Manfred Hammerl · Sascha Schwarz ·
Kai P. Willführ *Editors*

Evolutionary Social Sciences

A Tour

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Preface

Evolutionary theories and research findings have increasingly gained traction within the social sciences over the past few decades—albeit sometimes reluctantly. There has often been resistance and criticism, yet it can now be observed in many social science disciplines that evolutionary approaches have become established, influencing research to such an extent that this is reflected in terms such as evolutionary psychology, evolutionary sociology, or evolutionary demography. We now speak of evolutionary behavioral sciences or evolutionary social sciences. In an international comparison, evolutionary approaches were adopted rather cautiously in German-speaking countries and often viewed critically. Nevertheless, an increase in evolutionary research can also be observed here. This is expressed in an increase in publications and in the organization of conferences or evolutionary sessions at social science conferences, such as at the congresses of the German Society for Sociology (DGS) or the Austrian Society for Sociology (ÖGS). In particular, the MVE list[1] (Human Behavior from an Evolutionary Perspective), a mailing list and platform for scientists interested in evolutionary theory in German-speaking countries that has existed since 1999, has done and continues to do pioneering work and has been holding relevant conferences regularly since 2000.

Thus, in the year 2019[2] and in the year 2021[3] two MVE conferences took place, which explicitly addressed the relationship between evolutionary theory

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[1] Website of the MVE list: https://www.mve-liste.de/.

[2] MVE Conference 2019 at the Hanse Wissenschaftskolleg Delmenhorst: https://uol.de/mesf/mve2019. Organized by K. Willführ and S. Schnettler (Carl von Ossietzky University Oldenburg).

[3] MVE Online Conference 2021: https://www.tu-braunschweig.de/psychologie/methoden/mve-2021. Organized by N. Holzhauser, C. Ebner, F. Wille and F. Eggert (TU Braunschweig).

and social sciences. The contributions of the present book were largely presented at these two conferences. In addition, selected further contributions were invited to cover evolutionary social science research in the German-speaking area as broadly as possible. The present work is the first comprehensive overview of evolutionary social science research in the German-speaking area, which is intended to further promote the aforementioned increase in the importance of evolutionary research in German-speaking countries and make the many fields of evolutionary research accessible to a broad readership. After the German publication, this book was translated into English with the help of Large Language Models at the suggestion of the publisher in order to also reach a non-German-speaking audience.

Our thanks go to all the contributing authors of the anthology for their interesting contributions and their constructive cooperation, as well as to the publishing team at Springer VS, especially to Dr. Cori Antonia Mackrodt, who always provided us with advice and showed patience throughout the duration of the book project, with all its challenges and uncertainties.

We hope that this book provides an inspiring introduction for interested social scientists and students who want to deal with the evolutionary or biosocial foundations of human behavior and forms of human society. Ultimately, we hope that the book will also be received in the German-speaking as well as in the international scientific community.

Graz, Austria
Wuppertal, Germany
Oldenburg, Germany,
in November 2023

Manfred Hammerl
Sascha Schwarz
Kai P. Willführ

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Part II

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Evolutionary Social Sciences—An Interdisciplinary Fringe Project or a Small Revolution?

Kai P. Willführ, Sascha Schwarz and Manfred Hammerl

The word "evolution" literally means "development" and refers in biology to the gradual change of inheritable characteristics from generation to generation. Evolution is an essential property of life, just as gravity is an essential property of physical masses.[1] In the (natural sciences) scientific explanation and description of evolution, Darwin's theory of evolution has prevailed in competition with other approaches, such as Lamarckism, and when biologists speak of evolution

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[1] However, evolution does not mean a continuous advancement or improvement of living beings or characteristics. Throughout evolution, species or characteristics have repeatedly emerged that did not survive or could not (or were not) adapt to changed environmental conditions and became extinct.

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today, they (almost) always refer to Darwin. All species—including our own—are products of evolution and many scientists have argued that a self-release of humans from this natural process is impossible (Voland 2023). Following this view, not only would human biology be subject to this natural process, but social and cultural phenomena as products of these biological humans might also "only be understood in the light of evolution," to use the famous quote by *Theodosius Dobzhansky*. If one follows these considerations, this would further mean that any social or cultural science that leaves evolution out of its theoretical structures must inevitably fail. A social or cultural science without evolution would therefore be like astrophysics without a concept of gravity.

The (majority of) opponents of this radical naturalistic perspective accept the biological or evolutionary origin of humans, but argue that the social, culture, and technology have become independent phenomena that have largely dissociated from the (biological) evolution of humans. This standpoint is dominant within recent social and cultural sciences and at first glance this view is plausible, as the life course of modern humans seems to be shaped more by non-evolutionary institutions, social norms, and technologies than by biological evolution. Many non-evolutionary scientists therefore reject the inclusion of evolution in social or cultural studies as useless or even obstructive, as the laws of evolution do not seem to apply to society and culture.

However, at many points, critics of the evolutionary and biological perspective become thoughtful, as many research areas show that evolutionary processes do indeed play a major role in the emergence of social and cultural phenomena. For example, behavioral genetics shows that genes are partly responsible for the emergence of social inequalities, and concepts from evolutionary anthropology explain why blood relatives per se enjoy a different status than other members of society in all societies and cultures. Therefore, a reevaluation of evolutionary as well as biosocial perspectives is noticeable today within the social sciences. Under the umbrella term "Evolutionary Social Sciences," a multitude of research projects from various social science disciplines can be summarized, which, despite different theoretical structures and research subjects, have one feature in common: **They all try to fruitfully integrate Darwin's theory of evolution into their respective field of work.** The motivation to use evolutionary theoretical concepts in one's own research field can be very different. The range extends from the generally held hypothesis that an evolutionary perspective on humans is relevant for understanding social phenomena (without deeper references to evolutionary theoretical concepts), to the application of evolutionary biological theories for social science questions. It was the biological behavioral sciences, above all sociobiology, that have always used the theory of evolution to explain and describe social phenomena in animal and human societies. As the name suggests, the focus is on **behavior** and of particular interest are consequences for (biological) fitness. A strict distinction is made between proximate and ultimate research questions. Scientists who explain the biological factors of behavior control (such as hormones and genes) deal with the proximate questions, whereas questions about fitness maximization are of an ultimate nature. Concepts such as fitness, for example, are foreign to 'classical' sociology and the **action** of human actors in a social context, as opposed to 'mere' human behavior, has a long research tradition. As clear as these differences between the research perspectives may be, there are also astonishing similarities and the question arises whether we should not grant humans both, i.e., behavior and action.

Furthermore, the localization and naming of the various interdisciplinary projects is anything but clear. Sometimes the adjective "evolutionary" is prefixed to the name of the discipline to refer to the theoretical reference to Darwin and the interdisciplinary character of the research project. For example, one speaks particularly prominently of evolutionary sociology or evolutionary psychology. However, fields of work that use game theory, for example, also have a direct reference to evolutionary theory, even if their name does not immediately suggest this. The same applies to behavioral genetics or other biosocial approaches in the social sciences, which investigate the role of hormones or other physiological mechanisms for social phenomena and which also do not initially seem to explicitly refer to evolutionary or Darwinian concepts. However, this delimitation becomes blurred on closer inspection and often appears unjustified, as the functioning of these biological mechanisms can only be fully understood in the light of their (biological) evolution. Therefore, one initial goal of this book is to provide a first German-language—albeit not complete—overview of the wide range of applications of evolutionary perspectives in the social sciences, which are gaining more and more importance in the German-speaking world. After the German publication, this book was translated into English with the help of Large Language Models at the suggestion of the publisher in order to also reach a non-German-speaking audience.

In addition, Darwinian evolutionary theory offers a major advantage to an interdisciplinary social science: it can serve as a meta-theory, providing a common basis for exchange between disciplines. This applies to both the theoretical structure and the technical vocabulary. In our experience, interdisciplinary projects often fail because either (implicitly or explicitly) a lack of agreement on the relevant processes or concepts or a mutual misunderstanding of methodological approaches hinder interdisciplinary exchange. Darwinian evolutionary theory as a meta-theory can at least resolve disagreement about the relevant processes or concepts, as all evolutionarily informed scientists have an idea of what is meant by fitness or adaptation, for example, so that only mutual ignorance of the different methodological approaches of the disciplines could stand in the way of strong interdisciplinary exchange. Another advantage is that hypotheses can be formulated with relatively few premises and central concepts, such as ‘fitness’ or ‘adaptation’.

This book is interdisciplinary, just as the application of Darwinian evolutionary theory in the social sciences fortunately is today. We have divided the book into two parts. The first part collects contributions that provide a clear and generally understandable introduction to various research fields and central concepts of evolutionary social sciences. The second part contains contributions that deal with specific research projects from an evolutionary perspective.

The first chapter of the first part of this book was written by Christoph Antweiler and deals with niche construction in the Anthropocene. His contribution vividly shows the immense influence human action has on the planet and how the influence of humans for the environment impacts humans and their culture. Antweiler’s explanations make clear why evolutionary social sciences need to think big. The endeavor of evolutionary social sciences must not stop at the integration of Darwinian evolutionary theory. Humans are confronted with at least three different inheritance mechanisms: previous generations have not only passed on genes and culture(-techniques) to today’s humans, but have also significantly influenced their environment. Genes, culture, and environment are in complex interrelationships, and the mechanisms of Darwinian evolution represent “only” a central variable here.

The second contribution by Martin Diewald and Bastian Mönkediek focuses on the relevance of heredity for social phenomena and discusses to what extent genetically informed studies can be useful in explaining and interpreting social inequalities. Diewald and Mönkediek emphasize that social inequality research is just one example of the relevance of genetically informed studies within sociology in general. It should be noted that the methods of genetically informed research designs were not developed within sociology, but were brought into sociology from outside, namely from behavioral genetics. Many still view this import of foreign concepts into sociology with skepticism. However, this rejection is by no means a recent phenomenon, and Rosemary Hopcroft and Sebastian Schnettler deal with the history of this difficult relationship between sociology and biological concepts in the third contribution. Attempts have been made several times to integrate evolutionary as well as biosocial research and interpretation approaches into sociology—so far, however, these endeavors have not been successful for various reasons. The recent rapprochement between evolutionary theory and sociology is therefore not a debut, and it remains to be hoped that it will be successful this time.

The subsequent contributions of the first part of the book come from disciplines in which the integration of Darwinian evolutionary theory is already well advanced. Thus, Christine Hennighausen, Benjamin P. Lange and Frank Schwab discuss the benefits of integrating Darwinian evolutionary theory into evolutionary psychology in their contribution on media preferences. Media content and preferences can be excellently explained from the perspective of evolutionary psychology—this applies to old as well as new media. The authors also address the question of whether media phenomena are an adaptation to evolutionarily relevant problems or a byproduct of evolutionary adaptations.

Kai Willführ's contribution on Evolutionary Family Research emphasizes the difference between psychological preferences and actual behavior, and extends this to the behavioral effects or fitness consequences that result for the respective actor from his exhibited behavior. Willführ's contribution advocates for an interdisciplinary family research that is firmly anchored in the gene-centered perspective of behavioral ecology, but does not ignore the respective social and cultural context, as this significantly influences the individual cost-benefit balances of family members. Adolf Heschl's contribution deals with the concept of inclusive fitness and critically examines the genetic degrees of kinship used within sociobiology and behavioral ecology. Heschl argues that humans, like animals, behave more cooperatively than the gene-centered kinship concept of sociobiology predicts. His remarks thus contradict Willführ's contribution on Evolutionary Family Research, for which the kinship concept of sociobiology is central. We as editors consider it valuable to depict such scientific discourses and disputes in a book, precisely because they remind us that science is a lively discourse. Similar to Willführ's contribution, the contribution by Eva Brandl, Alberto Micheletti, and Ruth Mace also emphasizes that human behavioral ecology has always integrated culture into its research. In their contribution, Brandl et al. explain how vague and misleading the term "cultural evolution" has been used in the past, and advocate for using the term in the future only for the phenomenon and not for the underlying theories.

Andreas Diekmann's contribution deals with the fundamentals of game theory. A book on Evolutionary Social Sciences would be incomplete without game theory, as it has a significant influence on all behavioral sciences—both within evolutionary biology and in non-evolutionarily informed social sciences including economics. With the help of game theory, costs and benefits can be represented and modeled in various cooperation scenarios. Matthias Borgstede and Carsta Simon also present a mathematical model in their contribution, the so-called Multilevel Model of Behavioral Selection (MLBS). This model assumes that individual learning is a selection process that occurs simultaneously with natural (genetic) selection, with which behavioral changes at the population level can be clarified. The MLBS thus represents nothing less than a general theory of behavior.

A major strength of mathematical models like game theory or the MLBS is the sober consideration of results depending on set model parameters. Similarly sober, systematic, and largely free of observer bias should also be other methods in the social sciences. Susanne Schmehl, Kathrin Masuch, and Elisabeth Oberzaucher present human ethology as a discipline in their contribution, whose repertoire of methods allows behavior (of animals and also of humans) to be systematized and made observable. From our perspective as editors, the social sciences can benefit from the methodological competencies of systematic behavioral observation from human ethology, and it would be worthwhile to integrate these methods more strongly into social science research.

Frank Eggert and Nicole Holzhauser discuss in their contribution the relevance of evolutionary theory for psychology, but argue that previous research under the name ‘Evolutionary Psychology’ is essentially not an evolutionary discipline, but too similar to classical psychology. As an alternative, they propose the Behavioral Selection Theory, which would explain behavioral adaptations on the one hand through natural selection and on the other hand through rapidly changing or dynamic contexts, as a new evolutionarily grounded paradigm in psychology (and other behavioral sciences). The first part of the book ends with a contribution from Jörg Wettlaufer, who discusses why Darwinian evolutionary theory is only reluctantly acknowledged in historical sciences (as a classic humanities discipline). Wettlaufer shows, using the research of marriage and mating systems, that the evolutionary adaptation concept can indeed be helpful when it comes to explaining social historical changes. This example seems particularly noteworthy to us as editors, as it shows how every discipline that has even the remotest connection with (human) (social) behavior can benefit from an evolutionary perspective, if it so desires.

The second part of this book contains individual contributions that focus more strongly on specific topics.

Mirko Ruks and Martin Diewald show in their contribution the added value of genetically informed research designs for the study of educational inequalities. They impressively demonstrate how behavioral genetic methods can estimate not only the contribution of genetic effects, but also the contribution of social effects.

Martin Fieder, on the other hand, addresses a special case of in-group vs. out-group processes, namely the evaluation of migration. He shows that the evaluation of newcomers by those already settled is not only based on a genetic basis.

He further explains under which conditions xenophobic or xenophilic behaviors could have established themselves in the course of human history.

The importance of in-group vs. out-group processes is also a key element of the contribution by Hannes Rusch, who outlines a comprehensive research program that could explain on several levels why war and peace are part of the human behavioral repertoire and why conflicts between groups have always oscillated between phases of more or less war.

Michael Windzio's contribution focuses on the evolution of the social brain and, very similar to Martin Fieder and Hannes Rusch, assumes that a significant element of human evolution involves prosocial behavior (primarily) towards members of the in-group and rejecting behavior (primarily) towards members of the out-group.

A specific feature of the brain is also to generate emotions that are context-dependent. Emotions not only have the property of shaping one's own experience, but also the task of providing a signal function to the other (group) members. In her contribution, Christine Campen argues that the moral emotion of outrage, which she understands as a mixed emotion of (moral) anger and (moral) disgust, fulfills exactly these two functions (own experience and signal effect) in social groups.

Benjamin P. Lange and Sascha Schwarz, in their contribution, focus less on the categorization of people into in- vs. out-group, but rather deal more with the psychological processes associated with stereotyping. Using examples from modern media, they show that gender stereotypes in media preferences are not completely wrong, but are "exaggerated" in our minds.

The contribution by Lisa Klümper and Sascha Schwarz also deals with psychological processes, more specifically those that occur in the brain when we encounter potential partners in everyday life. They show how experimental psychological paradigms can be used to investigate which processes here apparently involuntarily, i.e., automatically, take place, and which do not.

The contribution by Alex Rieger, Annemarie Hartung, and Jan de Haan also deals with partner choice as a significant element for a relevant evolutionary theoretical variable: reproductive success. They focus on partner value as a known construct of evolutionary psychology and show how mathematical models (e.g., the MLBS, which is already generally introduced in Part I by Matthias Borgstede and Carsta Simon in the context of this book) can contribute to developing mathematically more precisely testable models from the purely verbal level.

Georg P. Müller also uses mathematical simulations with the help of game-theoretical considerations to model a completely different area of the scientific operation: The peer-review process. He shows from when it is expected that an old, already existing scientific paradigm will be replaced by new paradigms, and what role peer-reviewers play in this process. This contribution is exemplary for research projects in which evolutionary concepts are successfully applied to non-biological processes.

The second part concludes with Matthias Jung's contribution, in which he impressively demonstrates, using the example of Bronze Age axe blades, how the development of these tools can be described more sparingly than with alternative theories for explaining cultural change (e.g., the so-called meme theory). This contribution shows how interpretations of changes in disciplines such as prehistoric anthropology, where evolutionary theoretical assumptions are already very widespread, may be even easier to describe.

The introductory chapter of this book would be incomplete if it did not name some ethical implications and address the problematic relationship between evolutionary sciences and traditional social sciences. In the past, large gaps opened up that were more ideologically than scientifically justified. The theory of evolution and most disciplines of social sciences established themselves in the second half of the 19th century. There was initially an attempt to integrate the theory of evolution into social sciences—unfortunately with more than questionable results (see also Hopcroft & Schnettler in this book). Some movements in science and society, as represented by social Darwinisism and eugenics, misinterpreted or simply abused Darwin's theory of evolution (Darwinism) to justify their worldview. The arguments of such movements are referred to in German as "biologistisch" (not to be confused with the English term 'biologistic', which neutrally describes research in biology) and are summarized under the German term "Biologismus". It must not be forgotten that it was scientists thinking evolutionarily who gave the authoritarian and inhumane ideologies of the 20th century a supposedly scientific basis. Not least the often voluntary, not to say willing, cooperation of anthropologists and behavioral biologists with the Nazis led to the fact that after the Second World War in the German-speaking area practically every biological approach in the social and educational sciences was suspected of representing problematic worldviews. It may therefore not be surprising that the social sciences have only recently (again) dealt with the theory of evolution, even though the accusation of promoting "Biologismus" has not completely disappeared even today.

Every science can be in danger of being misused for ideological purposes. Scientists have little control over how their research results are understood or applied. However, the following principle must be observed in all natural science-oriented disciplines: Nature is not suitable as a model for any view or order. Any attempt to derive an 'ought' from 'is' inevitably leads to a naturalistic fallacy (Moore 1903) and is therefore doomed to fail. For example: If research results give reason to believe that despite all social construction of gender, persistent behavioral differences between men and women exist that have genetic causes, it does not follow that the genders in a society should have different rights or opportunities. Or: From the fact that intelligence is hereditary, it does not follow that a person's social position should depend on his or her IQ. Nature is amoral, and how we want live in our society cannot be derived from evolution or any other natural processes.

Curiously, the attempts to justify the inhumane movements of the 20th century are prime examples of poor scientific practice. When anthropologists in National Socialism measured the skulls of people of different ethnicities to prove the supposed superiority of the "Aryans", they must have completely ignored the studies of their colleague Franz Boas (Boas 1912).[2] Boas had also measured skulls of different ethnicities, finding that the skulls of Europeans and Africans differed, but he also showed that the skulls of African Americans resembled those of American whites more than those of sub-Saharan Africans. Boas concluded from this that the environment in which a person grows up must have a significant influence on their body. We can derive two insights from this early observation that are still valid today: First, that human biology is a social one. Environmental factors cannot be understood separately from genetic factors and vice versa. Second, that we should not fear research, even if it addresses the most sensitive questions. As long as research does not shy away from (justified) criticism and self-critically observes the generally accepted rules of good scientific practice, it should be allowed to research anything.

The Darwinian theory of evolution is one of the most successful theories that science has ever produced. Although it has been adapted and expanded over time, most recently by the niche construction theory (see also Antweiler in this book), it has passed all tests with flying colors. It would be a great pity if the social sciences were to leave its potential untapped. Fortunately, there is also an increasing exchange or convergence between the disciplines in the German-speaking world. This exchange is expressed through joint conferences, such as those organized by the MVE list (www.mve-liste.de) in Germany, or through joint ad-hoc sessions at large congresses such as those of the German and Austrian Sociological Associations (DGS, ÖGS). The book you are currently reading is also a sign of this fruitful convergence. It is particularly aimed at interested parties and researchers at all career levels, starting with students of all social science disciplines, up to more advanced individuals for whom the theory of evolution is not yet firmly anchored in their own field of work.

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[2] It should be noted here that Boas had Jewish roots and was a determined opponent of the National Socialists. His writings also fell victim to the book burning in Germany in 1933.

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Part I

Niche Construction in the Anthropocene

Elements of a geo-anthropological synthesis

Christoph Antweiler

1 Anthropocene

1.1 Global Geo- and Biotransformation

I will start with three examples; it's about plastic, animals, and concrete. First: Nowadays, every ecosystem on this planet and almost every organism contains micro particles of plastic. Second: Humanity currently consists of about eight billion people, but there are also around 25 billion broiler chickens on Earth. We are completely changing the fauna, for example, by our way of life causing the extinction of large parts of the megafauna. The extinction rate of animals, especially large land animals, since the 20th century corresponds to the last five "extinction events" in the biosphere, each lasting millions of years. Thirdly, please imagine the following: If you take all the materials transformed by humans (e.g., buildings, tunnels, concrete, asphalt) and spread them evenly over the land surface of our planet, you get 50 kg/m^2. This so-called technosphere thus consists of a hundredweight on each square meter, not on a hectare. I couldn't believe it and still don't want to believe it, but it has been proven by hard data (Zalasiewicz et al. 2017).

Even if we only consider these three examples, it becomes clear: the global environmental changes caused by humans, which are referred to as the "Anthropocene", definitely encompass more than just anthropogenic climate change.

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Humans today live in *Anthromes* instead of biomes (Ellis and Ramankutty 2008). Not a single ecosystem of our geosphere is completely untouched by humans anymore (Ellis et al. 2013; Lewis and Maslin 2018 as overviews). Natural scientists, especially from the Earth System Sciences, have been finding since the mid-1980s and increasingly since the turn of the millennium that human action has been shaping changes to the Earth's surface since at least the mid-20th century, perhaps even for thousands of years, that are unprecedented in history. These human influences on the Earth's surface, such as species extinction and ocean acidification, are now so strong, globally detectable and probably irreversible, that humans can be considered a separate "natural force".

1.2 A Conceptual Earthquake—Concept Development and Evolutionary Relevance

From a geochronological perspective, we live in the Holocene, the post-ice age, which began just under 12,000 years ago. The Anthropocene, often simply translated as the "Age of Man", would follow on from this. The Anthropocene is said to have begun 70 years ago (since 1950, according to the currently dominant consensus) to 200 years ago (according to the original thesis), and—if you ask archaeologists—it may even go back over 12,000 years. In the latter case, the Anthropocene would chronologically devour the Holocene. But from a geological point of view, all these periods are nothing more than a fleeting moment. Geologists think in deep time spans of billions of years and are very conservative when it comes to formally introducing new geological epochs.

The "Anthropocene" corresponds in its word formation to the names of other geological ages (Pliocene, Oligocene, Holocene). It is the name for the fact that humans are already shaping the Earth's surface and also the systemic material cycles so strongly that this will still be recognizable in the distant geological future. Since we are probably just leaving the geological Holocene, the comparatively stable post-ice age of 11,700 years, from an Earth system science perspective, the term "Anthropocene" was popularized by climate scientist Paul Crutzen and biologist Eugene Stoermer from the year 2000 onwards (Crutzen and Stoermer 2002). The term Anthropocene was thus not introduced by geologists, but by climate scientists and Earth system scientists. Geologists and paleontologists think firstly in very long time spans and only formally introduce such periods secondly when a worldwide synchronous marker can be demonstrated ("Golden Spike"). No wonder that geology only started paying more attention to the topic from 2009 onwards and the Anthropocene has not yet been definitively formally included in the official geological time scale. This step, which would certainly have significant consequences for the foundation in the sciences and for public attention, may be taken around the time this contribution is published.

Independently from Crutzen, but also in the year 2000, John R. McNeill, a pioneer of ecologically expanded global history, pointed out the dramatic increase in several phenomena in the global environment around the mid-20th century based on historical findings from a variety of sources. As a result, McNeill speculated that a historian looking back at the 20th century at the end of the 21st would probably emphasize less the two world wars, fascism, communism, and the women's movement, but rather the fundamentally changed relationship of humans to the environment (McNeill 2000, p. 17). McNeill then worked closely with earth scientists, such as Steffen and Crutzen, e.g., for a decisive essay (Steffen et al. 2011). As a historian, McNeill became a member of the Anthropocene Working Group of geologists, where he stands for the historically correct location of geoscientific knowledge (McNeill and Engelke 2016; Will 2021, p. 222). Today, more than twenty years later, environmental historians, who were first alerted to the global dimension of their topic by McNeill, are surprised at how much faster McNeill's assumption is likely to prove true according to current knowledge.

The word Anthropocene denotes a geological epoch, but the central empirical problem from a geological point of view is that it is set today and the beginning is supposed to be located in the present (around 1950). This is quite different from the usual practice in geology, where such periods are normally set *ex post* in the distant past, like the Holocene (11,700 years ago). Thus, from a geological point of view, the Anthropocene as an epoch definitely lacks the "dignity" of long duration (Müller 2021). Furthermore, the Anthropocene essentially forms a hypothesis. It includes many scientific assumptions, such as the permanence of anthropogenic sediments, and opens up a space for social scientific and political speculations about long futures. The central question about the Anthropocene can therefore be summed up in a paradoxical way: "What is the Anthropocene and what will it have been?" (Folkers 2020, p. 592).

The concept actually means a conceptual earthquake (Egner and Zeil 2019), but not everything is new. Precursors had already emphasized the comprehensive human influence on the geosphere in the 19th and early 20th century (Stoppani 1873; Vernadskij 1997). Since at least the mid-20th century, global effects of economy and communication media have been debated under the label "globalization". Earth system research has taught us since the 1980s to see the Earth as one system that consists of closely interlinked material and energy cycles. The human-caused share of climate change has been proven since at least the 1990s. The geosystem sciences increasingly speak of the highly dynamic "Earth-Human

System" instead of "System Earth" (Hüttl 2014). What is really new about the Anthropocene thesis are the insights that humans 1. significantly shape the entire geosphere and fundamentally change material cycles, and that this 2. happens at a pace that is unique not only in human history, but also in *earth history*, namely in the duration of a human life.

2 Concept Criticism and Systematization

The Anthropocene as a topic and concept arrived in the humanities and cultural sciences around 2010. The Anthropocene is on everyone's lips and thus the long-discredited concept of man has returned to the anthropological sciences with force. However, we do not yet know what exactly lies behind the term Anthropocene from a cultural scientific perspective. Is it a fact-based diagnosis of the state of the geosphere, a time-diagnostic formula for describing the world as a replacement for "globalization", or a scientifically dressed dystopia? It is difficult to determine what the Anthropocene actually is and above all, what it means for whom (cf. Antweiler 2024, pp. 76–81 for over 50 different assessments).

2.1 Criticism and Critique of Criticism—Welcome to the Neologismocene

The literature on the subject is already almost overwhelming, a good 20 years after the creation of the term and after a good ten years of cultural studies debates. Due to the diagnosed global environmental crisis and the political urgency linked to it, the topic is stirring and challenging scientists across disciplines. The lion's share of the debate takes place in the English-speaking and also strongly in the French scientific community. Colleagues in Latin America and in East Asia and Southeast Asia are beginning to take an interest in the concept (Bergthaller 2020). However, some are only beginning to warm up to the term, perhaps because it seems Eurocentric, and prefer to speak of "global environmental change".

Since around 2010, there has been a broad and also lively cultural, humanities, and social science discussion (Schlaudt et al. 2022 as a good overview). This has been reflected in the emergence of the rapidly developing interdisciplinary environmental humanities (*Environmental Humanities*) and in several journals specializing in the Anthropocene. Social science contributions, especially sociological ones in the narrower sense, are rather rare (see however Laux and Henkel

2018; Adloff and Neckel 2020; Thomas et al. 2020; Pries 2021; Schroer 2022). However, the popularity in sciences (and also in visual arts and media) also creates problems. The Anthropocene is often mistakenly used as a synonym for human-made climate change.

The term was and is obviously very stimulating, but in many cases “Anthropocene” is used as a buzzword without the geological implications. In the academic attention business, the word “Anthropocene” is often used as a catchy term to make other topics more interesting, such as criticism of capitalism or globalization. This is a pity, because I consider it too valuable scientifically and too relevant politically. The main criticism of Anthropocene theses comes from the humanities and cultural studies. On the one hand, the term is seen as an outgrowth of human hubris; it would convey the idea of human omnipotence. On the other hand, the concept would assume a unified humanity, thus ignoring inequalities between people, classes, genders, and societies. As a result, the Anthropocene should be gendered and decolonized (Sperling 2019; Alexandre et al. 2020; Mathews 2020; McEwan 2021).

The Anthropocene includes many topical aspects and they have been spelled out in science, art, and literature in various ways. This and the mentioned and other criticisms manifest themselves in alternative terms *(Capitalocene, Chthulucene, Plantationocene, Urbanocene, Technocene)* (Davis et al. 2019, as the best overview see Testot and Wallenhorst 2023, pp. 97–191, 255–311). The resistance to the term has many names. There are already about 140 alternative *-cene* terms (already almost 100 at Chwałczyk 2020); scientifically speaking, we live in the Neologismocene. However, most of these lose sight of a crucial perspective, namely the geological-deep time dimension (Antweiler 2024, pp. 155–162; on deep time Irvine 2020). They are rather time-diagnostic terms similar to that of the “knowledge society” or that of “postmodernism”. Moreover, an understanding of planetarity qua complexity of the phenomenon requires analytical clarity, which most of these terms lack. In my opinion, today’s planetary problem is too important for word games and academic trend surfing.

The two fundamental criticisms—namely the alleged hubris and monolithism—apply to some contributions to the debate, but the objections are often overstated and tend to throw the baby out with the bathwater. On the one hand, the concept conveys anything but the alleged omnipotence of man. It is precisely the unintended and uncontrollable effects of human action on the environment, i.e., the *impotence*, that have become clear through research on the Anthropocene. On the other hand, the criticism of the supposedly undifferentiated unity of humanity postulated by proponents of the Anthropocene thesis partly sets up a straw man. Crutzen and Stoermer’s epochal essay from 2002 clearly states that the Anthropocene is due to the activities of only about a quarter of humanity (Crutzen and

Stoermer 2002). Both the varying contributions to the causes and the differences in effects and vulnerability are now a normal assumption in almost all natural science contributions. The term "Anthropo" refers to man and thus the relevance of the *accumulated* effects of human behavior and actions. The Anthropocene represents a crisis diagnosis and discussions about the Anthropocene tend to dystopian narratives and often to misanthropy. In addition, there is the problem of conceptual diffuseness.

2.2 Facets of the Anthropocene—A Systematization

The Anthropocene involves both a fact-based thesis on a mega-macro phenomenon and the interpretation of this rupture and its societal relevance for politics. Given the fact that the term is used excessively, I suggest distinguishing four different meanings of the Anthropocene (Antweiler 2024, p. 81; cf. Toivanen et al. 2017, pp. 4–10 and Zalasiewicz et al. 2021, p. 9).

Anthropocene 1: A first understanding is guided by *earth system science* and refers to the earth-historical caesura in the status of the system Earth (new state) from around the mid-20th century. At its core, it is about the change of the geosphere with its linked spheres (atmosphere, hydrosphere, cryosphere, pedosphere) mainly due to the effects of human action as an important or even decisive geofactor.

Anthropocene 2: A second understanding is shaped by *geology*, the stratigraphic Anthropocene. This refers to the synchronous sum of events during the very short and currently ongoing geochronological "epoch". This includes all deposits during this time interval (synchronous), regardless of whether they are of anthropogenic, partly natural, or entirely natural origin, as a geological "series". This is the dominant view in the *Anthropocene Working Group* (AWG) of the International Geological Union (IGU). While archaeologists, historians, and humanities scholars set the phase boundaries diachronically (e.g., the regionally different starting points of the Stone Age), the horizons from a geological perspective must be globally detectable and synchronous (same time).

Anthropocene 3:A third understanding, more temporally open but spatially more limited, is primarily shaped by *archaeology and history*. It could also be referred to as the diachronic Anthropocene. This refers to the sum of all empirically verifiable influences of the Homo sapiens on the geosphere across all times, even if they start at different times and only show regionally. This is the view of the minority in the AWG and is similar to the concept of the "Archaeosphere".

Anthropocene 4: A fourth understanding comes from the humanities, culture, and social sciences. This is a *synthesis term for the* consequences of the epochal break caused by human-induced environmental change. This includes in particular political and ethical considerations and corresponding reflections on responsibility and the status of humans in relation to nature. This fourth understanding of the Anthropocene for the meta-level to the analytical levels of Anthropocene 1, 2, and 3 is filled extremely inconsistently in terms of content.

In the face of the Anthropocene, there is typically a divergence between human actions and their effects (Horn and Bergthaller 2022, p. 99, 106). Human actions are primarily locally oriented and usually follow an intention. However, their effects often occur first in other, possibly far distant places. Secondly, effects often occur in several or even many places. Often we do not know to what extent causes and effects are linked over great distances (*telecoupling*). This applies, for example, to resource extraction, long-distance waste transport, and biodiversity. In addition, the consequences are largely unintended and thus form a "tragedy" in the classical sense (Horn and Bergthaller 2022). This disjunction of action and effect is particularly relevant in the Anthropocene and could form a focus of socio-ecological research.

2.3 Agency—Agency versus Effectiveness

A second necessary differentiation concerns the term *Agency*. In discussions on global environmental issues, human action and human Agency are often referred to in an all-inclusive way. Or problems are identified that supposedly exceed human agency. This involves a complicated nexus of behavior, action, effects, intentions, and limited knowledge. Contrary to the usual loose language use, two forms of Agency should definitely be distinguished: Agency and Effectiveness (Horn and Bergthaller 2022, pp. 100 ff., 105, 222). Agency refers to intentional action, intentional Behavior, while Effectiveness refers to effects through non-intentional behavior or unwanted Side effects due to accumulated effects of intentional actions. Agency 1, as agency, represents the freedom of disposition or the possibility of action under restrictive conditions. Agency 2 means the effectiveness, the human impacts of action through non-intentional behavior, unintended or uncontrollable side effects of accumulated action intentions. This ranges from unintended effects and possibilities of tools (see Jung in this volume) to e.g. the "eternal costs" of final disposal of radioactive substances.

Agency as the first form of agency includes the potential for solutions, while effectiveness as the second form of agency in the Anthropocene is the actual problem. We are thus both drivers and driven: the cumulative actions of humans are a strong geofactor, but we are hardly able to control these effects. The potential effectiveness puts the assumption of the sovereignty of individual and collective actors to the test. Societies can significantly influence the geospheric system, but they cannot control it. Man partially steps back as a principal, Nature steps "into action". We humans deeply intervene in the planet and have thus become a geological power ourselves. But so far, we have not found a way out of the environmental destruction we have caused.

3 Coevolution—Cultural History meets Natural History

In the early Holocene, humans influenced the Geosphere only insignificantly, they were largely spectators of the development. The climate course in the Holocene, for example, was determined by three characteristics of the Earth's orbit around the sun: the ecliptic, the tilt of the earth's axis, and the fluctuations around this axis. The favorable Holocene warming for humans resulted from coincidences of astronomical situations from a human perspective, which increased solar radiation and then led to a relatively stable situation until recently about 12,000 years ago. In the Anthropocene, we have a truly new phenomenon that results from a complex interaction of systemic drivers and human forces at various scale levels (Thomas et al. 2020, p. 14; Thomas 2022 as the best overview).

3.1 Sociologization of Earth History—Ecologization of Sociality

Due to the complex intertwining of causal factors on the one hand and the temporal depth of human effects on the other hand, the Anthropocene requires a sociologization or Culturalization of earth history sciences. At the same time, in view of the Anthropocene, we need an ecologization and geologization of social sciences and historical research. Both have consequences especially for the research of social evolution in the sense of long-term courses of Human History. An evolutionarily informed analytical framework is required. This is because the question is tied to whether the distinction between Natural History (*res naturae*) and human History (*res humanae*) is meaningful, or whether a renewed, and broader, universal history is needed (Chakrabarty 2021, pp. 23–48, from a geological perspective Dartnell 2019). The Anthropos itself is a cumulative product of the entire coevolutionarily shaped history of the planet, more precisely the geosphere, on the one hand and the comparatively young political, economic and social changes in human history on the other hand.

The tricky thing about the Anthropocene, however, is that we are now unfortunately often dealing with the aforementioned *unintended effects of intentional actions*. Unintended effects are a frequently mentioned, yet under-theorized phenomenon in the Social Sciences. It makes a big difference whether actors are involved who (a) *can* have intentions, (b) *can* intentionally research these unintended effects, and (c) *want* to prevent these effects intentionally. If it's not just about description and analysis, but about intended change or desired societal transformation, the tension between intended and unintended "drivers" becomes insoluble (Thomas et al. 2020, p. 14). At the level of societal experience and especially individual experience, this distinction is of central importance because people orient themselves by what they can change in the world, in short: by culture.

From an evolutionary perspective, the core of culture lies less in the respective cultural contents, but in the special mechanism of extra-genetic transmission within and also between generations. The transfer of information between generations, which are relevant for phenotypic expression, occurs in humans not only through the genetic line, but through language and outsourced from the body in writing and material culture (see Brandl et al. in this volume). Boyd & Richerson proposed the model of "dual inheritance". This model has opened up a wealth of specific mechanisms and generated a flood of studies and also quantitative models (see Tab. 1).

The model of dual inheritance could, however, be expanded by reference to recent research from cognitive evolutionary research to illustrate the specifically human form of social learning. Cecelia Heyes, for example, argues that cultural learning is a special form of social learning using very specific cognitive tools (*cognitive gadgets*, Heyes 2018, p. 80, 219–222). These are primarily selective social learning, imitation, mindreading, instruction, and language. Thus, cultural learning is more than just a sophisticated form of social learning, i.e., learning with the help of social partners—contrary to the understanding of, for example, Michael Tomasello (2020), as well as some *cultural evolutionists*, like Joseph Henrich (2016).

Tab. 1 Factors of cultural evolution according to the dual-inheritance approach. (Slightly modified after Richerson and Boyd 2005, p. 69)

1 Randomness
1.1 Cultural mutation: individual, for example through false memory
1.2 Cultural drift: statistical anomalies in small populations
2 Directional forces (*decision-making forces*)
2.1 Guided variation (*guided variation*): changes during learning
2.2 Biased transmission (*biased transmission*)
2.2.1 Content preference (*direct bias*), for example through algorithm, cost-benefit analysis or learning inclination
2.2.2 Frequency-dependent bias (*frequency-dependant bias*), according to the usualness of a cultural pattern or rarity
2.2.3 Model-based bias (*indirect bias*): imitation of successful individuals or individuals similar to oneself
3 Natural selection of culturally transmitted variants
3.1 Selection at the individual level
3.2 Group selection

Simply put, according to Heyes, the special human cognitive ability lies less in the inherited intelligent brains of individuals than in the smartness shared in social interactions. The cognitive tools primarily emerge during childhood in a virtually culture-saturated environment. They are a result of cultural adaptation and functionally crucial for transgenerational transmission of culture. What remains underexposed in Heyes, however, is the realization that some of the cultural learning mechanisms are based on biotically given emotional inclinations which ensure the copying accuracy between generations. This was suggested in cross-cultural ethnological studies on emotional norm socialization (Quinn 2005, for examples Antweiler 2019). For human niche construction, it is relevant, although not addressed by Heyes, that many of these cognitive gadgets work through the mediation of *material* culture. An example is children who follow their leader, linked by a colorful band, by imitating each other. In human cultures, intelligence is extracorporeal in two ways: on the one hand in *specific* social interactions, on the other hand in artifacts, from objects to entire landscapes (see Jung in this volume). These extracorporeal objects contain the transgenerationally accumulated knowledge, metaphorically speaking, the sum of the standing-on-the-shoulders-of-giants to date.

3.2 Niche Construction and Multiple "Inheritance"

A certain gap in the model of dual inheritance concerns the precise analysis of the human-altered environment. There is a long tradition in cultural anthropology for this, because the ethnological concept of culture sees culture quasi as the sum of human environmental changes. In early ethnological cultural ecology, it was also worked out that the environment has a strong causal role for material culture but also other cultural areas. This was emphasized in cultural ecology with regard to long-term change in so-called neo-evolutionism (*multilineal evolution*). Most classical cultural ecological works were rather empirically oriented and focused on adaptation processes to the natural environment. More recent works, on the other hand, emphasize the active role of cultures in shaping the environment. In cultural anthropology The coevolution of societies and abiotic and biotic environment as such has only been addressed in recent times (Orr et al. 2015).

A central argument for the causal importance of the environment for long-term change of societies ultimately comes from evolutionary biology. In 2000, Richard Lewontin (1919–2021), a Marxist critic of narrow Darwinian concepts, published a book with the DNA-structure alluding title "The Triple Helix", which was translated into German with a ten-year delay (Lewontin 2010). The argument here is that the genetic heritage must be supplemented by an understanding of the intra-organismic environment in which the genes operate. Even more important for our context, however, is Lewontin's emphasis, already expressed in 1983, on sustainable modification of the environment by organisms: "Organisms do not adapt to their environments: they construct them out of the bits and pieces of their external world" (Lewontin 1983). The transmission of this extra-organismic environmental situation to the next generation is to be seen *as an independent instance of inheritance*. Organisms create (partially) their own environment through their behavior, and this environment in turn causally influences (1) the evolution of these organisms, (2) the evolution of their offspring, and (3) also the evolution of other organisms. Technically, this ecological niche construction was defined as:

> "… the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches. Niche construction may result in changes in one or more natural selection pressures in the external environment of populations. Niche-constructing organisms may alter the natural selection pressures of their own population, of other populations, or of both." (Odling-Smee et al. 2003, p. 419) A historically significant example of such ecological niche formation is the creation of atmospheric oxygen, which only dominated after the withdrawal of CO_2 due to the worldwide spread of marine cyanobacteria and later by land plants, which then set in motion large-scale photosynthesis (Lyons et al. 2014;

> Dartnell 2019, pp. 195–197). However, humans alter their environment not only based on genetic information, but also due to extragenetic information transmission (see Brandl et al. in this volume). Unlike other animals, humans do this actively, permanently, and globally. The persistence of the effects leads to these *culturally generated* environmental changes becoming (partially) permanent in a given generation at time T and forming the basis of the then supposedly "natural" living conditions in the next generation T + 1 (Fig. 1). This "ecological legacy", created mainly through cultural transmission from ancestors, such as in the form of tools, monuments, and pre-existing cultural landscapes, acts as a current condition of natural (sic!) selection. Consequently, humans are born into environments that have been shaped not only by contemporaries, such as parents and peers, but *significantly* by their ancestors. Since these environmental changes are based on an originally cultural transmission mechanism, which brings with it certain semi-autonomous processes, it is appropriate to speak of a "cultural heritage".

Lewontin's emphasis on the transmission of the environmental situation as an independent path of environmental inheritance and Boyd and Richerson's model of dual inheritance can be combined, making the evolutionary peculiarities of cultural transmission mechanisms clear. Thus we can thus distinguish three modes of inheritance: genetic inheritance, environmental inheritance, and cultural inher-

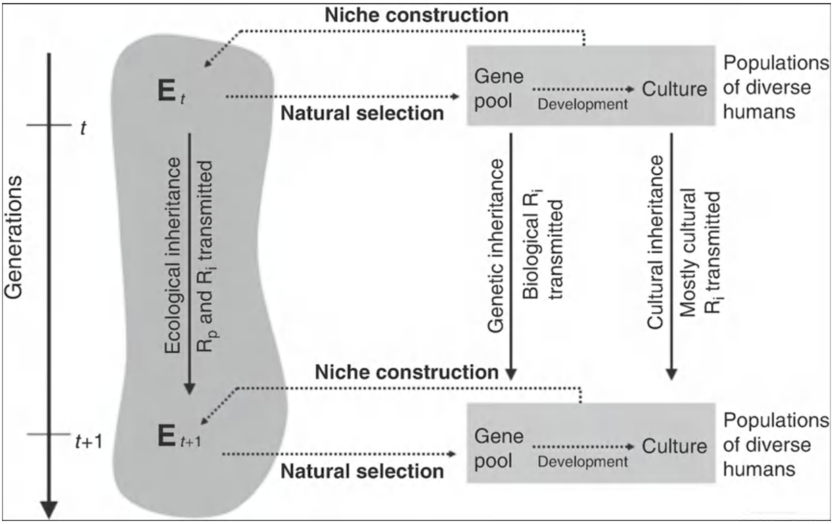

Fig. 1 Human niche construction (*niche construction*) in the *Triple-Inheritance* model according to Laland et al. 2000. (From Riede 2019, p. 340)

itance. So that we have the theory of multiple niche construction in humans (*human niche construction*) or, thought of temporally or diachronically, the model of a triple inheritance (*triple inheritance;* Odling-Smee 1988; Laland and Chiu 2020; Lange 2020, pp. 203−227). Independently of Odling-Smee, Laland, and Feldman, developmental psychologists had almost simultaneously come to similar ideas and had emphasized that this model helps to put any simplified notions of nature vs. nurture *ad acta*:

> “All organisms inherit parents’ genes, but many *also inherit parents, peers, and the places they inhabit as well*. We suggest the term *ontogenetic niche* to signify the ecological and social legacies that accompany genes. A formal name is needed to give the idea of the *inherited environment* equal status with its conceptual cognates; nature and nurture. We argue here that increased recognition of the inherited environment facilitates unification efforts within the developmental sciences by emphasizing the affinity, rather than opposability, of ontogenetic processes.” (West and King 1987, p. 549, emphasis mine) Strictly speaking, there actually exists a fourth mode of inheritance, also conceived by Lewontin. In higher organisms, organisms of other species live (as so-called “microbiome”), which pass on information in a non-genetic way. In animals, the (partial) inheritance of the microbiome occurs, for example, through coprophagy, in humans through the mucous membrane in the birth canal or breast milk (Roughgarden et al. 2017, p. 49, Table 1). We can see the microbiome as a community of life, which makes it part of the “external environment” of humans and thus part of the “ecological heritage”. But we can also see the human individual as a “holobiont”, which would make the microbiome part of the internal environment or part of the genome heritage (*hologenome*). In any case, we can speak of a multiple heritage, where the channels of tradition do not simply add up, but influence each other. The microbiome, for example, that is inherited, is subject to culturally conditioned changes in humans, such as by food preferences or cultural food laws (Schlaudt 2022, pp. 43–45 and there Table 1).

Therefore, I speak of a *multiple* inheritance of niches. In some organisms, the levels work together particularly strongly, as emphasized by Sonia Sultan, for example. Organisms change the selection they are exposed to, both through the physical change of their environment (*perturbation*), through the choice of their habitat (*relocation*). In doing so, their behavior can provoke a new selection (*inceptive*) or respond to an existing selection (*counteractive*). In addition, there is experience-related niche construction, through the way organisms change their *experiences* with the environment, without directly changing it themselves (Odling-Smee et al. 2003, Tab. 2.1). These aspects were already thought out in approaches by Jakob Uexküll in 1921 (Uexküll 2014). Especially humans not only factually change their environment, but can also perceive the environment as changed *perception*, act differently as a result, and thus further change it (Sultan

2015, pp. 38–44, 71–92 and the wonderfully informative website Niche Construction 2023). This model must and can also include forms of reciprocal causation (Laland et al. 2019; Bradley 2020). Multiple inheritance is a fundamental phenomenon of evolution for humans it is of fundamental causal importance, first for our all organismic survival as individuals and second for cumulative learning in collectives. This applies fundamentally and forms a basic engine of human becoming; in the Anthropocene, this is only shown in a global acceleration in the coevolution of humans and technology (Schlaudt 2022, p. 42 f.; see also Jung in this volume).

Such niche construction had very diverse effects in the history of humanity, on humans as well as other organisms and even the inanimate world. Broad anthropogenic changes, such as those of biodiversity, testify archaeologically to the expansion of humans in the late Pleistocene, the Neolithic spread of agriculture, the era of colonization of islands in the Mediterranean and Pacific, and the emergence of early urbanized societies and commercial networks (Boivin et al. 2016, pp. 6389–6393). This approach can be linked with further approaches to material culture to create a model that makes the natural and cultural factors of the genesis of the Anthropocene as well as the effects of the Anthropocene somewhat understandable, for which Fig. 2 provides an example.

Fig. 2 Triple cultural inheritance in Cologne, Germany: material culture, cultivated plants and partially anthropogenic atmosphere as multiple environmental heritage. (From Antweiler 2024, p. 351; Photo: Antweiler 2021)

The environmental aspect did not play a central role in the model of Boyd and Richerson, but this approach too has been further developed, fertilized by niche models, especially by the working group around Joseph Henrich. Methodologically, this involves the use of a whole spectrum of different methods and data types. Here, for example, field research and laboratory investigations as well as mathematical modeling and simulations play a role (Krauß 2015; Chudeck et al. 2016; Creanza et al. 2017). The precise distinction of the mechanisms of cultural transmission allows for a more precise understanding of the influences of culture on genetic evolution (*culture-driven genetic evolution*, Henrich 2016, pp. 59−60). Long-term field research is of central importance regarding the anthropocene effects on human collectives discussed above (Lansing and Cox 2019; Orr et al. 2015, p. 157).

The model of niche construction is, in my opinion, particularly versatile in its applicability for research. It allows for a bridge to social theories, because at the core of the niche concept—contrary to widespread perception—it is not a spatial niche that is meant, but a functional role of entities in an ecosystem. With the emphasis on activities or services instead of spatial niche occupation, a niche is comparable to a social role or a profession in the sociological sense. With the emphasis on the multiple construction of the niche, a connection to approaches of social constructivism is offered, at least if these are moderately constructivist. Another advantage is that the model allows for the examination of systems at the macro- and meso-levels, and also at the micro-level.

3.3 Coevolutionary Niche Dynamics—Desiderata on the Way to a Synthesis

What else needs to be done from a social science perspective beyond the approaches mentioned? There is a lot. First, this model could (in my opinion, should) be spelled out using a *holistic concept of culture*, as it dominates in cultural anthropology and is represented by some sociologists. Such a concept of culture understands culture as a phenomenon that permeates *various* forms of substance and is manifest both intracorporeally and extracorporeally (Antweiler 2024, pp. 338–342, Pries 2021; see Fig. 3).

Materiality, sociality, and practice already form a nexus among non-human primates. But since we are dealing with humans here, further differentiation is called for. First, a distinction must be made between material goods and organismic cultural components. This is a distinction *within* the category referred to in texts on material culture as “things as substance (in nature)”, which is separated

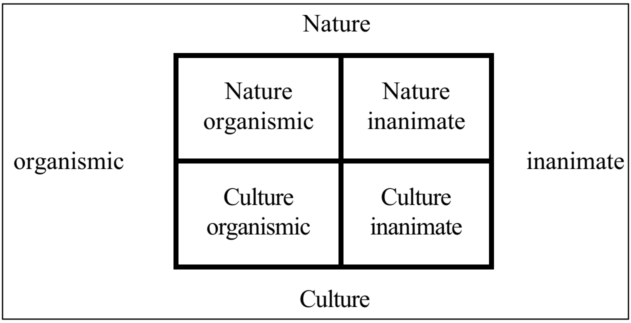

Fig. 3 Culture crosses different classes of material substance. (From Antweiler 2024, p. 339)

from concept-based "things as material culture" (Hahn 2014, p. 10). If material culture refers to the objects that are incorporated into the human lifeworld, i.e., understood as the sum of all objects that are used or meaningful in a society (Hahn 2014, p. 18), then domesticated animals and anthropogenic shaped landscape elements belong to it. However, living beings have significantly different properties and existential requirements (habitability) than other material objects or the abiotic nature.

With regard to the cultural shaping of living beings—in contrast to inanimate objects—adaptation, reproduction, generationality, and domesticability must be taken into account. Living beings have *non-circumventable* properties that differ from equally non-circumventable properties of other material things. According to this concept of culture, *which is open in terms of substance*, for example, cultivated plants are to be seen as components of culture. While the tree leaves in front of a building in Fig. 2 appear at first glance as an illustration of the contrast between nature and culture, the image can actually be seen as an example of different forms of *cultural* materiality. As part of the *animate* nature, however, they differ greatly in their properties, such as their generationality, from inanimate cultural components, such as buildings, which also have their own stubbornness, for example through weight and statics.

Consequently, culture plays a role both as part of the human-made environmental heritage and as a *partially* self-dynamic extracorporeal area in the coevolution of human communities (see Jung in this volume regarding artifacts). This applies fundamentally, for example, to the development of tool use with the evolutionary history of becoming human, because technology in the broad sense is not, as often said, only the second nature of humans. The, technosphere belongs to the first nature of humans. Here, for example, mechanisms of enabling new action spaces through tools or machines (invitation character, *affordance*) and especially innovations through the use of existing technology for functions that were not originally intended (*exaptation*, Gould and Vrba 1982) would need to be analyzed. In today's "Technocene", the fundamental importance of technology for culture is only revealed in a dramatically intensified way (see, for example, the extremely stimulating Schlaudt 2022, esp. pp. 7–11, 45–74, 120–158).

Secondly, co-evolution theories would have to deal with the explanation of social *macroevolution*, i.e., the long-term (at least trans-generational) development of entire communities, societies, and complex civilizations. Sociocultural macroevolution poses an even greater challenge than understanding human evolution on a micro level. This requires the inclusion of theories of social or cultural evolution from cultural anthropology, archaeology, cultural philosophy, complexity research, and historical sociology (Schnettler 2016; Antweiler 2017; Meißelbach 2019; Hammerl 2019; see Hopcroft and Schnettler in this volume).

A particular challenge lies in the development of an evolutionary model that also addresses the old, but far from resolved, topic of classical social evolutionism of the 19th century, namely the explanation of *directionalsocial evolution* (*anagenesis*, increase in complexity). The challenge is to identify the factors of the development of complex social systems towards *ian average*, but not teleological, increase in complexity. Recently there are promising syntheses that only partially spell out the potential of the concept of co-evolution (e.g., Van den Bergh 2018; Tang 2021; Turner 2020; Manning 2020; McCaffree 2022). Social evolution, including its thresholds and breaks, such as in the wake of digitization or currently in the face of the Anthropocene, needs to be addressed, but now with a genuine explanatory intent and in a co-evolutionary form, and this at all levels of scale (pioneering in this regard Löffler 2019).

For a truly bio-cultural understanding of social and cultural evolution, finally, insights from various theoretical strands would have to be tied together, perhaps less as an overarching theory but as a coordinated family of individual models. Elements of a yet to be created *synthesis* of social evolution are only outlined here in a thesis-like manner for the micro area:

1. To survive as organisms, humans *must* shape their natural environment through culture, in the form of socially shared and transmitted innovations. Thus, humans as individuals live in environments that are *always already* socially shaped.
2. *Niche construction* as a capability has become a necessity for Homo sapiens. The concept of niche construction reveals that the selection conditions

present at any given time are co-determined by the environment, which has been *culturally* shaped by previous generations.

3. The concept of *dual inheritance* shows the diversity of forms and effects of cultural transmission in particular, and also dynamics in certain areas, but largely ignores the environmental aspect and the material extrasomatic culture.
4. The model of *triple inheritance*, on the other hand, enables the analysis of a complex transgenerational mechanism of coevolution, including environments.
5. A *holistic concept of culture* conceives of culture as a phenomenon that is manifest both intracorporeally and extracorporeally and encompasses various forms of substance (thoughts, actions, material artifacts).
6. Within triple inheritance, *culture* thus forms a specific part as a self-dynamic area in the form of intra- and extracorporeal artifacts and thus a specific area within the selectively relevant environmental heritage for humans and other living beings.
7. *Technology* in the form of intracorporeal effects (e.g., nutritional effects in the brain, symbolic cognitive artifacts, pacemakers) and extracorporeal artifacts (tools) opens up or limits new action and innovation spaces by creating new environments.
8. The emergence of a *technosphere* in the Anthropocene intensifies an outsourcing of essential aspects of human metabolism into the natural and social environment that began with the use of tools. This fundamental externalized extracorporeal relationship with nature is a basic aspect of becoming human.
9. The cultural area itself contains semi-autonomous elements, fields with their own dynamics and dynamics of a coevolution, e.g., in the case of long-term cooperation involving anticipation among non-related individuals.
10. Only a comprehensive, but composed of clearly distinguishable elements, concept of *coevolution* can explain the mechanisms of long-term human societal change.

Human action in the Anthropocene changes essential cycles of the Earth system, which in turn has diverse effects on the conditions of existence and the options for shaping human existence. My conclusion is that debates on the Anthropocene, the largest mega- or macro-topic of social sciences and human sciences, show how fruitful it can be to bring together natural history and cultural history from a materialist perspective into a coevolution model. We need an eco-evo-synthesis (see e.g. Odling-Smee 2024). This would be an alternative to dividing science “cultures”, as is unfortunately still the case in the mainstream of the sciences of the human.

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The Potential Contribution of Genetically Informed Studies to the Explanation and Interpretation of Social Inequalities

Martin Diewald and Bastian Mönkediek

1 Introduction

It is unmistakable that genetically informed studies have increased in social science journals and conferences. However, this does not yet mean that they have found their place in the social sciences, and specifically in sociology. The expectations, hopes, and fears associated with genetically informed research are particularly diverse and varied in the social sciences (Martschenko 2022). They range from the hope of far-reaching new insights for the social sciences (e.g., Freese 2018) to the assessment that genetically sensitive research in the social sciences is more of a “dead end” (Robette and Reeve 2022). The position that genetically informed designs are a suitable means of controlling unobserved heterogeneity seems to be more accepted in the social sciences, without, however, expecting substantial contributions to social science questions and explanations. This view considers genetic influences more as a “disturbance factor” which can obscure the view of the importance of social influences. Distinct from this are studies that hope to gain insights about the underlying mechanisms through a consideration of the interplay of genetic and environmental influences (see Tabery 2014).

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If one generally concedes that the consideration of genetic influences could also be of interest for sociological questions and explanations, the subsequent question arises as to how genetic influences can be specifically “incorporated” into social science knowledge questions and explanations. This question is by no means trivial, because not only have genetic influences in sociological programming and theory so far had no established place, but conversely, genetically informed research has until recently taken place exclusively outside of sociology—and consequently has taken little notice of sociological explanation programs (e.g., Harden 2021). The answer to this question becomes even more relevant as sociology is increasingly confronted with findings suggesting that genetic influences could underlie some social explanations to a non-negligible extent (e.g., Liu 2018; Conley et al. 2015). From this, it is concluded in some places that the sociological theories and interpretations used for interpretation are wrong or comparatively insignificant (Plomin 2019). This calls into question the relevance of sociology as a science, especially where it makes a special claim to explanation: the explanation and interpretation of social inequalities.

Paradoxically, at the same time, attempts are increasing from outside sociology to position genetic influences and their investigation as an essential part of the explanation of social differences, and not least social inequalities. Turkheimer (2012) has generally referred to behavioral genetics as a social science, and Harden (2021) has declared genetic differences to be an essential part of the social inequality structure of societies. Consequently, the question arises whether it is not precisely the task of sociology to contribute more to this field of research (see Freese 2018), including a consideration of the question of how genetic differences are to be ethically evaluated, or whether they should result in imperatives for social and educational policy (Diewald et al. 2016; Freese 2018). Some sociologists, on the other hand, object to this, pointing to a largely incompatibility of genetic with social science research approaches (e.g., Fletcher 2022). However, the question arises whether such a strict separation is at all sensible, given the developments in the disciplines, and whether the social sciences could not benefit more from considering genetic influences than they have so far allowed. Conversely, in behavioral genetics or sociogenetics, it has long been prominently discussed that social science expertise is necessary to adequately understand the effects of genetic variation.

In our contribution, we would like to attempt to build such bridges between genetically informed designs on the one hand and sociological theories on the other. We focus on the field of inequality research and on clarifying two important questions that urgently require more attention: (1) How can the results of genetically informed studies, especially the parameters of the analyses, be linked with established sociological theories and concepts of inequality research? And following on from this: (2) To what extent is genetic variation relevant for ethical considerations in terms of equal opportunities or fairness of opportunities?

Social inequalities can be understood as structurally anchored differences in opportunities within society to achieve generally accepted life goals (Huinink 2022). These differences can refer to various desired life conditions—and thus dimensions of social inequalities—(including education, profession, money, health, or satisfaction with life). A detailed representation, including the possibilities of measuring such dimensions of social inequalities, is provided by Huinink (2022). However, our primary concern is not the extent to which such life conditions are unequally distributed within a society as a whole, but rather the extent to which the chances of better life conditions are unequally distributed among different social groups, such as between men and women or lower versus higher social origin (see Sect. 3).

In this article, we focus exclusively on genetic information as a population parameter and do not address additional questions arising from the possibilities of molecular and epigenetics for the *individual* determination of genetic chances and risks. We also do not go into detail about the various existing strengths and weaknesses of the typically used methods. This is not the focus of the present contribution and would go too far (see the contribution by *Ruks and Diewald in Part 2 of the anthology*). We only want to note at this point that all approaches are fraught with different problems of over- or underestimation of genetic and social influences, and only allow limited causal statements. However, they share these limitations with practically all social science methods.

2 On the Methodology of Genetic Variation

There is no reasonable doubt that everything that interests sociologists in their research is genetically determined to varying degrees. This applies not only to inequality parameters such as income, education, skills, status or life satisfaction, but also to the social experiences that influence such unequal life chances (Polderman et al. 2015). The latter means that social experiences are not completely exogenous influencing factors, but are partly determined by the genetic makeup of those who have these experiences. This happens, on the one hand, because individuals grow up in environments that are correlated with their genetic dispositions in that parents, who create these environments, partly pass on their genetic traits to their children (passive gene-environment covariation). Thus, children of particularly musical parents can not only be particularly musical because they grow up in a corresponding supportive environment. The special musicality of the children could also result from the genetic predispositions passed on to them by their parents. Furthermore, genetically determined characteristics of individuals can lead to certain social environments being sought and others avoided (so-called active *gene-environment covariation*). This is the case, for example, when people with a musical inclination are more likely to take music lessons instead of pursuing other activities. On the other hand, social experiences can be genetically determined in that other people (Alteri) react to genetically determined characteristics, such as personality, in the context of their social interaction with other individuals (*reactive gene-environment covariation*). To stay with the example of music lessons: If the teaching person recognizes a pronounced musical inclination in a music student, this can lead to more demanding, more challenging lessons. Another form of interaction between genes and environment, distinguishable from the previous examples, occurs when genetic predispositions only gain relevance through certain environmental experiences, or when the effect of social influences is different depending on which genetic predispositions are present. In such cases, one speaks of *gene-environment interaction* (Diewald et al. 2016). Perhaps the best-known example of this is the so-called Scarr-Rowe interaction, which assumes that genetic predispositions for cognitive abilities are more likely to unfold in resource-rich parental homes than in less resource-rich parental homes (Tucker-Drob and Bates 2016).

As these diverse examples illustrate, it is by no means the case that genes and social influences only influence social characteristics in an additive way, as the popular percentages à la “intelligence is half genetic and half determined by social experiences” suggest. Rather, genes and social environments interact in various ways. Both additive influences and the interaction of genetic variation and social influences can be modeled with the two main methods of genetically informed research, twin-based behavioral genetics and molecular genetics.

The classic twin-based approach first decomposes the total variance of a phenotype, such as the dimensions of social inequality mentioned above, into typically three variance components: the genetic variation (A), the environment shared by twins (C), and the environment not shared by twins (E). “Shared” here means that environmental experiences make twins more similar in their phenotypes; i.e., environmental conditions act uniformly and thus shape the lives of the twins towards certain patterns. Conversely, the “non-shared environments” make twins less similar in phenotype. This can involve experiences that each twin makes individually, as well as different perceptions and evaluations of objectively shared environments, such as the parental home. While this basic variance decomposition is subject to various assumptions and restrictions, further methods can be used to more precisely examine the extent to which the total variance of a phenotype is influenced by the interaction of genetic and environmental influences, also over time (see the contribution by *Ruks and Diewald in Part 2 of the anthology*).

In molecular genetic approaches, the work with so-called polygenic scores (PGS) currently dominates, which sum up which variations of the genome in the individual base pairs are significantly correlated with a certain phenotype—but mostly without knowledge of the mechanisms behind each one. Therefore, in molecular genetics, research practice remains with "black box" approaches as already with the ACE decomposition, even though there are possibilities in both cases to partly illuminate these (see Mönkediek and Diewald 2022 as an example for twin models). On the other hand, PGS, despite all existing restrictions, offer a possibility to directly include genetic variation as an influencing factor in the form of variables with corresponding coefficients in a regression equation, while in the context of twin-based approaches the conclusion on genetic variation is only indirectly possible via the variation of the phenotype between monozygotic and dizygotic twin pairs.

3 Integration of Genetic Variation into the Sociological Explanation of Social Inequalities

Both twin-based and molecular genetic approaches are now recognized to the extent that they are capable of testing phenotypic correlations, even in the field of inequality research, to examine their causal robustness, i.e., to determine to what extent correlations may be confounded by genetic differences. However, it is not only "noise" that is eliminated for the purpose of a "cleaner" determination of social mechanisms. Also, established theses are questioned and thus the empirical state of research is expanded, as has been shown not least by the example of the standard thesis on the high importance of cognitive abilities for educational success. While here, in part, only additive effects are assumed (e.g., Erikson 2016), i.e., cognitive abilities and social origin each contribute to educational success, genetically sensitive research suggests that the relationship between cognitive abilities and educational success is strongly confounded by both genetic and other environmental factors (Stienstra et al. 2021). It would therefore be mistaken to assume a causal influence of cognitive abilities on education, often taken for granted. Rather, both a higher genetic similarity and the same favorable environmental conditions favor both: higher intelligence and higher education.

The benefit of genetically informed designs for sociological research, therefore, lies in testing the relevance of social mechanisms. This does not necessarily mean that social mechanisms have no influence, but that purely phenotypic studies probably overestimate this. Such a review also says nothing about the extent to which existing correlations need to be supplemented or even replaced by other mechanisms, and what these mechanisms would be in detail. On the other hand, the benefit of genetically informed designs can lie in the fact that genetically sensitive research makes a substantial contribution to sociological inequality research. However, this is not a matter of course. Genetic variation as a factor is not explicitly considered in any inequality theory. However, we believe that the consideration of genetic variation can and must indeed connect to social science theory—especially against the background that research in this area will continue with or without a contribution from sociology (see Freese 2018). This is particularly true for the various forms of interaction between genetic variation and variation in social conditions, which would otherwise neither be adequately understood nor empirically identifiable. We want to make this clear at several points in the following.

3.1 Social Origin and Heredity

Is it not enough to know that the parental home provides unequal opportunities for the further course of life? Does it matter to distinguish between social and genetic origin? After all, it's the same parents we're talking about in both cases. Genetic and social transmission are intertwined from the beginning. However, there are two good reasons why such a distinction is significant from a sociological perspective. Firstly, sociology cannot isolate itself from an interdisciplinary state of science. A prima facie assumption that correlations between parental resources and behaviors on the one hand, and the development of offspring on the other, are exclusively, or even predominantly, social mechanisms, as discussed in inequality theories, is not convincing as long as this is not investigated including genetic mechanisms. This would leave the approaches presented by sociology unable to withstand criticism from outside. Paradoxically, given the advancing research also outside of sociology, a feared naturalization of social inequalities, i.e., a reduction of social differences to biological, especially genetic differences, can only be countered by genetically informed research, enriched by a sociological perspective, not by excluding genetic variation from the analyses. Previous genetically informed studies also do not suggest that theories of social mechanisms will actually prove to be largely meaningless, as the deep anchoring of human behavior in the social and cultural environment is not disputed. However, this does not exclude relativizations in individual cases, and alongside social mechanisms, genetic variation proves to be an additional significant contribution to the explanation of, for example, educational achievements (e.g., Isungset et al. 2022).

Secondly, genetic differences not only play a role as part of the intergenerational transmission of life chances, but potentially also as a basis for breaking through status reproduction towards social ascent or descent. Genes are both, both part of the intergenerational transmission of advantages and disadvantages, and opportunity and risk, to break the intergenerational status reproduction in one direction or another. After all, the individual combination of directly transmitted parental genes is not deterministically derivable from the parental genes—and even less so from the parental position in the inequality structure of society. Since children only inherit half of the genetic material of each parent, there is also much room for possible differences in genetic potentials and risks. Although there is the possibility that parents are genetically more similar due to the (increasing) tendency for homogamy in partner choice—a fundamentally very relevant topic for inequality research (Mare 1991). However, previous genetically sensitive research does not suggest that this has led to a substantial genetic similarity between partners (Conley et al. 2016).

3.2 Shared and Non-shared Environment in Twin-Based Variance Decomposition

Specifically, the twin-based variance decomposition into an additive genetic component (A), a shared environmental component (C), and a non-shared environmental component (E)—which nowadays often only forms a starting point for further analyses—not only identifies the importance of genetic differences compared to the social environment, but also distinguishes the relevance of the environment in terms of whether it influences individuals in a uniform or different way. This distinction shakes sociological certainties all the more, as sociological theories at least implicitly assume uniform environmental influences (Freese 2008). Behavioral genetic research proves the exact opposite, namely that the non-shared environment is usually more relevant (Plomin et al. 2001), at least after childhood, while shared environmental influences often tend towards zero (Turkheimer 2000). This does not mean that growing up together in the family has no formative power, but it directs attention to the significant differences in the development of children due to different activities, experiences, and also different perceptions and evaluations of the same situations (Freese 2008). The shared environment acts as a proxy for a uniformly shaping influence of the parental home, which can manifest itself in different contexts of the family household, but also in the parentally influenced experiential worlds in the neighborhood, school, and leisure activities (Diewald et al. 2016). Against this background, the comparison of the respective classification of results of corresponding studies for educational attainment from a behavioral genetic and inequality sociological perspective is revealing: In the sociological inequality perspective, the fact that for educational success the shared environment as a proxy for the influence of the parental home only accounts for about a third of the total variance may appear surprisingly small; especially compared to the approximately equally significant non-shared environment (Branigan et al. 2013). From a behavioral genetic perspective, the same result appears striking in terms of an unusually large importance of the shared environment (cf. Turkheimer 2000). Much more than most other characteristics, educational attainment is strongly shaped by environmental influences shared and uniformly experienced by children, which are primarily attributable to the parental home. This highlights the importance of parents, and how they influence their children's educational attainment through different behavioral and educational measures, in a more uniform and decisive manner than with other characteristics.

As "black boxes", the variance components do not allow statements about which experiences in particular have what significance, which is certainly a disadvantage compared to phenotypic analyses. However, this approach offers the opportunity to assess the relevance of shared and non-shared social environments in their entirety and in comparison to genetic variation, for example for educational success. The usual juxtaposition of the importance of the parental home compared to the competencies of the offspring suffers from the fact that even information-rich studies can hardly capture all relevant characteristics on both sides and that the competencies of the offspring cannot be considered exogenous to the characteristics of the parental home. However, ACE-based modeling allows to avoid the often considerable "omitted variable bias" in this and other examples, as well as to capture the overall influence of the parental home versus the characteristics of the offspring more completely. Genetic variation then stands for a developmental potential of characteristics linked to educational attainment—both risky and promising. This genetic potential can then be modeled as exogenous to the shared environment, i.e., the social influences of the family of origin (Mönkediek and Diewald 2022). To what extent this interpretation can be problematic, however, will be discussed in more detail by us at a later point in this contribution.

Last but not least, the combination of phenotypic and behavioral genetic analyses can shed some light on which experiences in particular might be important, for example through the step-by-step inclusion of covariates (Mönkediek and Diewald 2022). For this, the contribution by *Ruks and Diewald in Part 2 of the anthology* provides an overview.

3.3 Gene-Environment Covariation and the Accumulation of Advantages

The development of inequalities over a lifetime has increasingly attracted attention in sociological inequality research as "cumulative advantage" or "cumulative disadvantage" (e.g., DiPrete and Eirich 2006). The distinction and identification of active and passive forms of *gene-environment covariation* can be used to address such patterns of upward and downward spirals. *Active gene-environment covariation*, i.e., self-selection into certain environments that better match one's own goals than others, plays a significant role in the emergence of upward spirals of life success or its developmental prerequisites over time. This has been exemplified for the development of intelligence, a trait that is strongly genetically predisposed but can only unfold over time through spirals of such genetically influenced decisions (Nisbett et al. 2012; see also DiPrete and Eirich 2006). The more demanding and stimulating the activities and people one engages with, the more conducive this is to intelligence. It is assumed that individuals tend to select environments that are beneficial for them. Whether one follows this pattern (or can follow it) is not only significantly influenced by one's *own* genetic predisposition. In addition, the so-called *passive gene-environment covariation* also plays a significant role. Apart from self-selection into environments (active), environments, especially in early years, are largely created and influenced by parents (passive). The genetic predispositions of parents, which are partly inherited by the children, play a significant role in the created family environment. Finally, genetic predispositions can also generate reactions in the environment that affect the experiences made. This can happen when people we encounter perceive our genetically predisposed traits and let them guide their behavior towards us (*reactive gene-environment covariance*). So, as a child from a musical family, I can actively choose music lessons due to a present musical aptitude, while the person teaching me promotes me more or less based on the perceived musicality. This example illustrates that a positive genetic predisposition can affect the development of a talent or ability not only through possible passive and active gene-environment covariation, but also cumulatively, among other things, with a positive reaction in the environment.

3.4 Relational Inequalities: The Importance of Gene-Environment Interaction

What does a society make of the genetic predispositions for opportunities and risks of those who were born into it or who have immigrated into it? When this is compared for interrelated groups—such as men vs. women, low vs. high social origin, without vs. with migration background—this question conceptually corresponds to the theory of relational inequalities (Tilly 1998). In genetically informed research, such questions are also asked. However, these are not directly related to the phenotypic dimensions of inequality such as education, income, or profession, but rather to the degree of exploitation of a given genetic potential for factors that enable a better or worse positioning in society. Here, the existing genetically sensitive research increasingly focuses on the exploitation of genetic potentials for education (e.g., Isungset et al. 2022). In relation to this research, a suspicion that hovers over all purely phenotypic investigations and is occasionally raised is also dispelled, namely that differences between relational groups are not due to unequal social opportunities, but to genetic predispositions distributed differently between the respective groups.

In the context of this genetically informed research, the relevant social mechanisms generating inequalities are also increasingly being addressed. However, the construction of the relational groups should not remain at the rudimentary level of behavioral genetics, but should be based on the state of the art in sociological inequality research. Instead of compiling theory-free overall indices of social inequality, for example in the case of social origin, a distinction should also be made between the different resource dimensions (such as education, income, or profession), the effect of which can only be explained with specific mechanisms (Bukodi and Goldthorpe 2013).

Behavioral genetics and sociological approaches can usefully complement each other. Behavioral genetics works with the two main mechanisms of the *stress-diathesis model* and the *bio-ecological model* (Johnson 2007) (Fig. 1).

The *stress-diathesis mechanism* postulates that environmental stressors promote the development of traits for which there is a genetic predisposition (Johnson 2007). Most of the existing research focuses on the development of negative traits, such as disorders, diseases, and deviant behavior, which are assumed to have corresponding vulnerabilities in every human being to some extent. Latent

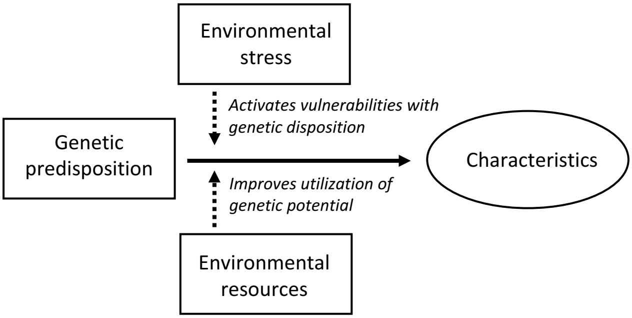

Fig. 1 Significance of environmental stress and environmental resources for the exploitation of genetic potentials for the expression of traits according to the *stress-diathesis mechanism* and the *bio-ecological model*

tendencies for such negative traits would then be activated and intensified by stress experiences (Arnau-Soler et al. 2019).

In sociological inequality research, the stress-diathesis mechanism is largely unknown, but it plays an increasing, albeit still very limited role. For example, inequality research is only slowly moving away from equating high status with low stress and rarely considers vulnerability as a prerequisite for how burdens differentially affect life chances. Here, sociological research can benefit from existing concepts in behavioral genetics.

The *bio-ecological model* discusses, in a relatively undifferentiated way, the importance of resource-rich environments for the realization of genetic potentials. In practical research terms, this, colloquially speaking, boils down to "more helps more", be it income, money, status, infrastructure. Here, sociological inequality research can offer far more elaborate concepts (Diewald and Faist 2011; Tomaskovic-Devey and Avent-Holt 2019). It distinguishes between different forms of social closure[1] up to social exclusion with the possible consequence of exploi-

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[1] *Social closure* refers to mechanisms that serve to preserve or gain advantages over potential competitors. This can happen, for example, through the granting or denial of rights, criteria for access to the labor market, such as certain educational titles or the German master privilege, or the formation of networks within companies. If such mechanisms condense to the point of denying "belonging", this is referred to as *social exclusion*. *Exploitation* arises in cooperations when a more powerful side can secure a disproportionate share of the value generated by the respective cooperation. (cf. Diewald and Faist 2011).

tation; the non-consideration of life situations and life plans in the welfare state agenda and the extent of social security overall; more or less self-determination, or conversely social control; and often cultural stereotyping and discrimination at the outset.

All of this can and should also be applied to models of gene-environment interaction for the genesis of inequality. Beyond this, the limits of genetically informed research should also be observed, which become particularly apparent when general characteristics from the sociological or psychological inventory are examined for heritability, but their effect is substantially dependent on the cultural or social context. This can be exemplified by the saying that a genetic predisposition for aggression puts one in jail if one lives in the ghetto, but in the boardroom if one is born into a mansion (see Conley 2009, p. 238).

In the investigation of such context effects, the elaborate state of historically and internationally comparative inequality research can provide basic starting points and inform genetically sensitive research. Against the background that the variance components determined in the context of twin analyses are time-specific population parameters, particularly internationally comparative studies offer a variety of research possibilities. Among other things, such rather rare studies could address the question relevant to inequality research, what role welfare states play for the significance of genetic predispositions.

4 Is genetic variation relevant for the ethical and political treatment of social inequalities?

It is a genuine interest of sociology to find out how societies deal with those who are born into them with unequal starting conditions. Sociology has dedicated itself to this interest with theoretical, methodological, and increasingly data-driven perseverance, without, however, paying attention to genetic differences. Rather, social origin, with its inherent resources and associated social mechanisms, is a place of social closure, with potentially lifelong consequences. Overcoming this social closure is the goal in order to achieve an open society in which life chances do not depend on the randomness of being born into better or worse-off families. The analysis of the conditions and mechanisms by which an origin-related distribution of opportunities comes about or can be overcome has always also served a social political agenda.

What changes now if one wants to take into account the fact that parents pass on not only their social advantages and disadvantages, but also their genes to their children, and one basically acknowledges that these genes also represent a starting capital for the further course of life? How are different degrees of heritability of social inequalities in different groups or societies to be interpreted? There have indeed been attempts to interpret overall heritability as an element of the inequality structure of societies, namely as an indicator of an openness of the societal opportunity structure in the sense that individual potentials can be developed as unhindered as possible. In twin-based variance decomposition, this then additionally stands in contrast to the shared social environment, which in turn is interpreted as a proxy for the relevance of social origin as social closure (e.g., Nielsen 2006, p. 207).

As already explained above, however, heritability estimates are difficult to interpret if they are not broken down more precisely in terms of the contributions they contain. This interpretation of heritability only makes sense if the genetic variation refers (almost) exclusively to genetic components of characteristics that are generally considered legitimate for unequal chance assignment—in the case of educational attainment, for example, genetic influences on competence acquisition (see also Freese 2008). Previous research suggests that, overall, there does indeed seem to be a correspondence between a high heritability of inequality characteristics and rather permeable structures of status acquisition and social mobility (Engzell and Tropf 2019; Selita and Kovas 2019). However, important arguments oppose such a substantial interpretation: On the one hand, heritability can also refer to characteristics that have a negative impact on success, such as the tendency to avoid stress and responsibilities, or mental problems or diseases. This makes it difficult to speak of heritability only in terms of the best possible exploitation of talent potentials and not also of the unhindered effect and development of genetic risks. However, exploiting talent reserves is also not synonymous with being exposed to genetic risks. Secondly, it can be quasi-hidden environmental influences, namely when certain ascriptive characteristics have no functional significance for educational and status acquisition, but are nonetheless hooks for social preferences and disadvantages, such as skin color, body size and weight, and these are genetically co-determined (see already Jencks et al. 1972, p. 137 with the example of discrimination against red-haired people). In such cases, corresponding shares of genetic variation indicate social closure processes instead of an openness of the opportunity structure!

A quite obvious other, almost opposite interpretation of heritability would be to see it also as an indicator of social closure, because if one cannot do anything for one’s parents, then this also applies to the transferred genes. Neither social origin nor genetic differences are to be understood deterministically, but both channel the development possibilities considerably. For such a reading, it is less important to distinguish between opportunities, risks, and ascriptive characteristics; one is bound in one way or another to the development spaces given by genetic predispositions. In twin-based variance decomposition models, both genetic variation and shared environment therefore represent the extent to which life paths are overall little open to coincidences and individual decisions against probability (Diewald et al. 2016; see also Harden 2021). Then the non-shared environment could conceptually be understood as a proxy for existing degrees of freedom or a lesser influence of origin in a society, as it captures individual deviations. However, this parameter is also not easy to interpret, as it contains the measurement error in measurement models, and also captures variation which is due to non-intentional action (coincidences).

In molecular genetic research, there are intentions to use genetic information not only for the characterization of societies and groups within societies, but also for individual profiles of opportunities and risks (e.g., Plomin 2019). Given the so far, with few exceptions, strongly limited explanatory power of genetic screenings, such attempts are still on shaky ground (Freese 2018). Also, for the so-called complex traits—including all personality traits, competencies, social characteristics, and almost all diseases[2]—genes are not deterministic, but probabilistic, i.e., they do not determine a specific development, but define possible developmental ranges. The actual development, e.g., of competencies, can then be driven up or down by the design of environments. However, this does not necessarily mean that such approaches would not be pursued further. Economic exploitation interests care less about this limited explanatory power and resulting stereotyping and discrimination, as long as their prediction models become somewhat better and thus profits can be made. It is all the more important that sociology familiarizes itself with the role of genes in the genesis of life chances in order to also be able to investigate and interpret their handling. To make a confession here will noticeably diminish the role of sociology in inequality research and the ensuing political debates sooner or later.

Overall, therefore, genetically informed research appears to be able to add some new aspects to the analysis of social inequalities, especially for the structure of relational inequalities between and within societies. This is particularly successful when the interaction of genetic variation with social conditions is investigated and the latter are based on the current state of phenotypic research (see also *Ruks and Diewald in Part 2 of the anthology*). To this, twin-based variance

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[2] Only a few rare diseases are solely determined by specific gene variants, such as Down syndrome or Huntington's disease; likewise, only a few physical characteristics such as eye color, but not body height.

decomposition adds the challenging, but also enriching, distinction between shared and non-shared environment for sociology.

The more attempts there will be to derive individual opportunities and risks from genetic markers or even to modify them with the possibilities of the genetic scissors, the more urgent the question becomes of how to ethically consider inequality-relevant genetic information, and whether this can lead to impulses for state regulations and policies. However, so far there has been no debate in the political-public sphere, as has long existed for poverty.

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Challenges and Achievements of Evolutionary and Biosocial Approaches in Sociology

Rosemary Hopcroft and Sebastian Schnettler

1 Introduction

In recent years, several scientific books on the evolutionary biological foundations of human (social) behavior have come onto the market that present research results on certain aspects of human biology (e.g., Harden 2021: genetics and social inequality; Tomasello 2020: ontogenesis) or bundle together certain behavioral complexes (e.g., Pinker 2011: violence; Raihani 2021: cooperation). Other books cover research on various biological subfields and various behavioral complexes (e.g., Sapolsky 2017). These and other books provide insight into research areas outside of sociology that deal with topics that are highly relevant to sociology in an informative way, including topics such as cooperation and conflict, mating and reproduction, human morality, and social inequality.

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Sociology has long avoided dealing with the evolutionary and biosocial foundations of social phenomena and has sometimes even devalued these as "biologistic", which in turn has been criticized both within and outside the discipline (e.g., Barkow 2006; Ellis 1996; Van den Berghe 1990). However, in recent years there has been a change in sociological engagement with biosocial and evolutionary approaches (see Schnettler 2016). In this chapter, we describe the history of evolutionary sociology and show the diverse ways in which sociologists today take up evolutionary and biosocial research. It will become apparent that in parts of sociology, the former often stereotypical understanding of what evolutionary and biosocial explanations of human behavior constitute has given way to an active engagement with evolutionary and biosocial explanations. The latter is evident in the fact that sociologists use such interdisciplinary approaches in their own empirical research and theory building and strive for consistency with them. For the most part, earlier sociological objections to biological treatises on human behavior (e.g., genetic determinism, racism/sexism, etc.) no longer apply to these newer approaches.

In the following, we refer to "evolutionary sociology" as sociological research that is dedicated to the relationship between evolved traits and predispositions and the social and material environment. This is to be distinguished from "biosociology", which examines the interaction of biomarkers (e.g., genes, hormones, polygenic scores, etc.) with the social and material environment. This differentiation roughly follows the classic distinction between "ultimate" and "proximate" causes. The term "ultimate" or "evolutionary" cause refers to the question of the evolutionary origin of physiological and psychological traits and the possible adaptive functionality of evolved traits. We attribute this perspective to evolutionary sociology. Biosociology, on the other hand, has a proximate focus and investigates the genetic, hormonal, neuronal, or other physiological processes that are (causally) involved in a behavior or perception (Laland et al. 2011; Mayr 1961; Tinbergen 1963).

As we will see in the following, the theoretical origin of evolutionary sociology and biosociology (henceforth briefly: "EBS") can be traced back to the Finnish sociologist Edward Westermarck and his work at the beginning of the 20th century. However, his influence on sociology disappeared later and, for most of the 20th century, evolutionary explanations played little role in US sociology (Degler 1991). The growing rejection of biological explanations of human behavior was, among other things, a reaction to earlier misinterpretations of Darwin's theory of evolution and its misuse to justify eugenics and racism. Other reasons for the dwindling influence of biological and evolutionary explanations in sociology were the emergence of extreme culturalism and the growing influence of

Durkheim's dictum, which postulated that sociology should explain social facts by social facts (Degler 1991; Udry 1995, p. 1267). A similar development was observed in Europe, where Westermarck's influence came to a halt by the middle of the 20th century.

This ignorance of evolutionary and biosocial approaches was briefly interrupted when some sociologists participated in the sociobiology debate or the "Sociobiology Wars" in the 1970s/80s (cf. Schnettler 2020). Individual researchers constructively adopted sociobiological concepts, but this development was short-lived and the majority of sociologists developed a critically rejecting attitude towards sociobiology applied to humans. This rejection was partly based on scientific concerns, but it was also partly politically and ideologically motivated, and it shaped sociology until a few years ago (Schnettler 2016; Segerstråle 1986, 2000). Only since the beginning of the 2000s has there been a significant renewed interest in evolutionary and biosocial approaches within sociology. The curiosity of sociologists, although sometimes very cautiously expressed, has increased in recent years and reached the mainstream (e.g. Bearman 2008; Massey 2000). After some declarations of intent and programmatic contributions, we now see more and more empirical research being published in top sociology and interdisciplinary journals, in which, for example, hormones and other biomarkers are implemented in relation to sociological questions (e.g. Goosby et al. 2018; Taylor 2012). There are also initial signs of the institutionalization of EBS in the form of new sociological and interdisciplinary subfields (Schnettler 2016), such as neurosociology and sociogenomics (Franks 2019; Mills and Tropf 2020; von Scheve 2011; Taylor 2012). These new developments are in contrast to the fact that numerous researchers in US and European sociology still hesitate to consider evolutionary or biosocial concepts in their work, and fear that a stronger reference could legitimize or promote inequalities based on gender or skin color. In addition, the degree of institutionalization of the various subfields of sociology that conduct research from an evolutionary or biosocial perspective varies considerably.

2 Edward Westermarck and the Origin of Evolutionary Sociology and Biosociology

Early sociologists like Marx, Spencer, Sumner, and Weber used evolutionary concepts in their theories about human behavior and applied Darwin's ideas—albeit selectively—to the phenomenon of sociocultural evolution (Baldus 2002; Degler 1991). This was even true for Durkheim (Runciman 2008; Schnettler 2010). However, for much of the 20th century, evolutionary and biosocial explanations played no role in sociology (Degler 1991), with the exception of metaphorical references, such as the analogy of society to the organism in structural functionalist theories (cf. Pries 2021).

Among the early sociologists, it was the Finn Edward Westermarck (1862–1939) who most comprehensively integrated evolutionary and biosocial concepts into his sociological work and can thus be considered the intellectual originator of EBS. Westermarck is today primarily known for the eponymous "Westermarck Effect", which states that children who have grown up together usually do not find each other sexually attractive as adults. Apart from this, he has largely been forgotten. However, at the beginning of the 20th century, Westermarck was one of the most famous sociologists in the world. He himself was strongly influenced by David Hume's and Adam Smith's studies on moral feelings, as well as by the works of Charles Darwin. The co-founder of the theory of evolution, Alfred Russell Wallace, was the mentor of the young Westermarck and wrote an introduction for his main work published in 1891, *"The History of Human Marriage"* (see Pipatti 2019). Westermarck was particularly impressed by Darwin's attempt (in *"Descent of Man"*) to explain the moral sense through the theory of natural selection (Pipatti 2019). Westermarck believed that moral ideas and moral judgments are at the center of sociology as a discipline and that these and the associated desire for retribution or reward are based on emotions, especially on compassion (ibid.). Emotions, in turn, are a product of evolution through natural selection. Thus, Westermarck held the evolutionary view that retributive emotions have evolved through natural selection because they tend to promote the interests of the individuals who feel them (Westermarck 1906, p. 108) and because in the environment of human ancestors, the interests of the individual and the group were largely harmonious (see also Pipatti 2019, p. 67). According to Westermarck, this common evolutionary heritage is the reason why moral rules show similarities all over the world.

While Westermarck pointed out the evolutionary, biological basis of emotions, he also emphasized the interaction between evolved predispositions and social contexts. He argued that emotional dispositions in human nature do shape the emotions underlying moral norms, but that the norms themselves are a product of the social context as the social context shapes how emotions are developed and expressed as norms. The social context and social learning lead to the emotions of moral approval or disapproval that people feel when they witness a social interaction typically being perceived as justified and generalizable because individuals have learned that almost everyone else in the social group would or should feel and react the same way. Furthermore, social processes determine who is included in the circle of sympathy and for whom the moral rules therefore apply.

While Westermarck's work *"The History of Human Marriage"* (1891) was a great success, his fame peaked with the work *"The Origin of the Moral Ideas"* published between 1906 and 1908 (Westermarck 1906). In the late 1920s, Westermarck's star in sociology began to fade. In anthropology, only Malinowski (1929, 1944) claimed that biology had an influence on social behavior. After Durkheim, most sociologists and social anthropologists began to reject any explanation of sociological phenomena that included psychology and/or biology. Structural functionalism and theories that explained social phenomena and social processes as a result of the needs and requirements of the social system itself became the dominant perspective in both areas in the years after World War II. The rise of behaviorism in the social sciences from the 1920s also meant that psychologists adopted the idea of social learning and conditioning. Thus, Westermarck's idea of universal evolved human emotions began to appear outdated (Pipatti 2019, p. 16). Further reasons for the growing rejection of biological explanations for human behavior at this time were the perceived closeness of evolutionary thinking to social Darwinism, which, however, represents a misinterpretation of Darwinian evolutionary theory. The eugenics movement of the early 20th century and its connection with scientific racism reinforced the tendency for social scientists to deny any role for biology in human social life (see Degler 1991).

3 The Sociobiology Debate

With his publication "*Sociobiology: A new synthesis*," entomologist and biologist Edward O. Wilson aimed to establish a new discipline that combines insights from various subfields of biology and deals with the biological foundations of social behavior in all social species, including humans (Wilson 1975, 1978). Sociobiology views and interprets behavioral characteristics as evolutionary adaptations to recurring problems in the environment. One of its central concepts is that of inclusive fitness and the associated shift in perspective from the individual to the gene as the primary unit of natural selection (Dawkins 2006 [1976]; Hamilton 1964a, b).

The sociobiology movement of the 1970s led to a reassessment of the role of biology in the social sciences. In sociology, Pierre van den Berghe (1979) used the idea of an evolved biological actor to explain the forms and variations that human families adopt in societies with different environmental conditions and subsistence technologies. Van den Berghe (1981) used the idea of inclusive fitness from evolutionary biology in interaction with the ecological and cultural environment to explain not only family groups but also larger groupings of tribes and ethnic groups.

With the advent of sociobiology and the individual- or gene-centered view of evolution in the 1970s, there was also a partial reassessment of Westermarck's work. Pierre van den Berghe (1979) wrote that in the first chapter of his great classic "*The History of Human Marriage*," "one finds an almost modern version of parental investment theory. This includes the idea of parental investment being asymmetric according to parental sex, a strong variation in paternal investment across species, and the idea that pair bonding is a mechanism for improving fitness." Some have claimed that Westermarck advocated group selectionist ideas and that his analysis was therefore outdated (e.g., Badcock 1994). However, Pipatti (2019) pointed out that although Westermarck was often vague about the unit of selection used and seemed to assume that characteristics serving individual fitness would indirectly also be useful for the group itself, his statements could certainly be sensibly classified within the concept of individual selection (p. 17). Stephen Sanderson recently referred to Westermarck as the "first sociobiologist" (2018b).

The fact that Wilson applied his approach to humans only in the last of over 20 chapters of "*Sociobiology*" was enough to ignite a controversial "sociobiology debate" (Schnettler 2020). As Segerstråle (1986, 2000) meticulously documented, this debate was highly politically charged. In this atmosphere, according to Segerstråle, the entire emerging discipline of sociobiology, like previous attempts to apply evolutionary and biosocial concepts to human behavior, was associated with the justification of social inequalities and racism. It even went so far as to equate sociobiology with "Nazi science" and assumed that even the claim to want to investigate the biological foundations of human nature, human social behavior, or the genetic differences between human groups could not be scientifically motivated, but could only spring from the worst political motives (Segerstråle 1991, p. 274).

Although a review in the prestigious *American Journal of Sociology* pointed out, shortly after the publication of Wilson's book, that Wilson's critics had largely misrepresented his scientific work (Eckland 1976; see also Segerstråle 2000), only a few sociologists followed Wilson's call to engage with the significance of sociobiology for sociology, apart from van den Berghe. In Germany, a few sociologists constructively, albeit critically, engaged with Wilson's sociobiology (Schnettler 2016), but often only in individual publications (e.g., Bogdany 1980; Giesen 1981; Hettlage 1984). An exception is the German sociologist Peter Meyer, who was early inspired by sociobiology and integrated an evolutionary perspective into large parts of his research program and into many of his publications. He worked on a biosocial theory of violence (e.g., Meyer 1977, 1981, 1982, 2000, 2010, 2011). Although he acknowledged past abuses of Darwinian evolutionary theory, he clearly advocated for considering biological factors underlying human behavior. According to Mayer, a taboo of research on genetic differences may be understandable in view of the disastrous consequences of past pseudoscience, but it does not change the existence of genetic inequalities, the significance of which he suggested warranted continued investigation (Meyer 1977, p. 14).

But apart from this plea and the occasional examples of constructive engagement with sociobiology, sociology remained stubbornly opposed to any inclusion of biology. Within sociology, a distorted image of sociobiology developed, resembling a greatly simplified and sometimes misunderstood caricature of evolutionary conceptualizations of human behavior and sociality (e.g., Richter 2005; cf. Schnettler 2016). This "biophobia" of sociology was emphatically criticized by individual sociologists who advocated for interdisciplinary engagement (Ellis 1996; Lopreato and Crippen 1999; Van den Berghe 1990), but for some time in vain: In the 1990s, biology largely disappeared from sociology (Machalek and Martin 2004).

4 Evolutionary Sociology and Biosociology in the 21st Century

4.1 Introduction

For a long time unnoticed by most sociologists, sociobiological research diversified in the meantime and was continued and further developed under various labels such as "evolutionary psychology", "behavioral ecology" and "cultural evolution" (Laland and Brown 2002). Although some of these approaches differ significantly in focus and methodology from sociobiology, they fall under Wilson's technical claim to want to explain social behavior and are largely consistent despite some different premises (ibid.). A few years ago, it was even suggested to reintegrate these approaches under the label of an "evolutionary behavioral science" (Brown et al. 2011). In addition to the mentioned research fields, which investigate behavior and culture from an ultimate perspective, great progress has also been made in the biosciences, which deal with the more or less proximate causes of behavioral traits. Scientists in areas such as neuroscience, behavioral endocrinology, and genetics investigate the neuronal, hormonal, and (epi-)genetic correlates and causes of perception and behavior (see Fig. 1 for an overview of the different fields). Research in these areas provides numerous examples of how biological and social processes are fundamentally intertwined (Schnettler 2016).

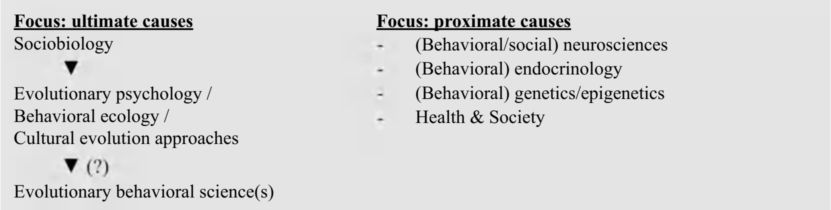

Fig. 1 Overview of the various Bio-/Evo-disciplines. (Note: This figure summarizes the various Bio-/Evo-areas mentioned in this section and roughly divides them into two groups: The focus is either on the ultimate or proximate perspective. The black arrows indicate a chronological order: Three new areas have emerged from sociobiology, which could be integrated into an evolutionary behavioral science today)

The preceding sections have shown that attempts to make biological and evolutionary concepts useful for sociology failed twice in the 20th century, each time immediately after major turning points in the biology of human behavior: in the decades after Darwin's "*Origin of Species*" and in the years after Wilson's "*Sociobiology*". However, with the sequencing of the human genome and the discovery of the genetic correlates of many social (and other) behaviors, there was a kind of upheaval at the turn of the 21st century: A milestone in American sociology was a much-cited article by Freese et al. (2003) that appeared in the prestigious "*Annual Review of Sociology*" and advocated for a stronger inclusion of biology in the discipline. Early American biosociologists like Booth et al. (2000) had previously written an overview of research on biosocial influences on the family; a continuation was published by D'Onofrio and Lahey (2010). In 2004, the section "Biosociology and Evolutionary Sociology" of the American Sociological Association was founded. With the publication of special issues on biosociology in two of the three most important journals in the field, "*Social Forces*" and "*American Journal of Sociology*", the (re-)introduction of biology into sociology was fully established (Bearman 2008; Guo 2006). For German-speaking sociology, Schnettler (2016) observes a similar, but time-delayed development. More and more programmatic contributions, advocating for a comprehensive examination of biosocial and evolutionary concepts, have appeared in recent years in prestigious sociology journals and in the common introductory handbooks to a variety of areas in sociology (Baldus 2002, 2018; Hank and Kreyenfeld 2015; e.g. Hill and Kopp 2013, 2015; Hurrelmann et al. 2015; Melzer et al. 2014; Steinbach 2015).

4.2 Following Westermarck's Footsteps

In contemporary EBS, the influence of Westermarck is clear. Jonathan Turner and Alexandra Maryanski adopted Westermarck's notion of the importance of emotions in human social life and, like him, traced the origin of human emotions back to our evolutionary history. In a series of works, they describe how central the selection for increased emotionality in humans was for the evolution of human sociality and that human emotions and the bonds they promote between individuals enable large human social groups (Turner 2000, 2002, 2007, 2010; Turner and Maryanski 2008). Using a cladistic analysis (a method for reconstructing evolutionary trees), they find that the last common ancestor of both the human and the great ape clade belonged to a solitary species (Maryanski and Turner 1992; Turner and Maryanski 2005, 2008, 2015). They argue that later human evolution led to an expansion of the emotion centers in the brain, which in turn enabled greater group solidarity, larger groups, and higher intelligence (Turner 2018; Turner and Maryanski 2008). In Turner and Maryanski (2005), they also explicitly include Westermarck's work on this topic.

However, the work of Turner and co-authors goes beyond the biosocial processes and human evolutionary heritage highlighted by Westermarck. Thus, Turner and Machalek (2018) argue that sociocultural evolution occurs through a societal selection process reminiscent of Spencer, in which societies resemble a social organism and are subjected to selection pressure along four axes or dimensions: production, reproduction, distribution, and regulation. They argue that a society will survive if it can effectively respond to this pressure; otherwise, it will disappear. In this respect, their work differs significantly from Westermarck's, who explicitly rejected the organismic analogy of society. He believed that the "biological-sociological" view of society as an organism was detrimental to the development of sociology (Pipatti 2019, p. 12).

Among the other evolutionary sociologists active in the US at the beginning of the 21st century is Stephen K. Sanderson (2001, 2014, 2015; Sanderson and Dubrow 2000). He has developed what he calls a "Darwinian conflict theory" of human sociality and supported it with extensive cross-cultural evidence, including from anthropology, as Westermarck had done before him. Darwinian conflict theory consists of a series of sub-theories and hypotheses that relate to a variety of human social behaviors, such as reproduction, parental investment, economic exchange, incest avoidance, sexuality, mate choice, kinship and marriage, gender differentiation and inequality, status and resource competition, geopolitics, aggression and violence, ethnic affiliation, and religious beliefs and rituals.

Since the turn of the century, there has also been work in the USA on the evolutionary sociology of religion, which can largely be seen as an extension of Westermarck's ideas about the evolutionary origin of human moral sentiment. Maryanski and Turner (2018) note how the human capacity for emotions, culture, and spoken language, in addition to a multitude of evolved predispositions and behavioral tendencies, underlie the human inclination towards religion. Turner et al. (2018) examine the Spencerian evolutionary processes that they believe give rise to religious institutions. Crippen and Machalek (1989) argue that emotional reactions predisposing individuals to religious feelings developed in small hunter societies as an adaptive mechanism to improve cooperation within kinship groups. As societies grew larger, these emotional reactions were adopted for larger, fictive kinship groups or religious groups, according to the thesis. Recently, Sanderson (2014, 2015, 2018a, c) suggested that a predisposition to religiosity offered rewards that could not be achieved in other ways, and that it was selected for because it increased individual reproductive success over the course of evolution. Hammond (2018) suspects the evolved neural structure of attachment behavior is a likely source of rewards for religious beliefs and behaviors. Marshall (2016) advocates a theory of religion as a product of the interaction of several evolved features of human nature and cognition within a common social and cultural environment.

In addition to developments in the USA, there are also a few specialist contributions in German sociology in which evolutionary theoretical approaches have been integrated into sociological theories of medium range or the work of individual scientists following such a perspective has been commended (Albert et al. 2016; Meißelbach 2019; Müller-Schneider 2019). An important insight from such theoretical debates is that evolutionary theoretical and social science approaches often do not contradict each other, but complement each other (cf. Schnettler 2016), and that evolutionary and bioscientists as well as sociologists have pursued surprisingly similar research programs and developed similar concepts independently of each other (cf. Fischer 2016; Pries 2021).

4.3 On Testing Evolutionary Biological Hypotheses

Since the early 2000s, hypotheses have been tested in sociology that were directly derived from evolutionary biology or from adjacent research areas. For example, the Trivers-Willard (TW) hypothesis (1973) has been tested. This states that in all sexually reproducing species with greater female than male investment, including humans, for females in good condition both offspring sex composition and parental investment is male-biased, while the reverse is true for females in poor condition. While the TW hypothesis in sex ratio form is empirically supported for many species, the evidence for the hypothesis in humans is mixed (Freese and Powell 1999, 2001; Hopcroft 2005; Hopcroft and Martin 2016; Kolk and Schnettler 2013; Schnettler 2010; Song 2018). Against the background of these mixed results, scientists also refer to the heuristic value of pursuing these and similar evolutionary hypotheses (Freese 2007; Schnettler 2010).

Another set of hypotheses from evolutionary biology that is being investigated by sociologists deals with differences between social (e.g., step-) and biological kinship relationships, e.g., in terms of (grand-)parental investment and relationship quality. Rotkirch (2018) even speaks of an emerging evolutionary family sociology in this context. This shows significant overlap with evolutionary approaches to family research outside of sociology (see Willführ in this volume). For example, Hamilton et al. (2007) investigated the hypothesis derived from the theory of inclusive fitness, whether biological kinship relationships are associated with higher investment in children than relationships between non-genetically related individuals. Specifically, it was investigated whether adoptive parents invest more in their children on average than parents in families with two biological parents. Although an initial difference was found in the study, this largely disappeared once the socio-economic status of the parents was controlled. These results suggest important differences between, for example, adoptive, step- and biological families with two parents, which make it difficult to attribute causality to the strength of genetic kinship. In newer studies, therefore, fixed effects at the family level were used to control for (unobserved) differences between the families. The corresponding studies show that, on average, adoptive and stepfamilies are disadvantaged compared to biological families in various respects (e.g., Gibby et al. 2021; Schnettler and Steinbach 2011). These results largely agree with the theory of kin selection in evolutionary biology.

Evolutionary theory also suggests that in social species, social status or rank is positively associated with the number of offspring, as status is associated with better access to resources and social advantages that facilitate pair bonding and reproduction. This aspect has been discussed in sociology and demography (Hopcroft 2006; e.g., Vining 1986). While this relationship is well documented for preindustrial societies, especially for men (see table in Hopcroft 2006), this does not seem to be the case in modern societies. Societies that are modernizing experience a drastic decline in the total fertility rate with the demographic transition. In societies that are in transition the relationship between status and number of offspring seems to reverse into the negative (Vining 1986). More recently, this conclusion has been nuanced to suggest that men with high status have more children on average than men with low status when status is measured as income. This has been found in the USA (Hopcroft 2006, 2015, 2019, 2021; see also Schnettler 2013), the United Kingdom (Nettle and Pollet 2008), Norway (Lappegård and Rønsen 2013), Sweden (Fieder and Huber 2007; Goodman and Koupil 2010), Finland (see also Jalovaara et al. 2019; Nisén et al. 2018), Japan (Ghaznavi et al. 2022) and Korea (Kim 2008). Men's personal income is also positively associated with the frequency of sex in the USA (Hopcroft 2006) and the number of extramarital sexual relationships in Finland (Haavio-Mannila et al. 2003). Interestingly, for married couples, the more a woman's husband earns, the more children she has, while men have fewer children the more their wives earn (Hopcroft 2022 for the USA).

4.4 On the Investigation of Proximate Causes

A growing number of sociologists and demographers have begun to use biomarkers in their research in recent years. Particularly successful, as measured by visibility in mainstream sociology, is sociogenomics (e.g., Diewald et al. 2015; Guang Guo 2008; Mills and Tropf 2020), which among all areas of EBS also shows the clearest signs of institutionalization as a research field (see Conley et al. 2014). Especially in sociological inequality research, genetically informed research designs are increasingly being used (see Diewald and Mönkediek as well as Ruks and Diewald in this volume). The reason for the success may lie in the fact that the various forms of sociogenomic research designs (twin studies, molecular genetic studies for the detection of individual genes, GWAS studies and the creation of polygenic scores) can be well combined with the standard methodological tools of the social sciences: the evaluation of survey data using regression analysis (see Schnettler 2016). Genetically informed sociological studies repeatedly show that genetic and social factors are not purely additive, but interact with each other. Gene-environment correlations can arise both from individuals being selected into certain social contexts by others due to their genetic characteristics, and from individuals selecting themselves into certain contexts. Genetic effects therefore often become even stronger over the life course (Guo et al. 2008; Plomin et al. 2013).

Another research area of EBS is neurosociology (von Scheve 2011). It has emerged from earlier work on the sociology of emotions and attempts to bring insights from behavioral and social neurosciences into sociology and integrate them into sociological models (Franks 2006, 2010; Franks and Turner 2013; Ten-Houten 1997). An initial step was to demonstrate the relevance of neuroscientific findings for central research areas of sociology and for the microfoundation of classic sociological concepts (Schnettler 2016; e.g., TenHouten 2013). Freese et al. (2003) estimate the potential for neuroscientifically informed sociological work as very high. In particular, the sociology of emotions could benefit from a stronger neuroscientific foundation (Franks 2006; Williams 2009).

Some sociologists have also used hormone measurements in their research. Since hormones are a direct interface between the social environment and individual behavior, endocrinologically informed research also holds great potential for sociology (Taylor 2012). Sociological contributions that investigate or summarize the relationship between hormones, social context, and behavior—such as in relation to deviance, family, gender, health, and status competition—often rely on relatively small and specialized samples (e.g., Booth et al. 2006; Mazur 2017; Udry 2000). Often the results of these studies are purely correlational in nature (see Mazur 2017). However, there are a few longitudinal and experimental studies that allow for causal statements, e.g., in studies on fatherhood and testosterone (Gettler et al. 2011) or on threats to masculinity and cortisol (Taylor 2014). Also with regard to the question of how constant discrimination processes "get under the skin", important sociological work with biomarkers for stress and inflammation processes has been carried out. By examining individual sections of the physiological causal pathways, this research shows how large-scale aggregated health gradients between subpopulations, differentiated e.g., by class or skin color, can be the result of constant experience of discrimination and racism (Cheadle et al. 2020; e.g., Goosby et al. 2018).

5 Conclusion

Although sociology largely ignored evolutionary and biosocial explanations of human (social) behavior and human perception for much of the 20th century, this noticeably changed with the turn of the millennium, first in the USA and then also in Europe. After an initial phase of (renewed) programmatic statements and calls for the integration of biological work into sociological work, more and more sociologists are now doing research using evolutionary and/or biosocial approaches. Fewer sociologists than before have a simplified and stereotyped view of biosocial and evolutionary approaches. Today, sociologists draw on concepts from the evolutionary behavioral sciences in their theory formation and empirical research. In addition, sociologists and demographers examine the interplay of genes, hormones, neural and other physiological processes and their interactions with individual behavior and the social context. That is, we see a tremendous variety of research in the area of EBS. However, the degree of institutionalization of these various subfields and specializations varies, with sociogenomics being the most advanced in this respect.

A considerable number of sociological researchers, however, still view biosocial and evolutionary explanations with skepticism. The positioning towards biosocial and evolutionary approaches within sociology seems to largely follow known fault lines in the discipline (cf. Voland and Meißelbach 2021). Given the breadth of engagement with evolutionary and biosocial fields and the cumulative research results that refute some of the strongest objections of sociologists to evolutionary and biosocial representations (reductionism, genetic determinism, naturalization of inequalities), the current developments, in our opinion, give reason for optimism that EBS, despite two failed attempts in the 20th century to integrate evolutionary and biosocial research into sociology, has now gained a sufficiently strong foothold in sociology to endure.

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Evolutionary Media Psychology

Christine Hennighausen, Benjamin P. Lange
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1 Media Use in the Digital Age

The use of media and the consumption of media entertainment have become indispensable in our daily lives. In the last decade, the use of online content and services has increased significantly due to digitalization and further technologization: While in 2012, 76% of Germans stated that they use the internet, just 10 years later, 95% of Germans are already online (Beisch & Koch, 2023). The most common form of internet use is receptive, mainly referring to the consumption of video and music streaming services, media libraries, live radio formats, and reading digital articles (Beisch & Koch, 2023). Similarly, annual expenditures for cinema visits have remained constant at around one billion euros over the last decade (excluding the "Corona years" 2020 and 2021; Federal Statistical Office of Germany, 2022). The computer and video game industry has also developed into a multi-billion dollar business (Dillon, 2016).

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These figures clearly show how much time and money people are willing to invest in media use and reception. How can this enormous human interest in media and media content be explained?

2 Media Phenomena from an Evolutionary Psychological Perspective

The production and use of media, as well as the reception of media content, have accompanied humans since their early developmental history (Schwab & Schwender, 2021; Tooby & Cosmides, 2001). Stone Age cave paintings bear witness to early media production and use; likewise, people have always told stories, through which they passed on important information from generation to generation and thus retained it in collective memory (Lange & Schwab, 2016; Matchan et al. 2020). In today's times, media use and reception have primarily shifted to the digital space due to the expansion of the internet and the spread of mobile devices—especially smartphones: Here, media content is permanently available and communication with fellow human beings is almost without temporal or geographical restrictions. Moreover, due to the low barrier, every media user can quickly and easily produce media content themselves ("Produser", a hybrid term combining *producer* and *user*).

How can media phenomena be explained? The discipline of media psychology aims at answering this question, as media psychology "deals with the description, explanation, and prediction of experiences and behavior associated with media, or that occur before, during, or after media use" (Trepte et al. 2021, p. 15; automatic translation by the publisher). Media phenomena can include media production ("who says"), media selection and use ("what in which channel"), and media effects ("to whom with what effect") according to the Lasswell formula (Lasswell, 1948, p. 37; see also Six et al., 2007). Media psychology considers both mass communication (press, radio, TV, cinema) and individual communication (telephone, email, messenger services; Winterhoff-Spurk, 2004).

Evolutionary media psychology (Hennighausen & Schwab, 2015a, b; Schwab & Hennighausen, 2016) describes and explains human behavior and experience in relation to the selection, use, and effect of mass or individual media by drawing on explanatory approaches from evolutionary psychology (Buss, 2004; for a brief overview in German see Lange & Schwarz, 2020) and considering psychological mechanisms that have developed through natural and sexual selection processes (Brill & Schwab, 2020; Hennighausen & Schwab, 2015a, b; Huskey et al., 2017; Lange et al., 2018; Schwab, 2010; Schwab & Hennighausen, 2016).

2.1 The Evolved Architecture of the Human Mind

Since modern humans were exposed to the mechanisms of natural and sexual selection during their evolution (Darwin, 1859, 1871; overview by Buss, 2004; Lange & Schwarz, 2020), the human body and human cognitive and behavioral structures can be understood as a product of evolution (Workman & Reader, 2008). Accordingly, the human brain should predominantly produce those behaviors that represent an adaptation to specific environmental conditions (Buss, 2004; Cosmides & Tooby, 1997; Lange & Schwarz, 2020). Thereby, it is assumed that specific evolved mechanisms have developed over the course of evolution to solve a particular recurring adaptive problem (Barkow et al., 1992; Buss, 2004; Schwab, 2010). Adaptive problems include all challenges that have evolutionary relevance, i.e., they are associated with differential reproductive success (mate selection and bonding, rearing of offspring) and/or survival success (food search, escape from enemies, and protection from diseases; Gigerenzer & Selten, 2001; Schwab & Schwender, 2021). These psychological mechanisms have evolved over the course of human history and represent an adaptation to the living environment of our ancestors (Tooby & Cosmides, 1992; for a critique of evolutionary psychology and the proposal to consider the Behavioral Selection Theory as an explanatory approach for faster behavioral adaptations to the environment, see also Eggert & Holzhauser in this volume). However, our modern, technologized, and mediatized living environment differs fundamentally from the environment of our ancestors, so that our once adaptive psychological mechanisms can lead to a *mismatch* of the evolutionary design (Workman & Reader, 2008). What does this look like in terms of media selection, use, and effects? Is this an evolutionary adaptation or (in parts) a mismatch?

2.2 Are Media Phenomena Adaptations or Byproducts of Evolutionary Adaptations?

As described above, evolutionary adaptations exist because they solved recurring and cross-generational problems of survival and/or reproduction of our ancestors. In contrast, evolutionary byproducts are not directly shaped by the mechanisms of natural or sexual selection, but can be understood as a side effect of an evolutionary adaptation (overview by Buss, 2004). For example, the umbilical cord is an adaptation, whereas the belly button, as a “remnant” of the once fundamental connection between mother and child, can be considered a byproduct of an adaptation.

Media production, selection, use, and effects are discussed both as evolutionary adaptations and as byproducts of adaptations. Miller's (2001) *ornamental mind theory*, for example, describes art and media entertainment as a product of sexual selection with great relevance in the context of mate choice. In the sense of a handicap, art and media entertainment are elaborate, costly, and time-consuming, so they can be interpreted as "costly" social signals that can communicate something about the "fitness" of the "producer" (Lange & Schwarz, 2013; Lange et al., 2013). In line with this, studies show that women in certain contexts are more likely to choose creative men as potential partners (Haselton & Miller, 2006; Schwab & Carolus, 2013) and that there is a correlation between creativity, the production of cultural goods, and the number of sexual partners (Lange & Euler, 2014; Nettle & Clegg, 2005). Furthermore, empirical evidence shows the evolutionarily predictable pattern that most cultural products and especially media products are produced by men of reproductive age (Lange, 2019; Lange & Euler, 2014; Lange & Schwab, 2018; Miller, 2001). In addition, media and entertainment can be understood as evolutionary adaptations, as they can be used in the sense of an "emotional simulation game" (Ohler & Nieding, 2006; Schwab & Hennighausen, 2016; Tooby & Cosmides, 2001). When consuming media content, individuals can fictitiously deal with complex social problems (= evolutionary challenges), mentally play through various solution approaches, and ultimately choose the course of action with the highest probability of success. This is also consistent with study results that show that media content repeatedly addresses mate search, mate bonding, status, and protection of relatives (Schwab, 2008; Schwender, 2006) and that interest in evolutionarily relevant content seems to be stable with little variation across epochs and cultures (Lange & Seethaler, 2015; for a cultural comparison see Uhl & Hejl, 2006). These contents are in turn anchored in the complex cultural patterns of human societies (Schwab & Lange, 2017). Learning ability and cultural ability are also products of adaptation through selection (culture by nature). Observable behavior may be optimal in terms of genes, cultures, both, or neither. Given the success of the human species so far, one might suspect that genes and culture mostly exist in a relationship of mutually beneficial interactions (Schwab, 2004).

In contrast to the adaptationist view of media phenomena, Pinker (1998, 2003) discusses media use as a byproduct of evolutionary adaptations. According to Pinker, humans have not developed specific psychological mechanisms for media reception, but respond to certain media-presented stimuli with pleasure and positive feelings, as it was advantageous in the living environment of our ancestors to respond to similar stimuli with a positive psychological mechanism. To illustrate this mechanism, Pinker uses the so-called cheesecake metaphor: Although humans have not developed a specific taste for cheesecake during their evolution, they have developed a preference for energy-rich food, as this provided a survival advantage in an energy-poor living environment. Cheesecake, due to its high fat and sugar content, stimulates the reward center in the brain, leading to positive feelings and corresponding approach behavior. The assumption that media selection, use, and effects are a byproduct of an evolutionary adaptation is supported, among other things, by study results that show that humans do not interact adequately with media (Media Equation: Krämer & Hoffmann, 2016; Reeves & Nass, 1996): If there are indications of social interaction, humans automatically react with social behavior in interaction with media figures, computers, and robots, although they are fully aware of the fact that technical artifacts do not have feelings and are not social interaction partners (Gambino et al., 2020; Krämer et al., 2015; Reeves & Nass, 1996).

3 Empirical Research in Evolutionary Media Psychology

3.1 Sex-specific Preferences for Media Content (Media Selection)

Evolutionary Psychology (Buss, 2004; Lange & Schwarz, 2020) allows for specific predictions regarding differences in experience and behavior that relate to sex and gender, respectively, which can be empirically tested (Bischof-Köhler, 2022; Euler & Lange, 2018). Thus, sex differences that can be observed in the selection of media content can be explained. There are robust and strong sex differences, for example in the preference for action-oriented media content with a higher preference among men. Women, on the other hand, seem to prefer content that focuses on qualitative mate selection and family aspects (e.g., Lange et al., 2021; Schwab, 2010; for a German-language overview see also Schwarz et al., 2018 and Lange & Schwarz in this volume). It seems plausible that women and men go through sex-specific emotional role-plays (Schwab, 2010) with their respective choice of certain media content (Lange & Schwab, 2016).

Interestingly, there are also gender stereotypes regarding the preference for certain media content: people have very clear ideas about which genres women and men prefer. These stereotypes usually go in the right direction, but they do significantly overestimate the true differences. It is conceivable that the culturally socialized stereotype amplifies the biologically predisposed dispositions and preferences. However, not all genres are overestimated equally: Lange and Schwarz (in this volume) provide an evolutionary explanation for why some genres lead to stronger overestimations of true gender differences in media preferences (film, TV series, and video game genres) than others.

3.2 Smartphones as a Social Signal in the Context of Mate Selection and Same-sex Competition (Media Selection, Usage, and Effects)

A number of studies use evolutionary explanatory approaches, particularly the theories of sexual selection (Darwin, 1871) and parental investment (Trivers, 1972), to explain *conspicuous consumption* of ostentatious luxury goods (Veblen, 1899). The consumption and ostentatious display of conspicuous luxury goods are interpreted as a waste of costly resources in the sense of a handicap (Zahavi, 1975), which can serve as 'honest' signals and thus as fitness indicators in mate selection and same-sex competition for reproductive partners. In line with this, studies suggest that primarily men might use conspicuous consumption to signal their quality as mates in the context of an uncommitted relationship (e.g., by immediate provision of resources; Griskevicius et al., 2007; Janssens et al., 2011; Sundie et al., 2011). Conspicuous consumption also seems to play a role in same-sex male competition when it comes to deterring potential rivals and communicating one's own social status with expensive and conspicuous luxury goods (Hennighausen et al., 2016; Hennighausen & Lange, 2016; Saad & Vongas, 2009). But women also seem to use conspicuous consumption as a strategy in same-sex competition. Studies show that in the context of same-sex competition, women particularly prefer those luxury products that make them appear more attractive and that women perceive other women who consume luxury products as more open to a short-term, uncommited partnership (Hudders et al., 2014). Moreover, women seem to show conspicuous consumption when they perceive their existing relationship as threatened by a potential rival: expensive luxury items, which could be a gift from the partner, are interpreted by other women as an indicator of the man's commitment to the existing relationship (Wang & Griskevicius, 2014).

In addition to conspicuous luxury items, studies also examine the signaling effect of expensive mobile devices in the context of conspicuous consumption. Findings show that men in the context of mate selection report increased purchase intentions for high-priced mobile phones and smartphones (Griskevicius et al., 2007; Janssens et al., 2011; Sundie et al., 2011) and suggest that men might use mobile devices as status symbols in the sense of a "cultural ornament" to attract the attention of potential female partners and deter possible rivals (Lycett & Dunbar, 2000). Relationship status also seems to play a role: Hennighausen and Schwab (2014) showed that only men who were single or reported being in an uncommitted relationship or affair indicated higher purchase intentions for a status-associated, conspicuous smartphone. Furthermore, both male and female participants particularly perceive an attractive man, who is presented as the owner of a conspicuous, status-associated smartphone, as a more suitable mate in the context of an uncommitted relationship, as well as a stronger rival and worse friend ("buddy") (Hennighausen, 2016).

The research results described provide a heuristically fruitful explanation for the selection of expensive, status-associated smartphones (Hennighausen & Schwab, 2014; Janssens et al., 2011; Sundie et al., 2011), the use of these devices (Lycett & Dunbar, 2000), and the effect that expensive, status-associated smartphones can have in same-sex competition and in the context of mate selection (Hennighausen, 2016).

3.3 Horror Fans and Morbid Curiosity (Media Selection and Media Effects)

Why do we voluntarily consume media content associated with negative emotions? Why do we like "tear jerkers" (Sad Film Paradox; Gleich & Vogel, 2016) or "scary movies"? From an evolutionary psychological perspective, emotions—especially negative ones—serve specific functions regarding reproduction and survival of the individual. They motivate us to exhibit certain fitness-enhancing behaviors (Lange et al., 2020).

The horror genre, for example, offers a special kind of emotional role-playing games that focus on the emotions of *fear* and *terror*. Why do viewers enjoy fictional, fear-inducing narratives? As an answer to this question, Scrivner, Johnson, Kjeldgaard-Christiansen, and Clasen (2021) hypothesize that media horror experiences can serve as simulations of actual experiences, through which people gather information and model potential experiential worlds and scenarios. To test their assumption, the researchers conducted a study during the COVID-19 pandemic, examining whether engagement with thematically relevant media fictions (including horror and pandemic films) was associated with better preparation for the pandemic and greater psychological resilience. The results showed that fans of horror films reported greater psychological resilience during the pandemic. In addition, fans of "prepper" films (alien invasion, apocalyptic films, and zombie films) reported both greater psychological resilience and feeling better prepared for the COVID-19 pandemic, and being able to better anticipate the events during the pandemic. These findings support the authors' assumption that viewers can practice coping strategies perceived as effective through engagement with frightening films, which are experienced as an advantage in real situations.

Since the study of Scrivner et al. (2021) is a correlational study, however, the direction of causality of the relationship between the consumption of horror and pandemic films and psychological resilience cannot be conclusively determined: Alternatively, it is also conceivable that individuals with higher resilience are more likely to be fans of "prepper" films and watch horror and pandemic films more frequently due to their higher psychological resilience.

This example nonetheless demonstrates how paradoxical phenomena in the area of choice, use, and especially the impact of certain media content can be profitably explained from an evolutionary perspective.

3.4 Talking Machines as Social Counterparts (Media Effects)

Google Assistant, Apple's Siri, Microsoft's Cortana, or Amazon's Alexa—also known as *smart speakers*—are increasingly entering our everyday life. They play music on demand, schedule appointments, provide information about current news, and control the smart home. Today, we can choose a life with intelligent virtual assistants and artificial intelligences by our side. Their popularity is steadily growing: The proportion of households in Germany that have at least one smart speaker has been continuously increasing and in 2021 already accounted for a third of households (Brocks & Bätjer-Gleitsmann, 2021). But how do we deal with this machine counterpart? What social behavior do we show when dealing with talking machines? Do we possibly treat them as if they were social actors?

The *Media Equation* approach refers to the tendency of people to "humanize" computers and other technical devices (Krämer & Hoffmann, 2016; Reeves & Nass, 1996). We behave as if these inanimate devices were an intentional and social counterpart (*intentional stance*; Dennett, 1987). Studies suggest that we even attribute emotions and thoughts to them (for an overview see Krämer & Hoffmann, 2016). After all, they seem to interact with us and direct their words specifically at us. Vacuum cleaners, lawn mowers, computers, mobile phones, and our TV screens are responsive and reply. Why shouldn't we also react socially and naturally—along our evolved mechanisms—to them and subsequently attribute human traits to them?

Schneider (2024) deals with the phenomenon of “computers are social actors” (= CASA) and applies this approach to the question: “Are voice assistants social actors?”. “Computers are social actors” (CASA; Nass & Moon, 2000) describes a paradigm that states that people thoughtlessly apply the same social heuristics and scripts they use for human interactions to computers—knowing well that these machines have no feelings, intentions, or human-like intentions. This happens when computers exhibit similar social characteristics, cues, and behaviors as humans, e.g., language or humor (e.g., Lange et al., 2019a; Lange & Pastau, 2018; Menne et al., 2018).

According to the CASA approach, certain features of machines trigger scripts for human interaction, leading an individual to ignore cues that point to the asocial nature of the machine. These features include text output, interactivity, or the ability to perform tasks usually carried out by humans. CASA has been extended to robots and artificial intelligence. To account for advances in technology, MASA (“machines are …”) has been proposed as a significant extension of CASA. Schneider (2024) develops a VASA approach (“voice assistants are …”) and investigates human-voice assistant interaction. He can show: People follow the social norm of politeness, especially the interviewer bias, in interaction with smart speakers. People show prosocial behavior towards smart speakers based on minimal cues, such as team affiliation. Gender stereotypes also become visible in human-smart speaker interaction and reciprocal behavior towards smart speakers depending on their previous helpful or unhelpful interactions with them.

3.5 Social Media Usage (Media Production and Effects)

In recent years, the importance of social media has largely increased, as steadily rising user numbers show (Beisch & Koch, 2021; Ortiz-Ospina, 2019). Social media are an essential part of Web 2.0 (“participatory web”) and are used by users to network with each other, communicate and cooperate over the Internet (Bendel, 2021). Since human cooperation and communication are significantly shaped by evolutionarily relevant fields of action (survival success, reproductive success, etc.), it is likely that this is also reflected in media phenomena observed around and in social media. In the following, we will demonstrate the added value an evolutionary perspective can have for explaining social media phenomena based on various findings.

3.5.1 Mate Selection in the Online Context: What Do Chat Texts and Nicknames Reveal about Their Sender?

In times of new social media, mate selection is largely shifting from the offline to the online world (Rosenfeld et al., 2019; for a German-language overview of online dating, see Aretz et al., 2017). It is assumed that similar sex differences are shown online as offline (Adler et al., 2018). Media psychological research on online mate selection has, among other things, examined the communication patterns that can be found in online mate selection. What does the sender communicate? And what conclusions can the recipient draw from it? A study by von Andrian-Werburg, Adler, Schwab, Schwarz and Lange (2020) showed, for example, that the intelligence of the interaction partner—an important mate selection criterion—can be inferred from the chat text of the interaction partner with above-average accuracy. However, none of the Big Five personality dimensions of the interaction partner were correctly recognized. An explanation for this could be, in line with theoretical assumptions from media and social psychology—*Hyperpersonal Communication* and *Social Information Processing Theory* (overview by Fischer, 2016) and *Impression Management* (overview by Eimler & Winter, 2016)—that the chat text is used by the sender to present themselves better, i.e., in terms of their characteristics, for example, more socially desirable. Research on online dating nicknames, i.e., pseudonyms used in online dating, on the other hand, found that the Big Five personality dimensions of the interactin partner, i.e., the nickname user, can be correctly assessed based on the nicknames. The nickname even allowed a correct assessment of whether the nickname user is more likely looking for a short-term or long-term relationship (Lange et al., 2019b). One could conclude that a whole text, simply because of the high quantity of language material, provides a good opportunity to deceive the interaction partner. A short nickname, on the other hand, reveals more about its producer and user. It indeed seems that the special characteristics of online dating (namely a certain anonymity and more time to compose asynchronous messages and thus more opportunities to present oneself better) make deceptions about mate selection relevant characteristics very prevalent. In line with this, research shows that deception is indeed practiced in online dating. For example, false information is given about physical attractiveness (women, for example, indicate a lower weight) or men conceal that they are actually pursuing a short-term strategy (Bischof-Köhler, 2022; Toma 2015; Toma & Hancock, 2010; Toma et al., 2008).

3.5.2 Gossip 2.0

Gossip ("chit-chat") refers to information about new, deviant characteristics or behaviors of other people (Arno, 1980). It is a universal human phenomenon: studies show that up to two-thirds of all conversations revolve around social topics (including mate choice and relationships; Dunbar, 1998a). But what makes gossip so significant? And what functions could gossip fulfill? Studies suggest that gossip serves as a "social glue" (Turner et al., 2003) as individuals network through gossip and gossip promotes the development of positive relationships (Foster, 2004). Following the Uses-and-Gratifications approach (Katz et al., 1973), gossip fulfills the need for information, influence, and entertainment (Rosnow, 1977). From an evolutionary perspective, gossip is of great importance as alliances are forged in the social group through gossip, which can increase differential survival and reproductive success depending on the extent (e.g., through an alliance against common enemies or devaluation of same-sex competitors through rumors; Carolus, 2012; Dunbar, 1998a, b). Dunbar (1998a) shows how gossip can even explain the evolution of human language.

Based on these theories, Carolus (2012) examined through a content analysis which topics are predominant in social networks (focus on the professional network *XING*[1] and the formerly active private network *wer-kennt-wen*)[2]. The results showed that many contents shared on user profiles were either associated with gossip regarding mate choice (e.g., information about relationship status) or with gossip regarding social reputation (e.g., photos showing the user with friends, number of friends).

3.5.3 Self-presentation in Social Networks

As part of the content analysis, Carolus (2012) also examined the self-presentation of men and women in the aforementioned social networks *XING* and *wer-kenn-wen.* The results of the content analysis of user profiles showed sex-differentiated differences, which would be expected due to the different parental investments (Trivers, 1972, see also above) and *the Sexual Strategies Theory*, which describes male and female preferences in mate choice based on this (Buss & Schmitt, 1993). The analysis showed that female profiles tended to have profile photos more often than male profiles, which is consistent with the fact that for men the physical attractiveness of a potential partner plays a major role (Buss

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[1] https://www.xing.com.

[2] https://www.wer-kennt-wen.de/ (active until June 2014; Wikipedia, 2022).

& Barnes, 1986). In contrast, there were no differences in the proportion of bare skin shown in the profile photos. Carolus also analyzed the relationship status information on the profile pages, insofar as the profiles provided this information. It was found that more women stated they were in a committed relationship than men (23% vs. 18%). For the relationship status "single", it was the opposite: here, men stated more often that they were single than women did (18% vs. 8%). This finding fits well with the predictions that can be derived from the *Sexual Strategies Theory* (Buss & Schmitt, 1993): women prefer a so-called qualitative mate selection strategy (see above), men have the option of a so-called quantitative mate selection strategy in addition to choosing a qualitative strategy as well (see Bischof-Köhler 2022). These examples from Carolus' (2012) content analysis show how self-presentation in social media can be better explained from an evolutionary perspective.

4 Summary and Conclusion

In this chapter, media production and, above all, media selection, use, and effects were viewed from an evolutionary perspective. It was shown that the theories of natural and sexual selection can contribute to a deeper understanding of how and why individuals choose media, use them (and produce them at all), and what effects media can have on people. Media production, as well as media selection, use, and effects, were discussed as an adaption to certain evolutionary challenges (*ornamental mind theory*; Miller, 2001; Media as an "emotional simulation game"; Ohler & Nieding, 2006; Schwab, 2008; Tooby & Cosmides, 2001) and as a byproduct of evolutionary adaptations (Cheesecake metaphor; Pinker, 1998, 2003). Further research must clarify in more depth which media phenomena are to be classified as adaptations and which as byproducts. The chapter finally presented various studies from evolutionary media psychology that show how media phenomena can be better understood and explained from an evolutionary perspective: Sex-specific preferences for certain media content, conspicuous consumption and display of status-associated smartphones, selection and effects of fear-inducing media content with pandemic and horror scenarios, social behavior towards smart speakers, and online mate choice, gossip, and self-presentation in social media.

Our brain and thus our mind or psyche are results of a biological evolutionary process (Buss, 2004). It is this mind that produces and uses media (culture by nature; see Schwab & Lange, 2017). Media and digitalization phenomena are thus on the one hand technologies and narratives of the present and are also cultivated through learning processes, but are also associated with the probability of an evolutionary mismatch. After all, these phenomena are always also results of our evolved nature. This allows—as research findings show - media production on the one hand and media selection, use, and effects on the other hand to be partly explained evolutionarily. In the course of the Darwinian process, humans have evolved into what they are today, and their handling of media always shows traces of the evolved mental apparatus of humans in its current form: We use "high tech-media" predominantly for our and with our "stone-age minds".

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Evolutionary Family Research—Cost-Benefit Balance at the Interface between Kin Selection and Social Context

Kai P. Willführ

1 Introduction

All human societies are based on some form of family. Which individuals belong to a family network, which of them live together in a household, how daily life in these family households is organized, and last but not least, the societal significance of the family, varies between regions, population groups, and periods. At the first glance, the phenomenon of the family appears too culturally diverse and the forms of family too dynamic in terms of their social changeability (Ruggles 2015), for an evolutionary perspective to offer more than an explanation of the pure biological foundations. Apart from biologically parenthood, many sociological explanatory models until now have rejected or ignored evolutionary or biosocial influences on human social behavior. According to these non-evolutionary approaches, the phenomenon of the family is exclusively a social phenomenon that needs to be explained with social theory. A parallel can be made to the relationship between the biological ability to develop language and language. Humans are capable of language due to a biological predisposition, but the language a person learns from an early age is determined by the cultural and social

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environment. Thus, any evolutionary approach that claims to explain the diverse social features of the family in different contexts seems doomed. This belief is widespread within the social sciences, which is why it is not surprising that many explanatory approaches in social science family research are purely cultural or social in nature (Fasang et al. 2016).

But appearances are deceptive. The cultural and social manifestation of the family is not only founded on evolutionary processes at several levels, but is profoundly influenced in its manifestation. Just as human language is based on an evolved universal grammar (Berwick et al. 2013; Chomsky 1995), the family, despite all its variance and dynamics, can be traced back to evolved, basic behavioral tendencies that prove to be remarkably constant over time and space. Without exception, all societies attribute significant value to blood kinship and especially to the parent-child relationship. This fact indicates that cultural and social explanatory approaches alone are not sufficient to explain the phenomenon of the family (Silk 1990).

For example, the social models of the 20th century, which devalued close biological relationships for ideological reasons, did not survive in the long term. In the early Israeli kibbutzim, children did not sleep in the parental household, but in the kindergartens. This was not accepted by parents and children in the long run, and so private family life was given more importance again. This example also points at an evolutionary basis for cohabitation in family households next to kinship relationships. Paleoanthropological research suggests that social groups of earlier representatives of the genus *Homo* were divided into family units and formed a kind of proto-household in which hunted and gathered resources were distributed (Manning 2023). Thus, living together in family households is not only a cultural universality, but is phylogenetically older than the species *Homo sapiens sapiens* itself.

This article discusses the relevance of the evolutionary perspective for family research. The theory of kin selection plays a central role in this. This theory not only explains why humans have the behavioral tendency to coordinate reproductive and productive activities within family networks, but also explains why humans differentiate between blood relatives and in-law family members in these networks. Even though the family ultimately traces back to evolutionary processes, the social context is not left out in the formation of family structures. As we will see, the social and cultural context influences the cost-benefit balances of familial (and non-familial) cooperation and competition. But before we turn to this in detail, Sect. 2 will firstdiscuss how evolutionary and non-evolutionary approaches to family research differ.

2 Location and Delimitations

2.1 Evolutionary vs. Non-evolutionary Research Programs

Evolutionary family research is, like all evolutionary approaches, a radically different research program to the theory of non-evolutionary informed social sciences. Tooby and Cosmides (1992) have tried to summarize the basic assumptions of non-evolutionary social sciences in the so-called *standard social science model* (SSSM), and have contrasted this with an *integrated model* (IM). While the IM considers evolution relevant in explaining all human behavior, according to the SSSM, any behavior can in principle be conditioned or learned. Individual (family) behavior can therefore be explained exclusively by social factors. To illustrate the SSSM, the human brain at birth is often compared to a blank slate or *tabula rasa* that can be written on at will. Just as the material structure of a sheet has no real influence on what is written on it, according to the SSSM, the brain has no influence on which family and social behavior it learns. Even though the SSSM has been criticized as inaccurate by non-evolutionary social sciences and psychology (Richardson 2007; Wallace 2010), it is undisputed that social sciences, with few exceptions, have so far not assigned a significant role to evolutionary explanatory approaches (see also Schnettler & Hopcroft in the same volume).

However, there are good reasons to believe that the evolutionary perspective is relevant in multiple ways for explaining human family. Humans do not come into the world as blank slates, but are born with a set of emotional, motivational, and cognitive adaptations. The theory of kin selection makes specific predictions about which behavioral tendencies or motivations can be expected from individual family members (see below). In family networks and households, the evolved behavioral tendencies of the members meet. Since these both differ and overlap, there is not only cooperation among family members, but also competition with considerable potential for conflict. Although the behavioral tendencies manifest themselves in the respective intra- and extra-familial social context into behaviors, i.e., the actual behavior, this socialization process is also controlled by cognitive mechanisms that are products of evolution (see below). The social context is thus involved in the formation of behaviors, but the control is subject to evolved mechanisms. In biology, such genetically controlled developmental processes are referred to as ontogenesis. Finally, the behaviors can have an effect on the actor and have an effect on their biological fitness. They therefore have an

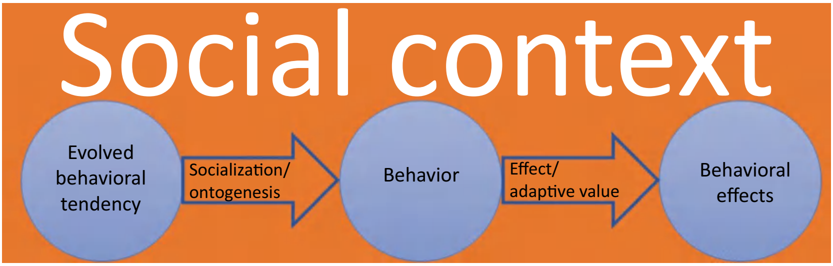

Fig. 1 Humans possess evolved behavioral tendencies at birth. These manifest themselves in the respective social context into behaviors. This socialization process is controlled by mechanisms that are also products of evolution (ontogenesis). The formed behaviors lead in the respective social context to effects that can have a feedback effect on the actor. These behavioral effects can be assessed in terms of their adaptive value

adaptive value, which can explain why some behaviors prevail in a population while others fail (Fig. 1).

2.2 Sociological and Evolutionary Biological Definitions of Family

The human family is sociologically defined as a community of life, established through partnership, marriage, civil partnership, adoption, or descent. Fundamentally, it is the affiliation of two or more generations related to each other in a mother and/or father-child relationship, who can live in a common household, but do not have to (Lexicon of Sociology). These communities enjoy a special status within societies and often the status of an institution. Members of a family gain a social position simply through family affiliation. The sociological definition explicitly emphasizes that social, not biological, kinship is decisive for the family.

The evolutionary perspective on family is based on the theory of kin selection. While it does not explicity exclude any of the family relationships recognized in sociological theory, here descent, i.e., biological kinship, plays a fundamental role. The affiliation of two or more generations related to each other must therefore have a biological character in contrast to the sociological definition. The basis of a biological family always consists of at least one, in monogamous partnerships two, and in the case of polygyny or polyandry, several reproductive individuals. The family includes the offspring of these reproductive individuals and is often extended by close relatives of the reproductive individuals. The latter are usually the parents and/or siblings of one or all reproductive individuals. In some traditional societies, adoptions are widespread, but the adopted children are usually blood relatives (Silk 1990; Volk 2011). Family forms such as step- or patchwork families cannot be explained by kin selection, but can be integrated into the evolutionary perspective. For example, in patchwork families, the support of stepchildren by the partner of the biological parent can be interpreted as an investment in the partnership.

Family researchers define family forms based on cohabitation and household forms. If only parents and children share a household, it is referred to as the nuclear family. If there are additional members living in the household, it is referred to as the extended family or multi-generational family. Cohabitation is certainly an important feature and can certainly be used to classify family forms, but a sharp distinction in practice is often not possible or sensible. For example, neolocal nuclear families can receive a high degree of grandparental support, such as daily childcare, even if the grandparents live in a separate household. Also, a greater spatial distance between the parental and grandparental household does not imply a greater emotional distance or that the grandparents are absent from family decisions.

2.3 Different Evolutionary Research Approaches

Evolutionary approaches to family research, which are oriented towards Darwinian evolutionary theory, are pursued in disciplines such as sociobiology, ethology, behavioral ecology, evolutionary anthropology, and evolutionary psychology. Voland (2023) assigns the evolutionarily oriented disciplines either to Darwinian Anthropology (DA) or to Darwinian Psychology[1] (DP). This division is based on the different definition of adaptive behavior, but both approaches share the assumption that evolved behavioral tendencies manifest in the respective social context. There are also different views on how to interpret the behaviors resulting from the manifestation in terms of their adaptivity, i.e., their ‘biological fitness’.

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[1] In the literature, ‘Darwinian Anthropology’ is often used synonymously with ‘Evolutionary Anthropology’. Similarly, ‘Darwinian Psychology’ is used synonymously with ‘Evolutionary Psychology’. Since there are other evolutionary theories besides Darwinian evolutionary theory, the attribute ‘Darwinian’ is more accurate than ‘Evolutionary’.

Approaches of DP designate behaviors as adaptive if their origin can be traced back to processes of natural or sexual selection. According to this definition, these behaviors have in the past, in the environment in which they evolved (*environment of evolutionary adaptedness*, EEA), on average increased the fitness of their actors. Under contemporary environmental conditions, however, these behaviors do not necessarily have to improve fitness. If environmental conditions change drastically, these behaviors can become functionless or even dysfunctional due to an environment-gene mismatch, thus reducing the fitness of the actors. In addition to mutation, inbreeding, genetic drift, gene flow, heterozygote advantage, and pleiotropy, these environment-gene mismatches, induced by rapid changes in the environment, are one of the causes for so-called 'maladaptations'(Crespi 2000).[2] For the behaviorally oriented approaches of DA, on the other hand, behaviors are adaptive if they are associated with the highest possible fitness for the actor under the given conditions and compared to all other realizable alternatives (Voland 2023, pp. 15–18). For an evolutionarily oriented family research, both interpretations can be useful, depending on the research question.

Box 1: What is 'Fitness'?

Fitness is a term from population genetics and represents a measure of the adaptation of an individual (phenotype) or a genotype to its environment. It is composed of the adaptation values of all characteristics of a phenotype or genotype. Individual genetic or phenotypic characteristics (e.g., behaviors) possess an adaptation value, but no fitness. An individual with higher fitness has greater reproductive success, i.e., more reproductively capable offspring, under the same environmental conditions than one with lower fitness. The reproductive success of an individual, in turn, is composed in social species of its own reproduction (*personal fitness*) and the reproduction of close relatives (*inclusive fitness*) (see Sect. 3.1). Fitness can be understood as a dimensionless ratio that cannot be directly measured (compare the concept of the 'latent variable' from the social sciences). In

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[2] The term *maladaptation*, like its German translation "Fehlanpassung", is actually an oxymoron, a contradiction in terms. While there are, as listed in the text, a number of mechanisms that can lead to biological characteristics being dysfunctional and thus reducing the fitness of the actor, natural selection is not one of them. By definition, it can only produce adaptations and never 'maladaptations'.

empirical research projects, proxies and indicators such as the number of (reproductively capable) children are therefore used. It is immediately clear that such indirect measurements are not without problems. Often, lifetime reproductive success cannot be determined due to short observation periods, and having many reproductively capable children does not guarantee that they will be successful in their own reproduction.

Conclusion: The term ‘fitness’ is closely linked to the theory of evolution, but a precise definition is difficult in practice, and there are different views regarding its exact meaning (Barker 2009).

DP primarily focuses on psychological preferences, for example in mate choice, while DA looks at behaviors and their effects on the actor’s fitness. In the research designs of DA, adaptation values or functionality of competing behavioral alternatives are compared, whose phylogenetic origins are initially not relevant and therefore do not require knowledge of the EEA (see Brandl et al. in the same book). But the approach of DP, on the other hand, requires exactly this detailed knowledge about the conditions of the EEA. We cannot observe our ancestors in their Stone Age environment. Statements about the EEA are therefore often assumptions derived from the research results of paleontology. Often, the criticism has been voiced, not entirely unjustifiably, that many research endeavors in DP merely deliver post-hoc explanations that largely evade scientific verification (Gibson and Lawson 2015). However, DP can do more than just tell stories from the Stone Age. With the appropriate empirical methods, these predictions and theory-guided hypotheses—in the spirit of Popper’s critical rationalism—can be falsified. This is particularly true for the evolved behavioral tendencies that can be derived from the theory of kin selection (see Sect. 3.1).

2.4 Important Evolutionary Concepts for Family Research

Some differentiations of the Darwinian theory of evolution are applied across disciplines and are particularly relevant for evolutionary-oriented family research. These include the theory of life history evolution (LHT, Alexander 1988; Roff 1992; Stearns 1989), the associated evolutionary theory of socialisation

(Belsky et al. 2007; Ellis and Boyce 2011) and the cooperative breeding hypothesis (Hrdy 2006, 2009). The LHT and the evolutionary theory of socialisation are key concepts when it comes to understanding the origin, i.e., the ontogenesis, of behaviours. The basic assumption is that life strategies, including attachment behaviour, are significantly influenced by the security or predictability of the social environment in childhood. Due to space constraints, this cannot be discussed in detail in this article. Interested readers are referred to the German review article by Störmer and Voland (2014). In contrast, the *cooperative breeding hypothesis* will be presented in the following, as it could be relevant not only for the evolution of the human family itself, but also for the historical development of the family household.

Human mothers do not raise their children alone, unlike many other mammalian mothers. They are supported by other individuals, very often by family members including the father. Many scientists have argued that the motivational and emotional ability to cooperate with family members is an important evolutionary adaptation that distinguishes humans from other great apes. Reproduction is organised in family networks in which parents and other individuals, also called *alloparents* (Hrdy 2009), cooperatively raise children. Drawing on the vocabulary of animal behavioural ecology, some scientists have referred to this as *cooperative breeding* (Hrdy 2006; Mace and Sear 2005). In this article, I use the broader term '*cooperative reproduction*' instead of *cooperative breeding*.

Cooperative reproduction is widespread among nest-building, flight-capable bird species. Usually, both parents share the care of the brood, and in some species, adult offspring from previous broods appear as so-called helpers-at-the-nest. These animals help the parents raise their younger siblings. Interestingly, the cooperation of the young birds can only partially be explained by kin selection, as it would be better for the fitness of the young birds if they were to breed in their own nest. Often, however, the parent birds enforce the cooperation of their adult offspring by sabotaging their nest building and mating attempts. The young birds are then faced with the choice of either not breeding at all or at least increasing their inclusive fitness as helpers at their parents' nest. Often, they can hope to eventually inherit the parents' breeding site (Kingma et al. 2014). To what extent such parent-child conflicts were important in the establishment of human nests, i.e., households, cannot be discussed here due to space constraints. However, it can be assumed that the parent-child conflict, as well as the lineage conflict between in-law related family members, is an indispensable characteristic of the human family.

Box 2: Is the human family household an extended phenotype?

The comparison to the bird's nest offers another interesting perspective on the human family household: Human family households could be interpreted as extended phenotypes (*extended phenotypes*; Dawkins 1982), similar to bird nests and spider webs. Extended phenotypes are not parts of the organism, but products of behavior, yet like the organism itself, they are under the control of its genes. Like morphological phenotypes, extended phenotypes vary in their plasticity. This is very low in spider webs, for example. Their construction, structure, and form are genetically determined and, apart from laboratory experiments, are almost unaffected by the environment. On the other hand, bird nests show some plasticity and can be influenced by environmental factors. For example, many urban bird populations use human settlement waste for nest building, often with fatal, but sometimes also with positive consequences (Suárez-Rodríguez et al. 2013).

In birds, it is assumed that the joint brood care of both parent animals was the evolutionary basis for alloparental cooperation at the nest. To what extent paternal investment or pair formation was the basis for cooperative reproduction in humans and for the formation of proto-households is controversial. To date, we do not know whether cooperative reproduction in humans arose from the cooperation of blood relatives, e.g., in grandmother-mother dyads, or whether, as in birds, parent pair formation was a prerequisite. Comparisons with other great apes species are of little help in this regard, as cooperative reproduction, apart from occasional sharing of food, is in practice not observed.

Even though we do not know exactly by whom, it can be assumed that the establishment of the first proto-households was primarily due to reproductive intentions. Once the households were established, everyday productive cooperations could then be organized with the human helpers-at-the-nest in addition to the reproductive ones. In this way, households could have become established beyond the purpose of reproduction. The fact that the household members are primarily relatives is partly a result of reproductive activity, as children are born into the household, and partly a result of individual and collective life decisions, as family members can join or be recruited to the household for various reasons. Regardless of how far this analogy between bird's nest and human family household can be stretched, it is undisputed that in both variants, closely related family members cooperate at one location. The reproduction of *Homo sapiens sapiens* in family households is a cultural universal and can, like its sociality itself, be considered part of its nature.

3 Evolutionary Family Research

3.1 Kin Selection: The Relevance of Common Descent

An important theoretical offer that evolutionary biology, more precisely sociobiology, made to the social sciences in the second half of the 20th century is kin selection theory or inclusive fitness theory. This theory describes why altruism among relatives can be evolutionarily stable in a world of 'selfish' genes. Its basic principle states that individuals can increase their biological fitness not only through their own reproduction (*personal fitness*), but also indirectly by supporting their close relatives in their reproduction (*inclusive fitness*). Hamilton's rule mathematically describes the relationship between altruistic behavior and genetic degree of kinship (Hamilton 1964a, b).[3] Simply put, it states that altruism between family members becomes more likely or intense with increasing genetic kinship. Thus, due to the different genetic degrees of kinship, it is more likely that an individual will be altruistically supported by his sister than by his cousin. With full siblings, one shares on average half of one's genes, while with first-degree cousins it is only an eighth. Again, the probability of being altruistically supported by a cousin is higher than the probability with which an individual can expect this from distant or unrelated persons.[4]

Hamilton's rule is very successful in explaining animal social behavior in all its facets. Many of its predictions also coincide with observations from family

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[3] According to Hamilton's rule, altruistic behavior can prevail evolutionarily or the genes responsible for it can spread in a population if the condition $K < r *N$ is met. Here, the costs (K) of the behavior for the altruist must always be less than the benefit (N,= gain in indirect fitness) multiplied by the degree of genetic relatedness (r).

[4] From the beginning, there were great misunderstandings with the theory of kin selection. These misunderstandings have contributed significantly to the rejection of this theory outside of evolutionary sciences. See Dawkins (1979) for this.

research. It is often the close relatives who are willing to support other members of the family over a long period of time, even if they do not necessarily expect to be compensated for the time and resources they have invested at some point (compare reciprocal altruism). This is particularly true for parents who raise their children, but also for grandparents who support their reproductive children or their grandchildren, as well as for aunts and uncles who support their nieces and nephews. It is also usually close relatives who are willing to save their relatives at high risk in dangerous situations. Friendships between non-close relatives, on the other hand, break up when resources flow in one direction for a longer period of time.

Even though such findings were reason enough for sociobiology to extend its explanatory claim to human social behavior, the degree of genetic kinship alone cannot explain human family relationships. Because if the relationship status of family members depended solely on their genealogical distance, very similar descriptions of kinship relationships would be found in all human cultures. But that is not the case. For example, some cultures and epochs differentiate between the brother of the mother and that of the father, while other cultures use the same designation for the brothers of both parents. Today in German, 'Onkel' can mean the brother of the father or the mother, while in the past the brother of the mother was referred to as 'Oheim' and the brother of the father as 'Onkel'.[5]

Furthermore, non- or distant relatives, such as adoptive or foster children, are granted the social status of a close blood relative in many societies. At first glance, such findings do not seem to fit the theory of kin selection, as parents here care for children who are not their own. Although Darwinian anthropology has always pointed out that genetic kinship relationships are still relevant in these cultures (Silk 1990), these findings have nevertheless led large parts of sociology and cultural anthropology to not only pay little attention to the evolutionary perspective on human family, but to reject it outright (Cronk et al. 2019). However, the cultural diversity of family forms between and within societies does not refute the relevance of genetic kinship. Instead, it merely indicates that factors other than genealogical distance also enter into the cost-benefit balance of the kinship relationship.

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[5] The terminology of kinship designations (*kin terms*) has always been the focus of anthropological research. See the classification of kinship designations according to Morgan (1871).

It should go without saying that inclusive fitness is the fundament of family but does not determine if family members cooperate. Hamilton's rule shows that close relatives enjoy a special status a priori. However, it does not imply that family members support each other regardless of the situation and under all circumstances. For example, siblings can forge reliable alliances, but at the same time compete relentlessly for the attention and resources of their parents (Fox et al. 2017). If the competition among siblings is great enough, even killing them can belong to the 'natural behavioral repertoire'. For example, some birds of prey exhibit Cainism, and the succession battles in the Mongolian and Ottoman empires provide an impressive example of human fratricide. In contrast to the Western royal families, who primarily practiced primogeniture, the succession in these empires was not legally established. As a result, there were almost always bloody succession battles in which brothers killed each other, and these 'sibling disputes' often escalated into full-blown civil wars (Dimitris 2005; Fletcher 1986).

For evolutionary family research, it is important to note on the one hand that genuine altruism is possible between close relatives. On the other hand, support and help are not granted unconditionally even among close biological relatives, but are offered on the basis of a cost-benefit calculation. As outlined below, these are highly dependent on the socio-economic and institutional context (Voland and Dunbar 1995; West et al. 2002).

Box 3: Caution: Genetic egoism ≠ psychological egoism!

One of the central assumptions of synthetic evolutionary theory (Huxley 1942), which is still valid today, is that genes that do not selfishly promote their own replication, but altruistically support the replication of other genes, cannot persist in evolution, as they disappear from the gene pool or cannot spread in it in the first place. Richard Dawkins referred to this existential property of genes as 'egoism' in his famous book *The selfish gene* (Dawkins 2016). Although there is nothing scientifically wrong with the explanations in Dawkins' book, he has often been accused of claiming that not only selfish genes, but also selfish individuals would be favored by evolution. However, this conclusion is incorrect, as it confuses the ultimate level and the proximate level. Cognitive scientist Steven Pinker has aptly put it: "Just as blueprints don't necessarily specify blue buildings, selfish genes don't necessarily specify selfish organisms. [...], sometimes the most selfish thing a gene can do is build a selfless brain. Genes are a play within a play, not the interior monologue of the players." (from: How the mind works. Pinker 1997)

3.2 The Lineage Conflict

Most animal species and almost all human societies avoid or prohibit sex between closely related individuals (see incest avoidance and incest taboo). Marriages or sexual relationships between siblings or between parents and children are taboo almost everywhere in the world, and even in many liberal European countries including Germany, consensual incest among adults is sanctioned with severe penalties (StGB § 173).[6] Some societies allow marriages between cousins and cousins up to the first degree or between uncles/aunts and nieces/nephews, while other societies, including many strictly Catholic ones, prohibit any form of cousin marriage. Usually, reproductive partners have a certain genealogical distance from each other. This has far-reaching consequences for family relationships: A family member is either blood-related or related by marriage to another. With blood relatives, one shares at least one ancestor at a relatively close genealogical distance (e.g., parent, grandparent, great-grandparent, etc.) and thus to a certain degree the same genetic traits. The common descent forms, as explained in Sect. 3.1, the basis for kin selection. On the other hand, family ties in the case of marriage are not created by close biological kinship or descent, but by marriage or partnership.

The distinction between marriage and blood kinship is not purely academic, but extends far into society and is reflected in its culture, social order, and legislation. An example of this are the different stereotypes of biological parents and in-laws. While the biological mother of the mother has the image of the caring grandmother who selflessly takes care of her grandchildren as well as her adult daughter, less positive attributes are assigned to the mother-in-law. The mother-in-law is also the target of socially accepted ridicule. Just think of the cactus that is offered to her as a seat in the German-speaking world (mother-in-law's seat, *Echinocactus grusonii*), or the door she is supposed to use in the English-speaking world when visiting (*mother-in-law door*). The list of these mocking meta-

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[6] Exceptions to the incest prohibition existed in many cultures for ruling families.

phors is long, and they are more than just linguistic tomfoolery, as they reflect a tangible genetic conflict between the parents' families.

Ultimately, it is evolutionary motivational patterns that lead parents to intervene in their children's reproductive attempts in order to increase their own inclusive fitness. There are (grand)parental motivations that are universally and cross-culturally effective. In particular, maternal grandmothers tend to support the reproductive activities of their daughters, as investing in female-line relatives (so-called uterine relatives) can increase their indirect fitness (Danielsbacka et al. 2011; Euler and Weitzel 1996). Many studies consistently show that the presence of the maternal grandmother in hunter-gatherer societies as well as in premodern agricultural societies has a positive effect on the survival of both her reproductive daughter and her grandchildren (Chapman et al. 2021; Engelhardt et al. 2019; Sear and Mace 2008; Willführ et al. 2018). The support in everyday life and the transfer of knowledge, for example about which measures effectively remedy emergency and illness situations, seem to be the cause of this positive influence (Scelza and Hinde 2019).

On the other hand, the effects of the paternal grandmother on the survival of her grandchildren are less consistent. Some studies report that the presence of the father's mother has no influence on the survival of her grandchildren, while others conclude that her presence increases the mortality of both her grandchildren and her daughter-in-law (Voland and Beise 2002, 2005). The inconsistent effects of paternal grandmothers can be explained by the different interests or perspectives on the partnership between their son and his partner. While every child that her son fathers increases her own inclusive fitness, this is only partially true for the children of her daughter-in-law. The father's mother primarily has no evolved interest in the life reproduction success of her daughter-in-law, but is only interested in her reproductive success as long as she gives birth to or takes care of her son's children.[7] Therefore, compared to the mother's mother, the father's mother has less incentive to consider the health of her son's wife. In extreme cases, she could even see her son's wife as dispensable and replaceable at any time after her death. She could therefore try to persuade her son's wife to have more children at shorter intervals than her daughter-in-law would do without her intervention. The scenarios of this intervention motivation of the mother-in-law, referred to in the literature as *kin priming* (Mathews and Sear 2013), range from friendly support and encouragement to reproductive and economic exploitation. Increased

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[7] A similar tension exists for the same reasons between the man and the mother of his wife.

fertility means that the intervals between births become shorter. Under premodern conditions, short interbirth intervals correlate with increased maternal depletion, resource dilution[8], and increased sibling competition. All three factors can increase both child mortality and mother mortality. The *kin priming* effect of the mother-in-law can therefore increase the mortality of her daughter-in-law and her grandchildren under premodern conditions, even if the mother-in-law is generally willing to support her son's wife.

4 The Genetic Lineage Conflict in the Social Context

In section 3, it was explained that the evolutionary perspective, based on kinship relationships, makes specific predictions about the behavioral tendencies to be expected from family members. It was described that the different lineage carries significant conflict potential for family members connected by marriage. This section will now focus on the role of the social context and show, using examples, how it can influence the lineage conflict in premodern as well as modern societies. An overview of how kin effects and lineage conflicts are researched using the methods and data of historical demography is provided by Willführ et al. (2024).

4.1 Example 1—Paternity Uncertainty, Inheritance and Residency Rules in Premodern Societies

Many evolutionarily informed scientists have interpreted the different influence of maternal and paternal grandmother as an expression of paternity uncertainty. Since the paternal grandmother cannot be completely certain that the children resulting from her son's partnership are indeed her biological grandchildren, the potential for conflict with her daughter-in-law could increase even further. In the animal kingdom, extra-pair copulations are widespread and these lead to increased genetic diversity among offspring. This genetic diversity can be advantageous in pathogen-laden environments and it also reduces the risk that all offspring suffer from the same hereditary diseases. However, the effect

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[8] Since parental resources (time, money or material goods) are finite, the resources available for each child inevitably decrease with an increasing number of children in the family. This circumstance is referred to as resource dilution.

of paternity uncertainty as a source of lineage conflict in humans is not generalizable. Because paternity certainty is largely determined by the social context and it guides the investment decisions of uterine and agnatic relatives. If paternity is secured, for example, through social control, there is initially no reason for grandparents to discriminate between the children of their sons and those of their daughters.

Especially from the perspective of the wife, the costs of extra-pair reproduction can quickly escalate, particularly in those contexts where the husband is willing to invest many resources in his (biological) children. In patrilineal societies, where paternal property is inherited by the sons, it is important from the perspective of the property-owning men that the children of their wives are indeed their own. In such societies, there is often a great moral pressure on women to be sexually faithful, and men often try to monopolize women reproductively (Strassmann et al. 2012). Against this background, it is not surprising that the residency rule of patrilocality prevails in many patrilineal societies. When the woman is integrated into her husband's extended family household after marriage, she is initially cut off from her blood family and is subject to a certain degree of reproductive control by her husband's family. But even if the woman could raise children from extra-pair copulations under such family circumstances, it is questionable whether these would socially look forward to a successful future. These children are stepchildren from the husband's perspective and therefore cannot expect support from him or his family.

The questions of which lineage generates resources, how these are distributed, and how the couple's residence is regulated are therefore decisive. In societies where intra-family transactions of resources and property are primarily patrilineal, it can be reproductively rewarding for the grandmother to invest primarily in the children of her sons rather than in the children of her daughters. These patterns can lead to a "patrilateral bias," as Pashos found for rural Greece (Pashos 2000). For the sake of completeness, it should be mentioned that due to heterosomal inheritance, the grandmother and the daughters of her sons have the same version of an X chromosome. Some studies suggest that paternal grandmothers invest more in their granddaughters due to this increased genetic kinship (Fox et al. 2010). For both, i.e., both for the patrilateral bias and the preference of the granddaughter by the paternal grandmother, a generally high paternity certainty is a prerequisite.

Residency rules are not only associated with the degree of paternity certainty, but also have a key influence on which lineage can invests more in the couple's children. Residency determines access opportunities of grandparents to their grandchildren in everyday life. In matrilocal societies, where men leave their family of origin and join the woman's family, the motivation of the maternal grandmother to support her reproductive daughter in everyday life can fully unfold. The same applies in neolocal contexts, if the households have a small geographical distance to each other. In patrilocal societies, however, where the married daughter lives with the man's relatives, even a high motivation of the maternal grandmother to support her daughter often cannot have an effect, either because the geographical distance between the households is too large, or because she is not welcome in everyday life. In most premodern societies, it cannot be assumed that paternal and maternal grandparents have the same access opportunities to their grandchildren in terms of geographical distance.

4.2 Example 2—Consanguineous Marriages in Pre-Modern Societies

Marriages between relatives can also influence the lineage conflict. Marriages between relatives or consanguineous marriages refer to partnerships in which the spouses show a relatively small genealogical distance to each other. Most consanguineous marriages are made between first or second degree cousins. Romeo and Bittles (2014) estimate that more than one billion people in North Africa, the Middle East, and parts of Asia live in population groups where more than 20% of marriages are blood-related connections. At the same time, numerous studies have shown that the offspring resulting from these blood-related connections suffer from the effects of inbreeding depression (Bittles and Black 2010a, b). Furthermore, from the perspective of older generations, reproduction in consanguineous connections leads to fewer offspring than would be the case with exclusively non-consanguineous reproduction (see Fig. 2). In reference to the genealogical term of pedigree collapse, also known as implex, this phenomenon is referred to below as descendant collapse.

Consanguineous connections occur in isolated populations, such as remote Alpine valleys or religious sects. In such societies, marriage markets are often severely limited, leading to blood relatives marrying each other, even though they might have avoided this under other circumstances. However, consanguineous connections are also observed in populations where the marriage markets are more relaxed. Then they can be interpreted in terms of an adaptive reproductive

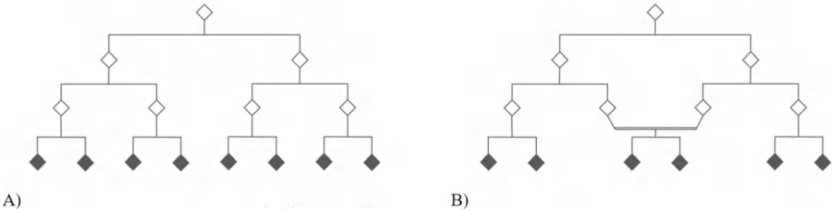

Fig. 2 Illustration of the descendant collapse. In these two fictional family trees, all couples have two children who in turn also bring two children into the world, etc. From the perspective of the great-grandparents, exclusively non-consanguineous reproduction of the offspring (A) leads to eight great-grandchildren. A consanguineous connection (B) among the grandchildren reduces the number of great-grandchildren to six

strategy, for example, to prevent non-relatives from accessing limited resources (Walker and Bailey 2014). For peasant societies, it has been repeatedly shown that a high degree of blood relationship is associated with an increased intergenerational transmission of land ownership through the patriline (Johow et al. 2019). Whether consanguineous marriage strategies are overall behaviorally ecological successful depends on the balance between the costs (inbreeding depression, descendant collapse) and benefits (social and political success, resource control, etc.).

Another behavioral ecological benefit of marriages between relatives that has so far received little attention in the literature could lie in the reduction of lineage conflict. In the case of a marriage between first-degree cousins, one parent-in-law is a biological aunt or uncle (see Fig. 3). Using the historical population of Krummhörn in East Frisia [1720–1874], my colleagues and I showed that the geographical proximity of the mother-in-law was associated with a lower mortality of her daughters-in-law (Willführ et al. 2018). This was particularly true for higher social, land-owning classes, in which the proportion of consanguineous connections was significantly larger compared to the landless population. Among the wealthy elite, to some extent, the genetic lineage conflict was neutralized by familial solidarity.

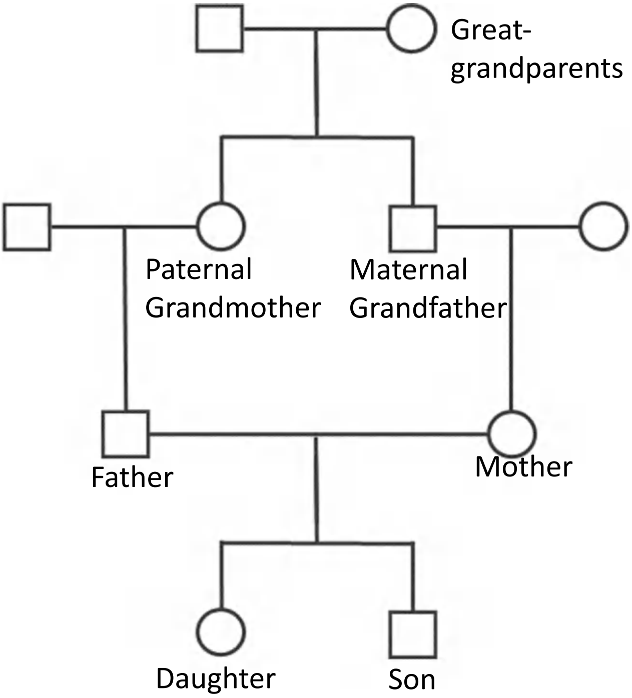

Fig. 3 In marriages between first-degree cousins, one parent-in-law is a biological aunt or uncle. In this illustration, the paternal grandmother, i.e., the mother's mother-in-law, is a biological aunt and the maternal grandfather, i.e., the father's father-in-law, is a biological uncle

4.3 Example 3: Grandmother Effects in Modern Societies

Major societal upheavals change the fundamental conditions that human nature faces (Borgerhoff Mulder 1998; Colleran 2020; Stulp and Barrett 2016). *Homo sapiens sapiens*, like its predecessors, is likely to have spent the majority of its evolution in (semi-)nomadic hunter-gatherer small groups (Marlowe 2005). If one follows the basic assumptions of DP, most of human cognitive and emotional abilities are adapted to this environment (see above). The sedentarization and the emergence of agricultural societies during the Neolithic Revolution about 12,000 years ago drastically changed the cultural and social context. Hunter-gatherer groups are either female bonded or male bonded, while there is a strong tendency towards patrilocality and patrilineality among agriculturally shaped societies. Upheavals of a similar magnitude occurred with modernization. One characteristic here is the dominance of the neolocal nuclear family, in which the couple lives with neither of the two lines (Ruggles 2015).[9] Even though social contexts arise through sedentarization, modernization or currently through digitization, which were previously unknown in human history, evolutionary behavioral tendencies remain relevant.[10] These arise from human genetic makeup and cannot simply be discarded in new environments. The questions that now arise from the evolutionary perspective are: First, in which behaviors do the evolved behavioral tendencies manifest in the new contexts? And second, what adaptive value do these behaviors have in the new contexts?

These two questions will be discussed in the following using the example of the effect of maternal and paternal grandmother and their transformation in the course of modernization. Using the Swedish census data from 1900 to 1910, my colleagues and I have examined how the geographical proximity of the grandparents affected reproductive success, measured by the number of surviving children, and the survival of the mother (Willführ et al. 2022). At the time, Sweden was largely modernized, i.e., industrialization had prevailed in most parts of the country, the demographic transition was in full swing, and the family model of the neolocal nuclear family dominated. In this social context, we find no evidence that the geographical proximity of the maternal grandmother influenced reproductive success or the survival of the mother. Interestingly, while the presence of the maternal grandmother in pre-modern societies made the survival of their reproductive daughters more likely, the Swedish women whose mother lived in the same household had the lowest reproductive success and the highest mortality. On the other hand, the influence of the paternal grandmother fits the predictions of the evolutionary perspective. The smaller the geographical distance of the

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[9] Parts of Western Europe may be an exception to this general pattern, as in these societies nuclear family households and thus neolocality were common even before industrialization (Hajnal 1983; Laslett and Wall 1972).

[10] The Neolithic Revolution, modernization, and digitization certainly represent important turning points in human history, but this selection of relevant societal upheavals is not exhaustive. Moreover, these event, generally speaking, rarely affect all people equally. Even today, there are still hunter-gatherer societies, traditional agricultural societies, and the current digitization does not affect all societies.

father's mother, the more (surviving) children the couple had. However, this *kin priming* effect was not associated with increased mortality of the mother, as has been observed in some pre-modern societies. Comparable results are reported by Hacker et al. for the USA for the same period (Hacker et al. 2021).

Critics might see the absence of the maternal grandmother effect as evidence that evolutionary explanations have no relevance in modern societies. However, the absence of the grandmother effect on mortality and fertility in modern contexts and under industrial mortality regimes is not a contradiction. The overall improved living conditions in modern societies may have led to grandmotherly support no longer being immediately vital for survival, even though there is evidence that it can, for example, reduce the risk of accidents (Tanskanen et al. 2020). From a behavioral ecology perspective, it is expected that grandmotherly engagement in such environments shifts to other areas. For instance, Swedish census data suggest that parental support helped unmarried women to marry well at the beginning of the 20th century. In contemporary populations, there is evidence that grandmotherly support increases the educational success of grandchildren. Even though these effects are partly due to various non-behavioral causes, grandmotherly investment is still relevant today (Liu 2018; Song 2016).

5 Conclusion

Evolutionary family research constructs a theoretical framework whose foundation is Darwinian evolutionary theory. Many theories based on Darwinian evolutionary theory are of particular relevance to family research. For example, the theory of kin selection is not limited to social behavior among animals, but also explains why humans in all cultures and periods organize their reproductive and productive activities in family networks and family households. Even though the willingness to cooperate in the human family ultimately rests on kin selection, it is not the only factor determining the relationships of family members. In a 'gene selfish world', genuine altruism between closely related family members is possible due to indirect fitness benefits, but family members are not only trusting allies, but also sharp competitors. Therefore, even among siblings or between parents and children, support and help are not granted unconditionally, but are offered based on a cost-benefit calculation. The costs and benefits depend on the social context. This applies to a comparative perspective between cultures and periods and the within-society perpsective used to analyze differences between social groups.

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Inclusive Fitness and Human Social Behavior

Adolf Heschl

The once strictly separated humanities and natural sciences are increasingly converging in terms of methodology and content, leading to speculation that there could soon be a potentially complete merger of the two major research areas. The emergence of a novel meta-discipline of “evolutionary social sciences” is already becoming apparent, as reflected in the full diversity of the contributions in this volume. A special role in this development is played by the theory of kinship selection, founded in 1964 by biologists William D. Hamilton, George R. Price, and John Maynard Smith, which assumes that the degree of genetic relatedness between individuals determines how they behave towards each other in different contexts. The extent of the resulting inclusive fitness has since reflected the ways in which individuals of a given species try to maximize their overall genetic fitness. For example, depending on the situation or environmental conditions, an individual can invest more in its own reproduction (direct fitness) or in that of its close relatives (indirect fitness)[1] or also in a combination of both. Here, *Hamilton’s inequality* $rB - C > 0$ applies, according to which the gain in indirect fitness rB (B … *benefit*, r … degree of kinship) through targeted support of relatives minus the loss in direct fitness C (C … *cost*) caused by reduced or even

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[1] In a certain sense, the Christian-Western demand “Love your neighbor as yourself.” (Mt 22:37) anticipates the idea of sociobiology, although today it stands as a humanistically generalized demand that considers “neighbor” to mean any other human being. Christ himself still saw this somewhat differently: “Whoever is not with me is against me.” (Mt 12:30).

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completely omitted rearing of one's own offspring must be greater than zero to be evolutionarily stable (Hamilton 1964a, b). In other words, true altruism without expectation of a return only pays off in evolution if it is directed at as closely related individuals as possible.

1 No True Altruism Without Kinship

In the animal kingdom, the general validity of this principle has already been demonstrated in a whole range of species (Bourke 2014). For example, the reproductive renunciation of worker bees is explained by their particularly close genetic relatedness with the privilegedly reproducing queen bee (75%), which due to the special reproductive system of the honey bee – haploid drones fertilize diploid queens - is always higher than that of possible offspring of the diploid workers (50%) (Trivers and Hare 1976). The situation is similar in cooperatively breeding mammals, where a single dominant pair reproduces and the rest of the family helps raise the young (e.g., some rodents, meerkats, canines, marmosets, humans). At the other end of the spectrum are species in which individuals form exclusively monogamous pairs that only raise their own offspring as in many bird species. A middle position is finally occupied by those species where social systems predominate in which promiscuously reproducing individuals mutually assist in raising the young which, with some likelihood, are related to all group members as in many socially living primates (e.g., chimpanzees, bonobos, macaques).

But even in the case of a monogamous pair, which normally only cares for its own offspring, the preceding mate choice already includes an indirect effect based on kin selection, which automatically also increases the inclusive fitness of both partners. Studies in a number of animal species, as well as in humans, have shown that individuals who want to reproduce do not choose any partner, but apply very specific selection criteria. In addition to phenotypically perceptible characteristics such as physical and cognitive fitness of a potential partner, parameters play a role that also concern specifically the genetic proximity to oneself. This phenomenon, known as assortative mating (Nishi et al. 2020; Allen et al. 2019), is based on the fact that sexual reproduction forces animals, against their will,[2] yet in the sense of an increased evolutionary adaptability, to accept foreign

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[2] The most effective form of reproduction is asexual reproduction, which, however, since the emergence of sexual reproduction about 800 million years ago in the Proterozoic, is no longer practiced as the main form of reproduction in most animal and plant species.

genes—this is the only reason why this type of comparatively elaborate reproduction, which rather reduces instead of multiplying the number of offspring (from 2 germ cells becomes 1 zygote), exists in nature at all—and these hence try to keep the proportion of foreign genes in their own offspring as low as possible. The result is a partner who is as closely related to oneself as possible, but still differs in those characteristics that could potentially bring a fitness advantage. The best-known example of this is the immune system, whose relative foreignness and thus potentially increased adaptation value for the recipient is usually determined by many animals including humans through the sense of smell (Milinski and Wedekind 2001; Havlicek et al. 2020).

2 Tit for Tat

True altruism in the sense of a completely selfless support of not closely related conspecifics at the expense of one's own fitness does not exist in nature, as any such organism would automatically take itself out of the race for reproduction and thus also the behavior that characterizes it. This has already been recognized by Darwin as the "problem of altruism":

> "He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature." (Darwin 1871, p. 130)

What does occasionally exist, however, is the mutual support of two partners who help each other in order to better survive and reproduce successfully. Such symbiotic relationships exist not only between different species that have become increasingly dependent on each other during their evolution (mutualism), but also as intentional cooperation between individuals of the same species. But even in such, rather rare cases in the animal kingdom of so-called "reciprocal altruism"[33] , where, as first described by evolutionary biologist Robert Trivers 1971, two partners apparently help each other independently of their degree of kinship

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[3] As soon as altruism demands a quid pro quo, it is no longer true altruism, but rather intentional cooperation based on the principle of *Tit for Tat*, an evolutionarily stable strategy of "an eye for an eye." This term, first introduced in the 1960s by American game theorist Anatol Rapoport (1964) and further developed 20 years later by Robert Axelrod (1984), has since become established.

(Silk 2013), genetic distance often plays a crucial role. Since mutual aid, if it is to function satisfactorily for both sides over a longer period of time, always requires a certain degree of mutual trust and social compatibility (Molesti and Majolo 2016), it has proven beneficial in the course of the social evolution of many vertebrates to be as selective as possible in the choice of potential cooperation partners in order not to fall victim to deception in the end (Campenni and Schino 2014; Roberts 2015).

Despite the great successes of modern sociobiology (see Voland 2013; for a current overview, see Willführ in this volume), it has not always been possible to apply its gene-based model of the evolution of animal social relationships 1:1 to humans. Although generally confirming the genetic approach, the observed relationships between degree of kinship and altruistic help or sacrifice were not always, as one would expect, strictly linear and if so, then often surprisingly weak. In an experiment by Madsen et al. (2007), the average willingness of test subjects to maintain a strenuous physical activity over a longer period of time for the benefit of a recipient differed only slightly (< 10 %) between close relatives (children/siblings: 50 %, grandchildren/nephew: 25 %, great-grandchildren/cousin: 12.5 % identical DNA) and "non-related" (< 6.25 % identical DNA) beneficiaries of the action, the latter characterized as "friends" or "acquaintances" (Fig. 1, Curve A). The same weak relationship between genetic kinship and selfless altruism was found even when the test subjects had to decide in a later experiment (Curry et al. 2013) how likely they would be willing to give something as precious as an organ (kidney) for a transplant to another person (Fig. 1, Curve B). The course of both curves differed significantly from the much steeper curve that is to be expected from classical gene selection theory first developed in 1966 by George C. Williams [4](Fig. 1, Curve C). This striking contradiction between biological theory and empirical data suggests that at least in humans there seems

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[4] Although Williams emphasized the importance of the individual gene for evolution in his book *Adaptation and Natural Selection* as early as 1966, it was Richard Dawkins who did this in a particularly explicit form: "The neo-Weismannian view of life, which this book represents, emphasizes the genetic replicator as the basic explanatory unit. I believe this plays an atom-like role in any functional, teleonomic explanation. If we want to speak of adaptations as 'for the benefit of' something, then this something is the active germ line replicator. This is a small piece of DNA, a single 'gene' according to the definition of the word." (Dawkins 1983, *The Extended Phenotype—the Gene as the Unit of Selection*, p. 113).

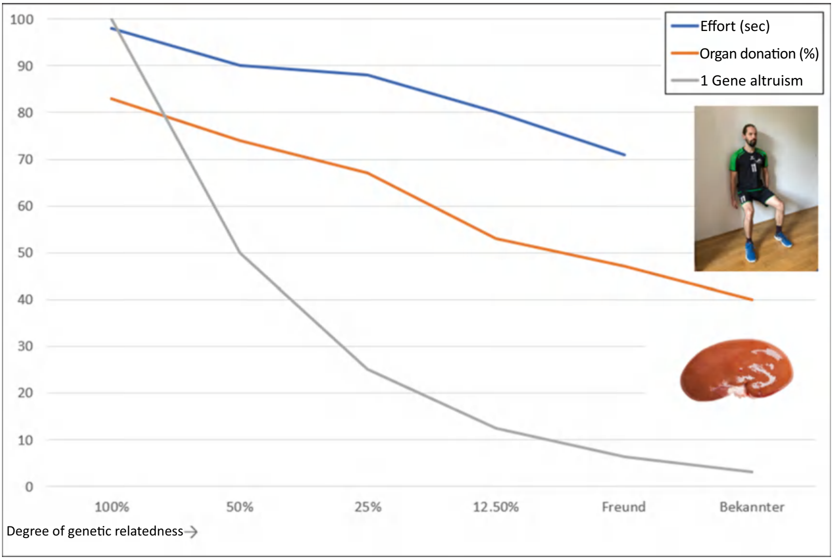

Fig. 1 Two revealing experiments on the relationship between genetic relatedness and altruism in humans. Experiment 1 (blue curve): Execution of a strenuous isometric exercise (pressing the body against wall), to give money to a recipient depending on its degree of kinship (Madsen et al. 2007). Experiment 2 (red curve): Willingness of test subjects to donate an organ (kidney) to a recipient depending on its degree of kinship (Curry et al. 2013). Gray curve (lowest): hypothetical curve derived from gene selection theory showing the inclination of social beings to act altruistically towards a recipient depending on its degree of kinship (reduction by half at each step).

to be a tendency to also confer to somewhat less closely related conspecifics a certain degree of altruistic assistance, which alone makes living together in larger groups possible.

3 Greenbeard Seeks Greenbeard

From a theoretical perspective, one would expect in Fig. 1 a similarly steep decline in the extent of altruistic-cooperative behaviors of the involved individuals under otherwise constant conditions—i.e., benefit B and cost C remain the same, only the degree of kinship r changes. However, as the data published by Madsen et al. in 2007 from various human cultures (blue curve) clearly show individuals defined as “not related” from a theoretical perspective are socially supported all over the world, without this happening on the basis of a strictly reciprocal tit-for-tat rule. To remedy this obvious empirical weakness of the single-gene concept, Richard Dawkins—building on earlier ideas from William D. Hamilton—developed the hypothesis of the *Green-Beard Effect*, which should make it easier for social individuals to recognize and promote like-minded individuals by wearing a conspicuous feature, such as a green beard. In this way, even an evolution of altruistic behavior completely independent of real kinship relationships would be conceivable, purely based on a few “selfish” genes that specifically promote each other. People with green beards would thus not only possess the necessary genes for the ontogenetic development of their special phenotype, but also genes that allow the recognition and promotion of other carriers of green beards. A mutually reinforcing “conspiracy” of a few selected selfish genes could thus arise, which would ultimately infiltrate and dominate entire populations and species through their high cooperativity (Gardner and West 2010).

However, an idea that seems helpful at first glance does not always have to be correct upon closer inspection. In the case of the Green-Beard effect, it turned out that its validity is essentially limited to intragenomic gene parasites, so-called *outlaws*—similar to certain types of viruses (e.g., Herpes, endogenous retroviruses; cf. Wildschutte et al. 2016)—which, once permanently integrated into the host’s genome, exploit its physiology for their own purposes (Biernaskie et al. 2011). This may sound convincing at first glance as a confirmation of Dawkins’ concept of the selfish gene, but ultimately fails because not all genes of a multicellular genome can code for parasitic green beards. But if, as Dawkins assumes, all genes of an organism are ruthless evolutionary egoists, then logically there are no more genes that commit themselves to the cause of the host. Then one must consequently also ask how—to use Dawkins’ provocative terminology—the “vehicle” host can still function at all if all its genes are mere freeloaders? It is therefore not surprising that the idea of the Green-Beard effect soon turned out to be a theoretical dead end, which raises far more problems than it claims to solve. This also explains the comparatively disappointing result after almost 50 years of continuous empirical research in sociobiology since the publication of Dawkins’ influential bestseller “The Selfish Gene” in 1976:

> “Research on greenbeards is still in its infancy, but it is clear that empirical work has made the plausibility of finding greenbeard genes in nature probable, and we now need to investigate their significance. … We tentatively suggest that greenbeard genes occur much more frequently than previously assumed, contrary to arguments against their biological relevance.” (Madgwick et al. 2019, p. 10)

But even the possible discovery of further isolated greenbeard genes would not be of much help when it comes to explaining the surprisingly pronounced helpfulness and cooperativity found in many animal species including our own one. On the contrary, according to the theory, real greenbeards primarily support only other greenbeards with exactly the same greenbeard genes and occasionally even go so far as to deliberately disadvantage non-greenbeard genes through directed "spite" and ultimately eliminate them from the population (West and Gardner 2010). However, this is the exact opposite of what behavioral researchers have demonstrated in recent decades, namely a surprisingly high social tolerance and willingness to cooperate in many species on this globe.

4 Cooperation and the Crisis of Sociobiology

Examples of interspecific cooperation include the regular associations of various African prey species (e.g., ungulates) as well as, although much less common, predators that form flexible coalitions among themselves to protect each other through herd formation from predators or to support each other in hunting prey (e.g., mixed groups of dolphins, seals, and gannets). In doing so, the individual species are quite selective, preferring specific partners for the respective purpose. For example, it is known that Hanuman langurs in Asia deliberately join forces with axis deer to benefit from their finely developed hearing when it comes to not becoming a victim of a tiger. The deer, in turn, prefer the proximity of the monkeys to benefit from their pronounced "foresight" when it comes to spotting a potential predator in the thicket of leaves and branches in time (Newton 1989; Ramesh et al. 2012). Also well-studied are the large gatherings of usually several species of ungulates in the African savannah, which try to protect themselves in this way from the large predators, especially the pack-hunting lions. What unites buffalo, giraffe, wildebeest, zebras, and gazelles primarily is the sheer fear of an attack by a predator. However, instead of just moving through the wide grassland with their own kind, the animals accept a significant additional food competition by deliberately joining other, similarly living species.

Now, the interspecific cooperation among ungulates threatened by large feline predators in the African savannah naturally has nothing to do with kin selection in the classical sense, which primarily aims to maximize the inclusive fitness of individual organisms (Wyatt et al. 2013). However, as far as the evolution of true eusocial structures in various species is concerned, in which certain individuals demonstrably forego their reproduction in favor of related conspecifics, an ideological split into two relatively strictly separated camps has developed in the last

10 years. The trigger for this split was an article written by Martin Nowak, Corina Tarnita, and the co-founder of sociobiology, E. O. Wilson, published in the prestigious journal *Nature* in 2010, in which the authors conclude with regard of the influence of Hamilton and Dawkins's kin selection on the emergence of complex social systems:

> "Eusociality, in which some individuals reduce their own lifelong reproductive potential to raise the offspring of others, underlies the most advanced forms of social organization and the ecologically dominant role of social insects and humans. Over the past four decades, kin selection theory, based on the concept of inclusive fitness, has been the main theoretical attempt to explain the evolution of eusociality. Here we show the limits of this approach. We argue that the standard theory of natural selection, in conjunction with precise models of population structure, represents a simpler and superior approach, allowing the evaluation of multiple competing hypotheses and providing a more accurate framework for interpreting empirical observations." (Nowak et al. 2010, Abstract)

The startled response of a selected group of colleagues, nearly 100 different researchers from all areas of the biological study of social behavior, ensued immediately:

> "Nowak et al. argue that the theory of inclusive fitness has been of little value in explaining the natural world so far and that it has led to negligible progress in explaining the evolution of eusociality. However, we believe that their arguments are based on a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature." (Abbot et al. 2011, p. E1)

This in turn immediately triggered a significantly sharpened reaction from the originators of the controversy:

> "Hamilton's work has stimulated many empirical studies and led to many measurements of kinship. But we have shown that we cannot rely on inclusive fitness theory to describe how interactions between related individuals influence evolution. Inclusive fitness theory is neither useful nor necessary to explain the evolution of eusociality or other phenomena. It is time for the field of social evolution to move beyond the boundaries of inclusive fitness theory." (Abbot et al. 2011, p. E10, authors' response)

But how do Nowak, Tarnita, and Wilson came to such a negative judgment about the concept of inclusive fitness or kin selection, which has seemingly provided valuable services in terms of the evolutionary explanation of social behavior for so many years? Well, their main argument essentially states that the development of complex social systems cannot occur due to the selection of one single gene, let's call it the "eusociality gene"—a variant of the green beard gene—but clearly requires a whole series of coordinated genetic adaptations. This suggests that the genome as a whole plays a crucial role in the evolution of social behaviors, as the latter must always be finetuned with regard to the behavior that primarily serves the survival and reproduction of the individual. This argument can be extended to the question if the classical procedure of calculating the degree of kinship in sociobiology based on Richard Dawkins' One Gene-dogma must also be questioned. If not individual "selfish" genes are the driving force of social evolution, then *all* genes of an individual must be taken into account. Or, argued the other way around, why should a single gene, arbitrarily isolated from the genomic context and moreover purely fictitious —no geneticist has so far discovered a "kin-love gene"— be the declared evolutionary engine of social altruism? In the sense of gene selection theory, it is rather to be expected that every phenotypically relevant gene should be just as interested in finding itself in the next generation as any other gene.

5 Genome-based Kinship Metric

If one takes the highly justified criticism of Nowak, Tarnita, and Wilson of the concept of inclusive fitness seriously, then there is no other choice but to calculate the degree of kinship between two individuals by using all known gene alleles of a given species. This would mean that instead of using the usual kinship gradations of 50% (children, siblings), 25% (grandchildren, nephews), 12.5 % (great-grandchildren, cousins) and so on for a specific, artificially isolated single gene, the summed probabilities of occurrence of *all known* alleles within a species have to be calculated. For this purpose, one needs the exact knowledge of the actual extent of heterozygosity of the respective species, in whose evolution one is interested. Then, the greater heterozygosity is, the more variable is also the genetic material of the species and accordingly more complex can be the genetic relationships between the members of the species. In humans, the first comprehensive molecular-biological comparative study done in 2015 (Genomes Project et al. 2015) assumes a degree of heterozygosity of about 0.6%. For this purpose, a total of 1.000 human genomes from various regions of the earth were used to create a general reference genome. In addition, 0.6% genetic variability initially only meant that all humans are genetically identical to no less than 99.4%, which already points to strongly reduced population sizes due to several genetic bottlenecks in our recent past (Amos and Hoffman 2010; Tang et al. 2022). However, this significantly changes the way of calculating degrees of kinship. Instead of the known steeply falling curve of 50%, 25% and 12.5% etc. for the calculation based on a single allele, the result is a much flatter course of 99.70% (99.4 + 0.6 x 0.5), 99.55% (99.4 + 0.6 × 0.25), 99.475% (99.4 + 0.6 × 0.125) and so on and so forth of kinship gradations for the entirety of our genome, consisting of identical homozygous genes and variable heterozygous alleles. And this would come much closer to the flat altruism curves of *Homo sapiens* as determined by the studies of Madsen et al. (2007) and Curry, Roberts & Dunbar (2013) than the so far calculated curves for single "selfish" alleles, whose potential for altruism drops steeply in comparison (see curves in Fig. 1).

6 From the "Primal Horde" to the National State

In this way, the recalculation of genetic relatedness adapted in this way to the biological conditions of the human species with its low degree of heterozygosity of only 0.6% makes it better understood why only humans have so far managed to form social structures that go considerably beyond the narrower circle of the nuclear family.[5] Did the human "primal horde"[6] after the separation from the last common ancestor with the chimpanzee about 6–7 million years ago still consist of an average of no more than 150 individuals (Dunbar 1993) until fairly recently, a trend towards larger group sizes started with the invention of agriculture and livestock farming and the resulting sedentary lifestyle, a trend which continues to this day. 12,000 years ago, at the beginning of the so-called "Neolithic Revolution" (Brown et al. 2009), there were only about 17 million people on earth (Zhu et al. 2021). Today there are already about 8 billion humans, an exponential increase in individuals of a vertebrate species, which is unique in the history of the earth. Group size expanded from an average of approx. 150 people of the hypothetical "primal horde" to up to 1.4 billion individuals (China, India) in the 21st century. In addition to the increase in the number of now "sub-jects" called

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[5] Lion and wolf packs usually consist of a dominant female alpha animal with parts of the female offspring of the last few years, supplemented by one or more migrated males. The largest individualized social structures on a matrilineal basis in the animal kingdom are probably found in killer whales (*Orcinus orca*): https://de.wikipedia.org/wiki/Schwertwal#Populationsstruktur.

[6] The term comes from Sigmund Freud, who in turn took it from Charles Darwin (https://de.wikipedia.org/wiki/Totem_und_Tabu).

members of the agricultural communities required by technological progress, increasingly violent conflicts over territories and their resources occurred, which promoted the merger of smaller groups into larger units, a trend which ultimately became decisive for the rapidly accelerating development of larger social structures. These new communities were no longer led, as still in the hunter and gatherer cultures, by a group of "equals among equals", but rather by a higher caste of privileged leaders and, at the latest with the beginning of the Greek antiquity, by a class of elitist experts in matters of "politics" (cf. "polis" in Ancient Greece).

7 Humanity as a "Family of Nations"

The astonishing thing about this development of the last 12,000 years is that despite the profound changes in social structures, the emerging agricultural societies continued to adhere to the model of a fictitious extended family. At least as a metaphor, most human groupings still see themselves as a kind of "large family" that has certain values and pursues specific goals. This still applies in various forms from the smallest community to the modern nation state (for a comprehensive treatment, see Johnson 1989). Even modern, multinational corporations, which should actually only be interested in the economic success of their company, often speak of their workforce in terms of "family" and "community", as if these were economically significant categories that were important for the success of the company. And even if the concept of family in many cases actually only has a rather purely metaphorical meaning—just think of the "family of nations" that, in 1920, founded the League of Nations as a precursor of the modern United Nations—one must also ask to what extent real genetic relationships influence the course of history, in the past as well as today.

8 Sociobiology and Politics

A concrete example of how cases of assortative, i.e., genetic kinship-based cooperation (for the method, see Joshi et al. 2022), can actually influence relevant societal developments is given by a sociobiologically inspired study that I conducted already some time ago on Mikhail Gorbachev's Perestroika (Heschl 1993). In this study, the main representatives of Gorbachev's political allies were subjected to a physiognomic assessment by 10 independent individuals, who were to judge the similarity of the faces published in PRAVDA of the participants of an important political meeting to the face of the initiator of the new movement. The resulting ranking of Gorbachev's Perestroika supporters not only revealed a significant association between physiognomic similarity to the party leader and loyalty to the content of his speech given at the 19th Party Congress of the CPSU in 1988, but in retrospect even proved to be of prognostic value. Some of the so-called "comrades" at the party congress who physiognomically resembled the party leader the least instigated an internal riot against Gorbachev three years after the publication of the study, but the endeavor finally failed (there were even suicides among the putschists). After the ultimate failure of Perestroika, Boris Yeltsin, who was quite close to Gorbachev in terms of physiognomy, ranking 10th among the 64 conference participants, took over Russia's political affairs after some severe turbulence[7] (Fig. 2).

Physiognomic comparisons can nowadays be carried out relatively easily with modern computer technology, and a recently conducted study with human doppelgangers has revealed that—which is to be expected from a theoretical point of view—physiognomic similarity correlates to a high degree with genetic proximity (Joshi et al. 2022). This would make extensive DNA comparisons a methodological quantum leap in social research. The foreseeable consequences of a metric adapted in this way to the biological conditions of a large-group species like *Homo sapiens* for future research would be considerable. Instead of limiting ourselves, as before, to the narrower familial surroundings of individuals, based on the 1-gene-based calculation of kinship still common in sociobiology (i.e. 50% → 25% → 12.5% → 6.25% = "not related"), we could now focus more on larger units such as companies, parties and other influential social structures and examine their special dynamics under evolutionary aspects. However, this would require the willingness of a larger number of test persons to have a more detailed genetic profile created of themselves. Genetic analyses have so far been viewed rather negatively in most countries, as their scientific use has often been accompanied by racist undertones (Lieberman 2001). However, this seems to be changing recently. For several years now, American companies from the gene sequencing industry have been offering private individuals genetic analyses based on saliva samples. Originating from the long-standing trend towards personal

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[7] Unfortunately, the current information policy of the Russian leadership makes it difficult to conduct a similar analysis of today's power relations in the Kremlin. However, it would be a surprise if Putin's closest circle, the so-called "collective Putin", did not also form a physiognomic—and thus also genetic—unity (see https://www.fr.de/kultur/literatur/kollektive-putin-11130954.html).

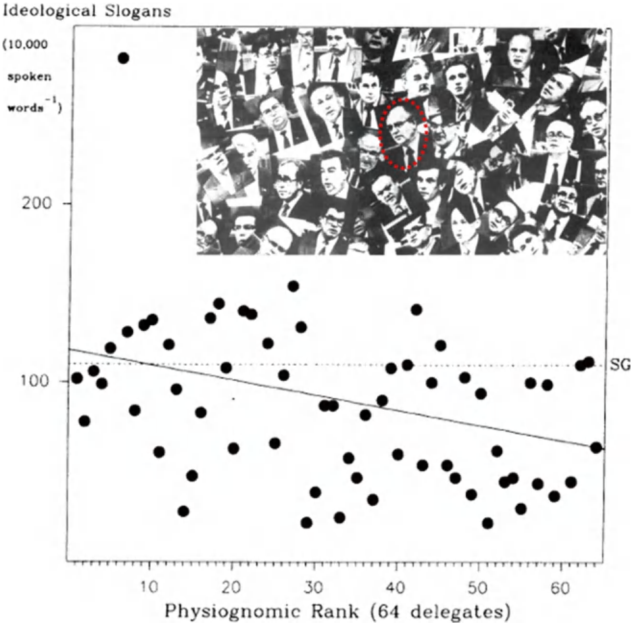

Fig. 2 Sociobiology and politics: Evidence of a significant association between physiognomic similarity to the party leader (x-axis: *Physiognomic Rank*) and political loyalty (y-axis: *Ideological Slogans*, e.g. Glasnost, Perestroika) in the speeches of 64 delegates at the 19th Party Congress of the Communist Party of the USSR in 1988 in Moscow. Red circle: portrait of Mikhail Gorbachev taken during the conference (*Secretary General,* SG ... number of slogans per 10.000 words in Gorbachev's speech). (reprinted from Heschl 1993)

genealogy research, such analyses have now developed into a veritable boom of individual self-discovery, which is not only of criminological significance,[8] but could also be made use of for scientific research in the sense of the future "evolutionary social sciences" as propagated in this volume.

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[8] As a buyer of such a genome analysis, one can voluntarily, i.e., with written consent, make one's data available to the executive.

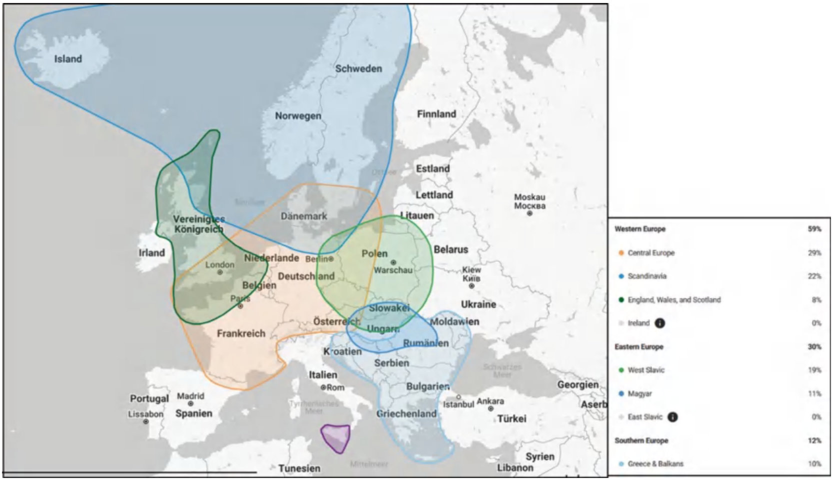

Fig. 3 Example of a genetic DNA ancestry analysis for an average Central European (place of birth: Austria). The data comes from a private DNA saliva test (*FamilyTreeDNA*), as they are now freely available worldwide. This shows how little sense it makes in today's Europe to assume sharply delineated national identities based on genetic similarities.

9 DNA Ancestry: A New Look at One's Own Origins

Finally, it should be briefly pointed out the possible socio-political consequences of an intensified use of individual DNA analyses for the purposes of sociological field research. Contrary to the still widespread belief of a geographically limited origin of one's own genetic make-up, such analyses nicely show how broadly scattered the composition of the genomes of all people living today is across the various continents.[9] When one sees one's own genetic profile as a geographical map on the globe plotted in colored fields for the first time (see Fig. 3), this helps to relativize any gene-isolationist view of oneself. Just hundred years ago, national and, from 1945, ideological borders between the people of Europe seemed insurmountable barriers, but this changed abruptly with the fall of the Berlin Wall and the subsequent dismantling of the Iron Curtain between East

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[9] Only a few ethnic groups in Africa south of the Sahara (Khoisan, Pygmies) deviate genetically somewhat more from the rest of humanity (Excoffier et al. 1987).

and West in 1989. Since then, the formerly separated populations of Europe and the rest of the world have been mixing more than ever before (https://www.cbs.nl 'imported' documents' 2002/05) and reflect what the genetics of the species *Homo sapiens* apparently had long prepared for, namely the unification of all people on the globe into a single comprehensive large social unit called "humanity".

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What is Cultural Evolution Anyway?

Alberto Micheletti, Eva Brandl and Ruth Mace

1 The Great Confusion – Is Cultural Evolution a Theory or a Phenomenon?

Cultural evolution is becoming a blanket term for any kind of human behavioral evolution. However, we believe that this is leading to confusion because the term "cultural evolution" is being used to indicate both a phenomenon—culture chang-

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ing through time—and an approach to study it—the focus on cultural inheritance and the potential role of transmission biases in shaping culture. This approach explores how learning processes influence the cultural transmission of behaviors (for example, conformity bias, i.e., the tendency to adopt practices observed by the majority of one's own social group, Henrich and Boyd 1998). This confusing use of the term is widespread in the literature and in informal discussion (we may even have been guilty of this ourselves). For example, Schulz et al. (2019: 1) state that "cultural evolution often favored some form of cousin marriage." Are they referring to cultural evolution as opposed to genetic evolution? Cousin marriage is surely a culturally transmitted behavior, so this comparison appears irrelevant here. Or, by cultural evolution, do they mean the action of transmission biases such as prestige bias (Henrich and Gil-White 2001), which can sometimes cause practices common among societal elites to spread to the general population? Or are they referring to the whole phenomenon of cultural change? If so, how can culture changing per se "favor" a particular outcome? After all, the evolution of genetically inherited traits does not in itself favor a particular outcome either; outcomes are instead favored by natural selection (where selection pressure causes individuals with certain traits to be more likely to survive and reproduce). The phenomenon of biological evolution therefore includes not only natural selection but also neutral processes (Kimura 1983) such as genetic drift (where the frequency of genetically inherited traits changes due to random events) and migration (where the frequency of a particular trait increases due to immigration from another population). The same is true for cultural evolution. In principle, the rate of cousin marriage in a particular society could increase due to innovation, migration (the immigration of people who already practice cousin marriage), or cultural drift (random events). But only some form of selection, genetic, cultural or perhaps both, may "favor" a given outcome. A second example reveals how this ambiguity can lead to confusion that is hindering progress in the field. A study by Barsbai et al. (2021) shows that human behaviors tightly fit local environmental conditions, following very similar patterns to those shown by mammals and birds living in the same area. Where birds and mammals hoard more food, humans also store more food; where human fathers contribute more to feeding their family, so do animal fathers; where more men are polygynous (i.e., married to multiple women), other male mammals are also more likely to monopolize females and male birds invest more in their plumage, which attracts more females; and where humans marry outside their own group, other mammals also travel longer distances for the purpose of reproduction, to name just a few examples (Barsbai et al. 2021). In a commentary on the study (Hill and Boyd 2021), the wording appears to present cultural evolution and adaptation to local ecology as alternative explanations for the diversity and distribution of these traits. They state: “Hence, the study appears to validate the basic premise of the evolutionary perspective called ‘human behavioural ecology’” (Hill and Boyd 2021: 236). Human behavioral ecology investigates whether and how human behaviors adapt flexibly to the natural and social environment and thus solve problems of survival and reproduction (see Borgerhoff Mulder and Schacht 2001). The authors write further: “However, it is a mistake to conclude from this that culture is unimportant” (Hill and Boyd 2021: 236). This seems to suggest that human behavioral ecology ignores culture. Yet, Barsbai et al. (2021) do not deny that the foraging, reproductive, and social behaviors they examine are culturally transmitted, at least in humans. Neither do they assume that cultural history plays little to no role in shaping the observed patterns, as seems to be implied by Hill and Boyd (2021: 236) when they state: “ecological factors explain much variation in human behaviour, but so too does cultural history.” Cultural phylogeny may indeed play a role. This term refers to the cultural relatedness between different societies arising from shared descent from a common cultural ancestor, from which certain practices were adopted (see Mace et al. 1994). For this reason, the authors control for the influence of cultural phylogeny in their analyses (Barsbai et al. 2021). In other words, the cross-cultural distribution of the practices they examined can indeed be traced back to environmental adaptation and not to the fact that polygynous societies descend from a common cultural ancestor. Barsbai et al. (2021) simply show that a variety of human behaviors—almost certainly culturally transmitted—fit local ecology in the same way as behaviors that are probably mostly genetically controlled in birds and mammals. Therefore, their analysis suggests that these cultural traits have been shaped by inclusive fitness interests. In other words, these practices improve the inclusive fitness of the people who practice them, i.e., they increase their number of offspring along with the number of offspring of their relatives. In line with a behavioral ecology approach, they are agnostic as to the mechanism leading to this fit. Behavioral ecology deliberately reduces behaviors to their fitness costs and benefits (i.e., how they either harm or improve the fitness of their carriers). How exactly a behavior is inherited—genetically, culturally, or both — or how it operates at the physiological or psychological level is irrelevant. It is possible that the adaptations documented by Barsbai et al. (2021) came about through one or more specific biases in cultural transmission or, more generally, because humans are flexible learners who make conscious, strategic choices about what to adopt, sensitive to payoffs (Burton-Chellew and West 2021). Although it is tempting to contrast adaptation to local ecology and “culture” or “cultural evolution” as two competing forces shaping the change of behavior through time, such a contrast is impossible. As Boyd has acknowledged elsewhere (Boyd 2018), adaptation to local ecology is an outcome of the process of cultural evolution, whereby cultural selection has favored a set of cultural variants because they are adaptive in a specific environment. This process is largely analogous to natural selection, although "cultural variants" are practices that are culturally, not genetically, inherited. They are therefore not innate but learned throughout life through contact with other people. Cultural variants can be very concrete things such as techniques and tools, but also include more abstract phenomena such as social norms that regulate the equitable distribution of game after hunting expeditions (on the role of cultural processes in niche construction see Antweiler in this volume). Due to this analogy to natural selection, the tools of behavioral ecology are always going to be needed to understand cultural evolution. Evolutionary biologists, too, have sometimes used language suggesting this unhelpful dichotomy between adaptation and culture. For example, Burton-Chellew and West (2013: 1043) ask: "Will culture be more important for certain classes of traits such as those less linked to fitness?" We suspect that these authors were meaning to suggest that fitness-insensitive cultural transmission mechanisms can sometimes result in non-adaptive outcomes (especially when a trait is less fitness relevant). This is certainly true. In all societies, people imitate various cultural practices that neither affect their chances of survival nor their number of offspring and are therefore not fitness relevant. However, the way they presented their argument can be potentially misleading. Behaviors can be culturally transmitted, and many human behaviors are, and yet they can still be shaped, at least to some extent, by the inclusive fitness interests of their bearer. In other words: fitness relevant practices that enhance survival are just as "cultural" as fitness-neutral conventions. While fur hoods protect the inhabitants of the polar region from hypothermia, due to the milder temperatures the version popular in many European cities is a comparatively non-functional fashion accessory. Yet both variants are aspects of human culture: "culture" is therefore not a synonym for behaviors that are neutral or not fitness relevant.

2 How to Explain Culture from an Evolutionary Perspective? With Tinbergen's Four Questions

As testified by the examples above, using the same term to identify both a phenomenon and a theory to explain it is unhelpful. It becomes unclear whether one is referring to an explanandum—what we are trying to explain—or an explanans—the set of statements we use to explain it (Hempel and Oppenheim 1948). This hinders discussion between researchers employing different approaches, as one may write about cultural evolution as explanans and the other might read it as explanandum. It leads to the false dichotomy between culture and adaptation to ecology that we have discussed above (for another example of the problem of diffuse terminology see Antweiler on the Anthropocene in this volume).

For these reasons, we believe that the term cultural evolution is best reserved for the phenomenon, not implying any one approach or theory. Just as the phenomenon of organic evolution and Darwin's theory of it are distinct (Brady 1985), so are cultural evolution and our explanations for it. Another term should be used to refer to approaches centered on cultural transmission (e.g., "cultural transmission approaches" or "social learning approaches"). In this way, it also becomes clear that behavioral ecology does not disregard culture. Behavioral ecologists aim to explain whether and how behaviors serve an adaptive function (Nettle et al. 2013), i.e., whether and how they improve the fitness of those who practice them, and most human behaviors are at least partially influenced by transmitted culture. Thus, much of human behavioral ecology studies the cultural evolution of human behaviors. It does so either by exploring the ecological incentives that shape the adoption of specific cultural traits, or by considering culture as part of the environment that determines cost-benefit scenarios faced by individuals (Mace 2014). In other words, "environment" includes not only the natural but also the social environment. For example, behavioral ecologists treat the inheritance of wealth in the maternal or paternal line as an outcome of inclusive fitness interests. Parents often preferentially distribute wealth to those offspring whose marriage prospects benefit most from it, which in turn allows the parents to have more grandchildren (see overview in Micheletti et al. 2023). Where resources benefit sons more on the marriage market than daughters, wealth is preferentially given to sons (Micheletti et al. 2023). Inheritance systems that favor a particular gender thus result from socio-economic and cultural conditions such as the economic and marriage system (Micheletti et al. 2023). These conditions create fitness incentives for individuals, which in turn influence cultural practices (for example, the socio-cultural context influences the costs and benefits of cooperation between family members, see Willführ in this volume). Cultural behaviors can be studied from a range of different perspectives. In the 1980s, three evolutionary approaches to human behavior emerged: evolutionary psychology (which focuses on cognitive adaptations that underly behavior; Tooby and Cosmides 1990), human behavioral ecology (Nettle et al. 2013), and a third one focusing on cultural transmission (often confusingly referred to as “cultural evolution”). Tinbergen’s (1963) four questions about behavioral evolution—mechanism, ontogeny, function, phylogeny— still offer a useful framework for organizing this research. Mechanism refers to physiological and psychological mechanisms that directly cause behavior; ontogeny refers to developmental processes, i.e. how the individual and their behavior are “built” during development and how they change over the life span; function refers to the adaptive problem that the behavior is designed to solve; and phylogeny describes how a feature has changed over the course of evolutionary history (Tinbergen 1963). These four levels of explanation are not mutually exclusive but rather complement each other. They are valid regardless of whether a behavior is genetically controlled, culturally inherited or a bit of both. In the domain of culture, mechanism includes psychological learning processes that enable us to copy other people’s behaviors (“She gives her child herbal medicine because most mothers in her village do so”); ontogeny describes how a person has acquired a behavior (“She learned the recipe for the medicine as a teenager”); function captures how cultural practices improve our chances of survival, for example (“Herbal medicine alleviates inflammation; therefore, mothers who treat their children with it experience less child mortality”); and phylogeny describes the cultural history of a trait (“The herbal medicine was developed a thousand years ago by the ancestors of the Y-cultures, when diseases increased dramatically due to environmental conditions. Since then, most societies in this cultural group have been using it”). Behavioral ecologists usually examine the adaptive function and the phylogenetic history of cultural practices; evolutionary psychologists explore the cognitive mechanisms underlying cultural behaviors; and many “cultural transmission approaches”, in addition to cultural history, focus on how individuals have acquired some behavior during their development (see Fig. 1). These approaches are complementary. Rather than being mutually exclusive, these three evolutionary approaches simply tackle human behavior, including cultural traits, at different levels of explanation (Fig. 1). Suggesting a dichotomy between culture and adaptation to local ecology, though perhaps intuitively appealing, is misleading: it generates confusion between function and ontogeny. In other words, stating that a behavior has an adaptive function does not deny that it could be culturally transmitted. Conversely, stating that people have acquired a behavior culturally, and not as a result of some genetic predisposition, does not deny that this behavior could have an adaptive function. Statements about ontogeny tell us nothing about function and the same applies vice versa. “Function” and “adaptation” are therefore not synonyms for genetically inherited biological processes.

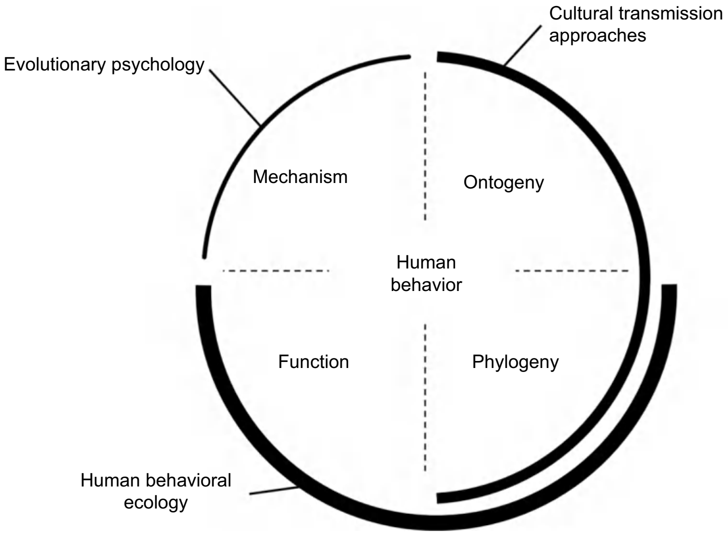

Fig. 1 Human behavioral ecology, evolutionary psychology, and the cultural transmission approaches ask different evolutionary questions about human behaviors. Note that some might extend the domain of interest of the cultural transmission approaches to include mechanism, and others might extend evolutionary psychology to cover ontogeny, depending on what definition of psychological mechanism is adopted.

3 How Best to Study Cultural Diversity - Based on Mechanisms or Function?

Models of cultural transmission derived from population genetics seek to predict the distribution of cultural phenotypes. “Cultural phenotypes” are observable cultural characteristics analogous to the observable properties of organisms in biology. Models derived from population genetics do this bottom-up, from transmission processes such as conformity bias. This does not entail that these models and related hypotheses disregard adaptation. In fact, major theorists have proposed that transmission biases have been selected for because they facilitate the spread of adaptive solutions via social learning (i.e., learning from other people) (Boyd and Richerson 1985; Boyd 2018). In other words: individuals whose learning was shaped by these transmission biases were more likely to adopt techniques and practices from others that improved their chances of survival and reproduction. However, the emphasis on transmission dynamics means that when addressing cultural phenotypes, mechanistic explanations (such as psychological processes that enable us to copy other people; for other mechanisms of cultural change see Jung in this volume) are favored. In contrast, behavioral ecologists seek to predict the distribution of cultural traits top-down, from the adaptive problems they are designed to solve. This entails that behavioral ecologists focus on functional explanations. In many cases, the top-down approach might generate results more readily than the bottom-up approach. With social learning processes showing few general rules (as multiple mechanisms are likely to be acting at the same time), predicting cultural diversity from the mechanisms of social transmission is going to be very hard. Models informed by inclusive fitness, and their test in the field, are key to help us understand cultural diversity; they build a clearer picture of the diversity of human behavior than cultural learning approaches alone can do. Cultural transmission dynamics can sometimes prevent the realization of inclusive fitness interests. This could be the case when people adopt cultural practices that harm their own fitness, for example by denying themselves the chance to produce offspring. More empirical research is needed to establish when this is indeed the case (the demographic transition from high to low fertility is one candidate; Colleran 2016). Yet, contrary to some suggestions, this does not mean that fitness-based models are inadequate or that only transmission dynamics should be prioritized as a matter of course.

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Evolutionary Game Theory

Andreas Diekmann

1 Introduction

Game theory deals with models of strategic action in social interactions. In doing so, it contributes to all social sciences such as economics, sociology, social psychology, political science, ethnology, and empirical legal science. It provides a precise, “unified language for the social sciences” (Gintis 2000) and tools for describing and analyzing social interaction. Game theory is, so to speak, the mathematics of social interactions.

For years, game theory has been an extremely dynamic field of research. Discoveries in the field have been awarded several Nobel Prizes. With models for repeated games, asymmetric information, signaling games, and evolutionary games, new fields of application have been opened up. With the rediscovery of game theory in economics, experimental game theory also experienced a rapid upswing.

Even though many applications of game theory relate to interactions of two or a few individuals, the models do not only deal with the micro-world of small groups. International conflicts, arms races, the exploitation of scarce environmental resources, trade relations and cartels, the collapse of financial markets, the exploration of the possibility of social cooperation among self-interested actors,

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exchange relationships, the emergence of social norms and conventions, the production of collective goods, trust and fraud in electronic markets, the credibility of announced threats and sanctions, and many other topics can be treated more precisely with game-theoretical models. Often, the theories lead to new and surprising predictions. The most powerful is not always the strongest, and under certain conditions, the weak can succeed in putting the powerful in their place or even exploiting them. A prerequisite for game-theoretical models is always that they involve strategic situations, in other words, the fates of the actors are mutually intertwined. Threats, bluff, asymmetric information (only the players know their true preferences, not the other players), honest and false signals are the salt of refined game-theoretical models.

Classical game theory, developed by John von Neumann and Oskar Morgenstern and further developed by John Nash and many others, however, relies on strict rationality requirements for goal-oriented actors. These are abandoned in evolutionary game theory, which is the subject of this article. Because in evolutionary game theory, it doesn't matter whether the actors act purposefully and strictly rationally. These models are therefore much closer to reality than strict rationality theory. It can happen that behaviors predicted by rationality theory evolve evolutionarily. In this case, the rationality solution is at the end of a competition among different behavior patterns.

Evolutionary game theory is by no means only important for biology, but also for the social sciences. Although it is not about inheritance in the biological sense, it is about cultural and social evolution. Social norms and institutions, behaviors, cultural patterns, linguistic idioms, organizational structures, technical innovations, and ideas can spread through learning and imitation. The sociologist Gabriel Tarde (2008/1890) already spoke of the “Lois de l’imitation”. Imitation often leads to “errors” or mutations. Successful patterns are imitated more frequently and spread, while unsuccessful patterns disappear.

Variation and selection, the building blocks of evolution, also have their place in cultural evolution. A central concept of evolutionary game theory is evolutionary stability or ESS, i.e., evolutionarily stable strategies that cannot be undermined by alternative strategies. Evolutionarily stable strategies are by no means always optimal. On the contrary, it can happen that a social process comes to a standstill in the “trap” of an unfavorable equilibrium. This happens, for example, with social norms when developments towards a “better” equilibrium are punished. A striking example is the graysome, almost thousand-year practice of foot binding young girls in ancient China (Mackie 1996). This article provides an insight into the principles and applications of evolutionary game theory and explains the basic concepts using examples. We limit ourselves to the static analysis of equilibria; hints on the dynamics of the processes and further literature can be found in the final section.

2 Evolutionarily Stable Strategies (ESS)

The pioneer of population science, Johann Peter Süßmilch, discovered a demographic regularity more than two centuries ago. Slightly more boys than girls are born, and the ratio, now called the "sex ratio," changes in favor of girls until it is about 1:1 at marriageable age. Süßmilch, primarily a pastor, saw this regularity as an expression of divine order. Biologists later put forward the secular explanation that the same ratio of sexes in most species is most favorable for species preservation. As we know today, this reasoning is incorrect. Not species preservation or group selection, but gene selection is the rule of natural evolution (Dawkins 1988). What is good for a gene does not necessarily have to be good for the group or species. Group selection only occurs under very restricted conditions. The explanation of the sex ratio, which is now essentially accepted as valid, was published by the statistician R. A. Fisher in 1930 (Maynard Smith 1976, 1982). It is based on the idea of gene selection. The probability of female or male offspring being born is (largely) genetically determined. This probability can change through mutation. However, only mutations that increase the "fitness," the number of offspring at reproductive age, will persist. Suppose a population consisted almost entirely of female organisms. Whoever has more male offspring in such a population will also receive more grandchildren. Genes with a higher probability for "sons" will spread in the species' gene pool. The same applies in reverse for a predominantly male population. Now it "pays" to have female offspring. Under certain conditions, which are met in many species, only a sex ratio of 1:1 in the population is evolutionarily stable. Without explicitly mentioning this, Fisher thus provides a game-theoretical explanation. The genes are quasi programs for the strategy of an organism (the "phenotype"). The payout to a strategy, the fitness, depends on how frequently other strategies are represented in the population. The fitness of a strategy is "frequency-dependent". Also in Axelrod's (1987) "ecological" simulation, the success of a strategy is frequency-dependent, and successful strategies were able to spread more strongly in the population.[1] However, there

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[1] Axelrod (1987) in his much-cited work on the "Evolution of Cooperation" let various strategies compete against each other in repeated prisoner's dilemma games in several

	Hawk	Dove
Hawk	(V-W)/2	V
Dove	0	V/2-t

Fig. 1 Game matrix Hawk-Dove game

were no mutationsand thus no new strategies. But these can potentially undermine the existing strategies. As soon as new strategies can appear, stronger requirements for the stability of anequilibrium are needed. The equilibrium must also be “evolutionarily stable”.

In a famous essay in “Nature,” biologists Maynard Smith and Price (1973) laid the foundations for game theory in biology on just three pages. With the concept of ESS, the “evolutionarily stable strategy,” the concept of the Nash equilibrium[2]is tightened. Evolutionarily stable strategies cannot be undermined by mutations—as inthe example of the sex ratio 1:1.

We consider an example from Maynard Smith (1976). In a population, there are two strategies, one aggressive, the other defensive, referred to as “Hawk” (F) and “Dove” (T). When two animals encounter each other, a conflict over a resource arises. A hawk fights until victory or until injury. The dove strategy involves holding position. If the opponent becomes aggressive, i.e., if it is a hawk, retreat is sounded before an injury occurs. The winner of a conflict receives a non-divisible resource, which increases fitness by V. An injury incurs costs of W. Two doves that “sit out” a conflict have costs (a fitness loss) of t each. In evolutionary biology, there is a simple currency, “fitness”. If two hawks meet, each has the same probability of emerging as the winner or loser from the duel. The payoff is therefore ½(V-W). The same applies to two doves. They can expect a payoff of ½V-t. A hawk always wins against a dove. The hawk receives V, the dove 0. The payoff can be found in the following game matrix (Fig. 1):

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tournaments. In the “ecological tournament,” the strategies scored points that determined the share of the strategy in the subsequent generation. Thus, successful strategies could spread, while less successful ones disappeared. After 1000 generations, the “Tit-for-Tat” strategy emerged as the winner. A brief overview can be found in Diekmann (2016: Chap. 7). See also further below.

[2] A Nash equilibrium is a combination of strategies (a “strategy profile”) such that no player has an incentive to *unilaterally* change his strategy. Applied to the example of the one-time, non-repeated prisoner’s dilemma: If both players do not cooperate (mutual defection), then neither of the two players has an interest in changing his strategy as long as the other player sticks to his strategy. Mutual non-cooperation is a Nash equilibrium in the non-repeated prisoner’s dilemma.

In the case of $V > W$, the population will be teeming with hawks. the hawk strategy is ESS. The game becomes interesting and more realistic when the cost of an injury exceeds the value of the resource ($V < W$). In this case, an ESS cannot be a pure strategy.[3] If there are only hawks, it is better to behave like a dove. If there are only doves,the hawks multiply. If $V < W$, it is a Chicken game.[4] The aggressive hawk strategy corresponds to"defection", the defensive dove strategy to "cooperation". Since the game issymmetrical, the payoff to the column player can be omitted in the game matrix.

Let's now define an ESS more precisely, in words and formally. "An ESS is a strategy with the following property: If all members adopt the ESS, no strategy that has emerged through mutation can undermine the population under the influence of natural selection" (Maynard Smith 1982, translation A.D.). In the case of cultural or social evolution, "natural selection" can be replaced by another selection mechanism, in economic models, for example, by competition in markets.

We call the strategy existing in the population the "native" strategy, a mutant strategy we also refer to as an "intruder".

A native strategy is an ESS if one of the following two conditions applies:

(i) The "natives" receive on average more from an encounter among themselves than a mutant strategy against a native strategy. Mutants cannot then spread, even if mutants achieve high payouts among themselves. (When mutants are rare, the probability of encounters between mutants is low.)

(ii) If the natives receive exactly as much among themselves as a mutant strategy against a native strategy, it must be the case: The native strategy gets more from an interaction with an intruder (a mutant) than the intruding strategies receive among themselves. If the additional condition is not met, the mutant would spread in the population through "genetic drift".

Formally written: If I is the "native" strategy and J is any "mutant strategy", then I is an ESS if one of the two conditions (i) or (ii) is met:[5]

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[3] A pure strategy means that the strategy is chosen with a probability of one. In a "mixed" strategy, alternative strategies $j = 1, \ldots, m$ are played with probabilities p_j, where the probabilities sum to one.

[4] In the "Chicken game", both players each have the choice between C ("Cooperation") and D ("Defection"). Defection is the exploitative, non-cooperative strategy.

[5] E denotes the expected value, the expected payoff, which the strategy listed first in the bracket receives. For example, E(J,I) is the expected payout to J in the interaction of strategies I and J.

	Hawk	Dove
Hawk	–10	6
Dove	0	1

Fig. 2 Example of a Hawk-Dove Game

(i) Either E(I,I) > E(J,I)
(ii) or E(I,I) = E(J,I) and E(I,J) > E(J,J).

(i) or (ii) must be fulfilled for every possible alternative J. If this condition is met, the native strategy I cannot be undermined.[6]

3 The ESS in the Hawk-Dove Game

For the simple case V > W, condition (i) is fulfilled for I = Hawk, i.e., the pure hawk strategy. J can be any pure or mixed alternative strategy. E(H,H) is always greater than E(J,H), where J = D is the pure dove strategy or any mixed strategy (with α for the probability of the Hawk-strategy and 1-α for the probability of the Dove-strategy). For $0 \leq \alpha < 1$, the following applies:

$$\mathrm{E(Hawk, Hawk)} = (\mathrm{V} - \mathrm{W})/2 > \mathrm{E(J, Hawk)} = \alpha(\mathrm{V} - \mathrm{W})/2 + (1 - \alpha)0.$$

In risky duels with W > V, E(Hawk, Hawk) > E(J, Hawk) does not apply. Nor does E(Dove, Dove) > E(J, Dove). A mixed strategy J beats the pure hawk and the pure dove strategy when the cost of an injury (W) exceeds the value of the resource (V). As already established, the two pure strategies are not evolutionarily stable in this case.

Is there an ESS for the case W > V? It would have to be a mixed strategy s = αHawk + (1−α)Dove. α must be determined in such a way that the ESS condition (ii) is fulfilled.

Let's first examine an example with the fitness points V = 6, W = 26, and t = 2. The payouts are shown in the game matrix (Fig. 2):

The mixed strategy is determined by the choice of α, the probability of the hawk strategy. We are looking for an equilibrium strategy α*, such that E(α*,α*)

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[6] At least not by individual mutants. However, if mutants come in groups ("clusters"), it is quite conceivable that the intruders could displace the natives, even if (i) applies.

= E(α, α*). Also, E(α*, α) > E(α, α) must apply for α ≠ α*. (Compare the two conditions (i) and (ii) for an ESS listed above. I corresponds to α*, J corresponds to α.) The first condition corresponds to a Nash equilibrium for mixed strategies. If α* is the equilibrium strategy, then deviation is not worthwhile, but it is also not punished. We can determine α* in a simple way: α is chosen so that the row (or column) is indifferent between choosing H or D.

Therefore, the following applies:

$$\alpha(-10) + (1-\alpha)6 = \alpha 0 + (1-\alpha)1.$$

Solving for α gives:

$$\alpha * = 1/3.$$

In evolutionary game theory, mixed strategies can be interpreted in two ways. First, it could be that an organism, so to speak, rolls the dice and in our case applies the hawk strategy with a probability of one third and D with a probability of two thirds. The second interpretation is that the composition of a population is polymorphic. In the population, one third of the members pursue the aggressive strategy and two thirds the defensive strategy.

Now we calculate the payoff of the α*-strategy. The expected value is:

$$\mathrm{E}* = 1/3\ \cdot 1/3(-10) + 1/3\ \cdot 2/3\ \cdot 6 + 2/3\ \cdot 1/3\ \cdot 0 + 2/3\ \cdot 2/3\ \cdot 1 = 2/3$$

According to the condition, E(α*, α*) = E(α, α*) applies. You can easily check the calculation by testing the expected value for the deviation to the strategy α = 1 and α = 0. Not surprisingly, the expected value in both cases is 2/3. (due to (−10)1/3 + 6 · 2/3 or 0 · 1/3 + 1 · 2/3).

However, we still need to prove that α* is an ESS. To do this, it must be shown that E(I,J) > E(J,J) for I ≠ J or E(α*, α) > E(α , α) for α ≠ α* applies.

$$\mathrm{E}(\alpha*, \alpha) = 1/3(-10)\alpha + 1/3\ \cdot 6(1-\alpha) + 2/3(1-\alpha) = 8/3 - 6\alpha.$$

$$\mathrm{E}(\alpha, \alpha) = (-10)\alpha^2 + \alpha(1-\alpha)6 + (1-\alpha)^2 = -15\alpha^2 + 4\alpha + 1.$$

Then, from E(α*, α) > E(α , α), α ≠ α*, the inequality $15\alpha^2$- 10α + 5/3 > 0 follows. The quadratic equation has a root only for α = α* = 1/3. For all mutant strategies α ≠ α*, the inequality is satisfied. The strategy α * = 1/3 thus has the property of an ESS.

As it turned out, the ESS strategy achieves a fitness of 2/3. This is less than the payoff for the dove strategy with a fitness of 1. Even more would a member of the population receive if all members α would "choose" so that fitness is maximized. The payout is then 57/45 (for calculation see below). It can be seen that an

ESS (as a result of gene selection) does not maximize the fitness of the group or species. (The genes could be better off if they made a contract and agreed on the dove strategy or on the α maximizing the expected value.)

The general solution for the ESS in the Hawk-Dove game (with V < W) can also be determined using the described method:

$$\alpha(\mathrm{V}-\mathrm{W})/2+(1-\alpha)\mathrm{V}=(1-\alpha)(\mathrm{V}/2-\mathrm{t})$$

Solving for α yields the ESS:

$$\alpha{*}=(\mathrm{V}/2+\mathrm{t})/(\mathrm{W}/2+\mathrm{t})$$

The expected value is:

$$\mathrm{E}=\alpha^2(\mathrm{V}-\mathrm{W})/2+\alpha(1-\alpha)\mathrm{V}+(1-\alpha)^2(\mathrm{V}/2-\mathrm{t})$$

If α is replaced by α*, the fitness of the ESS is obtained. The equilibrium strategy does not provide the maximum payoff, as we have already determined using the numerical example. If E is maximized with respect to α, the result is:

$$\alpha_{\max}=\mathrm{t}/(\mathrm{W}/2+\mathrm{t})<\alpha{*}$$

$$\mathrm{mit}\,\mathrm{E}_{\max}>\mathrm{E}_{\mathrm{ESS}}$$

In general, in the Hawk-Dove game, it is found that the maximum payofft (or fitness) is achieved for a strategy that is more defensive compared to the ESS or for a higher proportion of doves. Unfortunately, the optimal α is not an ESS. Only in group selection would evolution favor $\alpha_{\max}$.

4 ESS in the “War of Attrition”

The war of attrition is a bloodless battle. The winner is the one who holds out the longest. For example, two male representatives of a species wait for a female, the more impatient one loses the competition. For the Guinness Book of Records, people sit on poles for weeks or try to outdo competitors in marathon kissing, marathon dancing, or other curious disciplines. The level of fitness value of an entry in the Guinness Book is unknown, but numerous entries in the Guinness Book concern winners of a “war of attrition”. “Sitting out” is worthwhile in such a competition, but it also involves costs, which increase with the waiting time. Again, it is about a resource with the fitness value V. In the game, the waiting time is a (continuous) decision variable. The choice of a maximum waiting time is a pure strategy. The determination of a probability for each point in time (i.e., the choice of a probability distribution p(t) with $t \geq 0$) is a mixed strategy. The choice of a waiting time simultaneously determines the maximum costs that a player invests in the battle. The costs of player 1 are denoted by m_1, the costs of player 2 by m_2. If $m_1 > m_2$, player 1 wins. The winner gets $V - m_2$, the losing opponent bears costs $-m_2$ (for the game and the analysis cf. Maynard Smith and Price 1973; Maynard Smith 1976; 1982).

Even in the "war of attrition" there is no pure ESS. If a player were to choose a certain m, his opponent would only need to switch to a slightly higher value. If $m > V$, there would be an incentive for $m = 0$. An ESS would therefore have to be a mixed strategy.

It can be shown that a mixed strategy with an exponential distribution of waiting times is an ESS. The mean of the distribution is 1/V, provided the costs depend linearly on the waiting time (Maynard Smith 1982):

$$p(t) = (1/V)\exp(-t/V)$$

A remarkable study by Parker (1970) reports waiting times and mating success in dung flies (see also Wickler and Seibt 1991). These flies, nomen est omen, like to stay on cow dung, the fresher the better. Females prefer and come more frequently to fresh cow dung than to dry dung. A male fly waits until a female buzzes up to take a chance at copulation. But the competitors do the same. The fly could now wait on the dung, which is increasingly drying out, or fly on to another, fresh pile. Parker records the waiting times and determines the mating success. The waiting times approximately match the exponential distribution and the mating success is independent of the length of the waiting time. The latter observation in particular suggests an ESS (Maynard Smith 1976). The waiting times are distributed in such a way that no strategy can claim an advantage. If, for example, the length of the waiting time was positively correlated with fitness, it would be worthwhile to wait particularly long. More patient males would be rewarded and the distribution would change after a few generations. The constancy of fitness, on the other hand, is the actual evidence for the empirical validity of the model predictions.

5 Evolution of Cooperation and ESS

In Axelrod's tournament and computer simulation, strategies are referred to as "friendly" if they never initiate hostilities, i.e., they never choose the strategy Defection (D) first in the repeated prisoner's dilemma. Among the strategies that are friendly in this sense, "Tit for Tat" proved to be particularly successful. TFT is a Nash equilibrium strategy in the repeated game, provided the "shadow of the future" is large enough.[7] The question is, is "Tit for Tat"also evolutionarily stable?

Let's first test this with the defective strategy "Always D" as a potential intruder. The expected gain for the (infinitely often) repeated game of TFT against itself, E(TFT, TFT), is greater than E(Always D, TFT) with a sufficiently large "shadow of the future" (expressed by the discount factor). So "Always D" cannot undermine a TFT population. What about "Always C"? It holds that E(TFT, TFT) = E(Always C, TFT) and E(TFT, Always C) = E(Always C, Always C). The ESS condition is therefore not met. "Always C" can undermine a TFT population. And this applies not only to "Always C", but to any friendly strategy. Any friendly strategy can undermine any other friendly strategy! Even the strategy of "eternal damnation" (after a defection of the partner, D is chosen as punishment continuously) is not evolutionarily stable and can, for example, be undermined by "Always C". One could now say that this is not a problem, because all friendly strategies achieve the same score. The problem, however, is that the undermining friendly strategies can in turn pave the way for other, this time unfriendly strategies. TFT, for example, cannot be undermined by "Always D", but it can by "Always C". This strategy, however, can be displaced by "Always D". The scenario is thus that a TFT population is virtually stripped of its defenses by unconditional cooperation and then falls victim to defective strategies.

6 Outlook

Evolutionary game theory in the social sciences has the advantage that no strong assumptions about the rationality of the acting agents are required. Simple assumptions about learning and imitation are sufficient to represent evolutionary processes that lead to empirically testable statements. In this article, the equilibria resulting from evolutionary processes were analyzed. Beyond the static view, the dynamic analysis of the paths towards the equilibrium or equilibria is of par-

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[7] The "shadow of the future" refers to the value of future payoffs. If there is a probability after each game in the sequence of repeated games that the continuation of the sequence will be interrupted, future payoffs are less certain than current payoffs. The measure for the "shadow of the future" is the discount factor, a value greater than zero and less than one, analogous to the discounting in compound interest calculation.

ticular interest. A central component of this process is the replicator dynamics. Here it is assumed that the growth of a strategy is proportional to the difference between the success of the strategy and the average payoff. Shares of successful strategies grow in the strategy pool; on the other hand, shares of strategies that perform below average shrink. Formally, the replicator dynamics is expressed as a differential equation. Other types of learning processes can also be considered (Young 1998, see the overview by Sandholm 2017). An example that Young (1998) deals with in detail is the development of conventions in traffic. Rules of left or right-hand traffic varied historically even on the continent on a relatively small scale, until general rules gradually crystallized evolutionarily. Young (1998) describes the historical developments with evolutionary models. Nax and Perc (2015) show that a simple learning mechanism with limited information can indeed set a dynamic in motion that leads to stable cooperation in a social dilemma. In most studies on the evolution of cooperation, the repeated prisoner's dilemma or variants of the game such as the linear "Public Good Game" are used as a basis. Tutić (2021), on the other hand, investigates the dynamics of evolution in a non-linear contribution game, the "Volunteer's Dilemma".[8] Instead of the replicator dynamics, a stochastic modelis chosen in which players are replaced with a certain probability in the course ofevolution and the replacement depends on the success of the strategy. Tutić (2021) can show that the group size contributessignificantly to the emergence of cooperation and that a threshold value of two playersis crucial for whether cooperation emerges from the interactions or not. These andfurther investigations into the development of conventions and social norms as well as amultitude of studies on the evolution of cooperation touch on core questions of socialtheory (see the overviews by Newton 2018; Sandholm 2017). These are just some of theareas of application. Because evolutionary game theory provides precise tools that areused interdisciplinarily in social and natural sciences to understand the dynamics ofevolutionary processes.[9]

Note. This article is a revised text from Diekmann (2016).

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[8] The "Public Good Game" is a generalized prisoner's dilemma. In the "Volunteer's Dilemma", one of n players is sufficient to produce the collective good (Diekmann 1985). In both game situations, there is an incentive to free ride.

[9] Models of evolutionary game theory are used in numerous disciplines. From traffic sciences, which, for example, study the lane change of car drivers (Ji and Levinson 2020), to works on the growth of tumors in medicine (Wölfl et al. 2022). See also the overview by Sandholm (2017).

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Learning and Evolution: Individual-Level and Population-Level Selection of Behavior

Matthias Borgstede and Carsta Simon

1 Learning as a Selection Process

Over a century ago, Thorndike (1900) noted that individual learning processes, particularly classical and operant conditioning ("reinforcement learning"), can be conceptualized analogously to the process of natural selection. Similar to evolution, which describes the change in average trait expressions at the population level (phylogeny), learning can be understood as a selection process that describes the change in average behavior at the individual level (ontogeny) (Broadbent 1961; Gilbert 1970; Pringle 1951; Simon and Hessen 2019). The question how learning can be a form of "behavioral selection" has been answered very differently. Proposals range from the postulate of a common abstract principle (Skinner 1981), through the idea of a functional correspondence between genetics and neuroscience (Donahoe et al. 1993), to the idea of computational equivalence (McDowell 2004) and formal analogy (Baum 2017). As different as the answers may be, they have one thing in common: learning and evolution are conceptualized as similar (or analogous), but *separate* processes.

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However, conceptualizing learning as independent of evolution contradicts the view that the mechanisms underlying individual behavior have evolved at the evolutionary level through natural selection (cf. McNamara and Houston 2009). Specifically, learning evolved by natural selection because organisms that learn from the consequences of their behavior in their ontogeny are more likely to contribute to the gene pool of the next generation. A behavior analytic approach towards the theoretical integration of learning and evolution can be found in Baum (2012), who equates reinforcers with so-called "Phylogenetically Important Events (PIEs)". PIEs are events that are directly relevant to the survival and reproduction of a species, such as the availability of food or the absence of physical threat. According to Baum, PIEs act as reinforcers,[1] because they increase the expected evolutionary fitness of individuals. A similar concept is also pursued by Singh et al. (2010), who model the fitness consequences of reinforcers to explain the reinforcing effects of exploratory behavior by its indirect fitness consequences. However, neither Baum (2012) nor Singh et al. (2010) link their evolutionary concept of reinforcement with an explicit model of the selection of individual activities through their consequences.

This chapter addresses the question of how the two aforementioned discourses can be brought together within the framework of a general theory of behavioral selection. The aim of the analysis is to describe adaptive behavior in the form of a unified selection model that functionally links the levels of ontogenetic behavioral adaptations (learning) and phylogenetic behavioral adaptations (evolution)—the Multilevel Model of Behavioral Selection (MLBS). The MLBS was developed as a theoretical framework for explaining adaptive behavior at the evolutionary and individual level and aims to uncover basic principles of adaptive behavior and provide a general analytical framework for behavior analysis. Previous work on the MLBS has dealt with the implications of the theory of behavioral selection in the context of partner choice (see Rieger et al. in this volume), utility optimization (Borgstede 2020, 2024), operant and classical conditioning (Borgstede and Anselme 2022; Borgstede and Eggert 2021; Strand et al. 2021), adaptive behavioral dynamics (Borgstede and Luque 2021), and information processing (Borgstede 2021). The MLBS unites all of these phenomena within the frame-

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[1] The concept of the reinforcer in behavior analysis slightly deviates from the concept of reward, as reinforcers are defined solely by the fact that they change the probability of future behavior.

work of a general theory of behavior. For example, operant conditioning (or reinforcement learning) can be understood as a dynamic selection process that leads to (fitness-)optimal behavioral adaptations under certain conditions, and at the same time maximizes the predictability of fitness-relevant events (reinforcers).

Due to the high degree of formalization of the MLBS, the above-mentioned publications, however, require extensive mathematical prerequisites. A more accessible introduction to the conceptual framework of the MLBS in the sense of a general theory of behavioral selection does not yet exist. The aim of this chapter is to provide such an informal introduction. Therefore, all mathematical formulas were outsourced into separate boxes, such that the formal framework is comprehensible for those interested in mathematics, without disturbing the flow of reading.

2 Foundations of Selection Theory

The principle of selection was first described at the level of evolutionary adaptations of organisms to their environment (Darwin 1859). It is based on the interplay of variation, transmission, and differential reproduction. Evolutionary models can be used to describe the change of physiological characteristics such as body size or weight. On the other hand, they can also be used to describe the change of behavioral characteristics, such as parental care or courtship behavior (Davies et al. 2012). The evolution of general behavioral tendencies has increasingly drawn interest in psychology in recent years and has been implemented within the framework of evolutionary psychology (Buss 2019). However, the biological selection of psychological mechanisms is not the focus of this chapter. Instead, it is postulated here that psychological mechanisms themselves are realizations of a more general selection principle. The selection of behavior at the individual level is therefore a selection process in its own right that is inherently linked with the process of natural selection.

An abstract analysis of selection requires a clear conceptual framework. This framework is given by the so-called Price equation (Price 1970, 1972). Price recognized that differences in average trait values can be decomposed into a covariance term and an expected value term under certain conditions. The Price equation applies to all structures consisting of two sets that are linked in a certain way. The sets can contain arbitrary elements, such as individuals or groups, but also inanimate objects like stones, or even planets. It is crucial that the objects can be compared in terms of at least one property and that there is a relation between the two sets considered that assigns at least one object from set 1 to each

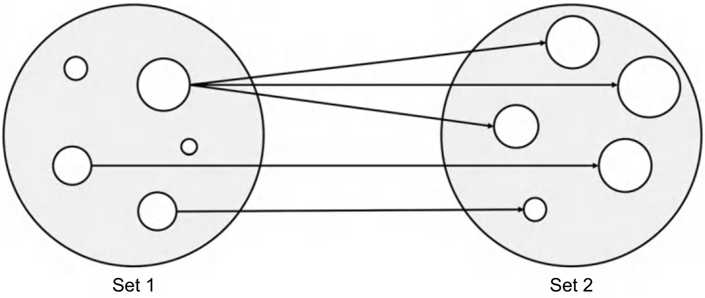

Fig. 1 Set-theoretical illustration of the Price equation. The change in the average trait value (here: diameter of the circle) from set 1 (parent population) to set 2 (offspring population) is a direct result of the covariance between the trait values in set 1 and the respective number of assigned circles in set 2. (©Matthias Borgstede, All Rights Reserved)

object in set 2[2]. In biological selection processes, set 1 is often referred to as the parent generation, set 2 as the offspring generation, and the relation between the sets corresponds to parentage.

Fig. 1 illustrates the structure underlying the Price equation at an abstract level. In the figure, the objects are depicted as circles and the property considered is the diameter of the circles. To keep the figure as simple as possible, each circle from set 2 is assigned exactly one circle from set 1 (indicated by the arrows). In addition, the circles connected by the arrows have a similar size. That is, there is a correlation between the diameter of the circles in set 2 and the number of circles from set 1 to which they are assigned.

In Fig. 1, the circles in set 2 have a larger diameter on average than those in set 1. Following the biological interpretation the Price equation, this corresponds to offpring inheriting their size from their parents. The circles in set 1 with a larger diameter are, on average, connected with more circles in set 2 than those with a smaller diameter. In the case of natural selection, this would mean that larger parents tend to have more offspring, thus contributing more to the offspring population than smaller parents. This contribution of parents of different sizes to the offspring population is called "fitness" in the context of the Price equation. The difference in the average diameter between the two sets can therefore be explained by the fact that the trait of interest (in this case the circle diameters in

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[2] See, however, Borgstede (2025) for a more general Price equation framework that can handle incomplete and even fuzzy setmappings.

set 1) positively covaries with fitness (i.e., the contributions to set 2). Price recognized that this covariance constitutes the essence of selection.

Box 1: The Price Equation

In his original publication, Price described the principle of selection in the context of population genetics (Price 1970). Price demonstrated that, given perfect inheritance of a gene, the change in gene frequency from a parent population to an offspring population always corresponds to the covariance between the parental genotype and parental fitness. If the gene's inheritance is not perfect (e.g., due to mutations), the deviation between the change in gene frequency and the covariance between genotype and fitness can be captured as the expected value of the change in genotype from parent to offspring. Formally, this corresponds to a decomposition of the gene frequency difference $\Delta\bar{z}$ into a covariance term $\mathrm{Cov}(z, w)$ and an expected value term $\mathrm{E}(w\Delta z)$:

$$\overline{w}\Delta\bar{z} = Cov(z, w) + \mathrm{E}(w\Delta z) \tag{1}$$

Here, w is the individual fitness and z is the individual genotype. $\overline{w}$ represents the average fitness of the parent population and $\bar{z}$ represents the average expression of the genotype z, which in the case of a single gene corresponds to the population gene frequency. $\Delta\bar{z}$ accordingly denotes the change in gene frequency from the parent population to the offspring population, and Δz denotes the change in genotype during transmission from parent to offspring. Eq. 1 is a mathematically exact description of the relationship between selection and covariance that is illustrated in Fig. 1.

The Price equation is considered one of the cornerstones of modern population biology (Luque 2017). It provides the analytical framework for a formal definition of selection that can be applied to any kind of system, as long as is has the same basic structure as a parent and offspring generation, where a parent trait is passed on to the offspring.

The scope of the Price equation is not limited to biology due to the high degree of abstraction of its underlying definitions. All set-theoretical structures that meet the above conditions allow a corresponding decomposition of mean trait differences into a covariance term and an expected value term. Thus, the Price equation can be used in various contexts to identify and formally describe the effects of selection processes (Price, 1995, written around 1971). The recognition of covariance does not provide computational advantages for the analysis of selection processes, but is of great value for theory development (Price 1970). Accordingly, it forms the conceptual basis of the theory of behavioral selection, and in particular of the MLBS.

3 The Theoretical Integration of Learning and Evolution

The question of how learning and evolution can be integrated in a common conceptual framework has been answered in various ways over the past decades. This section will elaborate on the already existing approaches to such a theoretical integration outlined in the introduction and discuss them against the background of a general theory of behavioral selection.

Skinner (1981) described "Selection by Consequences" as a causal explanatory mode that manifests itself at different levels of behavior. At the individual level, selection appears in the form of learning, at the group level in the form of culture, and at the species level in the form of evolution (Skinner 1981). Learning through reinforcement is therefore not only similar to evolution, but learning and evolution are both instances of a more abstract common principle. Skinner's view of selection as a general explanatory mode for adaptive behavior provoked mixed reactions in the scientific community (see, for example, the open peer comments on the re-print of the article in Behavioral and Brain Sciences in 1984 and in Norsk Tidskrift for Atferdsanalyse in 2016).

In behavior analysis, there have been few attempts so far to utilize the principle of selection within the framework of formal theory building. A necessary prerequisite for this was changing the level of analysis from the "molecular" to the "molar" perspective (Rachlin 1978). Instead of focusing on discrete behavioral acts (such as pressing a lever), the molar approach considers behavior at a higher level of abstraction and is therefore less concerned with the temporal proximity between discrete stimuli, responses, and consequences, but with average behavior and reinforcement rates that are aggregated over a longer period of time. Therefore, in the molar view, learning does not consist in the formation of associations or situational decisions, but in the change of context-dependent behavior rates over time (Baum 2002).

Baum (2017) was the first to link the molar perspective with a formal model of behavioral selection based on the Price equation. In his analysis, Baum identifies the behavior observed in individual trials of an operant behavior experiment with the individuals of a parent population, and the behavior in later experimental trials with the individuals of an offspring population. Baum thus describes the change in average behavior through the covariance between the observed behavior in the individual experimental trials (e.g., the time an individual spends on a certain activity) and the relative rate of recurrence of this behavior in a later trial. According to Baum, the recurrence of behavior is mediated by the presence of phylogenetically important events, such as the availability of food (abbreviated as PIEs, cf. Sect. 1).

Baum's (2017) "Behavioral Price Equation" can also be used outside the lab to describe changes in time allocation to various activitities. For example, changes in the daily time invested in resource acquisition (e.g., in the form of paid work) and in social interaction (e.g., in the form of shared leisure activities) can be explained by the covariance between the current time allocation and the resulting PIEs (such as the compensation of work or the support from other individuals). Baum's application of the Price equation allows for a previously unattained degree of precision with regard to the question of how individual learning could constitute a selection process. However, in Baum's approach, the process of behavioral selection is formulated independently of the principle of natural selection. A link between both levels of selection is only informally suggested by the postulated role of PIEs with regard to the recurrence of behavioral expressions, but is not implemented at the level of formal theory.

Borgstede and Eggert (2021) propose such a formal link. Building on previous work on the theory of behavioral selection, they propose a theoretical integration between behavioral adaptations at the population level and behavioral adaptations at the individual level within the framework of an integrative selection model, the MLBS. Like Baum's approach (2017), the MLBS is based on the abstract description of selection by the Price equation. However, individual behavior is not formalized as being independent of natural selection, but on both levels at the same time. This allows for a functional integration of learning and evolution within a common selection model. The core assumption of the MLBS is that individual learning processes can only be adaptive to the extent that they favor an increase in evolutionary fitness (according to Baum's PIEs). Therefore, the concept of evolutionary fitness forms the common starting point of natural selection and individual behavioral selection. Selection at the individual level (in the sense of operant conditioning) can therefore only take place if the selected behavior increases the expected individual fitness. Accordingly, reinforcers are defined as so-called fitness predictors (or fitness proxies) that enable the prediction of an expected increase in fitness.

If a positive fitness predictor (e.g., food) covaries with the occurence of a certain behavior (e.g., the lever press rate at different time intervals) within a certain context (e.g., in the context of an experiment on operant conditioning), the average behavior increases to the extent that it predicts an increase in evolutionary fitness. This fundamental relationship between reinforcement and evolutionary fitness is referred to as the “Covariance Based Law of Effect (CLOE)”. The CLOE describes the behavioral change of an individual over time within the framework of the MLBS, which, in addition to individual behavioral selection, takes into account the selection of average behavior at the population level in the form of natural selection. At the population level, the covariance between individual behavior and individual fitness leads to a shift in the population average of the behavior. This corresponds to the effect of natural selection as described by the Price equation. Correspondingly, the average behavior of each individual changes proportionally to the individually experienced covariance between the behavior in recurring situations and the availability of fitness proxies (i.e., reinforcersor PIEs). Depending on the extent of this covariance, the behavior is selected to varying degrees. Fig. 2 illustrates the postulated relationship between reinforcement and fitness prediction.

For example, if working overtime is associated with fitness-relevant consequences (e.g., mediated by appropriate compensation), the result will be a positive covariance, and the average working time will increase. The extent of this change through behavioral selection depends, according to the CLOE, on how strongly the covarying fitness proxy (in this case, the compensation) is associated with a change in average evolutionary fitness. Depending on the context, these fitness consequences can vary greatly. It is even possible for previously neutral events to become fitness proxies if they improve the prediction of already existing fitness proxies. These are then called conditional reinforcers. In the case of daily working hours, this could be praise from superiors, for example. Also, behavior itself can be reinforcing in this sense, provided that the execution of corresponding actions directly or indirectly contributes to the prediction of changes in evolutionary fitness. For example, the opportunity for physical activity can act as a reinforcer, as physical activity can be beneficial for evolutionary fitness under certain circumstances.

In addition, not only positive but also negative fitness proxies can covary with behavior. For example, an increase in daily working hours will only be selected for as long as the positive fitness effect outweighs negative fitness effects, even with appropriate compensation. Negative social consequences, such as criticism from a partner, can counterbalance or even reverse selection if they are directly or indirectly associated with changes in expected fitness. Under constant environmental conditions, the interplay of positive and negative selection factors will eventually lead to a behavioral equilibrium. Such a behavioral equilibrium may form an evolutionarily stable strategy under the given environmental condi-

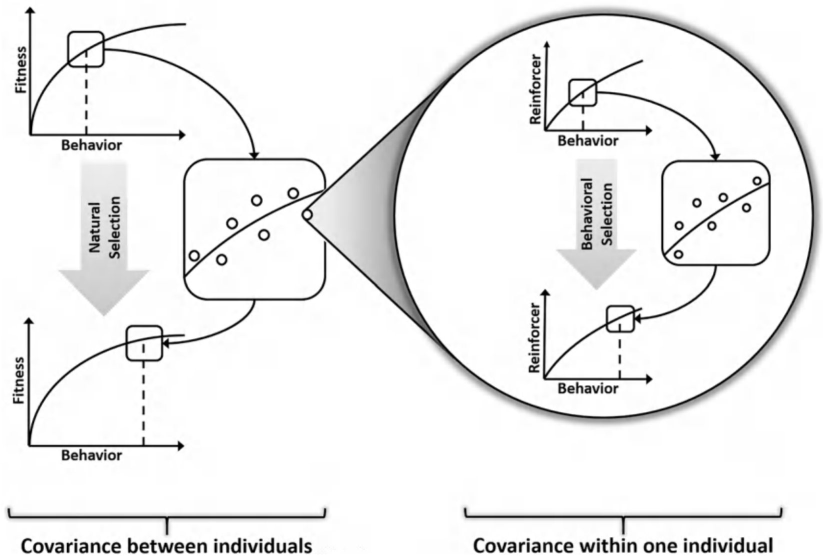

Fig. 2 The principle of behavioral selection as proposed in the Multilevel Model of Behavioral Selection (MLBS). The left side of the figure shows the process of natural selection (from top to bottom). The upper coordinate system represents the relationship between average behavior and evolutionary fitness. The depicted fitness function describes a monotonous positive relationship with a negatively accelerated curve, i.e., the higher the behavior rate observed in an individual, the higher is its expected fitness (with marginal fitness gain becoming increasingly smaller). Statistically speaking, such a relationship produces a covariance between the behavior and evolutionary fitness (represented by the points in the middle left box). According to Price (1970), this covariance implies a shift in average behavior through natural selection, which is reflected in an updated average behavior (lower left coordinate system). On the right side of the figure, the process of behavioral selection for a single individual is shown (also from top to bottom). The upper right coordinate system represents the relationship between individual behavior and (context-dependent) consequences in the form of fitness-relevant events (reinforcers). The depicted monotone relationship also produces a covariance, but within a single individual over time (represented by the points in the middle right box). Following the Covariance Based Law of Effect (CLOE), this covariance causes a shift in individual behavior, which is reflected in an updated behavioral allocation (lower right coordinate system). (©Matthias Borgstede, All Rights Reserved)

tions (see Diekmann in this volume). If the environmental conditions (and thus the covariance structure) change, such an equilibrium can be disturbed, leading to renewed selection until a new equilibrium is reached.

As a formal description of selection at the level of individual behavior adaptation, the CLOE defines the basic analytical units of behavior analysis at the highest possible level of abstraction, thus providing the conceptual framework for a theory of behavioral selection. This conceptual framework explains numerous empirical findings from behavioral psychology, such as the formation of conditioned reinforcers, the dependence of the effectiveness of reinforcers on their predictive power (Kamin 1969), the reinforcing effect of rarely performed behavior (Premack and Premack 1963), or the change in the reinforcing effects of different activities due to external contingencies (Timberlake and Allison 1974). Therefore, Borgstede and Luque (2021) argue that the CLOE can potentially serve as a fundamental principle of a general theory of behavior.

In addition, the CLOE opens up new perspectives on phenomena that are traditionally associated with cognitive sciences. For example, the often observed relationship between learning and information gain can be explained as a result of behavioral selection (Borgstede 2021). The predominant cognitive explanation for this relationship is that individuals are active decision makers who have an intrinsic tendency to search for information. The theory of behavioral selection, and especially its formalization by the MLBS, offers an alternative explanation. Instead of attributing learning and behavior to inherent psychological forces (such as intentions, goals, or will), the MLBS emphasizes the interaction of the individual with the environment (in the form of consequences). The core argument is that it lies in the very nature of selection to create order out of chaos. Therefore, if learning can be conceptualized as a selection process, it should be expected that, over the course of learning, increasingly more order – and thus predictability – emerges. From a formal perspective, predictability is nothing else but information (Shannon 1948). Consequently, individuals do not learn because they strive for information, but their behavior generates information because it is selected by its consequences.

In addition to these theoretical developments, the MLBS has already stimulated initial empirical applications. This shows that the theory of behavioral selection is not only an abstract interpretive framework for adaptive behavior, but also provides new impulses for the analysis and explanation of experimental data. For example, based on spontaneous reactions of pigeons to different food signals (so-called autoshaping), Strand et al. (2021) show that certain aspects of classical conditioning can be understood as behavioral selection in the sense of the

MLBS. Borgstede and Anselme (2024) further show how the interaction of different selection effects can bring about behavioral changes at the individual level in a study on food-seeking pigeons. They further describe an estimation method for the quantitative analysis of selection effects that can be applied in future empirical research.

Box 2: The Multilevel Model of Behavioral Selection (MLBS)

Formally, the MLBS consists of an extension of the Price equation. The crucial point is that the expected value term in Eq. 1 can be interpreted in terms of individual behavioral changes, provided that the analysis is limited to the survival component of evolutionary fitness (formally, this implies that every surviving individual from the parent generation is an “offspring” of itself). These intraindividual changes are themselves considered to be the result of a selection process that takes place within the individuals’ behavior. The Price equation can be extended accordingly:

$$\overline{w}\Delta\overline{z} = Cov_{\mathrm{i}}(z, w) + \mathrm{E}_{\mathrm{i}}\left(Cov_{\mathrm{j}}(z, w) + \mathrm{E}_{\mathrm{j}}(w\Delta z)\right) \tag{2}$$

Like in the simple Price equation, w corresponds to individual fitness and $\overline{w}$ to the corresponding population mean of evolutionary fitness. z denotes the behavior (e.g., the lever press rate in an experimental trial) and $\overline{z}$ the average behavior over several experimental trials. The change in average behavior $\Delta\overline{z}$ can now be partitioned into a covariance term at the population level ($\mathrm{Cov}_{\mathrm{i}}(z, w)$, corresponding to natural selection) and the population expectation value E_{i} over the individual behavioral changes. The individual behavioral changes are further partitioned according to the Price equation into an intraindividual covariance term ($\mathrm{Cov}_{\mathrm{j}}(z, w)$, corresponding to behavioral selection or “reinforcement”) and an intraindividual expectation value ($\mathrm{E}_{\mathrm{j}}(w\Delta z)$, corresponding to behavioral changes that cannot be attributed to selection). Finally, a functional link between both levels is established via statistical fitness predictors (for example, the expected amount of food), by replacing the fitness variation at the intraindividual level with variation in predicted fitness values. If this prediction is described by a linear regression of the form $w = \beta_0 + \beta_{wp}p + \varepsilon$, the individual selection part becomes:

$$w\Delta z = \beta_{wp}Cov_{\mathrm{j}}(z, p) + \delta \tag{3}$$

Due to the substantive similarity to the so-called "Law of Effect", Eq. 3 is referred to as the Covariance Based Law of Effect (CLOE). The CLOE is proposed as a general behavioral principle that underlies all forms of behavioral selection. Furthermore, it provides a formal definition of what is commonly referred to as reinforcement.

4 A General Theory of Behavior

This chapter addressed the question of how individual behavioral adaptations (i.e., learning over a lifetime) and population-based behavioral adaptations (i.e., evolution from generation to generation) can be consistently integrated within the framework of behavioral selection theory. Based on earlier work on the analogy between learning and evolution, a selection-theoretical framework was presented that allows the joint description of both selection processes within a single, overarching model—the Multilevel Model of Behavioral Selection (MLBS).

The MLBS describes individual behavioral adaptations as the result of a selection process based on the interarction of an individual with certain covariance structures. Depending on which behavior co-varies with fitness-relevant events (i.e., fitness proxies such as food, physical integrity, or social integration), and depending on which events prove to be reliable signals for such fitness proxies, different individual learning histories emerge, which do not only appear similar to evolutionary adaptations, but are in fact functionally linked with natural selection.

The advantage of a selection-theoretical perspective on behavior is that one general principle (i.e., the Covariance Based Law of Effect, CLOE) is capable of explaining numerous phenomena. Previous theoretical work shows that not only classical and operant conditioning, but also seemingly more complex phenomena from the field of information processing can be understood in terms of behavioral selection. Future research will show whether the MLBS proves to be a theoretically fruitful framework for constructing specific behavioral models that are capable of generating new empirical predictions. Empirical tests of such predictions will ultimately show whether the theory of behavioral selection can live up to its claim as a general theory of behavior.

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If You Want to Know What People Do, You Must Observe Them in a Structured Way

Susanne Schmehl, Kathrin Masuch and Elisabeth Oberzaucher

1 Why Human Behavior is Relevant

Insight into the behavior of organisms is crucial not only for research but also for everyday applications. Wherever organisms—whether plants, humans or animals—encounter their environment, their behavior is influenced by the opportunities for interaction that are offered. The behavior of an organism is defined as the totality of its movements, expressions (such as sounds, chemical emissions like scents, etc.) and body postures (Tinbergen 1955). In the following, the term "behavior" is used exclusively to refer to those events that are externally perceptible on an organism or emanating from an organism. Behavior here includes deliberate and spontaneous, intentional and unintentional, planned and unplanned actions. A distinction regarding underlying motives is subordinate in behavioral research, as it seeks first to observe—as objectively as possible—rather than interpret the causes and reasons behind actions.

This close interconnection of behavior and environment is particularly strong. For human behavior, Roger Barker coined the term "Behavior Settings" (Barker

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1968). The theory of Behavior Settings assumes that behavior cannot be understood independently of the behavioral environment. This also explains why the behavior of different people in one place has more similarities than the behavior of the same person in different places.

Behavior is influenced not only by the type of location—we behave differently in a supermarket than in an office, or in a restaurant—but also by the specific design of that environment, which further shapes our actions. Currently, especially in the design of interfaces between built or digital structures and users, knowledge of human behavioral tendencies can improve the usability of objects, applications, vehicles or devices, as well as their aesthetic qualities and functionality. Likewise, in interior design, knowledge of human preferences can be applied: if the evolutionarily developed preference for places that simultaneously offer a good overview of events (prospect), retreat opportunities(refuge) and escape possibilities are considered, attractive locations and spaces of high usability can be created (Appleton 1975; Fisher and Nasar 1992). The interior can thus be optimized to become effectively usable (Oberzaucher and Rueger 2018). An understanding of human territorial behavior can make public and private coexistence more harmonious by planning neighborhoods, office spaces and other buildings in such a way that the structures support the emergence of territorial identification (Fig. 1). Similarly, in digital and cognitive domains, understanding evolutionarily developed cognitive algorithms (Kahneman 2011) provides the basis for designing decision infrastructures in a targeted way. This can facilitate decision-making, or increase the likelihood of certain decisions through so-called nudging (Thaler and Sunstein 2011). Nudging is understood as an intervention in

Fig. 1 When territorial transitions are missing (left), and the public space directly borders private territories, the potential for conflict increases and private territories are hardly used. However, if a gradual division of territories is structurally implemented, and the public space is separated from private areas by semi-public and semi-private areas, fences are unnecessary (right). (Oberzaucher, 2017a)

people's decision-making processes, without however banning choices or significantly changing incentives, but by making the desired behavior easier and more cost-effective to achieve (Congiu and Moscati 2022; Thaler and Sunstein 2011). A well-known example of effective nudging is the city of Amsterdam, which changed its unaddressed mail distribution (e.g. advertisements) from an opt-out system to an opt-in system, thus saving around 6,000 kg of waste paper per year. Nudging is therefore one of the most important tools for influencing everyday decisions in favor of sustainable behavior (Schneider et al. 2022).

Various facets of human behavior have been and continue to be the subject of human ethological studies: facial expressions and gestures are not only significant in communication sciences, insights into them can be applied, for example, in pain therapy (Schmehl et al. 2016). Matchmaking agencies use human ethological data (Grammer et al. 2009), and numerous technology companies pride themselves on the intuitive and usable operation of their devices, which have been optimized through rigorous usability testing during their development processes (e.g. Mayer et al. 2013).

The application possibilities of behavioral science findings seem unlimited. However, the different disciplines not only differ in their theoretical approaches, but also in their methods of collecting data on human actions (see also Box "What is Human Ethology").

To capture human behavior, self-reporting through surveys is often used. With their application, complex issues can be quickly and easily adressed and large samples can be generated in a short time. With the option to make questionnaires accessible online, new possibilities opened up to collect data easily—both internationally and interculturally. For these reasons, one could conclude that, wherever the question allows, a survey would be preferable to an observation. The premise for this, however, is that both approaches deliver results of comparable quality. So far, some studies have compared the results of observation and survey. They suggest that observation and survey can lead to different results and interpretations. For example, Jenner and colleagues describe in a study on hand hygiene in the health sector differences between reported and observed behavior (Jenner et al. 2006). The observation showed that only 12% of the surveyed hospital staff behaved according to their previous statements. In general, participants tended to claim to wash their hands more often than they actually did. Corral-Verdugo also reports that people claim to recycle more conscientiously and behave more sustainably than they actually do (Corral-Verdugo 1997). Rundle-Thiele surveyed people about their alcohol consumption and subsequently observed their behavior in public places, finding only a very weak correlation between reported and actual alcohol consumption (Rundle-Thiele 2009).

These examples from the literature suggest that the sole use of questionnaires to collect actions and deeds of people may not lead to a truthful representation of actual behavior, especially in areas where certain behavior is socially desirable. It does not matter if self-deception or impression management is responsible, both lead to distortions in questionnaires and surveys.

However, even in areas without social pressure to behave in a certain way, surveys and observations can lead to contradictory results, as demonstrated by our study on tram passenger behavior.

In this study, people at a tram station were interviewed ($N = 120$, 61 women, 59 men, average age = 48 years) and observed in their actual behavior ($N = 200$, 102 women and 98 men). In a short interview, waiting passengers were asked how long (in minutes and number of stations) they prefer to spend their travel time standing, and from what distance they prefer to take a seat (Engelbogen 2019).

The behavioral observations were carried out on two different tram lines. At the starting station, with empty tram carriages, trained observers recorded how many people took one of the available seats and how many remained standing despite the available offer. The exit stop was noted for all travelers in order to calculate the travel distance. People with a visible physical impairment, heavy luggage or accompanied by children and/or dogs were excluded from data collection to minimize potential confounding variables. In this way, the behavior of 200 people (102 women and 98 men) was recorded. The age of the individuals was estimated to achieve as even a distribution as possible among the age groups.

In the survey on their preferences, 34.2% of the respondents indicated that they immediately look for a seat upon entering the vehicle, regardless of the distance to be covered ($N = 120$; mean = 4.8 stations; $SD = 9.34$ stations). The remaining 79 passengers reported that they prefer to stand for an average travel length of 7.3 stations (mean = 7.3 stations; $SD = 10.7$ stations). The behavioral observation led to the following results: 96% of all observed individuals immediately took one of the available seats ($N = 200$; mean = 0.07 stations; $SD = 0.38$ stations), regardless of the actual travel duration (mean = 5.38 stations; $SD = 2.6$ stations). Of the remaining 4% of observed individuals who did not take a seat, 4 people got off after one station, 2 people after two, and 2 people after three stations. Neither the survey nor the observation data show a difference between women and men ($n_{Survey} = 120$; $t_{Survey} = 1.151$; $df_{Survey} = 118$; $p_{Survey} = 0.252$; $n_{Observation} = 200$; $t_{Observation} = 0.792$; $df_{Observation} = 198$; $p_{Observation} = 0.429$). In a direct comparison of the two survey methods, there is a significant difference between the results ($N = 320$; $t = 7.137$; $df = 318$; $p < 0.001$), with reported standing travel times being longer than those observed (Fig. 2).

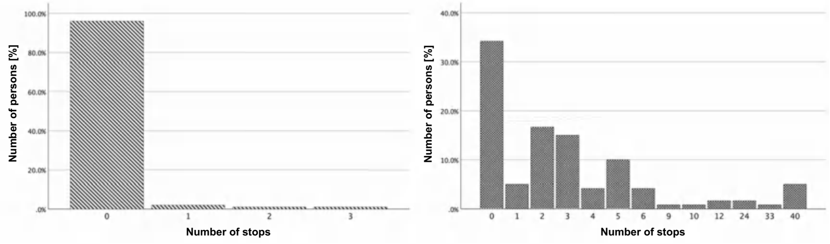

Fig. 2 Number of stations traveled standing according to observation (left) and survey (right). In the survey, people report traveling longer while standing.

The study on behavioral preferences in trams reveals significant differences between the survey and the displayed behavior. Since social desirability is unlikely to play a role in this context—that one remains standing in the train even though there are enough seats is not subject to any implicit social rules—the reason for the incorrect assessment of one's own behavior is probably due to people's lack of awareness of their own actions.

2 Humans as Witnesses of Their Own Actions

When we question people to gain insights into their behavior, the theoretical prerequisite is that the respondents provide truthful information about their actions. In most cases, however, we must assume that self-reports are subject to a certain degree of distortion—they are often inaccurate or even false. Different causes can be responsible for this "distortion":

Dishonesty: Verbal communication is largely governed by cognitive control, enabling individuals to deliberately send false signals at this level of interaction (Schmehl and Oberzaucher 2014). However, deliberate lying to mislead the interviewer is probably responsible for false statements in the rarest of cases.

Social Desirability: Individuals make statements intended to facilitate the building or strengthening of relationships with others (Cialdini and Trost 1998). Social norms help individuals in integrating into a community and establishing a position within society. Consequently, aligning oneself with the cultural conditions of a society generally exerts a beneficial effect on the individual concerned

(Mick 1996). The most well-known distortion effect in self-reports is the resulting undervaluation of socially less desirable behaviors and the overemphasis of socially desirable behaviors (Van den Mortel 2008; Brenner and DeLamater 2016). Individuals tend to suppress behaviors that are less socially appreciated and highlight their own achievements. This tendency to give desired answers can be observed both in direct questioning through interviews or conversations and in indirect questioning via (online) questionnaires. Although social desirability plays a role even without direct interaction with others, this effect is amplified by the presence of others. Numerous experimenter effects are described—for instance, regarding voting behavior (Bernstein et al. 2001), attitudes towards exercise and sports (Hadaway et al. 1998) and religious habits (Shephard 2003). The gender of the interviewer also influences participants' responses and behaviors—even extending to physiological reactions. For example, male participants show a higher pain tolerance when the experimenter is female (Alabas et al. 2012).

Intentions: Societal expectations and norms provide a general framework for desired behavior, but individuals also define at an individual level how they wish to behave. We have a certain idea of how we want to live our lives, and when we are asked about our habits, we tend to provide answers that align more closely with our intentions than with our actual behavior (Bein et al. 2015).

Cognitive (In-)Congruence: Cognitive congruence refers to the alignment between the cognitive self-image and personal behavior. When behavior does not correspond to one's self-image, memories of the behavior are often adjusted to restore consistency with the self-concept. This mechanism serves as a coping strategy to minimize self-inconsistencies (Bein et al 2015).

Ignorance (Unawareness): A predominant part of our daily behavior does not consist of conscious actions, but is instead carried out without deliberate reflection. Actions often occur below the threshold of conscious awareness. However, when individuals are asked in a survey to report on their actions and motivations they will mainly answer in a cooperative way. Reflecting on actions not processed consciously is inevitably prone to error, as the necessary knowledge base to offer a qualified statement is absent (Morsella and Poehlmann 2013).

A lot of small daily tasks and actions have long been automated through muscle memory and occur without active cognitive engagement. When asked about these activities, respondents are frequently compelled to guess or estimate, simply because they do not know.

These sources of inaccuracy consistently affect self-reports concerning behavior, motivations for behavior, or intended behavior. Although instruments exist to asses the general tendency towards distortion and false answers in questionnaires, these only serve to identify the individuals with the most inaccurate answers and do not solve the fundamental problem.

3 Learning to Observe to Understand Behavior

Instead of accepting that research results can only be considered valid to a limited extent, it makes sense to adapt the method of data collection, i.e., to either modify or supplement it.

Classical ethology offers a range of possibilities that can be applied to humans. Since its roots lie in the study of the behavior of non-human animals, this discipline was forced from the outset to develop methodological approaches other than surveys.

The exact method suitable for a behavioral biology study primarily depends on the research question. When planning the study, the first decision concerns whether the investigated behavior can be observed in a natural setting or whether an experimental setup is better suited to answer the research question. The former offers the advantage of greater ecological validity, while the latter enables better control over confounding variables. However, even in highly controlled experiments, influencing variables cannot be kept entirely constant—the state in which the participants enter the experiment varies considerably and can be recorded or standardized scarcely.

The standardization of experiments allows a detailed examination of processes, whereas the ecological validity of field studies enhances the generalizability of findings. Therefore, a combination of both approaches is recommended.

Whether employing an experiment or an observational study in a natural setting, the method of behavioral observation requires rigorous development. For a deeper engagement with ethological methods, the "Handbook of Ethological Methods" (Lehner 1996) is recommended.

Theoretical and practical considerations intersect in the selection and definition of behavioral categories: The human behavioral repertoire is very extensive. Therefore, it is necessary to identify those behaviors relevant to the research question. This usually involves referring to prior studies on the research topic. However, this approach carries the risk that research-relevant behaviors may be overlooked because previous studies have failed to consider them. Fischer (Fisher 2017) alternatively suggests starting with a survey and subsequently validating the results obtained through behavioral observation. While this approach may inspire researchers with new ideas, it still entails the risk that potentially significant behaviors—such as self-manipulation or social grooming (Nelson and Geher 2007)—may escape our attention because they are not reflectively recognized.

To minimize such biases, an empirical approach is recommended: Researchers should begin with ad libitum observation, during which all observable behaviors are recorded objectively and without functional interpretation. This method provides an initial, broad, and study-specific excerpt from the entire human behavioral repertoire ("ethogram", see also Eibl-Eibesfeldt 1967). From this unstructured description, clearly defined and reliably observable behavioral categories are subsequently developed. These initial observations can also serve as a pilot study to better plan further proceedings.

Hinde (1970) describes two groups of behavioral categories: Those defined according to morphological aspects (e.g., laughing, pointing, eating, etc.) or those classified according to consequences (e.g., approaching, fleeing, building a tower, etc.). Morphological behavioral categories are advantageous as they are initially free of interpretation thereby further reducing methodological bias.

Before a behavior catalog is employed in a study, it must be ensured that sufficient agreement exists regarding the definition of behaviors and that a high level of inter-observer reliability is achieved. If reliability is insufficient, the behavior catalog must be revised through an iterative process by further refining and clarifying the definitions. The measurement of reliability is not merely a tool for method development but, as an indicator of measurement accuracy, it is also an indispensable criterion for assessing a study's validity.

In the effort to describe events as objectively as possible, metric methods have been developed to create data bases free from interpretation. For example, conclusions about social relationships can be drawn by recording spatial proximity (Gelardi et al. 2020; Ogolsky et al. 2021). The Bern System decomposes body postures into individual angles, thereby enabling objective representation (Frey et al. 1981). The probably best-known method for describing behavior in a value-free and metric manner is the Facial Action Coding System (FACS), which refrains from emotionally interpreting facial expressions and instead records changes in expression based on the contraction of specific muscles and muscle groups (Action Units) (Hjortsjö 1969; Ekman and Friesen 1978). All these methods have the great advantage of minimizing interpretative bias. Although they can be labor-intensive, advanced methods of digitalization and automated image recognition technologies provide significant facilitation.

In addition to defining the categories to be observed, the specific procedure for data collection is crucial for the final data quality. Here, a distinction is made between **Sampling Rules** and **Recording Rules**. **Sampling Rules** determine WHO is observed and WHEN. A distinction is made between *ad libitum Sampling, Focal Sampling*, *Scan Sampling,* and *Behavior Sampling.* As previously described, *ad libitum observation* involves a value-free description of events, where observable behaviors are noted without any interpretation. *Focal Sampling* entails recording the behavior of a specific individual (or a dyad or other observation unit) over a defined period. During this precisely designated time, all actions of the individual, along with their sequence, are documented. This method provides not only a detailed insight into the specific behavior of individuals but also information about the temporal sequence and potential dependencies among individual actions. In *Scan Sampling,* all currently visible behaviors are recorded at regular intervals, regardless of the actors. For instance, when observing a classroom at a specific moment (time x), the behaviors exhibited by individual students are recorded precisely, without contextualizing them or considering preceding or subsequent actions. This method is particularly suitable for relating the behaviors of individual group members to one another. In *Behavior Sampling,* every occurrence of a certain behavior within the entire observed group is recorded, irrespective of which individual performs it.

Recording Rules determine HOW the behavior is recorded. Here, a distinction is made between ***Continuous Recording*** and ***Time Sampling.*** In ***Continuous Recording,*** the behavior under investigation is recorded throughout a previously defined observation period. To facilitate data collection, digital tools or video recordings are often employed. In addition to capturing the occurrence of behaviors, information about the duration and temporal sequence is also obtained. This is the method providing the most comprehensive view of the observed events. However, Continuous Recording is highly training-intensive and time-consuming, often requiring additional equipment, and typically allows the observation of only one individual at a time. Group behavior can only be recorded by repeatedly observing the same sequence, provided video material is available.

Slightly simpler to implement are the methods categorized ***Time Sampling:*** *One-Zero Sampling* involves a binary (1/0) recording of a certain behavior: each time a particular behavior occurs, it is noted. This approach allows for conclusions regarding the frequency of a behavior but does not provide information about processes or context. An intermediate stage to the previously explained methods is the so-called *Instantaneous Sampling:* here, at precisely defined points in time, for example at the end of a recurring time interval—i.e., every 30 seconds, all occurring behaviors at a place or in a group are noted. This creates the possibility of relating occurring behaviors to one another (Fig. 3) (Martin and Bateson 1993).

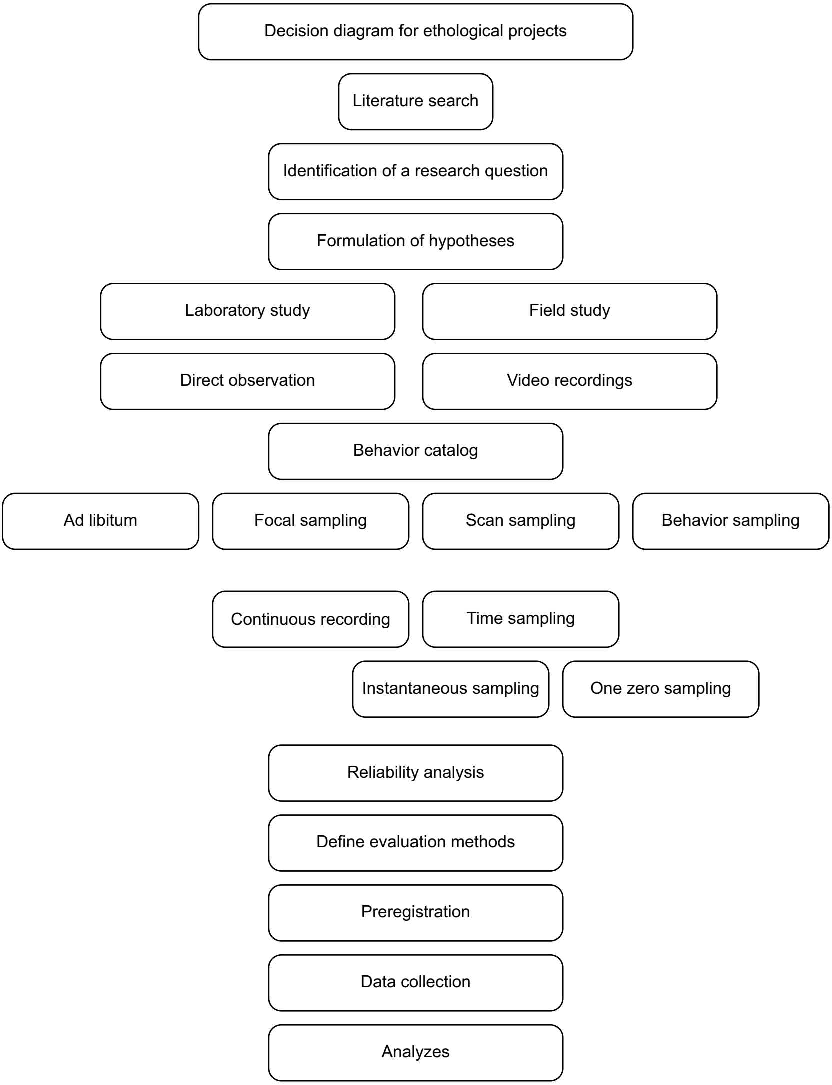

Fig. 3 Steps of a behavioral observation study

Developing a methodological framework for an ethological study requires careful validation and alignment with the research question. When achieved, this provides a solid foundation for the behavioral analysis.

4 The Path to Meaningful Data

Regardless of the chosen method, there are numerous techniques to capture behavior. In particular, digital technologies that support behavioral documentation have opened up new possibilities. With the help of specialized mobile phone applications, handheld computer programs, or digital audio and video recordings, behavioral observation becomes significantly more subtle and less intrusive than with traditional pen-and-paper methods or large video cameras. To reduce potential observer effects, among others, Rudolf Pöch and later Irenäus Eibl-Eibesfeldt used a 90° lens for their video recordings, which allowed them to film individuals without their awareness. From a research ethics perspective, however, this approach is highly questionable, as video documentation should only be conducted with the informed consent of participants. Audio and video recordings always present researchers with the challenge that informed consent potentially alter participants' behavior. This phenomenon, known as the "Hawthorne Effect"—i.e., the change in individuals' behavior simply due to being aware of the participation in a study—is often circumvented in practice by obtaining informed consent retrospectively. If the consent is not granted, the recordings are immediately destroyed. To protect personal rights, direct behavioral observation is always preferable to video analysis whenever the research question and the methodology allows it.

Regardless of whether live observation or video recordings are used, regular reliability checks are essential for quality assurance. This becomes particularly important when data are collected by multiple observers (Inter-Rater-Reliability). However, even if only one observer conducts the data collection, a reliability check serves to assess measurement accuracy (Intra-Rater-Reliability). Typically, reliability is assessed after a short training phase at the beginning of the data collection process and again toward its conclusion. It can be influenced by various factors: training and experience play a role, as do the duration of data collection and the associated fatigue of the observer. The frequency of the observed behavior can also affect reliability. For example, if a behavior occurs very frequently in a short time span, it may be difficult to document it reliably. An overly extensive behavior catalog can likewise lead to unsatisfactory reliability. In any case, reliability as an indicator of measurement uncertainty is an essential prerequisite for interpretating results—the more unfavorable the ratio of measurement accuracy to effect size, the greater the caution required in interpretation.

Thus, not only for pragmatic reasons, but also to ensure data quality, it is essential to align the behavior catalog as closely as possible with the research question.

The requirements for a behavioral observation are extensive if the resulting data are to be meaningful. The development of the ethogram (behavior catalog), the observation methodology, and the experimental design must be carried out rigorously. Trained observers are just as essential as an appropriate selection and number of participants. Field studies typically require larger data sets, as environmental parameters and potentail confounding factors are more difficult to control and document.

Although the prerequisites for behavioral observations are demanding, this approach provides insights into actions that cannot be obtained by surveys alone. The constructive combination of different methods allows the validation of the findings and the achievement of robust results. One of the most well-known examples in this context is the study "The Unemployed of Marienthal" (Jahoda et al. 1933). It is considered as a milestone in the development of empirical social research and a prime example of theory development through the integration of quantitative and qualitative data, both existing and newly collected. The Marienthal study investigated the effects of unemployment in the town of Marienthal following the 1929 closure of the factory that had originally led to the community's founding. During the Great Depression in 1931, unemployment and poverty worsened in Marienthal. The distinctive feature of this study was not only the finding that long-term unemployment led less to revolt than to loneliness and resignation, but also the pioneering application of triangulation (e.g., data-, method theory-triangulation) in capturing and portraying real human behavior.

5 Conclusion

In summary, it can be concluded that inaccuracies inevitably occur when human behavior is approached by using only a single method. A combination of various methodological approaches is indispensable for making reliable, reproducible, and robust statements about behavior. Behavioral biology and especially human biology offers numerous possibilities for investigating both the proximate and ultimate causes of human behavior.

Surveys are often preferred due to their relative ease of administration, but they may yield less reliable results. Observational studies, by contrast are labor-intensive and require a high level of expertise to ensure data reliability. This chapter introduces various methods and discusses their advantages and disadvantages. Using a case study, it demonstrates how questionnaire-based research and observational studies can be used to make predictions about actual behavior. Despite the increased effort required, structured behavioral observations remain essential for a deeper understanding of human behavior.

Human ethology can be highly valuable for researching and understanding human behavior, as it focuses on the study of human behavior in the context of their natural environment and attempts to analyze behavioral patterns and their functions. The focus of human ethology lies in the observation and analysis of human behavior as it occurs in real-world environments. With knowledge of various behaviors, their significance, and possible triggers, it becomes possible to conduct detailed observations and to identify specific behavioral patterns. In human ethology, behavior is observed in its natural context. Social, cultural, and environmental influences are considered, and this contextualization contributes to a more comprehensive understanding of behavior and its underlying motivations. An evolutionary perspective is employed to analyze human behavior, examining how certain behavioral patterns facilitate adaptation to the environment and how they may have evolved over time. This approach can provide important insights into the origins and functions of human behavior and can be applied across various practical domains. It can also help to adress issues such as discrimination and prejudice by expanding our understanding of the biological and cultural foundations of human behavior.

What is Human Ethology?

Human ethology, as a subfield of behavioral biology, is concerned with the study of human behavior against the background of evolutionary history that has shaped all living organisms. Human ethology is inherently interdisciplinary, incorporating elements from anthropology, biology, psychology, and sociology (see Eggert, F. and Holzhauser, N. in this volume).

A variety of methods are used in human ethology, including the observation of behavior in natural environments, experimental research, and the analysis of historical records.

Human ethology became popular in part through the work of Irenäus Eibl-Eibesfeldt, who studied human communication across different cultures and examined mechanisms of group formation and aggression regulation (Eibl-Eibesfeldt 1967). Beginning in the 1960s, Eibl-Eibesfeldt began building a cross-cultural film and sound documentation archive on universals of human behavior (*Human Ethological Film Archive of the Senckenberg Society for Natural Research),*[1] which continues to serve as a resource for cross-cultural studies of human behavior.

While Eibl-Eibesfeldt's approach was strongly characterized by the search for universals (behavior shown by all humans), contemporary human ethology has shifted its focus more toward the interaction between socio-ecological conditions and the expression of different behavioral repertoires.

Jane Goodall, a primatologist, conducted groundbreaking studies on chimpanzee behaviour, primarily in fieldwork. Her research significantly deepened our understanding of primate behavior and laid a foundation for the evolutionary classification of human behavior (Lawick-Goodall van 1971).

Richard Dawkins' book "The Selfish Gene" introduced key evolutionary metatheories, such as kin selection (Dawkins 1976; Hamilton 1964). Sarah Blaffer Hrdy, an anthropologist, investigated parental investment and social bonding in humans and other primates (Hrdy 1999). William C. Charlesworth primarily focused on the ontogenetic development of behavior, especially cooperation and social competence (Charlesworth 1973).

According to the ethologist and Nobel laureate Nikolaas Tinbergen, proximate, (immediate) and ultimate (fundamental, rooted in phylogenetic history) causes can be identified for each behavior (Tinbergen 1963). He expanded Julian Huxley's three foundational questions (Huxley, 1942) by adding a fourth—concerning phylogeny—resulting in the so-called "Four Whys" or "four fundamental questions of biological research":

1. Question about mechanism and form of occurrence: How does the behavior function (on a chemical physiological, neurological, psychological, and social level)?
2. Question about the causes in ontogeny: How does the behavior develop over the course of individual development?
3. Question about the biological function: To what extent is the behaviors useful to the individual (adaptive value)?

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[1] http://www.humanetho.de.

4. Question about phylogenetic history: What mechanisms have led to the development of a behavior over the course of phylogenetic history?

Tinbergen argued that behavior can only be explained multicausally, but never monocausally. Thus, modern human ethology includes both ethology and sociobiology, as well as learning theory, for example.

Central research topics in human ethology include human adaptation to the modern environment, social relationships, and reproductive decisions. Urban ethology, for example, explores how humans behave in modern—evolutionarily novel—physical and social environments, and how these environments can be designed to support well-being and healthy behavior. Topics addressed within urban ethology include residential satisfaction, behavior in public spaces, the effects of water and green plants on well-being, the role of public transport, and strategies for promoting more sustainable behavior (Oberzaucher, 2017b).

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Evolutionary Psychology: A Detour to an Evolutionary Paradigm for Psychology?

Frank Eggert and Nicole Holzhauser

1 Psychology

A long-observed fundamental problem in psychology is the lack of a unified theoretical foundation and the accompanying diversification of sometimes irreconcilable basic theoretical assumptions and perspectives. This diversity can be in part attributed to the prevalence of specialization within the discipline. The resulting fragmentation into theories of small and smallest scope, in turn, hinders the development of a unified theory of psychology. This circumstance has been repeatedly noted by leading representatives of the discipline. To illustrate this point, consider Gerd Gigerenzer's approach to theory and psychology, which is initiated as follows:

> "When discussing psychological research, what surprises every economist or physicist is that psychology has no theory. It has many local ones but no overarching theory, not even a provisional one." (Gigerenzer 2010).

Of greater concern, however, is the apparent absence of a fundamental theoretical perspective within the field, which is not only lacking, but also deemed unsuitable

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for the subject matter. This phenomenon may be attributed, at least in part, to the scientific culture and incentive system being designed in a manner that predominantly rewards the development of novel theories and concepts over the integration of existing approaches. From a theoretical perspective, however, the notion that the subject of psychology, the extensively cited "behaviour and experience," is such a complex and diverse phenomenon that it cannot be theoretically unified, appears to play a significant role and leads to the situation described by Gigerenzer:

> "Yet there is something even more surprising: a lack of awareness of the value of integration. Whereas the unification of theories, such as evolutionary theory and genetics, is a widely shared goal in physics and biology, it is barely visible in psychology. Few psychologists even consider theory integration as an objective." (Gigerenzer 2010).

The illustrations for the diagnosis expressed in these quotes can be found in abundance in psychology textbooks. The training and disciplining function of textbooks can subsequently results in students thinking within very specific theoretical frameworks. Concurrently, students may encounter difficulties in overcoming the resulting thought boundaries between different approaches. The theoretical unification of these concepts, or the aspiration towards such unification, may cease to be a part of the scientific discourse. This finding is consistent with Gigerenzer's subsequent assertion that, even when individuals specialise in a specific subfield, the following characterisation is frequently substantiated:

> "A textbook in economics starts with first principles that lead to an overarching theory and discusses how reality fits into this picture. A textbook in psychology lists dozens of theories in chapters on reasoning, intelligence, problem solving, and judgment and decision making—topics that appear closely related, but are populated by different researchers, published in different journals, and presented as independent enterprises. To the poor student, the relation between the various concepts in these different theories is never made clear." (Gigerenzer 2010).

The theoretical, methodological and terminological-categorical differences in psychology discussed here have developed in the wake of the so-called Cognitive Revolution in psychology. These differences are based, on the one hand, on the revival of concepts, methods and theoretical foundations from the mentalistic phase of psychology, In this phase, the human mind and its principles were considered the subject of this science, and introspection held a significant methodological position. On the other hand, these differences are to be understood as a counter-movement against the theoretical and methodological closedness of behaviourism and its claim to universality. The early form of behaviourism, which remained firmly rooted in associationist ideas, was initially developed by Watson in his seminal article "Psychology as the behaviorist views it", published in the esteemed Psychological Review. This article laid the foundation for a scientific programme of research in behaviourism. The essay commences with the following words:

> "Psychology as the behaviorist views it is a purely objective experimental branch of natural science. Its theoretical goal is the prediction and control of behavior. Introspection forms no essential part of its methods, nor is the scientific value of its data dependent upon the readiness with which they lend themselves to interpretation in terms of consciousness. The behaviorist, in his efforts to get a unitary scheme of animal response, recognizes no dividing line between man and brute. The behavior of man, with all of its refinement and complexity, forms only a part of the behaviorist's total scheme of investigation." (Watson 1913)

The Cognitive Revolution witnessed the decline of the behaviourist approach, its terminology, and its theoretical insights in mainstream psychological research and theory formation, which has since found a niche existence in the field of learning psychology. This development was largely driven by advancements in cybernetics and computer technology. The onset of the Cognitive Revolution is characterised by Stephen Pinker, a prominent figure in the field of cognitive psychology with a particular emphasis on evolutionary approaches, as follows:

> "In the mid-20th century, psychology was no longer "the science of mental life" (as William James had defined it), but "the science of behavior". Mentalistic concepts—thoughts, memories, goals, emotions—had been banned as unscientific, replaced by associations between stimuli and responses. But new ideas about computation, feedback, information, and communication were in the air, and psychologists realized they had enormous potential for a science of mind. Four Harvard scholars used them to launch the "cognitive revolution." George Miller chunked the "magical seven". Noam Chomsky instantiated a "universal grammar". Jerome Bruner solved problems. Roger Brown related concepts. In 1960, Bruner and Miller founded the Harvard Center for Cognitive Studies, which institutionalized the revolution and launched the field of cognitive science." (Pinker 2011)

The cognitive revolution, which occurred in the aftermath of significant advancements in information processing, precipitated a paradigm shift within the field of psychology. This shift entailed the re-emergence of information processing processes as the prevailing form of the formerly predominant mental processes. The revolution transpired over a relatively brief period culminating in a reversion to earlier mentalistic explanatory principles, that subsequently gained widespread acceptance.

> "A generation ago, a book like this one [Cognitive Psychology] would have needed at least a chapter of self-defense against the behaviorist position. Today, happily, the climate of opinion has changed, and little or no defense is necessary. Indeed, stimulus-response theorists themselves are inventing hypothetical mechanisms with vigor and enthusiasm and only faint twinges of conscience." (Neisser 1967)

Psychology thus returned—in contrast to the implications of the term "revolution" in reference to Kuhn's explanations of the structure of scientific revolutions (Kuhn 1962)—to its origins and sought explanations for behaviour again in mental events, in the structure and functioning of the mind. In this respect, the term "cognitive turn" appears to be more appropriate:

> "In this paper it is argued that the "cognitive revolution" in psychology is not best represented either as a Kuhnian "paradigm shift," or as a movement from an instrumentalist to a realist conception of psychological theory, or as a continuous evolution out of more "liberalized" forms of behaviorism, or as a return to the form of "structuralist" psychology practiced by Wundt and Titchener. It is suggested that the move from behaviorism to cognitivism is best represented in terms of the replacement of (operationally defined) "intervening variables" by genuine "hypothetical constructs" possessing cognitive "surplus meaning", and that the "cognitive revolution" of the 1950s continued a cognitive tradition that can be traced back to the 1920s." (Greenwood 1999)

This phenomenon, however, has now manifested itself under the guise of modern technical terminology. The advent of the computer metaphor, in conjunction with the concepts of programmability, algorithms, and the storage and processing of information that accompanied technical development, engendered the revitalisation of internal processes as explanatory factors of behavior.[1] This phenomenon, rather than the theoretical or empirical challenges inherent in behaviorism, served as the primary catalyst for the transformation within the field of psychology:

> "The various anomalies that eventually faced behaviorism, such as the "discovery" of biological limits on conditioning (Breland and Breland 1961; Garcia and Koelling 1966), and doubts about the ability of conditioning theory to accommodate linguistic performance (Chomsky 1959; Lashley 1951), did not result in the aban-

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[1] In this instance, an effect of societal-technological change and the promises of the information age can be identified as an external influence on the development of the theoretical orientation in psychology. Furthermore, the internal scientific competition for resources may have played a certain role, as key protagonists of both the "revolution" and the "old regime" were gathered in Harvard.

> donment of the central principles of operant or classical conditioning theories—the core theoretical elements of the behaviorist paradigm. … Nor were these recognized anomalies the primary stimulus for the development of cognitive theories in the 1950s, which was provided by outside developments in artificial intelligence and the computer simulation of cognitive abilities (Baars 1986; Gardner 1985).” (Greenwood 1999)

Following the behavioural revolution, introspection was eschewed as a method in favour of other approaches, due to its inability to facilitate intersubjective knowledge. However, it has bees reintroduced in a technological variant, as a test and questionnaire method (see Schmehl, Masuch and Oberzaucher in this volume), supplemented by statistical models that seek to model the relationships between introspectively accessible mental attributes and their objectively recordable indicators in behaviour (Lord et al. 1968). The objective measurement of behaviour was largely replaced by the recording of postulated latent traits, without these being able to meet the methodological criteria of measurements (Borgstede and Eggert 2023). The argument for the postulate of such internal processes and their scientific relevance did not always satisfy the criteria of a comprehensible argument, unless one accepted the connection of common sense and introspection as a reliable basis for concept formation in psychology:

> “The basic reason for studying cognitive processes has become as clear as the reason for studying anything else: because they are there. Our knowledge of the world must be somehow developed from the stimulus input; … Cognitive processes surely exist, so it can hardly be unscientific to study them.” (Neisser 1967)

The introduction of mental constructs established in everyday language, combined with a largely renunciation of restrictions on the introduction of new mental constructs, such as in the sense of Ockham’s Razor, has resulted in the development of a variety of theoretical terminology, often with very limited range.[2]

Theoretically, the cognitive revolution was accompanied by the fragmentation described at the beginning of this contribution. This was due to the postulation of different processes, such as specific motivations, emotions or cognitive

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[2] One of the factors contibuting to this phenomenon may also be found in the changing institutional conditions within the social system of science, encompassing university structures, publication systems and scientific reward mechanisms. These evolving structures increasingly incentivize scientists to prioritise expeditious research and publication prospects over theoretical and methodological rigour This, in turn, may lead to an exacerbation of theoretical fragmentation.

processing modes, which do not became theoretically integrated. However, these approaches appear to have a common basis due to their proximity to everyday understanding of mental processes and their significance, and because they can be more or less effortlessly classified into the metaphor of information processing. This suggests that they form a plausibly cognitive paradigm that unites them. However, a consistent and, above all, general design of a related context of theory and measurement, terminology and empiricism could not be developed in this way (Holzhauser and Eggert 2019). Psychology can be described as as a field that let "a hundred flowers bloom and a hundred schools compete" (Macfarquhar 1974) and it has developed into a theoretically inconsistent science on the one hand that is both, diverse and colourful on the other. This is in keeping with the observations made at the beginning of this contribution. Concurrently, the actors in this field—or, to remain within the metaphor of the aforementioned flower meadow—congregated beneath what was purpotedly a shared sky: a unified methodological toolkit, establishing a theory-free unity of the field of psychology by means of methodological-methodical ritualisation.

Consequently, the scientific method of experimentation was maintained, as it had already proven advantageous in the early mentalistic phase of psychology for the establishment of the new science and for the delination from competing endeavours such as philosophy (Holzhauser and Eggert 2020). However, the challenges inherent in the manipulation of not directly accessible independent features, in conjunction with the difficulties encountered in the measurement of psychological attributes as dependent features, have impeded the establishment of a consistent knowledge base (Muthukrishna and Henrich 2019). The unity of the subject was secured by methodical ritualisations, in addition to the described reinstitution of introspection as a recording method, for example in the use of (inference) statistical models, without their methodological prerequisites being sufficiently the subject of reflection (Gigerenzer 2004).

The absence of a unifying theoretical framework in psychology is identified as a key factor contributing to the empirical inconsistency and the problems with the reliability and reproducibility of empirical findings within the field. This issue was explicitly addressed in the context of the so-called replication crisis (Muthukrishna and Henrich 2019). The development of a coherent theoretical framework would represent a significant advancement not only for the status of theory in psychology, but also for psychology as an empirical science. The numerous methodological problems that Muthukrishna and Henrich address, in particular the unsolved measurement problem and the directly related problem of justifiable terminology (Holzhauser and Eggert 2019) can be traced back to inadequacies in theory formation and the lack of formal theories of sufficient generality (Borgstede and Eggert 2023).

2 Evolutionary Psychology

When considering psychology from the perspective of a natural science, and thus regarding behaviour and experience as properties of a biological system, it is evident that the theory of evolution should be referred to in order to develop a coherent theoretical foundation (Muthukrishna and Henrich 2019). A paradigmatic renewal of the discipline(s) oriented towards this is a hope associated with the development of evolutionary psychology (Buss 2020); similar expectations were also formulated for the sister discipline, evolutionary sociology (Lopreato and Crippen 1999).

> "Evolutionary psychology provides the conceptual tools for emerging from the fragmented state of current psychological science and linking psychology with the rest of the life sciences in a larger scientific integration. Evolutionary psychology provides some of the most important tools for unlocking the … mechanisms of mind that define what it means to be human." (Buss 2015)

The project of paradigmatic renewal of psychology through evolutionary psychology is predicated on the fact that the categories of behaviour and experience are redefined in such a way that the inherent indeterminacy in the prevailing conception is abolished. It is proposed that behavior and experience are reconceptualized as the result of structure-forming evolutionary processes:

> "Because evolution by selection is the only known process that is capable of generating complex functional organic design, evolutionary psychology appears to be the only viable metatheory that is powerful enough to integrate all these subdisciplines. This is the metatheory that seeks to present a unified understanding of the mechanisms of the mind that characterize this strange species of bipedal primates." (Buss 2015)

Assuming that the observable regularities in behaviour and experience are the result of evolutionary selectionist processes, a unified theoretical explanation for very different behavioural and experiential areas is posited. Despite the presence of diverse phenomena in these domains, a uniform theoretical explanatory approach is proposed.

The fundamental distinction between evolutionary psychology and other branches of psychology can be articulated in this manner: evolutionary psychology provides an uniform explanation for the regularities in behaviour and experience, whereas other psychological disciplines do not. In the preceding section, the concept of theoretical diversification in psychology was delineated, wherein principles of explanation with limited scope are employed to elucidate circumscribed phenomena. Within the purview of the sister discipline of sociology, this phenomenon is explicitly termed ‘theories of middle range’ (Merton 1968). In contrast, evolutionary psychology and evolutionary sociology postulate a fundamental, universally valid principle that is supposed to be able to explain the observed diversity and, above all, the regularities in behaviour and social phenomena.

The argument presented herein presupposes the premise, which is considered uncontroversial among scientifically oriented psychologists, that the phenomena relevant to psychology can be regarded as functional aspects of the central nervous system. Concurrently, the term “mind” is employed to encapsulate these functional aspects. In this manner, evolutionary psychology aligns with the prevailing trends in the field of psychology, positing that examination of cognitive processes (understood as the contemporary interpretation of the term “mind”) constitutes the fundamental objective of the discipline.

Evolutionary psychology aligns itself with the cognitive paradigm, which has been predominant as a basic orientation framework in psychology since the cognitive revolution. Consequently, it inherits the problems of this diversity in the postulated constructs, but attempts to counter this with a theoretical unification. From a sociological perspective, the rationale for this phenomenon may be attributed to the fact that evolutionary psychologists perceive themselves to be on the losing side in terms of the acknowledgement of their knowledge within the discourse should they not acquiesce to the prevailing theoretical power and authority relations inherent in the prevailing paradigm. Despite the apparent diversity it is evident that this paradigm exhibits a pronounced orientation towards cognitivism. In consideration of the extant anecdotal evidence pertaining to the contemporary discursive handling of (neo-)behaviourist approaches, this assessment is not unexpected.

However, the term “mind” is not without problems (Ryle 1949), as it is in a certain tension with a scientific conception that is otherwise claimed by evolutionary psychology through its embedding in the theory of evolution.

A review of the history of science and philosophy reveals that this tension can be traced back to the dualistic designs in the wake of René Descartes, who proposed the conceptual distinction between voluntary, mind-controlled behaviour and involuntary behaviour, which reacts quasi-reflexively to corresponding elicitors (Fearing 1929). In Descartes' design, voluntary behaviour, controlled by a fundamentally free mind, and involuntary behaviour, elicited by appropriate stimuli from the environment, are opposed. The hypothesis is that the organism is structurally anchored to react to certain environmental stimuli with certain involuntary behaviours, or, in modern terms, innate behaviours. From a contemporary standpoint, it is evident that natural selection functions as the fundamental structure formation mechanism in this context, thereby signifying that paradigmatically reflexive or, more generally, elicited behaviour is a product of evolutionary processes.

The development that began with the description of reflexes is then continued by Heinroth (Heinroth 1910), who founded ethology with his concept of species-specific instinctive actions. This concept was subsequently elaborated mainly by his student Lorenz (Lorenz 1937) and by Tinbergen (Tinbergen 1951), and the concept of instinct as a central idea for the explanation of behaviour was established.

In a manner analogous to the reflexes conceptualised by Descartes, behaviours governed by instincts are also initiated by external stimuli. In contrast to reflexes, the concept of instinct is characterised by an understanding of the internal causation of behaviour, with drives serving as a fundamental motivating principle. The categorization of stimuli as "key" or "releasing" is contingent upon the emphasis placed on the stimuli that govern behaviour, as opposed to the motivational underpinnings of drives. The advent of drives as a structuring factor for behavior has led to an approach to explanations for innate behaviour that mirrors that for voluntary behaviour governed by free will.

This is due to the fact that even voluntary behaviour demonstrates regularities and is, at least to a certain extent, predictable. Consequently, the existence of structure-forming processes that generate these regularities is imperative. Such structure-forming processes were also postulated earlier as principles or motives that the mind follows and that thus give direction to the will, as evidenced for instance by Thomas Hobbes' characterisation of hedonism (Chung 2016).

Evolutionary psychology is predicated on this tradition by postulating so-called Evolved Psychological Mechanisms as structure-forming mechanisms, which endow behaviour with an adaptive structure and can be characterised as follows:

> "An evolved psychological mechanism is a set of processes inside an organism with the following properties:

> - An evolved psychological mechanism exists in the form that it does because it solved a specific problem of survival or reproduction recurrently over evolutionary history. …
> - An evolved psychological mechanism is designed to take in only a narrow slice of information. …
> - The input of an evolved psychological mechanism tells an organism the particular adaptive problem it is facing. …
> - The input of an evolved psychological mechanism is transformed through decision rules into output. …
> - The output of an evolved psychological mechanism can be physiological activity, information to other psychological mechanisms, or manifest behavior. …
> - The output of an evolved psychological mechanism is directed toward the solution to a specific adaptive problem. …" (Buss 2015).

The postulated evolved psychological mechanisms are considered to be the result of natural selection, as also indicated by the following remark, which points to a central problem:

> "An important point to keep in mind is that a mechanism that led to a successful solution in the evolutionary past may or may not lead to a successful solution now." (Buss 2015)

The issue that a direct reference to natural selection raises is that many psychologically (and also sociologically) relevant phenomena require and demonstrate highly dynamic adaptations over a relatively short time period. It is an established principle of evolutionary biology that natural selection operates over the course of generations. Consequently, it can only, in principle, stabilise adaptations to relatively stable environmental conditions. In the event of behaviour being subject to rapidly changing selection conditions in terms of time and context, natural selection will be unable to select a simple evolutionarily stable solution. This issue has been explored in the context of evolutionary psychology, with the decision rules delineated in point 4 being put forward as a potential solution:

> "Psychological mechanisms are not like rigid instincts for another important reason—the decision rules. Decision rules are "if, then" procedures such as "if the snake hisses, then run for your life" or "if the person I'm attracted to shows interest, then smile and decrease distance." For most mechanisms, these decision rules permit at least several possible response options. Even in the simple case of encountering a deadly snake, you have the options of attacking it with a stick, freezing and hoping it will go away, or fleeing for your life." (Buss 2015)

In the context of evolutionary psychology, these decision rules constitute the fundamental unit of operation for natural selection. Rather than focusing on specific behavioural patterns, a mechanism is proposed that aims to align behaviour in a particular manner with changing environmental conditions. The conceptualisation of this mechanism as "decision rules" is likely attributable to the anchoring of evolutionary psychology in the prevailing paradigm of cognitive psychology. In the contemporary field of behavioural ecology, the concept of mixed strategies has emerged as a prominent theoretical framework. This framework encompasses a diverse array of tactics that are employed in response to the specific conditions present in relation to the organism or the characteristics of the environmental context (Davies et al. 2012).

Evolutionary psychology seeks to trace psychological phenomena back to decision-making mechanisms shaped by natural selection. These mechanisms refer to the emotional, motivational, and especially cognitive processes postulated in non-evolutionary psychology. The concept of a modular mind is pivotal to this theory, with modules providing specific solutions to problem situations that are of relevance to evolutionary adaptation (Barkow et al. 1995). This modularity is also regarded as a significant distinguishing factor when compared to a non-evolutionary cognitive psychology:

> "Unfortunately, the cognitive revolution carried over from behaviorism the core assumption of domain generality. Instead of domain-general learning processes applicable to all areas of human behavior, cognitivists posited domain-general information processes. Just as behaviorism posited no specialized learning mechanisms that might differ, say, from incest avoidance learning to food aversion learning, cognitivists posited no specialized information processing mechanisms. Just as you can program a computer to perform thousands of very different tasks, cognitivists assumed that domain-general information processers [sic!] could generate thousands of different behaviors. The domain-general cognitive metatheory also failed to provide something critical to human behavior—an explanation of the specific sorts of information humans and other organisms are designed to process. Evolutionary psychology furnished the conceptual tools for filling this key gap." (Buss 2020)

The integration of evolutionary psychology within the cognitive framework of psychology elucidates the fact that its purported revolutionary nature does not stem from its conceptualisation of a novel understanding of behaviour and its underlying causes and regulatory mechanisms. Instead, within the confines of the cognitive paradigm, evolutionary psychology merely postulates cognitive processes, that are practically adopted in their entirety and employed in psychology for explanatory purposes, as a consequence of evolution through natural selection.

The second point that is being made is the emphasis on modularity, as adaptive challenges are always specific. It is proposed that, given the specificity of the adaptation requirements, a corresponding specificity of behavioural solutions for these adaptation problems is derived. Assuming that all behaviour and experience can be understood as the product of such evolved psychological mechanisms, evolutionary psychology can claim to provide a rationale for the question of why there are these mechanisms and not others.

The seminal contribution of evolutionary psychology lies in its emphasis on evolutionary theoretical considerations within the field of psychology, thereby establishing evolutionary theoretical argumentation methods. The problematic aspect of evolutionary psychology lies in the theoretically unresolved tension between the postulated structure-forming mechanism of natural selection and the rapid and dynamic adaptation observable in behaviour.

This tension is addressed in an inadequate manner through the introduction of decision rules, which, when interpreted through the lens of natural selection, do not permit expeditious and dynamic adaptation. Instead, they delineate a more diversified behavioural regulation, which, nevertheless, remains inextricably linked to the temporal scope of natural selection spanning generations. If these decision rules are to enable rapid and dynamic adaptations of behaviour, their short-term specificity cannot be the product of natural selection. Instead, other processes must be added that are capable of producing such adaptations. Such processes are not postulated by evolutionary psychology. The aforementioned quote, which pertains to the distinctive function of evolution through selection in generating complex functional (i.e. adaptive) organic regularities, serves as a testament to this phenomenon. This assertion is further substantiated by the elucidations concerning the nature of man, which are designated as the central concept and explanandum within the framework of evolutionary psychology.

> “In this section we will address the core of human nature from an evolutionary psychological perspective. First, all species, including humans, have a nature, that can be described and explained. Second, we provide a definition of evolved psychological mechanisms—the core units that comprise human nature. Finally, we examine important properties of evolved psychological mechanisms.” (Buss 2015)

Evolutionary psychology is thus considered an integral component of evolutionary biology, addressing the psychological mechanisms that have emerged through the process of evolution:

> “Whereas the broader field of evolutionary biology is concerned with the evolutionary analysis of grandly integrated parts of an organism, evolutionary psychology focuses more narrowly on those parts that are psychological—the analysis of the human mind as a collection of evolved mechanisms, the contexts that activate those mechanisms, and the behavior generated by those mechanisms.” (Buss 2015)

Despite the aforementioned distinction between evolved psychological mechanisms and rigid instincts, the theoretical conception remains, in principle, fully compatible with ethological considerations of the instinct concept. Evolved psychological mechanisms can be defined as slightly more complex innate eliciting mechanisms that respond to combinations of relevant stimuli or are additionally dependent on the state of the organism. They do not merely depict simple stimuli-reaction relationships, as are paradigmatic for reflexes.

Consequently, the fundamental issue concerning the evolutionary theoretical foundation of psychology remains unresolved. Evolutionary psychology can be criticised for its inability to provide a satisfactory explanation for the rapid and dynamic adaptations in behaviour and experience that have been observed. This flexibility and capacity for rapid adaptation in rapidly changing contexts, especially in the domain of social behaviour, is a fundamental characteristic of human behaviour and experience. The introduction of a greater number of diversified “decision rules” does not resolve the issue to any more extent as the introduction of conditional strategies and tactics, which were utilised in an attempt to resolve the issue in behavioral ecology. It is important to note that both mechanisms are subject to the restrictions under which natural selection operates. It has been demonstrated that the capacity for adaptation by natural selection is constrained, in principle, to alterations of eliciting stimuli, behaviors, and the consequences of fitness, which remain constant across successive generations. In the event of rapid and dynamic change, natural selection is unable to evolve an adaptive solution. However, it has been demonstrated that natural selection can favour and facilitate the establishment of mechanisms within organisms that enable more expeditious and dynamic adaptation of behaviour.

3 Behavioral Selection Theory

In order to comprehend these mechanisms, it is beneficial to re-examine the psychological theory strand that historically emerged in the context of American pragmatism and positivism of the early 20th century and was subsequently abandoned during the cognitive turn: the behaviourist approach. This step back is not a regression from a modern behavioural theoretical perspective, but on the contrary, the continuation of a theory tradition that set out to develop a coherent theoretical understanding of its subject, behaviour.

In this context, the cognitive revolution, which restored psychology to its mentalistic origins that it had previously abandoned, can be regarded as a counter-revolution against the established behaviorism of the era. Miller, a prominent figure in the Cognitive Revolution, makes reference to this:

> "The cognitive revolution in psychology was a counter-revolution. The first revolution occurred much earlier when a group of experimental psychologists, influenced by Pavlov and other physiologists, proposed to redefine psychology as the science of behavior. They argued that mental events are not publicly observable. The only objective evidence available is, and must be, behavioral." (Miller 2003).

The early behaviorism referenced by Miller, as previously stated, exhibited a pronounced methodological orientation, seeking to establish an empiricist psychology that placed emphasis on the identification and description of behavioural regularities derived from objective behavioural data. The utilisation of mental processes as an explanans for these behavioural regularities is deemed unfeasible, as such a postulate is in principle empirically inaccessible and therefore cannot be subjected to empirical testing. This negative critique of mental processes as explanans is superseded in the course of the further development of behaviourist concepts, especially by Skinner, by a positive critique that establishes the consequences of behavior as explanans and leads to the principle of "Selection by Consequences" (B. F. Skinner, 1981). The behaviour exhibited by the organism is selected by the consequences of that behaviour and thus established or inhibited in the organism's context-specific behavioural inventory.

In order to provide a comprehensive explanation for the manifestation of a particular behavior within a specific context, it is essential to elucidate the selection conditions under which said behavior is exhibited in that particular context. It is therefore evident that these provide the explanation as to why this particular behaviour is exhibited in this specific context, and not any other. This shift in the explanans signifies a methodological departure from classical, mentalistic psychology (as described by Miller) and a theoretical reorientation with regard to the causation and explanation of behavior. The question of the explanans of behaviour is thus addressed, and it is this which becomes the fundamental difference between a behaviourist and a cognitivist-mental explanation of behaviour:

> "Cognitive science is the creation science of psychology, as it struggles to maintain the position of a mind or self. … Watson attacked introspection in his behavioristic manifesto of 1913, and for that or other reasons introspection was essentially

> abandoned. … Cognitive psychologists tried to restore the status quo. … What they hoped dead was the appeal to selection by consequences in the explanation of behavior. The mind or, failing that, the brain must be restored to its rightful position. Because of its similarity to the vernacular, cognitive psychology was easy to understand and the so-called cognitive revolution was for a time successful." (Skinner 1990)

The employment of mentalistic causes hinders the capacity to discern the underlying explanations, thereby impeding the transition of psychology into a recognised natural science. This theoretical orientation gives rise to significant challenges in empirical research, which remain obscured by a methodological approach oriented towards the natural sciences (Borgstede and Eggert 2023).

As previously discussed, this relationship between theoretical assumptions and methodological and methodological problems has been highlighted in the context of the behaviourist project of psychology as a natural science:

> "There is a sense in which it can be said that the methods of science have scarcely yet been applied to human behaviour. We have used the instruments of science; we have counted and measured and compared; but something essential to scientific practice is missing in almost all current discussions of human behaviour. It has to do with our treatment of the causes of behaviour. (The term 'cause' is no longer common in sophisticated scientific writing, but it will serve well enough here)." (Skinner 1976)

It is important to highlight a common misunderstanding regarding the assumed status of the internal processes of mental events:

> "The objection to inner states is not that they do not exist, but that they are not relevant in a functional analysis." (Skinner 1953)

This quote is pivotal in establishing the centrality of the argument concerning inner states. It is not a denial of their existence; rather, their logical role as explanans is called into question. Consequently, these inner states become explananda of a psychological theory, a role they fulfilled in principle even before this, despite having been assigned a causative function in relation to behaviour. These states in themselves are phenomena that require explanation.

Should a motivation—or in the context of ethology, a drive—be deemed causative of behavior, then the question of its origin will be immediately pertinent. A comparable scenario emerges in the context of neuronal processes as explanans for behaviour. This raises the fundamental question of the underlying mechanisms that give rise to these neuronal processes and their unique characteristics.

The fact that these questions so often do not immediately come to the fore, but explanations based on internal or neuronal processes are relatively uncomplainingly accepted as explanans, may point to a deeper theoretical and methodological problem of current psychology.

The fundamental premise underlying the notion of explaining behaviour in terms of structural conditions of the mind (or the neural system) is the implicit assumption that such explanations are inherently complete. This assumption suggests that the concept of a particular form, whose inherent structure is not subject to further explanation, is already sufficiently comprehensive. An evolutionary explanation of behaviour contradicts this approach, as it does not consider the structural properties of organisms, including humans, to be "given"—as is still the case in the doctrine of creation or its modern variant of "Intelligent Design". Instead, these properties become the subject matter that needs to be explained, and thus cannot represent the ultimate explanans for behaviour (B. F. Skinner, 1981):

> "There is a much more important reason why we have been so slow in discarding mentalistic explanations: it has been hard to find alternatives. Presumably we must look for them in the external environment, but the role of the environment is by no means clear. The history of the theory of evolution illustrates the problem. Before the nineteenth century, the environment was thought of simply as a passive setting in which many different kinds of organisms were born, reproduced themselves, and died. No one saw that the environment was responsible for the fact that there were many different kinds (and that fact, significantly enough, was attributed to a creative Mind). The trouble was that the environment acts in an inconspicuous way: it does not push or pull, it selects. For thousands of years in the history of human thought the process of natural selection went unseen in spite of its extraordinary importance. When it was eventually discovered, it became, of course, the key to evolutionary theory." (Skinner 1971)

The pivotal insight concerning the development of the theory of evolution pertains to the explanatory function of environmental conditions (or, in contemporary terminology, the context) and the contingency structures that prevail within them. These structures delineate the relationships between individual behaviours and the concomitant consequences, thereby establishing them as explanans for the adaptability of organisms. Consequently, this provides the foundation for an evolutionarily justifiable explanation of behaviour. Consequently, regularities in behavior and experience are indicative of regularities in the environment. It is not necessary to employ a structuring mind in order to explain these regularities, just as it is not necessary to posit a more or less intelligent creator in order to explain all the other regularities of nature:

> "As a science of behaviour adopts the strategy of physics and biology, the autonomous agent to which behaviour has traditionally been attributed is replaced by the environment—the environment in which the species evolved and in which the behaviour of the individual is shaped and maintained." (Skinner 1971)

A retrospective analysis of the psychological underpinnings of the cognitive turn reveals notable parallels with approaches in the field of evolutionarily based behavioral biology. This agreement pertains to the type of explanation of behaviour, the explanatory principles employed, the central concepts, and the empirical-experimental methods used to investigate behaviour.

In classical ethology, internal constructs such as drives occupied a central position in the formation of theories as the main explanans. In modern behavioral ecology, however, there is a clear recourse to the contingency structures of the environment, thereby enabling the explanation of adaptive strategic and tactical behaviour. If the characterisation of human nature is in the foreground in classical human ethology, the adaptivity of behaviour, especially in its dynamics, becomes the predominant theme of human behavioural ecology.

The present paper sets out to explore the ways in which Behavioral Selection Theory builds on these developments, and to what extent it can be developed into an evolutionary paradigm for psychology. Should this approach be extended not only to internal psychological processes, but also succeed in theoretically embedding social behaviour, communication, artefacts, and symbolic processes in a consistently coherent manner, it could also enable fruitful theory formation in the field of sociology.

In this domain, too, a comparable scenario is observed, characterised by a paucity of theoretical unification and the frequent consequence of incompatibility. These phenomena are further compounded by the concomitant empirical challenges. Despite the fact that evolutionary sociology has now gained some recognition and acceptance as a subfield within the field of sociology (Schnettler 2016), it continues to grapple with the same fundamental problems as evolutionary psychology (Holzhauser and Eggert 2021). The issue of how evolutionary adaptations can be used to explain the variable and dynamic processes that give rise to the search for universals is a subject of particular interest, as is the question of how a theoretically consistent argument can be formulated that links the complexity of societal phenomena with processes of natural selection. This desideratum also appears here to be a significant obstacle that can explain why both evolutionary subfields seem to find it so difficult to implement their claim to paradigmatic renewal of the discipline.

In order to develop such an evolutionarily based paradigm for psychology, it is necessary to 1) explain how adaptations—even rapid and dynamic ones—can arise in behaviour and experience, and 2) explain how the underlying adaptation mechanisms are linked to natural selection. A thorough exposition of the solution to the aforementioned issuess would exceed the purview of this article; however, a concise delineation of the potential solution should be endeavoured:

The regulation of behavior is facilitated by a variety of behavioral control mechanisms. It is these characteristics, rather than the behaviors themselves, that are understood to be the result of evolutionary processes, thus shaped by natural selection. Behaviour is the result of these mechanisms, which are in turn the product of the aforementioned processes. It can thus be concluded that the explanans for the emergence of certain behaviours is constituted by the consequences associated with these behaviours. The relationship (or regularity) between a specific behaviour and the subsequent consequences is delineated by the concept of contingency. The contingency structure delineates the relationships between potential behaviours and their associated contingencies. It is acknowledged that contingency structures may vary in nature depending on the specific circumstances, and this variability is typically observed in practice. Consequently, varying contingency structures define different ‘contexts’ in which they are employed. The selection of behaviour is context-dependent in this sense. Natural selection operates on the contingency structures between variants of the same behavioural control mechanism, which are shown by different organisms, and selects these variants over generations. Operant selection is defined as the process selecting variants of behaviour within the same behavior control mechanism, which are exhibited by the same organism. These variants are selected over repeated confrontations with a specific context.

The most elementary forms of such behavioural control mechanisms are reflexes and instincts. These phenomena can be comprehended within the theoretical framework of Behavioral Selection Theory, which posits that they represent solutions to adaptation problems fixed by natural selection. The mechanism of natural selection operates on the aforementioned relations of specific eliciting stimuli and specific reactions, whose expression varies between organisms. It is evident that, over the course of evolution, natural selection is instrumental in stabilising the variant or variants that are associated with the most favourable fitness consequences for the organism. In instances where such a distinction is not feasible, or where it is deemed more advantageous, a more intricate behavioral control mechanism is selected. This mechanism entails the specification of the eliciting stimulus exclusively in specific instances of confrontation. In such cases, the result are imprinting effects that fix the eliciting stimulus during ontogenesis (Lorenz 1978).

The general advantages of anticipatory behaviour regulation, which also lead to the development of sexual selection, where the fitness consequences for the offspring are quasi-regulated in advance by selecting potential mating partners, favour mechanisms that allow reliable signals for the appearance of eliciting stimuli to be identified. Should this prove successful, behaviour can be adaptively modified in anticipation of the occurrence of the eliciting stimulus, thereby altering the fitness consequences that arise from its occurrence. The aforementioned mechanism is represented by classical conditioning, in its modern interpretation as signal learning (Rescorla 1988).

Operant conditioning in its contemporary interpretation as operant selection of behaviour, signifies a mechanism that can adapt behavior in a flexible and dynamic manner to rapidly changing contexts. The selection of behavior is determined by the consequences that ensue from the behaviour in question. According to the principles of behavioral selection theory, the connection to natural selection is made through the quantitative structure of the reinforcement value, which can be interpreted as a predictor of fitness consequences (Borgstede 2020). Anticipatory mechanisms, such as the identification of discriminative cues, facilitate the adaptation of behavior to changing contexts without the need for repeated selection. In addition to the immediate experience of contingencies, i.e., relations between behaviour and consequences, mechanisms of observational learning, instruction, and insight have the capacity to accelerate selection processes and detach or even abstract them from real existing contexts (Skinner 1990).

From this perspective, internal processes can also be conceptualised as behaviour and integrated into a general selectionist theory of behaviour. The present paper sets out to give a hint how the aforementioned theoretical framework provides a comprehensive theoretical foundation within which all phenomena that can reasonably be understood as behaviour can be consistently described and explained with a theoretically founded terminology. Initial approaches to a basic formalisation of this theoretical corpus have already been undertaken (Borgstede and Eggert 2021).

Behavioral selection theory is predicated on a unified explanatory principle for behavior, which was previously proposed by Skinner (B. F. Skinner, 1981): Selection by Consequences. Should this fundamental notion be consistently applied, the mechanisms of behaviour regulation hitherto described—ranging from reflexes to instincts to classical and operant conditioning—can be classified into a unified theoretical framework. In this manner, they can be explained as special cases of this general principle.

Behavioral selection theory provides a comprehensive explanation of the behavioural adaptations discussed in ethology and evolutionary psychology through the lens of natural selection Furthermore, it has the theoretical capacity to comprehend behavioural adaptations to rapidly changing contexts and dynamically changing conditions. In this manner, and through the integration of internal processes, it may provide the hoped-for evolutionarily grounded paradigm for a natural science psychology.

In contrast to the principles of evolutionary sychology, behavioral selection theory is predicated on the integration of cognitive phenomena, which are regarded as special cases of behaviour, into a general selectionist paradigm. This relativises the difference between behaviour and experience, thus rendering psychology, in conjunction with behavioural ecology, a natural science-based and evolutionary theory-based science of behaviour. Behavioral selection theory can thus also be considered a fundamental paradigm of evolutionary psychology, but it claims a broader validity by also classifying adaptations that cannot be directly explained by natural selection into a general selectionist explanatory scheme. These adaptations, which emerge through operant selection, are not independent of natural selection; however, they can also not be explained by this selection mechanism alone. Furthermore, the theoretical framework of behavioral selection theory extends beyond the conventional paradigm of behavior by encompassing phenomena that are traditionally regarded as antithetical to it. This is due to the attribution of these phenomena as internal explanans for behaviour, consequently rendering them unsuitable as a subject to general explanatory principles.

Evolutionary psychology, as characterised in this paper, concerns itself with highly specific cognitive processes that have been shaped by natural selection and which regulate behaviour. It is therefore possible to classify the theory in question as falling within the framework of behavioral selection theory. However, it is the authors’ opinion that the theory does not represent the new paradigm of psychology. In this instance, the classical psychological approach is overly extensive, whilst the revolutionary elements of the conception are insufficiently developed. Evolutionary psychology is closely intertwined with classical ethology and the cognitive paradigm of psychology, even if it includes newer ideas about mixed strategies from behavioural ecology (albeit under a different name). The transition from classical ethology to modern behavioral ecology in the field of behavioural biology offers a valuable orientation for the necessary transformation of psychology, as it aspires to evolve into a scientifically grounded discipline based on evolutionary theory.

The extent to which this approach can also be fruitful for the social sciences in general depends primarily on whether more complex social and societal phenomena and symbolic processes can be linked to the mechanism of operant selection in a theoretically consistent manner. Should this endeavour prove successful, it is conceivable that behavioral selection theory could serve as a theoretical framework within the domain of psychology, while concurrently facilitating a meaningful interface with other branches of the social sciences. In the event that the endeavour to establish such a foundation for more complex social phenomena reveals the necessity of alternative selection mechanisms to natural and operant selection are required for explanation, this could also contribute to a clarification of the concept of cultural selection, which is often still too vaguely formulated in many respects.

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The Long Road to an Evolutionarily Informed Social History and the Paradigm of Adaptation

Jörg Wettlaufer

1 Introduction

When looking back at the origins of an evolutionarily grounded or informed historical science (cf. Wettlaufer 2002, 2015) and temporarily setting aside Darwin's dictum of the light that his theory of evolution would shed on the history of mankind (Darwin 2000, p. 564), one would first turn to the West, more precisely to Ann Arbor in Michigan (USA). There, towards the end of the 1970s, the so-called *Darwinian History* emerged, which originated from the local adaptationist school of thought inspired by the synthetic theory of evolution and the associated "Adaptationist Program" (Betzig 1992d, cf. Gould and Lewontin 1979). The open question that this new research direction dealt with was to what extent culture could be understood as a "product of striving" by individuals to maximize their genetic reproduction (Alexander 1979, p. 67).

Around the same time, a completely different yet related school of thought developed in Europe, which sought to use the findings of ethology (later human ethology) to explain human culture, including culture in historical periods. The focus was less on questions of adaptation and selection, but rather on seeking analogies between the behavior of human and non-human primates and establishing a phylogenetic connection. A prominent representative of this research was Otto König, the founder of the so-called cultural ethology (Kulturethologie) with a focus on European ethnology. More prominent in public perception was the

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founder of human ethology, Irenäus Eibl-Eibesfeldt, who also examined phylogenetic adaptations of representations of human behavior in art (Eibl-Eibesfeldt and Sütterlin 1992). Therefore, a sidelong glance at Munich and Vienna is also worthwhile to complete the picture of the prehistory of an evolutionarily informed historical science.

In the US, initial work focused on the hypergynous marriage practice in socially stratified historical societies and the associated competition for dowries (Dickemann 1979, 1981). Eventually, Laura Betzig published her much-noticed dissertation on despotism and differential reproduction (Betzig 1986, see also Betzig 1982, 1991, 1992a, b, c, 1995a, b). She examined the relationship between the political system and the "mating system" in humans, both cross-culturally and over time. Betzig found that despotic and strongly hierarchical political systems usually lead to polygamous marriage systems, specifically a polygamy of the powerful. Democratic social orders, on the other hand, harmonize better with monogamous marriage systems. Betzig explained this relationship using a rich, partly anecdotal material, which she drew from descriptions of despotic rulers by classical writers or from modern historiographical works as well as from the ethnographic literature, especially the HRAF (Human Relations Area Files) (Murdock et al. 2006). On the one hand, the lack of critical handling of historical sources may have led to this work being practically ignored by historians, despite its obvious relevance for historical sciences (see however Herlihy 1995). Instead, interest remained in an "evolutionary bubble" and in political science (see summarizing Wettlaufer 2002). In evolutionary behavioral ecology and psychology, however, the results sparked an intense debate about why the correlation between power and polygyny or genetic fitness no longer exists in modern industrial societies of Western influence (see Hopcroft and Schnettler in this volume). Kevin B. MacDonald, an American personality psychologist and now, due to his books suspected of anti-Semitism, the *enfant terrible* of evolutionary psychology (see most recently Alexis 2022), had taken up this crucial question of why the reproductive advantage of powerful men had disappeared in modern societies and tried to answer it by suggesting that so-called socially imposed monogamy (SIM) has gained the upper hand in Europe since the 12th century (MacDonald 1990, 1995a, b). This perspective, which was more in line with the "empirical findings", i.e. the prevailing view among historians, was based on a multivariate, non-deterministic theory that denied a direct connection between mating system and social system and instead attributed a shaping influence on the motivational system of individuals to institutionalized controls of reproduction, such as those exercised by the church. Here, "culture" comes into play as a mediating factor between adaptation and behavior. Because it functions idependently or genetic replication, culture enables behavioral flexibility, unknown in natural systems. David Herlihy 1995, one of the few historians interested in evolutionary explanatory models, argued similarly. He postulated a transmission of genes and culture, which, like genetic material, influenced human behavior (Herlihy 1995b). On the side of the adaptationists, however, there was continued speculation about the reasons for the demographic transition and the continued success of monogamy, and new hypotheses were developed (Borgerhoff Mulder 1998; Betzig 2012).

Even after intense debates on the entire “Adaptionist Program” (cf. Laland and Brown 2002, p. 95 ff.), the problem essentially remained unsolved. The *Darwinian History* and its interpretive approach from the paradigm of adaptation subsequently quieted down—the term disappeared from the discourses and new perspectives such as *Deep History, Neurohistory* and *Evolutionary History* took over the field, in some cases without including the work, results and questions of the *Darwinian History* in their own considerations. However, historians’ discomfort with integrating explanatory models of behavior from biological and thus evolutionarily explainable adaptations continued to persist. Only the *Deep History* (Smail 2007; Shryock and Smail 2011) and the *Genetic History* currently seem to be rekindling the dialogue between natural sciences and the humanities (Marcus 2020).

The following contribution aims to trace the role of adaptation (adaptive traits) for the development of culture and human behavior using empirical data from historical periods against the background of these different efforts to explain human behavior. This is done by examining the recent debates on the history of human mating systems. In doing so, it contributes to a better understanding of the possibilities for an evolutionarily informed history in the tension field of the dual heritage of natural and cultural adaptation.

2 The Concept and the Term of Adaptation

The term adaptation in the context of evolutionary theory refers to a characteristic (adaptive trait) occurring in a population of a living organism that is advantageous for the transmission of its genetic material to the next generation. These are usually characteristics that have arisen through mutation and subsequent selection. Adaptations can refer to the physiology, morphology, and behavior of a species. Adaptation refers to both the process of adaptation and the product of this adaptation of an organism in the course of a selection process.

Adaptionism, also known as biological functionalism, is thus the view based on Darwinian evolutionary theory that many physical and psychological characteristics of organisms are evolved adaptations to the environment in which these organisms live. The fundamental forces that produce these adaptations are variation and selection in evolutionary theory. Selection can, in the context of sexual reproduction, be further distinguished in natural and sexual selection. In both cases, however, it is about the transmission of the organism's genetic and cellular material to the next generation. Most of the organism's lifetime is under selective pressure, as the "goal" or ultimate criterion for evolutionary success is only achieved with the successful reproduction of the next generations. The basic mechanisms were described by Darwin himself, with Darwin's perspective on adaptation being multi-layered, as Thimothy Shanahn impressively demonstrates in his book on "The Evolution of Darwinism" (Shanahan 2013, pp. 93–114). In Neo-Darwinism or Synthetic Theory, which established itself from the 1940s and was supported by people like Julian Huxley and Ernst Mayr, adaptation as a consequence of variation and selection played an increasing role. Once the carriers of information were identified with Mendelian genetics, many biologists saw adaptation as the decisive factor of selection. This perspective was formulated in 1966 by George C. Williams in his classic "Adaptation and Natural Selection" (Williams 1966). A major impact on the "Adaptionist Program", which was the prevailing school of thought at the University of Ann Arbor in Michigan in the 1980s, was also made by Richard D. Alexander (1929–2018), who held a professorship in evolutionary biology there. In his book on "Darwinism and human affairs", particularly in the second chapter on natural selection and culture (Alexander 1979), he laid the foundations for the subsequent engagment of *Darwinian History* with the explanation of human behavior from the perspective of individual fitness.

Adaptations are thus the phenotypic characteristics of a species that were shaped by selection in the past. However, it is also conceivable that, as George Williams formulated, adaptations are only characteristics that are "a priori conform to a specific design" (Williams 1992, p. 40, cit. after Shanahan 2013, p. 145). The idea of adaptation in an evolutionary past has become the basis of the adaptation paradigm in Evolutionary Psychology, which seeks to understand adaptations functionally according to the Environment of Evolutionary Adaptedness (EEA). These adaptations, which were usually acquired in the Pleistocene, can also be dysfunctional in the modern environment of humans or may have new functions in social interaction (so-called Exaptations) (Barkow et al. 1992). For an application in media psychology, see the contribution by Hennighausen, Lange and Schwab in this volume (see also the critical objections by Eggert and Holzhauser in this volume to the concept of adaptation in Evolutionary Psychology).

3 Critique of Adaptationism and State of the Discussion

This one-sided adaptationist view of the formation of phenotypes was criticized by Stephen Jay Gould and Richard Lewontin in their 1979 work "The Spandrels of San Marco and the Panglossian Paradigm". Evolutionary biologists, according to Gould and Lewontin, have the habit of routinely proposing adaptive explanations for every feature, without also considering possible non-adaptive alternatives for feature formation. They also criticized the conflation of adaptation with the argument of the process of natural selection. Plausibility alone for the explanation of adaptations is, according to the methodological objection, not a sufficient argument as long as it is not possible to falsify these explanations (Gould and Lewontin 1979). The criticism of Gould and Lewontin was taken up by Ernst Mayr and Daniel Dennett, who in turn argued for a more rigorous methodology for identifying adaptations or pointed to already existing methods. Mayr, who considered the organism as the level of selection, stated in 1983: "He [the evolutionist] must first attempt to explain biological phenomena and processes as the product of natural selection. Only after all attempts to do so have failed, is he justified in designating the unexplained residue tentatively as the product of chance" (Mayr 1983, p. 326, quoted after Shanahan 2013, p. 140). Daniel Dennett, for his part, pointed out in 1995 that evolutionary biology has always been looking for hidden constraints. "Good adaptationist thinking is always on the lookout for hidden constraints, and in fact is the best method for uncovering them" (Dennett 1995, p. 261, quoted after Shanahan 2013, p. 140). Thus, constraints in the observed adaptations are not necessarily a counter-argument, but part of the explanation. Richard Dawkins most clearly positioned himself on the side of the critics of Gould and Lewontin. In his book "The Extended Phenotype: The Gene as the Unit of Selection" (Dawkins 1982), he gave various reasons why adaptations can be limited. This includes the time lag that can occur between adaptation and changes in the environment. An example he cites in this context is the hedgehog's reflex to curl up when in danger. Under the changed conditions of modern human transportation, this is often a deadly decision for the animals (Dawkins 1982, p. 35). A milestone in the discussion about adaptationism was finally the book "Dawkins vs. Gould: Survival of the Fittest" by Kim Sterelny (Sterelny 2001), in which the author was able to clearly work out the differences in the arguments of the opponents. According to Sterelny, Gould and Dawkins differ mainly in the relative role of selection and variation. They also set different priorities with regard to the development of organisms. Developmental constraints are fundamental to Gould's criticism of adaptationism. Dawkins, on the other hand, attaches less weight to this aspect and was more interested in extended possibilities that are open to lineages as a result of developmental revolutions. For example, the evolution of segmentation increases the possibilities for variation. "Major transitions in evolution are developmental transitions, transitions that enable new variants and thus new adaptation complexes" (Sterelny 2001, pp. 77–78).

4 Double Adaptation in Culture and Nature—and the Resulting Implications…

Parallel to the development of the "Adaptionist Program" and its criticism by Gould and Lewontin, another school of thought established itself early on, which assumes a coevolution of natural selection and culture. This view is closely associated with the name of Edward O. Wilson and sociobiology. Together with Charles Lumsden, Wilson published "Genes, Mind, and Culture. The Coevolutionary Process" as early as 1981 (Lumsden and Wilson 1981). While their approach was even more firmly rooted in the field of genetic evolution, the work of Cavalli-Sforza and Feldman focused on the exploration of cultural transmission mechanisms (Cavalli-Sforza and Feldman 1981). The theory of a dual inheritance (also known as Ddual Inheritance Theory) was finally introduced by Richard Boyd and Peter Richerson towards the end of the 1980s. (Boyd and Richerson 1985; Durham 1991). Their perspective continues to shape our understanding of the relationship between biological and cultural development to this day (see Currie et al. 2021).

On both levels, nature and culture, adaptation processes can thus be observed. In this context, Eckart Voland describes the relationship between nature and culture as intertwined and views culture as an extension of the behavioral repertoire evolved from natural adaptations. Nature and culture are thus in constant interaction. Natural adaptations are culturally reinforced and in turn become part of a cultural system themselves. At the same time, culture changes environmental conditions, reduces selection pressure, and may bring about new rules and behavioral norms that can in turn selectively influence the transmission of natural adaptations (Voland 2000). An example of such an interplay between nature and culture is the social use of human shame. Genetically predisposed and equipped with its own physiological and phenotypic manifestations, shame has experienced and continues to experience diverse cultural expressions, some of which can be interpreted functionally as stabilizers for cooperation in groups and the enforcement of common norms. The investigation of the cultural use of physiological adaptations in historical and recent cultural settings remains a research desideratum (Wettlaufer 2015, 2023). Another topic that lies at the heart of evolutionary history is the development of human mating systems as shaped by the interplay between nature and culture from the perspective of a "Deep History".

5 Human Mating and Marriage Systems in an Evolutionary Perspective

The starting point is the discussion described in the introduction: the thesis put forward within the framework of *Darwinian History* of the variable adaptation of the human mating system to the imperative of fitness optimization in the biological sense. From this assumption, it is difficult to explain the dominance of monogamy as a form of marriage in the Western cultural sphere since the High Middle Ages, especially since systems of mild polygyny are the rule in cultural comparison (Ford and Beach 1969). This direction is also indicated by comparative evidence placing humans within the spectrum of mammalian mating systems (Harcourt et al. 1981). Observing mating systems embedded in human cultures comparatively over long time spans reaveals the strinking range and flexibility with which homo sapiens sapiens reproduces successfully and adapted to the respective environments. Walter Scheidel summarized the state of the discussion about the success story of monogamy in 2009, using Greco-Roman societies as an example. He demonstrated how difficult it is to attribute a fixed function and a general understanding of the monogamy imperative of predominantly Western societies as "Socially Imposed Monogamy" (SIM) so far. Basically, the occurrence of non-marital sexuality within "officially" monogamous societies undermines efforts to derive societal advantages such as reducing competition among men and strengthening cooperative behavior from the prevailing form of marriage. Instead he suggested that the Christian tradition adopted the Greco-Roman view of monogamy as the only legitimate form of marriage (Scheidel 2009, p. 287; Scheidel 2011) and then the ongoing success story of monogamy began with Christianity.

The tradition of a monogamous marriage system may even date back further. In her work, Laura Fortunato reconstructs early Indo-European and Proto-Indo-European marriage systems as primarily monogamous with predominant virilocality (woman lives with the man and his family) and alternative neolocality (couple lives neither with the bride's parents nor the groom's, but establishes their own household). Her findings broadly align with earlier conclusions drawn from linguistic and ethnographic data (Fortunato et al. 2006; Fortunato 2011, 2015).

Fortunato and Archetti argue that the main advantage of the monogamous system lies in inclusive fitness, i.e., the indirect improvement of reproductive success through the support of closely related individuals (Fortunato and Archetti 2010). Walker and colleagues seek to rekonstruct an "original" human marriage system through comparative observations in hunter-gatherer societies (Walker et al. 2011). The reasons for the transition from a polygynous to a monogamous marriage system are manyfold. Henrich, Boyd, and Richerson try to explain the "puzzle of monogamous marriage" through the positive effects in competition between groups. By suppressing intrasexual competition and due to the reduction of the number of unmarried men and the reduction of conflicts within a household, monogamy as a marriage system offers advantages over a polygynous system (Henrich et al. 2012). Sadettin H. Citci, on the other hand, holds the increased income opportunities of women in modern societies responsible for the system change (Citci 2014). Francesconi and colleagues see the decisive factor in the particularly pronounced overlap in the care of children of different ages in a family (Francesconi et al. 2016). Bauch and McElreath explore the relationship between the spread of sexually transmitted diseases and the establishment of the SIM using a simulation—and naturally find a connection (Bauch and McElreath 2016). Another aspect that could also argue for the development of monogamy as the preferred form of marriage are the advantages that monogamous families have in the joint upbringing of offspring, the so-called cooperative breeding (Boomsma 2009, 2013; Schacht and Kramer 2019, pp. 66–67).

The most comprehensive attempt to solve the puzzle has recently been undertaken by Ross and colleagues in a large-scale study. They modified the standard polygyny threshold model with *female choice* into a model of equal partner choice and then tested this model with a new, extensive dataset, including data from historical populations. Provided two conditions are met, this model could also make monogamy the predominant form of marriage in very unequal societies, with a highly unequal distribution of resources. However, the study also classified serial monogamy as a form of polygyny, which complicates comparability with other explanations. The analysis showed that with the transition to stratified agrarian economies: (i) the frequency of individuals with sufficient wealth to secure a polygynous marriage decreases, and (ii) the marginal fitness returns decrease and prevent extremely wealthy men from marrying as many women as their relative wealth would otherwise predict. These conditions together, according to Ross and colleagues, lead to a high probability of monogamy in farming populations (Ross et al. 2018). All culturally transmitted norm settings are, even in this model, only subordinate adjustments to the fitness advantages that are supposed to result from monogamy.

Considering these different explanations, one can fully agree with the view of Schacht and Kramer in the latest literature review on this topic. A consensus on a human-typical mating system is and remains elusive in the literature. In all modern human societies, monogamous, polyandrous, polygynous, and short-term mating patterns are present, with most societies exhibiting multiple types of marriages and mating relationships. A further complication of a simple classification of the mating system are the various possible interpretations of biological features that are typical for humans and that are used to indicate mating patterns of our ancestors. In summary, Schacht and Kramer derive three core statements. 1) Although polygyny is socially sanctioned in most societies, monogamy is the dominant type of marriage within a group across cultures. 2) Sexual relationships outside of marriage occur in all societies, yet the paternity rates of such relationships in humans are relatively low compared to those of socially monogamous birds and other mammals. 3) While the timing of the evolution of certain anatomical features is disputed, the degree of sexual dimorphism in humans and the relative size (in relation to body weight) of the male gonads indicate a divergent history of sexual selection compared to our closest relatives, the great apes. Thus, while there are many ethnographic examples of differences between human societies in terms of mating patterns, the stability of relationships, and the ways in which fathers invest in their offspring, the close pair bond in cohabitation remains a ubiquitous feature of human mating relationships. This pair bond sometimes manifests in polygyny and/or polyandry, but is most often observed in the form of a monogamous marriage, which is often serial and characterized by a low degree of paternity uncertainty and a comparatively high degree of paternal care (Schacht and Kramer 2019, p. 68).

6 Conclusion

It's time to take stock again. Since the German-language publication of the article "Evolutionary Biology and Historical Sciences" by Nancy Wilmsen Thornhill in the volume edited by Eckart Voland on "Nature and Culture in Interplay", thirty years have passed (Thornhill 1992). That contribution sought to demonstrate—using the example of changes in marriage restrictions in American society of the 18th and 19th centuries—how principles of evolutionary theory can help explain cultural phenomena. It bridged the gap between natural and humanities sciences and is part of the diverse efforts of Behavioral Ecology to find explanations for behavior and reproductive decisions in historical populations from historical-demographic data (Kindworth and Voland 1995, Voland 1990, 1995). However, few scholars from the humanities embraced this approach and continued on this path (cf. Herlihy 1995; Kroll and Bachrach 1990; Bergstrom 1994; Scheidel 2014). In the natural sciences, initial interest also waned when tangible interdisciplinary successes failed to materialize. For most Humanities scholars, the evolutionary perspective appeared to narrow interpretive possibilities and offered little space for critical discussion and discourse. While areas such as kinship, reproduction, reproductive strategies, parental investment or even marriage rules and systems provided points of intersection, domains such as history of ideas, art- and cultural history in the narrower sense remained untouched by evolutionary theories. An exception in this regard is the less theory-based and more analogy-based field of human ethology, which has yielded some remarkable results in this context.

The central obstacle for broader acceptance of *Darwinian History* among humanities scholars lies in its perceived overemphasis of fitness maximization. Regardless of behavioral complexity, every cultural trait was expected to be justified in terms of reproductive advantage. Thus, *Darwinian History* bordered on circular reasoning and invited the charge of biologism. Similar to sociobiology, the criticism ignited at the denial of the autonomy and dynamics of sociocultural phenomena (Wuketits 1999). Cultural behavior patterns developed out of traditional societies, when examined more closely, usually do not hinder reproduction. Collective celibacy in religious communities, as it was developed, for example, in the Catholic Church, is a typical example of a behavioral norm that cannot be explained by direct fitness advantages. Of course, celibate priests can help relatives to advantages, which in the end also pay off in fitness. But the focus on the aspect of fitness falls significantly short here to fully understand the emergence and spread of this cultural phenomenon.

Despite these criticisms and limitations, the idea of “evolutionary historical science” continues to attract interest among historians. *Deep History* and *Neurohistory* are just two research fields that have been discussed for several years (Smail 2007, 2014; Shryock and Smail 2011; Wettlaufer 2012). *Evolutionary History* or evolutionary historical science today includes both a historically and evolutionarily informed environmental history (Russell 2011) and research with a focus on cultural and emotional history (Wettlaufer 2023). Humanities scholars are currently particularly open-minded about the so-called *Genetic History,* which is able to answer questions about the spread of populations and even the genetic prevalence of individuals using modern methods of molecular genetics. This approach creates new bridges to *Genealogy* and *Public History.* With the populations come languages and cultures, whose dispersal can now be investigated on a new empirical basis. Even if the historical unique event, the singularity, continues to elude an evolutionary explanation, it seems that *Genetic History* is currently reviving the dialogue between natural sciences and humanities (see, among others, Weigel 2001; Zerjal et al. 2003; Marcus 2020, Liu et al. 2021).

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Part II

Genetically Informed Research Designs in Sociological Inequality Research. The Example of Educational Attainment

Mirko Ruks and Martin Diewald

1 Introduction

Various studies have shown that on average, about 40 % of the variance in educational success can be attributed to genetic differences (Branigan et al. 2013; Silventoinen et al. 2020). Therefore, anyone interested in educational inequality cannot ignore genetic influences. Against this background, we would like to demonstrate in this chapter the added value of genetically informed research designs (*cf. Diewald and Mönkediek in Part 1 of the anthology*) for the sociological exploration of social educational inequalities. For this purpose, essential genetically informed research designs will be briefly introduced, and then it will be shown what contribution such genetically informed designs can make, exemplarily for two central research fields of educational research: the intergenerational transmission of educational inequality and the question of to what extent parental behavior compensates or accentuates the educational potentials of their children. *Methodologically,* genetically informed designs can generally be advantageous as they can control for unobserved environmental and genetic heterogeneity, thus enabling more precise estimates of social effects. At the same time, we show what contribution genetically informed designs can make to a better *theoretical understanding* of both aspects of the genesis of educational inequalities. It would

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be too short-sighted to understand genetic effects exclusively in terms of unobserved confounding variables. Given that genetic influences have been reported on almost every sociologically relevant characteristic (Polderman et al. 2015), it is theoretically advisable to also include genetic influences in the explanation of social inequalities, especially since they do not only operate independently alongside social influencing factors, but also operate in conjunction with social influences—and thus the social influences can be better understood through them.

2 Genetically Informative Research Designs

We would like to briefly introduce the three most widely used approaches to genetically informed research: 1) Fixed-Effects (FE) models with sibling data, 2) variance decomposition models with twin data, and 3) molecular genetic methods. Sibling data offer the opportunity to control for various types of unobserved heterogeneity and thus obtain more precise estimates of social effects. Typically, FE models are calculated for this purpose, which control for all unobserved factors shared between siblings. Different types of siblings involve different degrees of control for unobserved heterogeneity. Conventional siblings and dizygotic twins share on average 50 % of their genes and shared environmental experiences, the latter being born at the same time and thus the extent of controlled shared environmental experiences is significantly larger. Monozygotic twins, on the other hand, are genetically identical, so an FE model here controls not only for all unobserved shared environmental factors as in the case of dizygotic twins, but—with few random mutations—also for *all* unobserved genetic heterogeneity.

While the approach of FE models with sibling data primarily considers genetic influences as a source of biased effects that need to be controlled, genetic influences in variance decomposition models with twin data are explicitly modeled (Knopik et al. 2017; Neale and Maes 2004). The classic twin model is based on the comparison of monozygotic and dizygotic twins, which allows to decompose the variance of a trait into additive genetic (A), shared (C) and non-shared environmental influences (E). The twin models are calculated as structural equation models, in which the variance components are modeled as latent factors. There are a number of extensions for this basic twin design. For example, multivariate twin models can be used to investigate which factors mediate the genetic effect on the dependent variable, while in more complex models, such as the various forms of the so-called “extended twin family designs”, additional family members are included, so that, among other things, social and genetic intergenerational transmission effects can be distinguished (Keller et al. 2009).

In addition to the use of family data, molecular genetic methods are another form of genetically informative designs. While there are various molecular genetic methods (see Harden and Koellinger 2020; Mills et al. 2020; Mills and Tropf 2020), we limit our discussion here to so-called "polygenic scores" (PGS). PGS measure the genetic predisposition for a certain characteristic, e.g. educational attainment or intelligence, and are calculated based on so-called genome-wide association studies (GWAS). The aim of a GWAS is to calculate associations between the characteristic of interest and so-called "single nucleotide polymorphisms" (SNPs), i.e. differences in individual base pairs of DNA. Based on the results of the GWAS, a PGS can be calculated as the sum of the gene variants weighted by the strength of the GWAS association. To control for bias in the effects due to geographical clustering of gene variants, "principal components" are calculated based on a factor analysis carried out with the GWAS data, which are considered as covariates in a regression model like other social characteristics.

3 The Contribution of Genetically Informed Designs: Compensation vs. Accentuation

An increasingly prominent topic in inequality research is the strategies used by families with a higher socio-economic status to maintain their status, and by families with a lower status use to achieve upward mobility. In particular, the question is discussed whether a high socio-economic status can compensate for lower performance, or whether it even accentuates good predisposition. Analyses for France (Bernardi and Cebolla-Boado 2014), Italy (Bernardi and Triventi 2020) and Spain (Troiano et al. 2021) largely confirm the compensation thesis, while Heiskala et al. (2021) report mixed results for Finland. However, all studies have in common that they sometimes mention genetic influencing factors conceptually, but do not investigate them empirically.

A *methodological* advantage of genetically informed designs is that they can control for various types of environmental and genetic unobserved heterogeneity. For example, Holm et al. (2019) investigate for Denmark whether the effect of early school performance on the level of secondary school attended later varies with social origin. Compared to OLS models, the effect of the grade point average in FE models with monozygotic twins is more than halved, suggesting a significant bias of the OLS estimates due to unobserved genetic and social factors at the family level. Also, the differences according to social origin in the FE models are much more pronounced. Thus, substantial differences in the results already arise from an effective adjustment for such biases, which do not necessarily have to go in the direction of a relativization of social mechanisms. Gil-Hernández (2019) investigates for Germany whether the effect of cognitive abilities on the probability of attending a grammar school varies with social origin and estimates an FE model with monozygotic and dizygotic twins for this purpose. In the FE models, the effect of cognitive abilities is reduced by more than half, which is a clear sign of the genetic and social confounding of the association between cognitive abilities and attending a grammar school. Stienstra et al. (2021) investigate a similar question, but calculate an ACE-beta model for this purpose (Kohler et al. 2011). This model, like FE models with monozygotic twins, controls for possible biases due to unobserved genetic factors and social factors at the family level. At the same time, however, the confounding genetic and social influences are explicitly modeled as latent factors, i.e., we know to what extent confounders are social or genetic. Also in this study, the authors show that the effect of cognitive abilities is substantially reduced as soon as genetic and social bias is controlled for. Thus, about 34 % of the association of cognitive abilities and school type can be attributed to unobserved social factors, about 48 % to unobserved genetic heterogeneity, and only about 18 % can be explained by the actual effect corrected for these. The authors can also show that the origin differences in the effect of cognitive abilities are biased: While the "raw" association between cognitive abilities and school type is stronger for individuals with a low social origin in the sense of the compensation thesis, no origin differences can be observed once unobserved social and genetic heterogeneity is controlled for. Overall, these three studies not only show that the relevance of school grades and cognitive abilities in conventional designs is significantly overestimated due to unobserved heterogeneity by genetic and shared environmental factors, but also suggest that the tests for compensation or accentuation could be confounded (Holm et al. 2019; Stienstra et al. 2021). This shows that controlling for unobserved heterogeneity using genetically informed designs is of central importance for the compensation vs. accentuation debate.

Although substantially different results are achieved in these examples by controlling for genetic variation, genetic factors are still not part of the explanatory program under investigation. In addition to controlling for unobserved heterogeneity, another advantage of genetically informed designs is that they allow for the first time to investigate genetic influences as a theoretically significant part of explanations and to integrate the role of the interplay of genes and environment in explaining educational inequalities. For the debate on compensation and accentuation, this is done, for example, by studies on the social stratification of genetic influences. Here, it is investigated whether the realization of a genetic predisposition for educational success depends on social origin. Specifically, it is investigated to what extent in higher social strata a low genetic predisposition for education or school performance is compensated for or the realization of a genetic potential is accentuated. Methodologically, this field relies on both the classic twin design and molecular genetic methods.

The state of research on such an interaction of a genetic predisposition with social origin is quite heterogeneous. Some studies show for Germany (Baier and Lang 2019), the USA (Papageorge and Thom 2020; Uchikoshi and Conley 2021) or Finland (Erola et al. 2021), that the realization of the genetic disposition for educational success is intensified in higher social strata in the sense of the accentuation thesis. On the other hand, there are reports of a lesser realization of genetic potential in higher strata in the sense of the compensation thesis for the USA (Harden et al. 2020; Lin 2020), Sweden (Baier et al. 2022b) and Germany (Ruks 2022), while other studies for the USA (Figlio et al. 2017) and Norway (Isungset et al. 2022) find a moderation of the genetic influence neither in one direction nor the other.

While most studies only test *if* the realization of genetic disposition for educational success depends on social origin, multivariate twin models can differentiate *which* specific genetic dispositions are conditioned in their realization by social origin. For example, Tucker-Drob and Harden (2012a, b) show for the USA that a moderation of the genetic predisposition for school performance by social origin is specifically due to a moderation of genetic dispositions for intellectual interest and learning motivation. Similarly, Ruks (2022) shows for Germany that a large part of the interaction between social origin and genetic predisposition for tertiary education participation is specifically due to a different realization of genetic disposition for cognitive abilities. In this case, it is shown that offspring from higher social strata need to exploit their predisposition for cognitive abilities less in order to attend a university.

In addition to the use of genetically informative designs to control for unobserved heterogeneity and thus obtain more precise estimates of *social* effects, these can also be used to investigate the role of *genetic* effects as part of inequality-generating mechanisms. Despite heterogeneous findings, it can be clearly stated that social inequalities in the realization of genetic predispositions for educational success are a crucial component of the explanation of social educational inequalities in the sense of compensation and accentuation. Therefore, if the aim is to provide as complete an explanation of social inequalities as possible, these findings cannot be ignored.

4 The Contribution of Genetically Informed Designs: Intergenerational Education Transmission

Intergenerational educational transmission has traditionally been a central research area in empirical inequality research. Numerous studies here show a strong correlation between social origin and educational success (e.g., Jackson 2013)—either through the calculation of social origin effects in regression models (Erikson 2019) or by using sibling correlations as an indicator of the "total origin effect" (Grätz et al. 2021). A special role in this context is played by the question of the relationship between "ascription" (closure) and "achievement" (openness), i.e., to what extent educational success is quasi laid in the cradle for children from higher parental homes or must be achieved through individual merits. However, determining the extent of social closure by calculating social origin effects in regression analyses or sibling correlations is problematic, as both approaches ignore that (a) parents not only provide their children with access to resources but also pass on their genes to them, and (b) that the similarity of siblings is not only due to shared social origin, but also to common genes. This problem can only be addressed in genetically informed studies. This is not just about the *methodological* question of controlling unobserved heterogeneity, but about the *theoretical* and almost popular discussion beyond science about whether life fates are determined more by *nature* or *nurture,* and what this implies for the possibility of socio-political influence. Thus, it has been argued in part that considering genetic influences can contribute to a better understanding of the relationship between social closure and openness in status acquisition (such as Nielsen 2006), by using the heritability of a status characteristic as an indicator of open opportunity structures. According to this interpretation, the heritability estimate quantifies the possibility of realizing one's own genetic potential, so that high heritability can be interpreted as an indicator of open opportunity structures and low heritability as an indicator of social closure. This interpretation of genetic effects has been adopted in many studies (e.g., Guo and Stearns 2002; Nielsen and Roos 2015), but is also criticized (see *Diewald and Mönkediek in Part 1 of the anthology*).

Studies that investigate how genetic effects on status-relevant characteristics vary over time or between societies, among others, contribute to this debate. Thus, Engzell and Tropf (2019) show that genetic influences on educational success are stronger in egalitarian contexts, and Heath et al. (1985) show that the heritability of educational success is increasing for younger cohorts, which the authors explain with more open access to education. This is consistent with findings by Herd et al. (2019), who show that with the decrease in structural access barriers to education for women, the gender difference in the heritability of education also decreases. Rimfeld et al. (2018) also show that the genetic influence on educational success in Estonia has significantly increased with the end of the USSR, which they also justify with a reduction in structural access barriers to education. Overall, these studies seem to confirm the thesis of stronger genetic influences in egalitarian social contexts, despite theoretical objections to such an interpretation.

One criticism of the thesis of heritability as an indicator of open opportunity structures, however, is that it is based on the (implicit) assumption that genetic effects are exclusively due to the realization of dispositions for meritocratic characteristics and that social closure mechanisms play no role in the unfolding of the genetic effect (see *Diewald and Mönkediek in Part 1 of the anthology*). The question of which genetic dispositions are relevant for educational success can be addressed through multivariate twin studies or the calculation of genetic correlations based on GWAS data. Thus, many twin studies show that a significant portion of the heritability of education can be explained by competence-related or performance-relevant characteristics such as intelligence (Plomin and Deary 2015) or conscientiousness (Starr and Riemann 2022). This is consistent with the fact that about 75 % of the heritability of school grades is explained by cognitive and non-cognitive abilities (Krapohl et al. 2014). At the same time, purely ascriptive characteristics such as BMI, body height, or other health-related behavior also play a (smaller) role (Bulik-Sullivan et al. 2015), which could indicate social closure or discrimination processes. In summary, it can therefore be said that even genetically sensitive designs do not provide a comprehensive answer to the question of openness vs. closure. Nevertheless, they should be considered an important building block of the toolkit for researching the opportunity structure of a society, which complements well-known methods (e.g., social origin effects or sibling correlations).

In addition to these more theoretical-conceptual reasons for considering genetic influences in the analysis of intergenerational educational transmission, genetically sensitive designs can also contribute to making more precise statements about the *social* reproduction mechanisms of educational inequalities by controlling for unobserved heterogeneity. As already mentioned, parents pass on not only access to resources but also their genes to their children. This phenomenon of passive gene-environment correlation (see *Diewald and Mönkediek in Part 1 of the anthology*) can lead to biased estimates of the social reproduction of educational inequalities: individuals with a positive genetic predisposition for educational success are better educated and achieve a higher socio-economic status (Belsky et al. 2018). Now they can support their children in acquiring education not only through access to these economic, cultural, and social resources, but also pass on their genes that are beneficial for educational success. Therefore, there is a risk that part of the effect of social origin on educational success is not due to social, but to genetic transmission effects, so it is necessary to control for genetic transmission effects in order to make meaningful statements about the social reproduction mechanisms.

A number of studies use more complex twin models to distinguish between social and genetic transmission effects. Baier et al. (2022a) calculate a so-called “Multiple-Children-of-Twin Design” (MCoT) using data from the Norwegian Twin Registry, which takes into account twins and their children and thus allows distinguishing between social and genetic intergenerational transmission mechanisms. They show that the correlation between parents’ education and children’s education can be fully explained by genetic transmission. Similar results are reported by Eifler and Riemann (2022) as well as Wolfram and Morris (2022) for Germany. They calculate a “Nuclear Twin Family Design” (NTFD), which takes into account not only the twins but also their parents and siblings, and show that the intergenerational correlation between parents and children for both the highest school degree and the years of education is fully explained by genetic transmission. In addition to the twin-based designs, there are some studies with a molecular genetic design that examine how much the social origin effect is reduced when controlling for the parents’ PGS. Both Conley et al. (2015) for the USA and Isungset et al. (2022) for Norway report that only a small part of the origin effect can be attributed to genetic transmission. However, these molecular genetic studies should be treated with caution, especially in the context of the so-called “missing heritability” (Mills and Tropf 2020), i.e., the generally known, significant underestimation of total heritability in molecular genetic studies compared to twin-based studies. It is therefore not surprising that the molecular genetic studies reveal less genetic transmission than the twin-based studies. The fact that the molecular genetic studies come to less drastic results should not be understood as a reassurance to the sociological audience in the context of the “missing heritability”. In summary, it can be said that especially the twin-based studies raise strong doubts about the sociological narrative of social reproduction mechanisms and point to a significant distortion of the estimation of social reproduction mechanisms by unobserved genetic transmission. The frequently replicated and very strong social origin effects could thus largely be the result of unobserved genetic heterogeneity and attributable to genetic transmission effects. This should be a clear call for non-genetically informed inequality research to deal with the possibility of genetic transmission mechanisms.

5 Conclusion

The aim of this article was to demonstrate the specific contribution that genetically informed study designs can make to the investigation of social educational inequalities. It should have become clear that this is much more than calculating a proportion for educational indicators that is attributable to genetic variation rather than social influences. It is not just about the undoubtedly important question of controlling for unobserved heterogeneity, which has demonstrably also produced grossly distorted estimates for the state of research on educational attainment. Rather, it also involves the substantial question of how a significant part of the prerequisites with which we start life shapes life courses, and to what extent social conditions, including welfare state programs and measures, weaken or strengthen the significance of our genes overall and of certain genetic imprints. This literature review has thus shown that genetic predispositions are highly relevant for sociological questions. If the aim of sociological theory formation is to understand social behavior, it is therefore well advised not to ignore the relevance of genetic dispositions for social behavior. The question of "Nature vs. Nurture", which in the sense of a zero-sum game asks whether genetic or social factors are important, is long outdated in behavioral genetic research. Rather, the aim is to understand the complex interplay of genetic predispositions and social environmental conditions. In this sense, the evidence presented here does not make sociological theories obsolete, but rather complements them in terms of more theoretical and empirical precision, thus making their claims more credible. For the topic of education, this means for example: (1) The hope of being able to completely influence educational processes with education-related measures is naive. (2) Nevertheless, a strong genetic influence on educational success does not mean the irrelevance of environmental influences. On the one hand, even with a heritability of 40 %, around 60 % of differences in educational success are due to environmental influences. On the other hand, it is also worthwhile to ask which environmental conditions enhance or prevent the realization of a genetic disposition with regard to the genetic influences. (3) This includes the finding that the importance of genetic predispositions becomes greater the more educational pathways are opened. (4) This means in consequence that instead of the distribution of opportunities according to social origin, the distribution of opportunities according to genetic differences increases, but the general importance of the family of origin does not necessarily have to decrease, since genetic differences are also an inheritance from parents. (5) Finally, against this background, it is also appropriate to review the theoretical mechanisms of intergenerational educational transmission and not only to consider a genetic transmission alongside the social one, but also to think about how and under what conditions social origin can influence the realization of genetic dispositions. Even this rough overview makes it evident that genetically informed designs can both confirm and significantly supplement classic social science findings.

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Why are we Friendly to Strangers and/or Xenophobic? An Evolutionary Analysis.

Martin Fieder

1 Introduction

For most people in Europe, especially in Germany and Austria, the year 2015 will be remembered as the year in which our recent history experienced an unprecedented influx of people from regions outside Europe (e.g., Syria, Afghanistan). In total, more than 80,000 people came to Austria in 2015, and, in the years 2015 and 2016, more than a million to Germany. The arrival of these people led to massive, highly emotional discussions in families, among friends, in the media, in short, in the whole society, which continue to this day. The reactions to the displacement of a significantly larger number of people from Ukraine as a result of the Russian invasion in 2022 were, at least so far (as of October 2022), much less.

However, "to be remembered" often means something different, depending on personal attitude. For some, 2015 was an opportunity to demonstrate humanity and stand up for their own values, for others, 2015 meant pretty much the opposite: their own values, their own culture, seemed threatened to them.

But why is that so? And why does the topic of "us" and "the others" polarize so much? Is it only due to "education", the environment, "political education", the media, etc.? Can it only succeed with the help of the "right environment" to move people in one direction or the other?

An impressive example that the environment alone cannot explain everything is provided by political attitude (Eaves and Eysenck 1974; Martin et al. 1986), which

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is also related to the “us and the others” (Haidt 2012). Twin studies have shown that our individual political attitude (“left” vs. “right”) has a substantial genetic basis: i.e., whether we are politically more “conservative” or more “progressive” is partly due to our genetic makeup (studies estimate up to 60%, reviewed in Lockyer and Hatemi 2018; Hatemi and McDermott 2012). The same applies to our xenophilic vs. xenophobic attitude, as we will show in detail in the following section based on several studies: the genetic predisposition explains, depending on the characteristic examined, between 19% and 79% of the individual differences in attitude towards foreigners. However, most “genetic studies” have the limitation that they were usually conducted based on Europeans or people of European descent. These statements therefore initially only apply to Europeans.

It is very similar with our moral ideas, which can be quite different individually: what is morally required for one group, the other group rejects for equally moral reasons. Accordingly, one group accuses the other of “moral deficiencies”. Since the epochal studies by Jonathan Haidt (2012), a US moral psychologist, we know about the diversity of moral ideas. Accordingly, the perceived moral obligation to one’s own group or the “others” also differs significantly: while some prefer their own group, others also have sympathies for the “others”.

2 Evolution, Behavioral Genetics & Historical Migration Movements

To better understand the genetic foundations for our attitude towards the “us” and the “others” or xenophobia vs. xenophilia, a brief digression into behavioral genetics is necessary. According to the three laws of behavioral genetics by Turkheimer (2000), every trait also has a genetic basis, which explains part of the variance of this trait. The extent can vary greatly depending on the trait, ranging from low (a few percent) to very high (e.g., body height over 80%; Silventoinen et al. 2003). These values were obtained in twin studies, which calculate the proportion that genes, the common environment, and the individual environment explain in the variance of a trait through statistical procedures from the comparison of the similarity of identical twins (de facto genetically identical) and fraternal twins (on average 50% genetic information in common).

A completely different methodological approach is pursued by the so-called *genome-wide associations studies* (GWAS, in German, “*Genomweite Assoziationsstudien*”). GWAS analyze the relationship between the entire genome (usually millions of so-called Single Nucleotide Polymorphisms (SNPs), which are individual differences in the DNA sequence at the level of individual nucleotides of a large number of people, and one or more phenotypic characteristics (Mills et al. 2020). With this method, in addition to twin studies, another measure for determining the overall genetic influence on a characteristic is available. One of the most important methods derived from GWA studies are the so-called "Polygenic scores". These allow a statistical estimate of the respective individual genetic predisposition of individual characteristics. In terms of results, the values of twin studies and GWAS are quite similar. However, GWAS, and especially the derived "Polygenic Scores", currently explain a smaller proportion of genetic variation than twin studies (Mills et al. 2020).

At the time of writing this article (December 2022), there are no GWAS on the topic of xenophilia vs. xenophobia. The following section will therefore deal exclusively with twin studies.

However, we should first move away from the very broad terms of xenophilia vs. xenophobia and focus on terms that probably characterize our long evolution much better. Because most of our evolution did not take place in such large units as states, nations, religious communities, etc., but in groups of probably no more than 150 individuals (Dunbar 1993). The "foreign" was therefore not another people, another culture, or another religion, but simply another group of also about 150 people, with which our own group often maintained both genetic and cultural exchange (more on this later), but with which there could also be hostile and thus lethal conflicts (Chagnon 1988).

Therefore, in the discussion about the "we" and the "others", we should start from small groups: *our group* vs. *the others*. The group can actually be the original small group, but our "group feeling" can also extend far beyond to peoples, states, and religions. Although we no longer have an actual relationship with these large associations , we still apply the attitudes that have formed in and for the original small groups during evolution to much larger associations.

Does this in-group vs. out-group attitude also have a genetic basis? Definitely yes, although the amount of the genetic component varies greatly depending on how exactly this attitude is measured or asked, and how the "group" is defined. As already mentioned above, previous studies found a range of heritability from 19% to 79% (Kandler et al. 2015; Lewis et al. 2014; Loehlin 1993).

2.1 Results of a Twin Study on Attitudes Towards Strangers

The following section summarizes the questions, hypotheses, and results of a study already published by Fieder & Huber (Fieder and Huber 2021).

Based on the "MIDUS Twins Study" (a part of the "*midlife development data sets of the USA*"—https://centerhealthyminds.org/science/studies/midlife-development-in-the-united-states), we were able to achieve very similar results in this study, like those studies cited above. The MIDUS Twin Study includes 159 male and 181 female monozygotic twin pairs, 108 male and 184 female dizygotic twin pairs, and 220 different-sex twin pairs aged between 25 and 74 years. In the MIDUS study, 3 sets of questions were asked about "*in-group behavior*" regarding religion, ethnicity, and race.[1] Based on the twin data, we calculated a so-called ACE model, where A stands for the "*additive genetic variance*" of a characteristic, i.e., the variance of individual differences of a characteristic explained by genetics, C is the "*common environment*", the variance essentially explained by the common parental home, and E, the "*non-shared environment*", the variance explained by the environment that the twins did not experience together, essentially everything that is not genetics and not parental home. Like other studies, we found that the genetic predisposition between the individual *"in-group vs. out-group"* questions varies greatly in complexity. We found the least genetic predisposition for the question "*how close you are to your own race*" (19%), the highest (45%) for the question "*is it important to marry in your own race*". As in all other studies, the parental home—with the exception of the question "*is it important to marry within own religion*" (25%)—has a rather small share in the "*in-group vs. out-group*" attitude (Tab. 1). Just like in many other studies, the individual environment (i.e., everything that is not the parental home) has the relatively greatest influence on the "*in-group vs. out-group*" attitudes, followed by the genetic predisposition (Tab. 1). Even though the individual environment has the greatest influence, we must therefore also expect a relevant "genetic" influence on this topic. However, the extent of the genetic influence is on average less than, for example, that on political attitude.

Even though these results show that our attitude towards strangers also has a genetic basis, they by no means imply that we would be helplessly at the mercy of our biology and that our biology would be our insurmountable fate.

This result can be well illustrated using the example of genetic predisposition to education based on a theoretical illustration: if there is no school, there can be no genetic predisposition to school success, as all children have the same school degree—namely none. Only when the environment places "value" on school

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[1] "Race" is a technical term in the USA, defined by the Bureau of Census and asked in census and other surveys, unlike the term race in German, which implies significant biological differences also in the sense of a "valuation".

Tab. 1 ACE Model MIDUS Data: Genetic predisposition, shared environment (family home), and individual environment towards "in-group" attitude for the question complexes Religion, Ethnicity, and Race

		genetic predisposition	shared environment	individual environment
Religion	**identify own relig. group**	43.82 %	5.95 %	50.27 %
	prefer people same relig.	34.69 %	9.12 %	56.10 %
	important marry same relig.	22.94 %	24.01 %	53.00 %
Ethnicity	**identify ethnic group**	39.31 %	0.00 %	60.68 %
	prefer ethnic group	22.37 %	13.03 %	64.48 %
	important marry same ethnicity	21.72 %	10.50 %	67.73 %
Race	**how close own race**	19.01 %	1.00 %	79.92 %
	prefer same race	27.77 %	0.00 %	72.25 %
	important marry same race	45.83 %	0.00 %	54.17 %

success and promotes it, do measurable genetic differences occur (Plomin 2019). Similarly, one can imagine the genetic predisposition for xenophilia vs. xenophobia: only when the topic is relevant, can one also measure clear genetically conditioned differences between people.

In addition, many characteristics do not have a "must for one direction", but only a predisposition that individually points more in one direction or the other. Knowing this is particularly important in our view in the case of friendliness towards foreigners vs. xenophobia. Genetics is therefore "*not fate*", but always manifests itself in interaction with the environment. This is very impressively demonstrated by civilization, which has made us humans—a species that has a substantial predisposition to violence—a relatively peaceful species in most state societies (Pinker 2011). To go into more detail on the methodology and especially the consequences for social science research would far exceed the scope of this contribution, which is why reference is made at this point to the contribution by Martin Diewald and Bastian Mönkediek in this anthology, which deals with both methodological and substantive aspects of behavioral genetics in the social sciences using the example of the interpretation and explanation of social inequality and in particular also discusses the possible future significance of behavioral genetics for the social sciences in detail.

2.2 Historical Migration Movements and Their Evolutionary Consequences

Having discussed the genetic foundations of our attitude towards strangers in the previous section, the question now arises as to how this dichotomy of xenophilia vs. xenophobia, which has the potential to divide our societies, could have evolved. Essential for all evolutionary explanations is the understanding that our behavior and attitudes are shaped by life in small groups, which we have led over long periods of time.

An evolutionary cause for xenophobia can therefore also be suspected in the competition and the associated violence between groups, which is already found in our closest relatives, the chimpanzees. When two male chimpanzee groups meet, there is often a fight, especially when one group is significantly smaller and the other group recognizes that they could have an advantage. The "victorious group", after a frequently lethal confrontation, then integrates the females of the losing group into their own group (Wrangham 2019).

Even among hunters and gatherers, there is sometimes increased violence between groups, even though there can be familial relationships between the groups, as impressively documented in the case of the Yanomani (Chagnon 2013). Violent conflicts between groups are also documented for Papua New Guinea (Eibl-Eibesfeldt 1996; Wiessner 2019). Since we cannot have behavioral observations from the Old Stone Age, such data on aggression between groups of still living tribal cultures provide an important clue to the aggression of early hunters and gatherers. For the Yanomani, violence and raids on the "others" also paid off reproductively. Violent men were married more often and had more children than less violent men. The same, although on a much larger scale, applies to Genghis Khan, whose descendants today make up 0.5% of the world's population. The conquest wars of Genghis Khan and his descendants have thus also paid off reproductively (Zerjal et al. 2003). Today, in modern societies, the importance of violence has radically changed. Violence is punished instead of rewarded—civilization has worked (Pinker 2011).

Nevertheless, violence and conflict between groups have likely shaped our development over long periods of time. Numerous archaeological finds of battlefields and massacres attest to the sometimes violent encounters between groups, such as the Neolithic massacre of Schletz (Wild et al. 2004) in Lower Austria's Weinviertel, the massacre of Halberstadt (Meyer et al. 2018) in Saxony-Anhalt, or the massacre of Koszyce (Schroeder et al. 2019) in today's southern Poland, as well as the Bronze Age battlefield at the Tolense (Jantzen et al. 2011). In most cases, the victims were men and only rarely young women—a fact that is also clearly proven by new genetic data. The arrival of the Yamnaya culture in the western part of Europe about 5000 years ago probably did not occur without violence. This was one of the most massive and male-dominated migration movements Europe has ever experienced (Fu et al. 2016; Goldberg et al. 2017; Reich 2018), and it dramatically changed the genetic landscape of Europe, especially in terms of the male lineage. However, the Yamnaya migration of that time is in no way comparable to today's migration in terms of its relative size. In terms of numbers, it would be comparable to an immigration of one billion people to Germany in 2015 (Krause and Trappe 2019).

The Yamnaya were an Eastern European culture of the late Copper and early Bronze Age, mainly settled in the Pontic Steppe. About 5000 years ago, there was a massive wave of emigration to the western part of Europe, and to the east into present-day India. The domestication of the horse likely played a significant role in the rapid spread of the Yamnaya culture. One consequence of the spread of the Yamnaya culture was that the proportion of resident Y-chromosomes in Europe was displaced by the Y-chromosomes of the newcomers, i.e., the resident men apparently could not pass on their genes. We do not know what happened to the resident men, but their genetic signature is hardly found in our genomes anymore. They were apparently displaced by the men arriving in significant numbers (Goldberg et al. 2017).

The genetic data also show that there was a mixing of the newcomers with the resident female population (Reich 2018). Since the Yamnaya did not only migrate to the west, but also to the east onto the Indian subcontinent, similar genetic patterns are also found there (reviewed in Reich 2018). A comprehensive historical analysis of the "replacement of male populations" by newcomers can also be found in Scheidel (2021). By the way, the plague also spread with the Yamnaya (Krause and Trappe 2019), which probably made the Yamnaya migration particularly lethal. However, the plague cannot explain the selective displacement of only the resident men from the gene pool.

A similar displacement of the resident male population from the "gene pool" is also found after the Anglo-Saxon immigration to England (Weale et al. 2002) or during the colonization of the two Americas. In the case of the Americas, in addition to a mass dying of the indigenous population, mainly due to introduced diseases, there was also a displacement of the resident male population from the gene pool (Reich et al. 2012).

All in all, these data make it clear that men in particular had problems, especially due to male-dominated migration. However, in this context, the distinction between migration and conquest campaigns based on archaeological data is usually impossible. Campaigns and subsequent migration may have overlapped and/or alternated (Schahbasi et al. 2021)

However, if migration takes place slowly and is not male-dominated, it probably proceeds more peacefully, as shown for example by the slow migration of mainly families from Anatolia to Europe about 9000 years ago (Fu et al. 2016). But even this migration was not only peaceful, as newer data from the Pyrenees document (Alt et al. 2020)

Since not only our physical [morphological] characteristics, but also our behavior and attitudes are “products” of evolution (Barkow et al. 1995), it can be assumed that these immigration processes, and all the unknown conflicts between groups of people, have left their mark on our cognition and attitudes over the extremely long period of our evolution. Therefore, it makes “*evolutionary sense*”, when some members of groups warn against encounters with strangers, and against too much trust in strangers (as Laokoon did in Homer’s Iliad). Xenophobia could therefore also have had an adaptive value. And since it was the men who probably often took the higher risk in encounters with strangers, it would not be surprising if they were on average less friendly towards strangers than women. Indeed, our data show that men’s attitudes towards strangers are on average less positive than those of women (see below). Also, Michael Windzio comes to similar conclusions as we do in this anthology on the basis of group competition and group cooperation, identifying an ambivalence of the social brain, which consists in the fact that prosociality within a group could result from the same evolutionary mechanism as ethnic-cultural boundary drawing between groups. Precisely our “self-domestication” can therefore also lead to the dehumanization of the “others” and thus to the rejection of the “outgroups”.

2.3 Inbreeding and Ethnocentrism

But what about the friendly attitude towards strangers? Again, our early life in small groups comes into play, because these small groups had a central problem: If reproduction only takes place within a small group, it means that sooner or later more or less related individuals will have children with each other. This in turn leads over a longer period to the accumulation of mutations, to the so-called inbreeding depression and to homozygosity (i.e., identical DNA sequences over large stretches on both chromosomes), with all their mostly negative effects on cognitive abilities, health, and fertility (Clark et al. 2019). In fact, we were recently able to show based on US-American (Wisconsin Longitudinal Study; N ~ 9000) and Australian data (Brisbane Twins Study; N ~ 8000) that the higher an extremely ethnocentric, xenophobic attitude of a person is (the more important, for example, someone's own ethnic and national identity is), the more frequent and longer are their so-called *Runs of Homozygosity* (ROH—identical genetic sections over large stretches on both chromosomes)—an indication of a higher frequency of marriages among relatives in the past (Fieder et al. 2021).

2.4 Results from the European Social Survey on Attitudes Towards Migration

If one always stays within one's own group, not only is the exchange of genetic material missing, but also the exchange of ideas and innovations. The group stagnates at best. Therefore, it makes sense for a part of a group to seek exchange with other groups and therefore must be more friendly towards strangers. In this context, "female dispersal" comes into play: We know that in most cultures, women have moved into the group of their future husband (Huber et al. 2017). Based on genetic data, we also know that this could indeed lead to migration movements over large distances. For example, data from the Stone Age of northwestern Russia (Sikora et al. 2017) show that women have migrated over larger distances. The same applies to groups in the Bronze Age Lech Valley: about two-thirds of the women immigrated from outside into the communities of the Lech Valley (Mittnik et al. 2019). So it was apparently women, and especially young women, who provided the genetic and cultural exchange between the groups. Therefore, one would expect women, and especially young women, to be more friendly towards strangers than men, as they often had to integrate into the "foreign group" of their husbands in the past. Therefore, based on data from modern societies, we analyzed whether women or men are more friendly or hostile towards strangers, i.e., whether these *"real world data"* actually coincide with our *"evolutionary expectations"* (Schahbasi et al. 2021). To test these hypotheses, we analyzed data from the European Social Survey (https://www.europeansocialsurvey.org) from the years 2002 to 2016. The European Social Survey is conducted every two years and includes representative surveys from a total of 33 countries beyond the EU. We analyzed the data of 44,223 men and 39,511 women with regard to their attitude towards migration. In particular, questions about

Tab. 2 European Social Survey—Questions on attitudes towards migration by origin. Sum of all countries and surveys from 2002–2016

	Same Ethnicity		Other Ethnicity		Poorer Countries	
	N	%	N	%	N	%
allow many to come and live here	20,101	24.56	12,232	14.94	11,410	13.99
allow some to come and live here	37,293	45.57	33,849	41.33	31,513	38.65
allow only a few to come and live here	18,592	22.72	25,606	31.27	25,977	31.86
allow no one to come and live here	5,852	7.15	10,206	12.46	12,640	15.50
Sum	81,838	100.00	81,894	100.00	81,540	100.00

attitudes towards three different groups of migrants were of interest (Tab. 2). First of all, Tab. 2 shows that the acceptance of migration of people of other ethnicities or from poorer countries is lower across all questions than for people of the same ethnicity. To investigate which factors influence attitudes towards migrants, we calculated multiple regression models, which can determine which factor/factors among several are significantly associated with attitudes towards migrants.

The results of the multiple regression models suggest that higher education is associated with a more positive attitude towards migration, especially towards migration of other ethnicities and from poorer countries. This may be due to the fact that education conveys a more open attitude (Craft 2017), or that educated people have a more open attitude. It may also be related to the fact that more educated people have more resources and are therefore less affected by potential distribution issues with the newly arriving people (Collier 2013).

The comparison of women and men shows, as expected, that men have a more negative attitude towards migration than women. However, women's attitudes towards foreigners become more negative with increasing age, especially when there is a child in the household. This also fits our expectations: young women, who have usually emigrated to their husband's family, should have a more positive attitude; but with the birth of a child, the concern for the child (or children) predominates, which may lead to a more cautious and thus negative attitude.

Finally, people with a more right-wing political attitude have a more skeptical attitude towards migration than those with a left-wing attitude. Since both, the political attitude and the attitude towards "us" vs. the "others" are closely linked, this also meets expectations. Religious people, on the other hand, have a more positive attitude towards migration, especially towards migration of other ethnicities, which may also be explained by the integrative character of religion. After all, integrating people of various origins under one value system is a central characteristic of the major religions and the so-called "big gods" (Norenzayan et al. 2016).

3 Discussion

Our results support the assumption that evolutionary processes were involved in the "ambivalent attitude" towards strangers, which was sensible for our survival in small groups: on the one hand, a group of "stranger-friendly" people who ensured genetic and cultural exchange, and on the other hand, a group of "stranger-hostile" people who warned of potential threats from encounters with strangers. The apparently greater acceptance of the refugee movement as a result of the Ukraine war in 2022 in the host countries reflects both the higher willingness to accept people of a similar ethnic background in Europe, similar to the Yugoslav war in the 1990s. However, it also shows that the male-dominated migration of 2015 and thereafter was probably a very significant reason for the lower acceptance of this immigration. The greater acceptance of female-dominated migration in the course of the Ukraine conflict also points to substantial differences in acceptance by gender. However, we still lack data to prove this. The negative attitude towards young men probably results, in addition to possible evolutionary causes, directly from the fact that young men of any origin represent the group of people who are most frequently noticeable due to violence and generally antisocial behavior (the "young male syndrome") (Beaver et al. 2014). Some studies also show that a surplus of men can be destabilizing overall, because many men are then unable to find a partner (e.g., male surplus due to selective abortion of female fetuses in India and China; Hudson and Den Boer 2004). However, newer longitudinal, historical data from North America also show that this does not necessarily have to be the case: a surplus of men in immigration leads, according to these data, to women marrying earlier, men marrying later, so that the surplus of men, probably due to increased mortality among men, does not have to lead to more unmarried men, and thus to conflicts (Filser and Willführ 2022).

Of course, evolutionary adaptations in our past cannot be transferred 1:1 to today. We no longer live in tribes, among which the men fought massively and often lethally. Also, our populations are so large that an institutionalized, genetic exchange like "the emigration of young women" is no longer necessary, nor do we need migration to transfer culture—the internet does this much faster and more effectively today. But these, our evolutionary adaptations and our genetic heritage continue to exist. Biology influences us more strongly than we have so far suspected or wanted to admit. We should always keep this in mind in the highly emotional discussion: we are also discussing our evolution and genetics. This is especially true for our moral ideas. We often consider our moral judgments to be rationally founded and therefore without alternative. In reality, however, it is the other way around: our already existing moral ideas are rationalized by our mind afterwards (Smith and Hatemi 2020). Our moral ideas also have evolutionary and genetic foundations.

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War of the Genes? Violent Intergroup Conflicts from an Evolutionary Perspective

Hannes Rusch

1 Introduction

With the open Russian attack on Ukraine in February 2022 at the latest, it is clear that the hope for a steadily more peaceful world, which one might have been able to harbor as a 'Westerner' after the revolutions in the Eastern Bloc states of the early 1990s, has been disappointed. Looking at the time since the World War II, there is, especially since around 2010, a sobering trend (see Fig. 1): the number of armed conflicts worldwide is increasing.

If one wishes, one can argue vigorously about whether these numbers also imply an increasing relevance of warlike events for humanity as a whole. If one relates the number of conflict-caused deaths to the growing world population, this does not necessarily seem to be the case—Pinker (2011). Similar calculations can be made by comparing the annual number of war deaths with numbers of disease-related deaths—in Germany alone, for example, about twice as many people die of cancer each year as there are war deaths worldwide on average since 1989.

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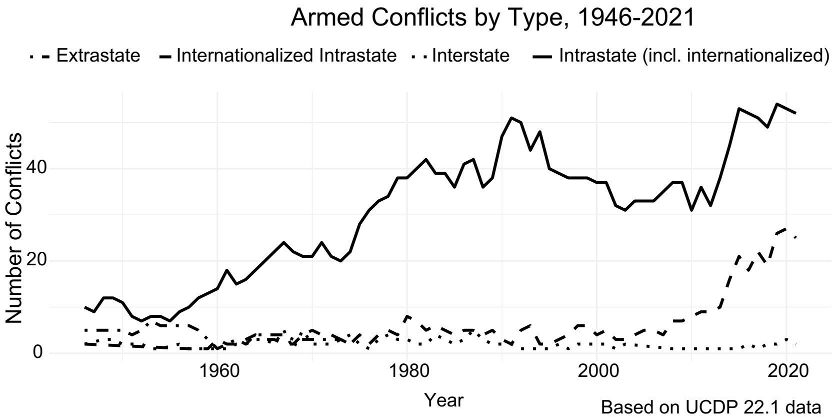

Fig. 1 Overview of the number of armed conflicts over time since 1946, separated by conflict type; data source: *Uppsala Conflict Data Program*—Davies et al. (2022)

What can unfortunately be determined without doubt is: ‘war is somehow not to be killed’. And if one looks back further than 1946, it is also undisputed that the history of mankind has been continuously influenced by violent conflicts between various groups at least since antiquity, if it has not even ‘structured’ by such.

Therefore, it is naturally tempting to raise the question of whether the inclination to warlike behavior, which is manifested in this ‘history of violence’, occupies a similar rank in the human behavioral repertoire as ‘loving’, ‘helping’, ‘eating’, ‘learning’, etc., whether it thus represents an adaptive solution to a problem that has repeatedly occurred over evolutionarily relevant periods. The answer can obviously not be as simple a ‘yes’ as for ‘eating’: going to war means, at least in a first approximation, a significantly higher risk to life and limb than trying unknown food—Tybur et al. (2013). A decidedly behavioral ecological analysis seems more appropriate here, asking: under what conditions can such risky behavior pay off for whom in evolutionarily relevant currency?

Let us try to shed some light on the possible answers to this question in a more systematic way. Tinbergen’s famous four questions are helpful for this—Tinbergen (1963); see Tab. 1. Any complete evolutionary explanation of a behavioral trait must provide convincing answers to at least these four questions. In relation to warlike behavior, as with most other behavioral complexes, this means work of at least one researcher’s lifetime per question. The cursory treatment in the following should therefore be excused.

Tab. 1 Tinbergen's four questions for evolutionary explanations

	Proximate	*Ultimate*
Static	What is the mechanism?	What is the function?
Dynamic	How does ontogenesis proceed?	How did phylogenesis proceed?

2 Mechanisms

Let's start proximately static, that is, with the mechanisms: What happens when people start and wage wars? At least three levels of description should be considered here, which have already been intensively researched from a behavioral ecological, anthropological, and evolutionary perspective, namely (i) 'Culture and Technology', (ii) 'Group Processes and Dynamics', and (iii) 'Individual Motivations'.

2.1 Culture and Technology

On the first level, 'Culture and Technology', the primary question investigated is under which (cultural-)historical-technical-geographical conditions violent conflicts between groups are more or less likely to occur. Of course, no historical situation is exactly like another, and the more details one considers, the more differences one will be able to discover. Moreover, the respective historians rarely agree on the description of these details. The logical consequence is the coexistence of countless historical case studies and associated interpretations.

Nevertheless, there are attempts to extract 'larger' patterns from the available data. The works of Peter Turchin and co-authors, who have set themselves the task of quantitatively capturing the cultural evolution of human institutions and mathematically modeling them, should be highlighted here—Turchin et al. (2013, 2017, 2021). With regard to the occurrence and intensity of wars, the work of Turchin and colleagues emphasizes the insight that the success of state formation and its stability in the period from 1500 BC to 1500 AD critically depend on the military technologies available in the respective world region at the respective time, which in turn are subject to rapid technical evolution and are culturally 'inherited'—Turchin et al. (2013).

This means: assuming that the basic genetic outfit of *Homo sapiens sapiens* probably has not changed much in these 3000 years, we observe a high degree of variability in the way warfare is actually conducted during this part of recent history, and see what drastic consequences this has for the organization and stability of human societies in the same period—consider, for example, the difference between ‘traditional’ forms of warfare as sporadic *raiding* (see Sect. 2.3) and the institutionalized armies of the 20th century, often with forced recruitment.

On the level of ‘Culture and Technology’, the following can therefore be stated: As humans, we have intensively used our cultural ability, i.e., the talent to reflect on our behavior, to codify recommendations for action as techniques, to pass them on, and to optimize them over time, to develop the craft of war step by step into a highly differentiated cultural technique. To put it pointedly: Just as we can feed many times the number of people per hectare of arable land today, we can also kill many times the number of people per bomb. For our question about the evolution of warlike behavior, this mainly means complications. Because any possible underlying similarities of warlike conflicts are overlaid by the variable forms of the current state of the art of warfare.

2.2 Group Processes and Dynamics

What about the second level, ‘Group Processes and Dynamics’? Are there recurring patterns in the organization of the mobilization of group members for violent group conflicts? Are there perhaps also recurring patterns in the emergence of the collective decisions that lead to such conflicts? Two dimensions play a crucial role here: first, the relationship *between* the conflicting parties, this Sect. 2.2, and second, the organization *within*, which we will touch upon in Sect. 2.3.

A fundamental distinction at the intergroup level is that between *offensive* and *defensive* aggression—Rusch (2014a, b). Who exactly ‘the own’ group is may vary from conflict to conflict. In most cases, however, the own group includes those people who should be particularly important to a given individual in evolutionary logic, namely the own family—but see Sect. 2.3. If this group is now threatened by external circumstances, be it natural forces or human aggressors, often a lot is at stake biologically: one’s own survival, that of one’s own children, that of the partner, that of the parents, siblings and other ‘helpers at the nest’—Clutton-Brock (2002); Burkart et al. (2009). The defense of these and other vital ‘resources’, even with violent means and at high personal cost, usually appears to us as morally justified and heroically exemplary as it should pay off in the long run in evolutionary calculus, taking the genotype’s ‘superindividual’ perspective—Rusch (2013). It is therefore not surprising that defensive aggression in intergroup conflicts can be easily and reliably provoked experimentally—Böhm et al. (2016); de Dreu et al. (2016); de Dreu and Gross (2018), especially also preventive-defensive aggression—Abbink and de Haan (2014); Böhm et al. (2016); Halevy (2017). Equally unsurprising is the observation that in the self-description of the conflict parties in most cases all sides claim to be 'only defending'. Examples from recent history abound: Putin allegedly 'defends' Russia against NATO and 'liberates' the Ukrainian territories, the USA allegedly 'protected' themselves and the world with the attack on Saddam Hussein's regime from his weapons of mass destruction, the Third Reich undertook the elaborate false-flag operation 'Tannenberg' to be able to claim on September 1, 1939, to merely be 'shooting *back*', etc.

For defensive aggression at the group level, we can therefore preliminarily state that an evolutionary explanation could indeed have starting points here: The defense of the own group represents a survival-relevant problem and seems to reliably evoke corresponding individual reactions. An important open question in this case, however, is domain specificity: Is this a special adaptation or rather collectively organized self-defense against a generic threat?

And there remains the other side: What about collectively organized *offensive* aggression? That, I think, is *the* key question for the next years of evolutionarily informed research on warlike behavior. Unfortunately, the systematic scrutiny of this question is complicated by the aforementioned tendency of offensive aggressors to disguise their actions as self-defense, as well as the notorious difficulty of clearly identifying causes of war. Nevertheless, there are informative research approaches here.

A current large-scale research agenda, for example, is investigating to what extent and in what forms *'carrying capacity stress'* could be responsible for the emergence of conflicts—de Dreu and Gross (2018). Roughly simplified, this agenda is based on the question of how human groups react to what types of resource scarcity or uncertainty with what forms of intergroup aggression. Initial works from this agenda actually show that offensive aggression can be experimentally induced by creating resource uncertainty—de Dreu et al. (2022). Interestingly, however, this approach also assumes morally comprehensible reasons on the part of the aggressors. Offensive violence is seen here as a preventive measure to avert or at least mitigate collectively impending damage due to scarce available resources. The guiding idea here is thus something like collective petty larceny of food.

Even less systematically illuminated are other possible incentives for collective offensive violence. Obvious motives here are resource appropriation without existing or impending scarcity, subjugation and enslavement, and perhaps ideological motives. Whether 'religious wars' etc. should constitute a category of their own, or whether existing affiliations to religious and other groups are merely used as a means to the end of marking favorable targets for aggression, would have to be discussed separately—Fearon and Laitin (2003); Esteban and Ray (2011).

It should be emphasized at this point that there are, of course, countless works on the emergence of offensive warlike aggression; case studies—Phillips and Axelrod (2004); Martel (2012)—as well as review works—Gat (2008). What is missing is evolutionarily informed, systematizing work that develops behavioral theory from the micro level of individual incentives and their recurring occurrence, derives predictions about triggers and forms of collective violence from this, and then tests these against available and newly collected data. The aforementioned works by de Dreu and colleagues are a promising approach that can be expanded upon.

2.3 Individual Motivations

At the level of individual incentives, there are also initial works that point to possible recurring patterns in the emergence of offensive aggression between groups. Particularly interesting here are the anthropological works, for example, by Glowacki and colleagues, who deal intensively with the forms and consequences of intergroup conflicts among semi-nomadic people in southern Ethiopia—Glowacki and Wrangham (2013); Mathew and Boyd (2014); Glowacki and Wrangham (2015); Glowacki et al. (2016). The deadliest form of violence between groups here is collective raids on neighboring groups of other ethnicities. The aim of these *raiding* campaigns is to loot livestock such as goats and cattle while minimizing individual risks for the attackers. These ‘robber gangs’ cleverly use the element of surprise and/or any possibilities of deception and camouflage to keep themselves safe—which also succeeds in most cases. Contrary to what one might suspect, these raids are rarely based on a communal decision of the entire group. Rather, it is usually individual, well-connected, young men who gather ‘troops’ of volunteers around them and then set off without obtaining the approval of their larger group—Glowacki et al. (2016); Glowacki and McDermott (2022).

What motivates these raids? Glowacki convincingly argues in this context that the young men derive direct individual benefits from their behavior. Although they initially have to hand over the looted animals to their community, which they often do reluctantly, particularly successful robbers gradually earn a higher social status through these tribute payments, which ultimately pays off for them in evolutionary currency. When they reach marriageable age, they also have the greatest claims on the community’s livestock, which often allows them to marry more women and consequently father more children than less successful robbers can—Glowacki and Wrangham (2015). A similar observation was also made by Chagnon among the Yanomamö in Amazonia, where more successful warriors also marry more women and father more children than less successful ones—Chagnon (1988). In a quantitative analysis of available anthropological literature, Glowacki and Wrangham also found that the documented existence of cultural reward systems for successful warriors in a given society correlated positively with the respective number of conflict deaths per 100,000 per year—Glowacki and Wrangham (2013). In Doğan et al. (2018), finally, we were able to show in an economic experiment that the exogenous assignment of higher shares of the achievable loot also increased the individual willingness of the so privileged conflict participants to participate in esp. *offensive* aggressive group behavior, whereas defensive-aggressive behavior remained independent of individual privileges.

Of course, the studies cited here represent a small sample and a selection. It should be noted that there are major differences of opinion in anthropology as to whether these scenarios can be considered representative. Counterarguments are provided, for example, by Beckerman et al. (2009) and Moore (1990). A large-scale, more balanced literature review is offered by Glowacki et al. (2020).

The picture that emerges for this possible model of early ‘warfare’ is thus one of communal violence for personal advantage, initiated by particularly ‘brave’ young men, and whose consequences for the involved groups are initially ambivalent. In a more recent piece, Glowacki (2022) sharpens this model to the provocative question: If this is the ‘original state’, shouldn’t we rather think about an ‘evolution of peacefulness’ and understand this as something that needs explanation?

3 Ontogenesis

Let’s move on to the next Tinbergen question. The development of warlike behavior in the individual lifespan, its ontogenesis, is first and foremost, purely descriptively, characterized by a clear gender difference. Even though military career paths have been open to women in many countries for some time, their participation in wars as soldiers and the number of their entries into the military are limited—Carreiras (2006). It should be noted that the chicken and the egg are impossible to separate here: It could theoretically be that male dominance in military professions emerged purely by chance and then deterred women from entering this ‘man’s world’ and thus the difference perpetuates itself. Conversely, it could also be that men simply ‘prefer’ to go into the military more than women.

If one looks at the history of warlike conflicts, one finds that the division of labor between the genders in the practice of warfare, which continues to this day, has a long tradition—Gat (2008). Women, as far as is known, took on supporting roles such as supply, catering, and medical care in the wars of prehistoric and historical societies, while men primarily took on the fighting and dying—Keeley (1996). Exceptions such as the Scythian archer women (Gat, 2008) or the women's regiments of Dahomey (Alpern, 1998) do exist, and the role of female rulers in initiating wars should not be underestimated—Dube and Harish (2020).

Looking at developmental psychological work, one finds that boys seem to have a more pronounced interest in 'war games' than girls—Caffrey (2019); Pellegrini (2015). The chicken and the egg are of course not clearly identifiable here either. However, there are interesting cross-cultural studies that find that playful practice of aggression ('*rough and tumble play*') is less common in boys in more egalitarian gatherer societies than in more socially stratified farmer societies—Boyette (2016). So there is some flexibility in learning aggressive behavior in youth. But even in these societies, it is primarily boys who engage in these games.

In later life, it is also predominantly young men who engage in warfare and/or advocate warlike solutions to conflicts—McDonald et al. (2012). An interesting parallel exists here between the fundamental data of criminology and that of conflict research: Young men not only make up the largest group of military personnel, but are also the main protagonists of most criminal activity, especially violent crimes—Flowers (2003); Blattman (2022). Against the background of the work of Glowacki and colleagues on the raids carried out by young men among the Nyangatom and other groups against neighboring ethnic groups, the question arises: Do the beginnings of war perhaps lie in the channeling of youthful male aggression away from violence within the group/family towards violence against neighbors?

On the female side of events, adolescence is also a critical phase. In broad strokes: While men at this time hardly miss an opportunity to show off their daring, skill, and bravery, for which group conflicts also provide a suitable stage, young women have the agony of partner choice. A number of studies suggest that male war heroism in this context could serve as an honest, because costly, signal of special advantages—Rusch et al. (2015); Rusch and Störmer (2015); Margana et al. (2019). According to this, women would benefit from choosing proven heroes as partners because they have proven their bravery and physical fitness through their deeds. In addition, such heroes rarely rank low in the male dominance hierarchy, which can also offer advantages for their partners.

Conversely, the threat of failing these female selection criteria also provides a huge incentive for young men not to too lightly avoid the 'war test'. Well documented, for example, is the stigma that hit so-called ‘4-F’ men in the USA of the 1940s: Anyone who was rejected from general military service had poor chances as a man on the ‘home front’—Smith (2013). The shaming of potential ‘shirkers’ was even more directly used in Britain during World Wars I and II. Here, so-called ‘*White Feather Brigades’* of young women were formed, who combed the cities and handed out white feathers to non-uniformed young men. The effect of this systematic public *‘shaming’* on the enrollment rates in the British military was considerable—Becker (2022).

To my knowledge, there is little systematic research from an evolutionary perspective on attitudes towards warlike behavior and its effects after adolescence. Of course, we can extrapolate from recent trauma and violence research that veterans may not be the most easygoing parents—Beaver et al. (2014); Sherman et al. (2016); McGaw and Reupert (2022). However, it is unclear to what extent this has effects on parental performance that would be severe enough to lead to evolutionarily relevant disadvantages for the respective children.

4 Phylogenesis

What does it look like phylogenetically, that is, in the comparison of species? For a long time, humans were considered the only species that wages war. However, it is now well documented that other species are also capable and often willing to do so—Hardy and Briffa (2013); Rusch and Gavrilets (2020); Morris-Drake et al. (2022). Of course, any listing of the relevant species always depends on the underlying definition of ‘war’. This can always be tailored so that in the end only humans wage ‘real’ wars. However, we learn little from such definitional exercises. With a sufficiently generous definition, we learn more, e.g. ‘War is collective aggression with the purpose of killing or permanently displacing conspecifics’. Such behavior is then found in humans and chimpanzees, but also in such diverse species as certain mongooses, termites, ants or even giant anis (a cuckoo species)—overviews are provided by: Morris-Drake et al. (2022); Rusch and Gavrilets (2020). In addition, many species of bacteria have entire arsenals of ‘biological weapons’ that they use in costly battles against competing colonies—Niehus et al. (2021).

One of the few constants that connects the various forms of non-human intergroup conflicts is the observation that close relatives rarely fight against each other. Here, ‘close’ is relative: sisters do indeed fight together against cousins, and cousins together against second cousins. However, the goals pursued by these coalitions, as well as the chosen forms of organization and means, vary greatly.

For the question of human propensity for war, our two closest relatives, chimpanzees and bonobos, are of particular interest. Jane Goodall's famous works on 'chimpanzee wars' disturbed many, as they clearly demonstrated how systematically and brutally these primates closest to us can go about killing members of other groups—Goodall (1986). Initially, it was suspected that human influence on their living conditions could have provoked this behavior. However, today there is little doubt that this organized form of violence is part of the natural behavioral repertoire of *pan troglodytes*—Wilson et al. (2014). Bonobos, on the other hand, are considered peaceful, tolerant and are known for their tendency to soothe conflicts through mating acts.

In a recently published work, Glowacki extensively and critically deals with both the available evidence and the arguments for and against the suitability of chimpanzees and bonobos as models for the evolutionary origins of human warfare—Glowacki (2023). It is particularly noteworthy here that both species, chimpanzees and bonobos, are commonly misjudged. Bonobos are not always peaceful, they too often resort to violence when representatives of different groups meet—Moscovice et al. (2022). Conversely, chimpanzees are not always as aggressive as perhaps assumed. For some populations, for example, no violence between groups is known at all—Wilson et al. (2014).

For the question of whether the propensity for aggressive intergroup conflicts has been ingrained in our behavioral repertoire since the last common ancestor (LCA) of humans, chimpanzees and bonobos, whose lines separated according to current research sometime between 13 and 4 million years before our time, this variability unfortunately mainly means one thing: uncertainty. All possibilities are conceivable: LCA could have been warlike, which is why this behavior breaks through in some humans and some chimpanzees in 'suitable' situations, whereas this behavior could have weakened in bonobos because it was less frequently needed. Conversely, it could also be that LCA lived rather violence-free, which is reflected in the behavior of the bonobos, whereas chimpanzees and humans could have gained new advantages through increasingly violent behavior. We simply do not know.

Even though this look at our closest relatives is rather unsatisfactory, the comparative perspective of species is not completely uninteresting. Future analyses should, however, shift away from chronological reconstruction attempts towards a better understanding of convergent evolution. As soon as we can better describe what the most common cost-benefit structures of human engagement in violent conflicts between groups look like, measured in evolutionarily relevant currency, we can also more specifically search for the occurrence of the same or sufficiently similar interaction structures in other animals. First steps in this direction are currently being taken—Morris-Drake et al. (2022); Rusch and Gavrilets (2020); for a discussion of the genetic foundations of human attitudes towards foreign and own group members, see also Fieder (in this volume).

5 Function: Qui bono?

This brings us directly to the fourth Tinbergen question: What is the ultimate function of warlike behavior? Does someone, on an evolutionary long-term average, gain a fitness advantage from it? If so: who and when? Two approaches can be heuristically distinguished here: the analysis at the group level and the individual level.

5.1 Group selection?

In light of the horrific events of the 20th century, it may seem plausible to assume that wars have the potential to annihilate entire 'peoples'. If mathematical-theoretical models are based on the assumption that the victory of a warring party almost automatically always means the extermination of the defeated group/s, then conditions actually arise under which group selection in the Darwinian sense is possible—Rusch (2014a, b). The logic here is briefly as follows: As soon as a group contains a sufficient number of (geno-)types that provoke such total wars *and* 'heroically' sacrifice themselves for the victory of their own group in these wars, such groups can gain an advantage over more peaceful groups and displace them by extermination. This leads to the paradoxical effect that the individually disadvantageous willingness to self-sacrifice in war can nevertheless prevail via group selection. *Nota bene*: under quite extreme, purely theoretical assumptions!

In fact, however, it is empirically not clear how strong the effects of wars on the differential survival of certain types of individuals, i.e., the composition of the human gene pool, are at all. Theoretical biologist Laurent Lehmann uses the term 'demographic' effects of wars for this—Lehmann (2011). The demographic conditions under which group selection is theoretically possible are opposed in reality by at least two essential factors. First, wars of annihilation with explicitly genocidal goals are rather unlikely. Rarely, if ever, after achieving strategic war objectives, e.g., conquest of certain regions, capture of certain resources, is it in the interest of the victors to completely annihilate the defeated party—Esteban et al. (2015). On the one hand, this is simply too laborious, on the other hand, it deprives oneself of a valuable resource: namely subjugated labor and/or tribute payers. On the other hand, after the subjugation of enemy groups, there is often a mixing of victors and vanquished through (forced) marriage but also through (work) migration.

Reliable and detailed data on the demographic effects of historical wars are unfortunately very hard to find. We have little better than rough estimates of the numbers of war dead in relation to the population size of selected historical societies—Falk and Hildebolt (2017). Worse still, as long as these values are available without the associated migration rates and estimates of other 'gene flow' between the relevant groups, even these numbers are not particularly meaningful in terms of the group selection question. In conclusion, we will not be able to answer this question here, and perhaps never in general. However, the idea of group selection through warlike behavior is not particularly plausible. Accordingly, one of the best attempts so far to estimate the relevant numbers at least for hunter-gatherer societies and compare them with the theoretically required values for functioning group selection concludes that the real values are far too little extreme to enable group selection—Dyble (2021).

5.2 Warrior Cultures?

So what are the alternatives? Three possibilities present themselves. First, it could be that warlike behavior simply offers no systematic advantage, but is also not sufficiently disadvantageous to be selected out in the long term. It would therefore be 'just there', without having lasting consequences from an evolutionary perspective. However, this is contradicted by the observation that similar behavior can also be observed in other animals, as discussed in the previous section. This would be surprising if warlike behavior did not follow any evolutionary logic at all.

The same applies, secondly, to explanatory approaches that want to make humans' exclusive cultural abilities responsible. On the one hand, such approaches do not explain why warlike behavior also occurs in less 'cultured' species, and, on the other hand, why other species that have the ability to transmit behavior through learning are not warlike. Mind you: to what extent, for example, the mentioned variance in the occurrence of intergroup aggression among chimpanzees can possibly be explained by local 'tradition' is, to my knowledge, not yet investigated; there could well be an informative correlation here. In addition, the above-mentioned works by Turchin and colleagues impressively show the cultural influences which human warfare is subject to. That our cultural ability influences how we wage war is therefore beyond question.

Thirdly, a more differentiated view remains. As discussed above, attack and defense must first be distinguished. The emergence of a willingness to collectively defend, even if it can become very risky individually, is comparatively easier to understand from an evolutionary perspective—Rusch (2013, 2014b). Collective offensive-aggressive behavior is more difficult. As explained above, individuals can indeed benefit from such warlike behavior. On the one hand, through direct resource appropriation, i.e., collective raiding (including for humans), and displacement of competitors, and on the other hand, through status effects within their own group, ultimately improved reproduction chances—Rusch et al. (2015); Rusch and Störmer (2015).

However, within groups there is always a tension between these individual interests and the collective security risk that arises from overly aggressive group members when they uncontrollably start conflicts with other groups—which can indeed happen: Glowacki reports, for example, that ‘raiders’ in some societies hide their plans from the group because they know they would not get communal consent—Glowacki (2022). In addition, successful warlike actions are always ‘teamwork’, so they always need a critical mass of willing combatants within their own group.

Recent theoretical works take all these individual, collective, and strategic factors into account and look for critical conditions under which offensive-warlike behavior evolves and stabilizes in the long term; the works of Laurent Lehmann should be particularly highlighted here—Mullon and Lehmann (2022); Lehmann and Feldman (2008); Lehmann (2011). And indeed, there are such conditions. However, the resulting equilibria are rarely monomorphic; rather, in the long term, states emerge in which various types of behavior differentiate, coexist, and on average keep each other in check, in the classic sense of ‘mixed equilibria’—Maynard Smith (1974); Rusch and Gavrilets (2020).

6 Conclusion

Even though the currently most differentiated evolutionary models for the emergence of warlike behavior do not make very simple predictions, the dynamics they describe are at least qualitatively plausible: War in human history is not a permanent state or the absolute exception; rather, societies have always oscillated between phases of more and less war.

Understanding the critical conditions under which this pendulum swings in one direction or the other seems to me to be the primary task of evolutionarily informed conflict research. Formal economic and political science theory building in this field is capable of illuminating the material and power-political incentives in the pros and cons of individual and collective conflict entry decisions—Esteban et al. (2012); Garfinkel and Skaperdas (2007); Chowdhury (2021); Rusch (2022). However, a better understanding of our conflict psychology and its deeply rooted evolutionary components can make crucial contributions here by refining our analysis of the reaction of 'real' people to these incentive structures and, where necessary, correcting it—Böhm et al. (2020).

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The Evolution of the Social Brain Between Prosociality and Ethnic-Cultural Boundary Drawing

Michael Windzio

1 Introduction

In the course of human evolution, we became social beings. During climatic changes and the transition to life in the savannah, the ability to cooperate within the group proved to be vital. The neurological prerequisites for cooperation were the sensitivity to the emotional states of others, and, related to this, the ability to mentalize, which developed with the increasing (relative) size of the neocortex, meaning that the intentions of others could be understood. With increasing social cognitive capacities, the abilities for imitation and vertical transmission of knowledge improved. Cultural development increasingly came to the fore (Henrich 2016). The dependence of early humans on the cultural knowledge of the group, adapted to the respective niche, such as in food search and preparation, made them sensitive to markers of group affiliation. Cultural markers are indications of shared vital knowledge and the validity of shared social norms. A result of the evolution of the social brain is thus also a coalitional psychology. Due to the vital importance of the specific culture, this psychology is oriented towards group differences (see Fieder in this volume). The self-domestication of the genus Homo proceeded parallel to cultural evolution, which occurred in a process of multilevel

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selection through competition and conflict between groups. Mediated by the neuropeptide oxytocin, this self-domestication also facilitates the dehumanization of the out-group (Hare and Woods 2020).

2 Cognitions and Emotions of the Social Brain

Cognitions and emotions of the social brain are proximate factors of human sociality. Humans and other primates use emotions in facial expression and voice intonation in communication. People find communication strenuous and awkward when an appropriate emotional connotation is lacking (Turner 2000, p. 121–122; de Waal 2010, p. 78–82). Within a few weeks after birth, human infants are able to recognize emotions and imitate the facial expressions of close family members (Turner 2021, p. 101). Infants six to eight months old react emotionally when they observe unfair behavior by geometric figures with googly eyes (Greene 2015, p. 46; Bloom 2013, p. 26–27).

It has been found in neuroscientific studies of macaques that observing the motor actions of others triggers neuronal activities that resemble those that accompany the execution of such actions themselves. Although the debate about the role of so-called mirror neurons for observational learning and empathetic responses continues (Sapolsky 2018, p. 538–541), their activation could be a prerequisite for "mentalizing"[1]: They could contribute to the ability to mentally reproduce what a person is doing, which in turn is important to understand *why* they are doing it (Lieberman 2013, p. 150). People tend to take an *intentional stance,* i.e., to assume that they are surrounded by intentional agents and to attribute intentions to organisms and objects in their environment, such as the intention to eat, to flee, or to mate (Dennett 2017, p. 85). Sometimes, we angrily attribute malicious intentions even to our computers! An evolutionary precursor of the intentional stance could have been the Hyperactive Agency Detection

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[1] Usually, *mentalizing* is used synonymously with the concept of *Theory of Mind* (Premack and Woodruff 1978). However, *Theory of Mind* is misleading insofar as the chimpanzee studied by Premack and Woodruff does not have a "theory", but is only able to "… (to) impute wants, purposes, or affective attitudes to another individual" (Premack and Woodruff 1978, p. 526). Therefore, other authors prefer the term *mindreading* (Mercier and Sperber 2018, p. 94) or, like Lieberman (2013, p. 108), *mentalizing* as a *concrete application* of a Theory of Mind, which in itself only consists in stating that others probably also have intentions and emotional states.

Device (HADD) (Barrett 2000): It is safer to mentally represent a snake that possibly *wants* to bite us, than to mistake a snake for a piece of wood (LeDoux 1998, p. 166). In this process, the detour via the sensory cortex is avoided, which is why one is initially not aware of these processes. The selective advantage of an intentional stance is greater if it produces more false-positive than false-negative results (Guthrie 1980, p. 190).

The difference between the HADD or the neuronal shortcut from the sensory thalamus to the amygdala on the one hand, and the emotional-cognitive ability of mentalizing on the other hand, is that mentalizing requires a minimum amount of self-control (von Hippel 2018, p. 112). Mentalizing means having a subjective idea about the subjective idea of another person. This can be extended in recursive sequence to higher orders of intentionality: "I think that you assume that I don't know that you tried to make me believe that I assumed something wrong". A minority of people are able to cognitively process more than the fifth order (Dunbar 2016, p. 45–46; Dunbar 2021, p. 121).

A specifically human cognitive component of cooperation is described by Tomasello as "joint intentionality" (Tomasello 2018, p. 50). This concept emerged from comparative experiments on the cooperative behavior of young human children and adult great apes (Tomasello 2018, p. 76–77). In humans, the creation of a cooperative "we" represents a new epistemic level. Each of the cooperative partners adds the perspective of the other to their own perspective, so that "… as she is collaborating the individual imagines being in the partner's role and perspective ... and also imagines how the partner is imagining her role and perspective" (Tomasello 2018, p. 55). Joint intentionality shifts cognition to the higher level of "second-personal agency" (ibid., p. 57) and cooperative identity (ibid., p. 57, 62). We develop a joint commitment to the cooperative goal and a responsibility to treat our partner as an equal individual, as well as a feeling of guilt when we fail to meet the expectations of our joint "we" (Tomasello 2018, p. 73, 108).

In accordance with the above argument, Lieberman summarizes our neural predisposition to sociability: First, the brain is active even when we seemingly do nothing, i.e., when we are not working on a specific task. In this case, the brain's activity pattern is similar to that which occurs when we think about other people and our social relationships (Lieberman 2013, p. 19). Second, human brains process physical pain and social pain (pain due to social stress) in a similar way. Both activate the dorsal anterior cingulate cortex (dACC), which exists only in mammals, not in reptiles (Lieberman 2013, pp. 50–51). Physical and social pain are based on the same neural structure, which serve as an alarm system. The dACC detects whether a desired state is present and triggers negative emotions otherwise (Lieberman 2013, p. 62). Third, we tend to attribute agency to our environment, that is, to think about the intentions of others. In this case, the "mentalizing system" (see above) in the human brain is active, involving the dorsomedial prefrontal cortex (DMPFC) (Lieberman 2013, p. 117). Fourth, humans experience their own self not only as their own self-concept ("I"), but also as a concept of how the self could be perceived by others ("me") (Mead 1934). Chimpanzees and other intelligent mammals recognize themselves in the mirror, but only humans are capable of thinking about adjectives that describe themselves. When they do this, the medial prefrontal cortex (MPFC) is active, suggesting that "… our conceptual sense of self is strongly associated with the … MPFC" (Lieberman 2013, p. 186). According to Lieberman, the neural activity generating the social self ("me") has a harmonizing effect: humans are sensitive to the reactions of their social environment. They compare their own self-concept (e.g., "I am a friendly person") with the assumed viewpoint of others, e.g. their family or at work (Lieberman 2013, pp. 191–192). This cognitive module involves a "panoptic self-control": we assume that we are constantly evaluated and judged by others. In line with Tomasello's considerations on joint intentional activity as a precursor to a shared sense of "we" (Tomasello 2018, p. 75), this ability harmonizes our behavior with morality, norms, and social expectations, thus increasing our willingness to cooperate (Lieberman 2013, p. 228).

Humans are also willing to bear the costs of punishing norm violations (Dunbar 2021, p. 241). This *altruistic punishment* (Bowles and Gintis 2011, pp. 24–26) is still practiced today in small communities of hunters and gatherers (Boehm 2000). The community itself thus ensures cooperative behavior and compliance with norms. Symbols of belonging represent group-specific norms and sanctioning systems that ensure cooperation and are therefore vital for human survival. That's why these symbols have a strong influence on whether we classify others as potential cooperation partners or not.

People select others as members of coalitions or alliances by interpreting hard-to-control emotions (Frank 1988, p. 125–130; de Waal 2019, p. 68, 147) and cultural markers (Berreby 2008, p. 225; Boyd 2018, p. 37) as indicators of potential social deception, i.e., a lack or insufficient reciprocity in social exchange, by using specialized cognitive modules. Humans rely on indicators of shared knowledge and norms to establish cooperation, including emotional expression, dialect, behaviors, religion, and other beliefs (Tooby and Cosmides 2010; Tomasello 2018, p. 88–98; Henrich 2016, p. 200–201; Boyer 2018, p. 45–46; Moffett 2019, p. 146–147). People interpret these clues as indicators of shared norms that are essential for cooperation, integration, and survival of the group (Sober and Wilson 1998, p. 173). However, the definition of groups, alliances, of "us and them", can be very flexible and is often adapted to the needs of the current situation (Berreby 2008, p. 212–213). This is the basic idea of the coalitional psychology (Tooby and Cosmides 2010): we tend to apply social categorizations quickly and unconsciously (Berreby 2008, p. 137–139) and try to sort out with whom we can form coalitions and with whom we cannot. This coalition psychology may have a genetic component (see Fieder in this volume), but the definition of concrete group boundaries strongly depends on contexts and situations.

3 Cultural Group Selection Led to Self-Domestication, Altruism, and Parochialism

Proximate conditions of human cooperation lie in the neurological structures that enable us to prosociality and compliance with norms. What are the *ultimate* factors of the social brain, i.e., which evolutionary processes did (presumably) stabilize it? Interestingly, the relative brain size of Australopithecines (about 4 million years ago) was probably not larger than that of today's chimpanzees (Dunbar 2016, p. 100). Probably, initially important for cooperation were the *emotions* involved in social interaction and communication (Damasio 2018, p. 114). The subcortical areas of the brain expanded to enrich the primary emotions (e.g., aversion-fear and satisfaction-happiness) with variants, mixtures, and different intensities (Turner 2021, p. 57–59), so that social interactions were accompanied by a variety of emotions. The brains of hominids successively oriented themselves towards the ability for empathy and imitation (Lieberman 2013, p. 153). Emotions were therefore important for the evolution of human sociality (Turner 2021, p. 129). How did this come about?

While smaller monkey species occupied the most nutrient-rich core areas of the forests, communities of early apes lived scattered over many square kilometers on the barren margins. Individual foraging was the most efficient way to utilize the scarce resources. This resulted in networks with rather loose ties, but probably not in integrated groups. This type of social organization still exists today in orangutans (*Pongo*) in tropical rainforests (Maryanski and Turner 1992, p. 18–19; Turner 2021, p. 34), i.e., in habitats that ecologically probably resembled those of the early apes.

Assuming that the social behavior of the LCA (last common ancestor) of orangutan and human (approx. 12–18 million years, Turner 2021, p. 31) was similar to that of the orangutans, leaving the rainforests posed a great challenge. Due to climatic changes, these LCA had to adapt to the living conditions in the grassland (Hippel 2018, p. 33), but their predisposition to "… low density networks, low sociality, and strong individualism" (Maryanski and Turner 1992, p. 13) was very different from life in the open grassland. Along with bipedalism (two-legged locomotion), more intense social ties and group solidarity now represented a selective advantage (Humphrey 2002, p. 42).

By cooperating, hominids created niches on which their lives depended. Following the logic of the prisoner's dilemma, non-cooperative individuals in such groups, who did not contribute to the collective good, would have had a reproductive advantage, so their characteristics would have spread in the population. However, we know that humans evolved into a highly cooperative and social species (Bowles and Gintis 2011), possibly also because *cultural group selection* (Boyd 2018, p. 99) acted in addition to individual selection.

In evolutionary biology, however, researchers "… look with deep suspicion on any suggestion that benefits accrue solely for the benefit of the group and against the interests of the individual" (Dunbar 2022, p. 17). Even *cultural* group selection (see below) is not universally accepted today as a mechanism of human sociality (Sterelny 2021, pp. 152–153). In the following, the term group selection is used in the sense of multilevel selection (see below), as selection also operated at the individual or even the gene level. However, when Dunbar (2016, p. 313) argues that a sense of obligation and a bond to the group make compliance with norms more likely, and that religious ceremonies such as trance dances in particular strengthen social cohesion among hunter-gatherers (Dunbar 2022, p. 70), and that cohesion and cooperation promote the spread of the group at the expense of other groups, he is effectively describing cultural group selection in the sense of Boyd (2018). Culture in terms of shared knowledge is passed on intergenerationally within groups and is thus a characteristic of the *group*—even if cooperation also increases individual fitness in the long term.

Selection between groups becomes important when efficient cooperation within groups is necessary to be successful in competition between groups, e.g., in big game hunting, when groups compete for resources, or of course in violent conflicts between groups (Turchin 2016, pp. 82–90). The better the individuals cooperated and the better a group was able to keep non-cooperators and cheaters under control, the better the group could exploit the resources in their environment, and the better the group could defend their resources against competing groups.

This process of multilevel selection was demonstrated in an experiment on the laying performance of hens kept in cages with 4 to 8 other hens (Wilson 2019, pp. 84–86). In the first variant of this experiment, the most productive hen in each cage was selected to breed the next generation (individual level). However, after several generations, productivity in the cages of subsequent generations did not increase, but decreased, because the highest-performing hens achieved their productivity by bullying other hens. Each subsequent generation inherited the disposition to bully. When housed together in a cage, the offspring of the high-performance hens became highly aggressive and began to harass and even kill each other. This extreme stress led to a decline in productivity. In the second variant of the experiment, on the other hand, the *entire group* with the highest overall performance was selected for reproduction (group level). The offspring of the highest-performing group remained healthy, their productivity increased by 160%. If this experiment were continued over longer periods of time, the population would eventually consist almost entirely of tame, cooperative hens.

Applied to human evolution, multilevel selection means that more cooperative groups have an advantage over less cooperative groups, both in resource competition in overlapping niches and in violent conflicts between groups (Turchin 2016, p. 116). As group-level selection was driven by competition or intergroup conflicts, we humans developed a tendency to distance ourselves from out-groups, or at least to limit our prosociality to those within our circle of ~150 people whom we have categorized as friends or cooperation partners (Dunbar 2021, p. 93). However, altruism based on genes and phenotypes could only arise in rare situations with comparatively strong selection between groups (Boehm 2000, p. 206; Bowles 2009, p. 1294), which was given in the experiment on artificial selective breeding just described. Archaeological data on adult deaths caused by prehistoric wars and violence support the thesis that group selection based on genetic dispositions was possibly strong enough to produce a cooperative species (Bowles 2009; Wilson 2012, pp. 72–73) (see Fieder in this volume).[2] However, the role of the group level for selection, as indicated above, is controversial in biological evolution (Boyd 2018, pp. 106–109). Moreover, the significance of prehistoric wars and violence for human evolution is highly controversial in anthropology (Fry 2015). Regardless, *cultural* evolution was a likely driving force for the pronounced differences in norms and practices between groups (Boyd 2018; Henrich 2016). Within the respective niche, cultural reproduction was, among other things, vital, because it enabled cooperation and collective goods.

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[2] This is plausible if prehistoric communities were strongly structured by kinship and the assumptions are met under which the Price equation of multilevel selection is mathematically equivalent to Hamilton's equation of kin selection (Birch 2019, pp. 86–87).

4 The Rejection of Outsiders by Common Culture and the Conditions of Cooperation

Our tendency towards group-related prejudices and negative attitudes towards out-groups might have evolved from the need to protect collectively created goods from exploitation by outsiders. Cooperative groups had to ensure that the products of their joint collaboration were not "open access" resources for outsiders who did not contribute to the collaboration (Greene 2015, p. 49). Joint collaboration requires shared knowledge and a common culture. Culture enabled a rapid response to ecological change, but also the exploitation of extremely different niches, ranging from the tropical rainforest (Yanomami), the Kalahari desert (San) to the Arctic (Inuit). Survival in ecological niches requires very specific knowledge that must be maintained through learning and teaching within the group (Henrich 2016; Laland 2017, p. 190). Without culture and its active transmission, human existence is not possible.

A *conformist transmission* of knowledge and culture facilitated cooperation and the creation of life-sustaining niches: people copy dominant cultural practices without testing possible alternatives themselves (Henrich 2016, p. 48; Boyd 2018, pp. 40–41). If individuals consistently follow simple rules of whom they copy, e.g., from the most successful members of the group (Boyd 2018, pp. 36–37), individuals will become more similar *within* the group, but at the same time, the cultural difference *between* groups increases (Turchin 2016, p. 93). According to the Price equation[3], the selection at the group level becomes increasingly

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[3] According to Price's equation, altruism operates at the level of genes, organisms, groups, tribes, etc. Let's take the example of two levels, the individual and the group (see Bowles and Gintis 2011, p. 53): w_{ij} is the fitness of individual *i* in group *j*, p_{Aj} is the average proportion of altruists (A) in group *j*, p_{Aij} is the probability that individual *i* is an altruist. Since altruism is costly for the individual, the effect of β_i on fitness w_{ij} is negative, while β_j is positive when group *j* outperforms other groups in terms of average fitness.

$$w_{ij} = \beta_0 + \beta_j p_{Aj} - \beta_i p_{Aij}$$

In this two-level model, altruism prevails in the long term if the effect β_j at the group level outweighs the effect β_i at the individual level and if the variance of A *between* groups (the distribution of A between groups) is higher than the variance *within* the group (the individual probability of being A) (Turchin 2016, p. 82):

$$\left|\beta_j\right| > |\beta_i| \cap \mathrm{var}\left(p_{Aj}\right) > \mathrm{var}\left(p_{Aij}\right)$$

More generally, the proportion of altruists will increase if the ratio of the variance of the proportion of A between groups $\mathrm{var}(p_{Aj})$ to the variance within groups $\mathrm{var}(p_{Aij})$ is greater than the ratio of the selection strength β_i on individuals to the selection strength on groups β_j (Turchin 2016, p. 82):

$$\frac{\mathrm{var}\left(p_{Aj}\right)}{\mathrm{var}\left(p_{Aij}\right)} > \frac{\beta_i}{\beta_j}$$

important the higher the variation var(p_{Aj}) of the prevalence of a cultural trait between groups is compared to the variation var(p_{Aij}) of this trait within the group (Turchin 2016, p. 87). Imitation and social learning fuelled cultural evolution at the group level and reinforced the cultural boundaries between groups, not least through the transmission of norms and methods of detecting and avoiding norm violations (Henrich 2016, p. 189). The various elements of a culture had to fit together to form a viable system of knowledge and practices. It was dangerous not to adhere to norms and practices of hunting, food preparation, tool use, or other elements of the evolved culture. One example of conformist transmission are the food taboos of the Fijian islanders. Pregnant women avoid marine animals that contain pathogens (Henrich 2016, p. 158), but in most cases cannot justify why they do so. They report that other people, usually older women, advised them to avoid these foods (Boyd 2018, p. 24). The individual only had to "… conform to the right way of doing thinks" (Tomasello 2018, p. 86), so that the behavior meets the requirements of the group in the respective ecological niche.

To ensure whose knowledge fits into the symbolic universe of a group, human cognition relied on hard-to-fake observable markers such as body ornament, language or dialect to decide from whom to learn and who likely shared the same norms of cooperation (Henrich 2016, p. 201).

Selection at the group level probably occurred through culture, shared knowledge, norms, routines, and practices, rather than through genes (Boyd 2018, p. 108). Environmental changes were likely too rapid for genetic adaptation and simultaneously slow enough for the intergenerational cultural transmission of adaptive practices (Turchin 2016, p. 92). As a result, human "… social groups became maximally distinctive from one another in language, dress, and customs, and they competed with one another. Those with the most effective social practices thrived relative to others" (Tomasello 2009, p. 94).

Cultural markers serve as signals for coalitions and alliances, but also for potential conflicts between groups (Tooby and Cosmides 2010, pp. 206–207). We can therefore explain the human tendency to negatively evaluate markers of cultural differences by interpreting these markers as signals for potential cooperation (Greene 2015, p. 67; Boyer 2018, p. 50). The rapid and mostly unconscious decoding of cultural markers is important for our coalitional psychology as well as for the establishment and maintenance of group boundaries (Tooby and Cosmides 2010). Certainly, during human evolution, when most people lived as hunters and gatherers, there were not many opportunities to encounter a person whose skin color was significantly different (Greene 2015, pp. 52–53; Boyer 2018, p. 48). The assumption that racism is *not* part of our biological dispositions (Kurzban et al. 2001) is consistent with empirical findings about three-year-old children. For them, skin color does not matter when it comes to accepting a toy from someone or participating in an activity with someone (Bloom 2013, p. 114). However, we are very sensitive to cultural markers as indicators of group boundaries. In experiments, for example, small babies were given the opportunity to switch between audio tracks with different languages by sucking on a pacifier. As a result, these babies showed a high preference for listening to the language they are accustomed to (Bloom 2013, pp. 110–111). In addition, babies prefer to look at people who speak without a foreign accent. All of this suggests that our sensitivity to cultural group affiliation is anchored in our neurological dispositions.

5 Rejection of Outgroups and Dehumanization are Explained by Self-Domestication

Another factor that stimulated tendencies towards group-related exclusions and tribalism is self-domestication. The domestication syndrome has been analyzed by geneticist Dimitri Belyaev in captive foxes. The selection of foxes based on their tameness affects a complex system of genes and traits, which changed the anatomy of the brain as well as the production and emission of neuropeptides. Side effects of selection for tameness are the forehead blaze common in domesticated cows and horses, but also curled tails and floppy ears (Wrangham 2019, pp. 70–71). Many dog breeds differ in this respect from wolves, their non-domesticated ancestors. Other symptoms of domestication are smaller bodies, shorter, more juvenile faces, reduced sexual dimorphism, and smaller brains (Wrangham 2019, pp. 62–63; Hare and Woods 2020, pp. 84–87).

Symptoms of domestication do result also from *self-domestication*. Bonobos, for example, are close relatives of chimpanzees, but much less aggressive and significantly more prosocial (Wrangham 2019, p. 102). Compared to the ancestors of Homo sapiens, modern humans also show features of domestication. Domestication led to a high degree of prosociality, a pronounced ability for self-control, and low aggression, which are prerequisites for strong bonds among non-relatives and intensive cooperation within the group. In addition, human social organization strongly depends on communication and mentalizing, which is greatly facilitated by eye contact. Only in domesticated animals and humans is the pigmentation of the sclera of the eyes, the area around the iris, missing (Hare and Woods 2020, p. 73). Although this lacking pigmentation may have been just a side effect of human self-domestication, it now facilitates communication (Dunbar 2021, p. 352) and mentalizing (Clifford and Palmer 2018), as it allows direct eye contact and tracking of gaze direction.

There is intense debate in anthropology about how human social behavior compares to that of our closest genetic relatives, the bonobos and chimpanzees. In contrast to the pronounced xenophobia and intergroup aggression of chimpanzees (Wrangham 2019, p. 231–232), encounters between different groups of bonobos often proceed very harmoniously and end in extensive sexual contacts, so bonobos can rather be described as *xenophilic* instead of *xenophobic* (de Waal 2019, p. 194).[4] The human heritage probably consists of a *mixture* of the behavioral dispositions of our two closest relatives: our tendency towards spontaneous, "hot" and reactive aggression is significantly reduced by our ability for self-control (as a result of self-domestication) compared to chimpanzees. But this also comes along with the ability for proactive, i.e., controlled, planned and "cold" aggression (Wrangham 2019, p. 38), which has not yet been documented in bonobos, but does occur in humans (Boehm 2000, p. 80–82; Wrangham 2019, p. 159–160). Thus, self-domestication at least in humans corresponds with a dark side of human sociality, namely dehumanization, i.e., the denial of the other as a full-fledged human.

Dehumanization is a prerequisite for the most severe antisocial atrocities that humans have ever committed against each other, and this is also due to the ambivalent role of the neuropeptide oxytocin. Prosocial effects of oxytocin are detectable in the parental care relationships of mammals (Hruschka 2010, p. 36; Lieberman 2013, p. 92). In this sense, parental care relationships accompanied by neurochemical processes are already domesticated. However, oxytocin is more of a "mama bear" hormone (Hare and Woods 2020, p. 109, 114; Lieberman 2013, p. 93) than a hugging or love hormone. Oxytocin is also released when a mother observes someone threatening her child. The influence of oxytocin on our behavior suggests that the human disposition towards prosocial and moral feelings arose in connection with the mother-child bond: We care intensively for those we feel close to, but at the same time react sensitively to perceived external threats (Bloom 2013, p. 174–175). Oxytocin seems to increase our willingness to blindly

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[4] For a possible explanation of the different developmental paths of chimpanzees and bonobos over the last 2–3 million years, see Wrangham (2019, p. 106–108). He refers to the food competition of the LCA of both species with the gorillas. Bonobos originated from a fission that migrated to the south side of the Congo River, where, in contrast to the north side, no gorillas lived. Due to the good food supply here after the river level rose again, the females increasingly moved around in groups and thus brought male bullies under control. Now the reproductive chances of the less aggressive males increased, whose proximity the females rather tolerated.

trust our partners and friends and take risks with them (Hruschka 2010, p. 40). But treating hamster mothers with oxytocin also increases the likelihood of violently attacking a male they believe is threatening their offspring. Similarly, male rats show an increased oxytocin level when they mate with a female and care for it, but they are also more likely to attack strangers they believe are threatening it (Hare and Woods 2020, p. 109). So oxytocin is by no means a universal love drug (Haidt 2012, p. 271). Oxytocin increases cooperation in experiments, but not if the other player is in a different room or remains anonymous. Oxytocin even reduces cooperation with strangers (Berreby 2008, p. 242; Haidt 2012, p. 173; Sapolsky 2018, p. 116). In addition, oxytocin reduces the ability to recognize facial expressions that show pain or fear of people who belong to a different ethnic group (Hare and Woods 2020, p. 114).

Equally important is that oxytocin reduces the neuronal activity required for more complex thoughts about the subjectivity of others. Under the influence of oxytocin, we stop mentalizing. This "… allows us to blind ourselves to the humanity of people outside our group when we feel threatened" (Hare and Woods 2020, p. 111). In raids on other groups of hunters and gatherers (Boyer 2018, pp. 58–60; Wrangham 2019, pp. 236–238; Bowles 2009) or when parents protect their children from acts of violence, dehumanization overrides empathy and the suppression of targeted aggression. This is precisely what the concept of dehumanization describes: the perception of the other *as a human* is impaired, our tendency towards prosociality and empathy is reduced, making targeted aggression significantly easier for us.

Oxytocin thus appears to be involved in both prosociality within a group and dehumanization between groups. These arguments do not contradict coalitional psychology, which argues that evolution has led to cognitive modules for detecting deception as well as recognizing potential coalitions and cooperative alliances (Tooby and Cosmides 2010). Rather, the concept of dehumanization gives coalitional psychology a neurochemical basis (Koch 2020). This basis influences our behavior probabilistically, but by no means inevitably.

Sociological analyses of human sociality should take evolutionary origins into account in order to arrive at an appropriate image of the *homo socialis*. This image should not be drawn one-sidedly, i.e., neither only as "naturally good, but alienated by society" in the sense of Rousseau, nor as *homo homini lupus est* in the sense of Hobbes. As a product of evolution, both aspects, i.e., pronounced prosociality within the in-group as well as the tendency to draw boundaries based on cultural markers, are two sides of the same coin. Of course, this does not imply that humans alsways surrender to a potentially xenophobic coalitional psychology. The group boundaries drawn are often situation-specific and can be based on various different cultural markers. Thus, language serves in various ways as a cultural marker, for example for ethnic-cultural, religious or increasingly today for political affiliations. Against the background of societal polarizations, it can be helpful to become aware of these tendencies, in others, but especially in oneself.

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The Socio-Evolutionary Development of the Moral Outrage

Moral Outrage as a Result of Human Evolutionary Adaptation to Life in Social Communities and Societies

Christine Campen

1 Outraged Durkheimians

We live on the planet Durkheim, concludes an article by Haidt and Graham (2008). The authors refer to the sociologist Emile Durkheim in their naming of Earth. The designation says less about the planet than about its inhabitants: Humans are characterized as moral beings who live in complex social dependency structures. Morality is considered the basis of human coexistence and is thus central to the survival of the planet Durkheim.

Morality is closely linked with emotions, which on one hand contribute to strengthening the moral order through the human tendency to avoid negative stimuli, and on the other hand, through their communicative effect, indicating moral misconduct by individuals. Moral outrage (in German Empörung) forms a special form of communication of morality. While shame and guilt are self-referential moral emotions and moral anger and moral disgust refer to others, moral outrage can be applied to abstract constructs:

> “Were it not for this reservoir of moral indignation, the mechanisms of social control would be severely limited in their operation. They would be confined only to

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> the action of people who are *directly* disadvantaged by nonconformist and deviant behavior. In actual fact, however, moral indignation and disinterested opposition to nonconformity and deviant behavior serve to lend greater strength to the mechanisms of social control, for not only the relatively small number of people directly injured by deviance -- for example, the parents of the kidnapped child -- but also the larger collectivity, adhering to the culturally established norms, are activated to bring the deviant (and, by anticipation, other prospective deviants) back into line." (Merton 1968, p. 417).

Moral outrage as a communicative tool works without a direct subject and can thus be used (in political discourse) to clarify one's own moral position and accuse (un-)named opponents of moral misconduct. In the course of the pluralization of society, outrage becomes a rhetorical move. Whether it's Alice Weidel, who is outraged about the federal government's immigration policy, or Karl Lauterbach, who expresses moral outrage in the debate about advertising bans for abortions: In politics, moral outrage is used to politicize, moralize, and mobilize.

In research, moral outrage is associated with two basic emotions anger and disgust (see, among others, Batson et al. 2007; O'Mara Kunz et al. 2011; Pizarro et al. 2011; Salerno and Peter-Hagene 2013; Uehara et al. 2014). It is assumed that either anger or disgust dominates depending on the topic, or one of the two emotions is the emotion that expresses moral outrage. However, this would mean that moral outrage is not an independent, communicable emotion.

This understanding of moral outrage is questioned here and instead it is assumed that moral outrage is a mixture of anger and disgust, which arose as a reaction to the differentiation of society. From a historical perspective, it can be assumed that this process began druing the Neolithic Revolution, about 10,000 years ago (Weisdorf 2005).

This origin will be considered in the following. First, the connection between morality and emotions will be explained. Subsequently, the development of moral emotions will be examined from an evolutionary perspective, in order to finally trace a possible path of the emergence of moral outrage as a product of increasingly complex social relationships.

2 Morality: Two Perspectives

In the sociological view of morality, the importance (of morality) for social coexistence is emphasized: Durkheim assumes, "[…] that the realm of morality begins where the social realm begins" (Durkheim 1995[1984], p. 111). Sociality and morality thus go hand in hand. And so it is not surprising that Durkheim assumes that there is society without morality: Only the complexity and the content of morality varies (ibid., p. 81). He defines moral action as an action that is oriented towards collective interests and regulates the behavior or actions of the individual (ibid., p. 81 ff.). With this, Durkheim emphasizes the function of morality for society and the people living in it: The "egoistic" tendencies of the affects are restricted by morality, thus constructing a form of regularity in which relatively many individuals (with individual desires and goals) can coexist. Transgressions of moral rules can lead to exclusion from the respective society (ibid., p. 84).

In his view on morality, Durkheim follows Kant (1959 [1797]), who understood morality as a rational decision between two alternatives of action (the moral and the amoral one). This conception of morality was also adopted in psychology (Kohlberg 1996; Piaget 1986 [1984]). In this view, moral action is tied to rational considerations and independent of emotions (Prinz 2013 [2009]).

A different view on morality is represented by David Hume (2003), who suspected the root of morality in man's ability to empathize. In the sociological view, Simmel (1911, 1992 [1901]) in particular follows Hume's interpretation when he emphasizes the importance of the emotions that accompany (a-)moral actions. The emotional reaction to (a-)moral action was later taken up by Goffman (1963, 1967) and analyzed in social interactions. It is this connection between emotions and morality that is gaining weight in current research. Representatives of this line of thought assume that morality is a product of human evolution (see, among others, Chapman et al. 2009; Kitcher 1998; Turner 2010). The result of this evolution, according to the thesis represented here, is the emergence of moral outrage as an emotion.

3 The Development of (Facial) Emotions

It is hardly disputable that other mammals also have a certain range of emotions (Turner 2010, p. 127). Different primate species show emotions that are quite similar to human emotions (Chevalier-Skolnikoff 1973). Turner (2010) assumes that particularly with the increase in complexity and perception through the eyes and the associated decrease in perception through the nose and ears, the communicative effect of emotional expressions emerged.

Darwin (1872) assumed that the facial expressions of emotions in relation to humans are universal. In "The Expression of Emotion in Man and Animals" he describes three principles, "[…] which appear to me to account for most of the expressions and gestures involuntarily used by man and the lower animals[…]" (ibid., p. 27):

> "1. The principle of serviceable associated Habits.
>
> Certain complex actions are of direct or indirect service under certain states of the mind, in order to relieve or gratify certain sensations, desires, &c. ; and whenever the same state of mind is induced, however feebly, there is a tendency through the force of habit and association for the same movements to be performed, though they may not then be of the least use (ibid., p. 28)."

The first principle describes, according to Chevalier-Skolnikoff (1973, p. 13), how conscious behavior of animals, such as flight, would be associated with emotions (fear) that would be triggered by habituation in similar situations even when the conscious behavior (flight) is not necessary.

The second principle is called "principle of Antithesis" by Darwin (1872, p. 28). He assumes that opposing conscious impressions trigger opposing emotions and behavioral tendencies:

> "As the performance of ordinary movements of an opposite kind under opposite impulses of the will, has become habitual in us and in the lower animals, so when actions of one kind have become firmly associated with any sensation or emotion, it appears natural that actions of a directly opposite kind, though of no use, should be unconsciously performed through habit and association, under the influence of a directly opposite sensation or emotion (ibid., p. 65)."

So if fear is mistakenly triggered because the individual perceives an object or an animal as dangerous, an opposite emotion can arise when it is recognized that it is not a source of danger. In this case, relief, which is often accompanied by almost hysterical laughter and releases the tension that has built up through the previously felt fear.

In both cases, it can be assumed that the emotional reaction has adaptive potential: If we go back to the example of fear, it is easy to see that the increased tension of the muscles and the increase in heart rate that accompany the emotion of fear facilitate escape from potential enemies. On the other hand, it seems equally sensible to reduce this tension as quickly as possible if it turns out that the perceived danger is not dangerous at all.[1]

The last principle "the principle of actions due to the constitution of the Nervous System" (ibid., p. 28) is based on Darwin's assumption that increased stimulation of nerves causes a discharge and thus can generate behavior (ibid., p. 66 ff.). This principle explains the emergence of emotions such as surprise and

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[1] For the physiological processes of the emotion fear see Darwin (1872).

is distinguished by Darwin from the first two principles. The startle reflex as a reaction to a suddenly occurring danger could thus have formed into the emotion of surprise. Darwin therefore assumes that emotions arose through behavior and the associated changes in consciousness. The behavior shown, which is understood by individuals today as an expression of emotion, had certain functions, such as widening the eyes in fear to enlarge the field of vision, or showing the teeth in anger to demonstrate the size of these as a deterrent to the opponent. However, Darwin also assumes that sociality played a role in the emergence or development of emotions (ibid., p. 265).

A century later, these theses were taken up by researchers, especially with regard to humans, and the first basic emotions were defined with a potential biological basis (Ekman et al. 1969; Izard 1971; Kemper 1981; Plutchik 1970). In the recent past, research has been able to further substantiate the thesis of universal emotions: Ekman and colleagues were able to prove the emotions of anger, happiness, disgust, surprise, fear, contempt, and sadness as culturally independent (i.e., universal) through cultural comparisons (Ekman 2013 [1972]; Ekman and Rosenberg 2009).[2] This also means that the facial expression of emotions can be understood by other individuals.[3] Darwin already addressed this signaling function: “As most of the movements of expression must have been gradually acquired, afterwards becoming instinctive, there seems to be some degree of a priori probability that their recognition would likewise have become instinctive” (Darwin 1872, p. 358 f.).

Shariff and Tracy (2011) describe the adaptive advantage of understanding emotional expressions by pointing out that significant environmental changes could be read from nonverbal behaviors. Thus, a saber-toothed tiger did not have to be seen by the individual itself to trigger a flight reflex. Instead, the facial expression of fear byanother individual is sufficient as a sign of potential danger. It is advantageous in this context that in a group of individuals, only one needs to recognize a potential danger and can warn the others through facial expression.

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[2] For an overview of research on universal emotions, see: (Matsumoto et al. 2016).

[3] The fact that the basic emotions are shown in the same way all over the world (and to a large extent are also described very similarly) suggests that they must have originated before the first major migrations of the ancestors of humanity. That is, up to 300,000 years ago (Rito et al. 2019).

4 Moral Emotions

Moral emotions have not yet been mentioned in these considerations, and it is still disputed to what extent their facial expression could be universal.

In research, a distinction is made between self-related and other-related emotions (Haidt 2003; Lefebvre and Krettenauer 2019; Rozin et al. 1999; Stets et al. 2008; Tangney et al. 2007). Self-related moral emotions are mainly understood to be shame, guilt, and embarrassment (Rozin et al. 1999; Tangney et al. 2007; Turner 2010). According to Turner (2010, p. 551), these emotions are triggered when second or third parties indicate to an individual that they have crossed moral boundaries. A more precise distinction between the self-related emotions can be found in Prinz (2013 [2009], p. 76 ff.): He assumes that guilt is felt when moral rules of the legal order are broken and/or individuals are affected who are emotionally close to the individual who has broken these. Shame and embarrassment, on the other hand, he considers as gradations, with embarrassment being triggered when social rules of behavior are broken that do not lead to a loss of social status. If there are violations that can be associated with a loss of status, shame is felt.

The emotions have a prosocial effect insofar as they motivate the individual's behavior or actions to compensate for the amoral action or to clarify that the moral transgression has been recognized and regretted by the individual (Stets et al. 2008, p. 232 ff.).

Other-related moral emotions include disgust, anger, and contempt (Rozin et al. 1999, p. 375). These emotions are directed at the moral transgressions of others. They are also referred to by Prinz as “reactive moral emotions” (Prinz 2013 [2009], p. 69). According to Prinz (ibid., p. 70 f.), moral anger is felt when the rights of others have been disregarded, whereas moral disgust is a reaction to violations of the natural order. With the latter, Prinz associates, for example, mass murders in which the bodies of the victims were mutilated or sexual offenses (ibid., p. 73). Contempt, as the last of the other-related emotions, is directed against hierarchical moral rules (of decency) (ibid.).

Haidt refers to the three emotions as “guardians of the moral order” (Haidt 2003, p. 839). The fact that the other-related emotions in particular are referred to as the guardians of the moral order seems sensible insofar as it can be assumed that in situations where an individual does not feel any of the self-related moral emotions when violating moral guidelines, the other-related emotions can act as a sanction that either trigger the corresponding emotions or signal that the individual does not want to comply with the moral principles of the group and should therefore be excluded from the group.

5 Evolution and Morality: Kin-Selection and Mutual Altruism

Two additional mechanisms of evolutionary biology could also contribute to the formation of moral emotions: kin-selection and mutual altruism.

Kin-selection is based on the assumption that the genetic variation between closely related animals is less than that between other members of the same species, and it is therefore biologically sensible to ensure the survival of these close relatives in addition to one's own survival. Dawkins argues (2006[1976], p. 114 ff.) that the spread of one's own genetic information through siblings and their offspring can be just as advantageous as one's own reproduction. Kin-selection thus explains why help is given in raising other's offspring (Clutton-Brock 2002).

Mutual altruism follows assumptions of game theory, which considers mutual cooperation as one of the most sensible strategies in social associations (Axelrod and Hamilton 1981). The extent to which this assumption is correct is still disputed. Initial research observed that vampire bats shared their food with unrelated members of the same species, placing value on reciprocity: A vampire bat was more likely to share with members of the same species who had already shared food with it than with other members of the same species. (Wilkinson 1984). According to the researchers, this leads to a gradual exclusion of members of the same species who do not share, which in an evolutionary context means that the probability of reproduction (and thus the transmission of one's own genetic information) is highest among the vampire bats willing to share with others.

In combination, these two mechanisms could be considered as a starting point for the emergence of morality and explain how this can have a positive evolutionary effect.

6 Migration into the Savannah

Most species of monkeys live in communities. These are usually composed of a mature male, several mature females, and their common offspring (Maryanski 1995; Turner 2010). Even in these groups, there are basic moral rules that favor the survival of the group: Maryanski (1995) assumes that one of the first moral rules was the prohibition of incest, which is why the grown offspring usually left the parent-group. Mature males would result in mating competition, while mature females are not relevant for mating and therefore do not provide a significant advantage for the group. Turner (2010) assumes that the ancestors of humans migrated into the savannahs of Africa. The new environmental conditions (it is assumed that the ancestors of humans previously lived in densely forested areas) favored creatures that lived in larger communities, as the group provided protection from predators in an environment where escape to the trees was no longer possible. In the course of this development, the ancestors of humans became more emotional, according to Turner (ibid.), attributing this to the enlargement of certain brain areas: While the limbic system increased emotional diversity, the enlargement of the neocortex made more complex thinking possible. Social bonds formed and emotional expressive behavior emerged as a nonverbal language of emotions and emotional states:

> "For millions of years, a few hominids survived in open country savanna by virtue of new kinds of emotional ties to each other. Given preadaptations for language and for self-recognition, a language of emotions emerged, as the association cortices were usurped by natural selection to generate a language built around the visual reading of face and body for its emotional content, and as this language evolved, it was increasingly used for self evaluations as selection worked on the neo-cortex and subcortical emotion centers responsible for such evaluations." (ibid., p. 141)

This combination of self-reflection and a larger emotional repertoire led to the emergence of the emotions shame and guilt: "Morality cannot exist without guilt and, to a lesser extent, shame. Moreover, guilt and shame are powerful mechanisms of social control, in several ways." (ibid., p. 136). Turner's theses are supported by other authors who argue in a similar way (Buchanan and Powell 2015; Kitcher 1998; Moll et al. 2003). If one follows this interpretation, moral emotions took their beginning here.

7 The Problem of Punishment

Shame and guilt, which for Turner constitute the beginning of moral emotions, are closely related to other-oriented moral emotions. However, Turner does not explain the emergence of moral anger and moral disgust. It can be assumed that these emotions must have developed along with self-related moral emotions in order to maintain moral order. An argument for this assumption is the fact that amoral behavior at the individual level generally offers advantages as long as the behavior is not sanctioned by others.

In contrast to shame and guilt, moral anger and moral disgust are based on basic emotions that have changed over the course of human development to address moral misconduct. Disgust in particular has been taken up in research and will serve as an example of the development towards a moral emotion:

Haidt and colleagues (Haidt et al. 1997) assume that disgust originally was a reaction to bad taste and thus "warned" an animal against potentially toxic or spoiled food. In doing so, they pick up on what Lazarus (1991) referred to as "core relation themes". The themes that trigger the emotion are firmly established (i.e., inherited through evolution), but can be changed (Ekman 2012). Over the course of human development, according to Rozin and colleagues (Rozin et al. 2009), the animal nature of humans became triggers for disgust. The adaptive function of this change is described as follows: "This process had adaptive value, because by making things or thoughts disgusting a culture could communicate their negativity and cause withdrawal from them" (ibid., p. 1180). Only in the third step of the development of disgust, however, do moral themes become triggering factors: Rozin and colleagues refer to "[…] a class of moral offenses involving violations of purity and sacredness […]" (ibid.). With this step, the problem of punishing moral transgressions is solved and the system of moral control is complete insofar as it can now react not only to self-related moral misconduct, but also to moral transgressions of others. "Punishment and indirect reciprocity facilitate the evolution of investment in community interests because they help deter cheating […] and reinforce community-oriented behaviours […]" (Flack and de Waal 2000, p. 15). This suggests that this development took place when the ancestors of humans first formed larger communities in which it became necessary to control the behavior of the individual (Hill et al. 2011; Kaplan et al. 2009). It is suspected that anger and contempt have undergone a similar change.

8 From Morality Through Anger and Disgust to Outrage

In the historical consideration so far, the description has remained in a time when no larger societies have yet formed (Wilson 1985, p. 317). The emotions that have so far sanctioned amoral behavior are most likely limited to shame, guilt, embarrassment, anger, disgust, and contempt. The assumption represented here is that the emotion of moral outrage developed during the transition from small communities to larger societies.

The moral emotions of anger, disgust, and contempt have changed in the course of human development insofar as they are felt and shown in response to amoral behavior of others. This change made it possible to sanction amoral behavior and thus maintain the moral order. It is assumed that moral anger and moral disgust differ in the moral misconduct they respond to: Haidt (2003, p. 856 f.) describes moral anger as "[…] a response to unjustified insults […]" to oneself as well as to second or third parties, while he considers moral disgust as a reaction to violations of social and group-internal moral rules.

In research, moral outrage is associated with these two basic emotions (see, among others, Batson et al. 2007; O'Mara Kunz et al. 2011; Pizarro et al. 2011; Salerno and Peter-Hagene 2013; Uehara et al. 2014). However, moral outrage as an emotional response to abstract constructs and subjectless moral transgressions seems neither moral disgust nor as moral anger.

The larger a group living together is, the higher the probability that a moral plurality will emerge. It could be assumed that moral outrage as a moral emotion only arose when there was no longer one morality that united everyone, but several moralities, as can be found in today's societies. The transition from communities where individuals know each other to societies with complex interdependencies, in which individuals are not known to each other, could be the point of origin of outrage.

Campbell (1975) assumes that the complexity of the social interdependencies of human societies cannot be compared with other social communities of mammals. The mutual dependence of the individuals living in a society today makes obedience to social rules indispensable in order to ensure smooth or low-friction cooperation. The moral order forms the foundation that guarantees sociality in general. If we now assume that the communities in which people have lived together have steadily grown and thus the dependencies of people have become greater, leading to an increase in the complexity of the moral order, at some point direct sanctioning of (a-)moral behavior is no longer sufficient. Moral constructs become more abstract and the number of people who need to be morally monitored also become more diverse and larger. Moral outrage as an emotion that can punish not only personally experienced amoral actions, but can also be applied to abstract constructs and larger entities, could fulfill the function of a control instance here. Moral outrage as a communicative means seems to be used particularly in political speeches or in scandal representations (Hitzler 1989). Moral outrage is used as a means to dramatize one's own moral integrity on one hand and amoral concepts (with and without named representatives) on the other.

The emergence of moral outrage would be a two-step process:

1. In the first step, the triggering topics of the basic emotions anger and disgust changed to communicate moral anger and moral disgust.

2. Based on these two emotions, a mixed emotion in the sense of Plutchik (2001), who assumes that two similar basic emotions can mix into so-called "primary dyads" emerged.

The last step would explain why no uniform picture of moral outrage could emerge in research so far and at the same time support first analyses of mimic representations of moral outrage (Campen and Dimbath 2020). If one follows these considerations, moral outrage would be a mixed emotion, that isthe product of adaptation (of humans) to changed social conditions.

9 What Next with Moral Outrage

Morality appears to be a biologically inherent part of humans. The emotions associated with it clearly indicate that this morality has become more complex during human development and has thus adapted to the increasingly complex social interdependencies. Moral outrage seems to represent the current end of the development chain.

The considerations presented here can only be understood as a first step in further research into the emotion in particular and moral emotions in general. Further research in the area of facial expression is necessary to obtain an accurate picture of the emotion of moral outrage and to clarify whether it is universal or only emerged relatively recently. An interdisciplinary approach to the topic seems to be the most fruitful variant, as the sub-disciplines can benefit from each other: Moral outrage is undoubtedly a social emotion that can be beneficial in the examination of social phenomena. However, psychology and (evolutionary) biology, with their own explanatory models, can fill the gaps that would remain in a purely sociological consideration.

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Gender Stereotypes Compared to Gender Differences Using the Example of Media Preferences: Accurate, just Exaggerated or Completely off? An Evolutionary Psychological Perspective

Benjamin P. Lange and Sascha Schwarz

1 Introduction

Gender differences in experience and behavior are a popular field of research in the social sciences (overview by Bischof-Köhler 2022) and especially from an evolutionary perspective (e.g., Schwender et al. 2018). The starting point of evolutionary psychological research on gender differences is often the sex-differentiated reproductive conditions (theory of parental investment; Trivers 1972; overview by Bischof-Köhler 2022), from which precise predictions about gender differences can be derived and then subjected to empirical testing (overview by Bischof-Köhler 2022; Euler and Lange 2018), such as regarding differential grandparental care, gender differences in the experience of jealousy (Euler and Lange 2022) or partner choice (see Klümper & Schwarz, in this volume).

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In addition to the assumption of (presumably real) gender differences, gender stereotypes, i.e., assumptions about socially shared characteristics and properties of women and men, are also a popular field of research (e.g., Hyde 2016; for an overview see also Bischof-Köhler 2022). Are women and men psychologically completely different, the former from Venus, the latter from Mars (Gray 1992)?

Gender differences have also been considered from an evolutionary psychological perspective in the areas of communication and media (Adler et al. 2018; Hennighausen and Schwab 2015a, b; Lange 2018; Lange and Schwab 2018; see also Hennighausen, Lange & Schwab, in this volume). For example, gender differences in media use or media preferences have already been investigated—e.g., regarding the preference for different film genres (Wühr et al. 2017; overview by Schwarz et al. 2018).

In this chapter, we discuss gender differences in the preference for different film, television series, and video game genres from an evolutionary psychological perspective. The biological sex of the consumers is seen as a factor influencing the preference for the respective genres. Furthermore, we address the question of whether and to what extent these empirically investigable preferences are gender stereotypes or real preferences.

2 Gender and Media Preferences

Scientific debates on the topic of gender differences in media preferences can be divided into four different categories: theories dealing with media content, biological approaches, evolutionary psychological theories, and socialization theories (overview by Schwarz et al. 2018). In the following, we will focus primarily on proximate-biological and specifically ultimate-evolutionary psychological aspects.

Proximate-biological approaches, for example, assume hormonal differences between women and men as a possible cause for differences in media preferences (Goldstein 1998; Malamuth 1996). Testosterone, which is present in significantly higher concentrations in men on average than in women, is associated, among other things, with an increased sex drive and aggressive behavior (Mazur and Booth 1998). Prenatal testosterone seems to play a role in this, which could partly explain gender differences in adult film preferences (Schwab 2010), and possibly even early media preferences of preschool children (Lange 2015). Thus, testosterone could be partly responsible for the fact that men, on average, prefer genres with violent content. Conversely, more ‘female’ hormones could explain the genre preferences of women on average (overview by Schwarz et al. 2018).

Complementary to the above-mentioned proximate-biological aspects, evolutionary psychological approaches focus on the ultimate function of gender differences (Bischof-Köhler 2022; Euler and Lange 2018), i.e., the question under which selection pressures of evolutionary past psychological gender differences and thus also gender differences in media preferences could have arisen. Hennighausen and Schwab (2015a) postulate on the basis of the theory of parental investment (Trivers 1972) that women prefer media content that deals with the choice of a suitable romantic partner from an evolutionary psychological perspective, while men prefer content that deals with rivalry, status, power, and the acquisition of resources (overview by Schwarz et al. 2018; see also Hennighausen, Lange, & Schwab, in this volume).

In summary, both biologically proximate and evolutionary (biologically ultimate) approaches exist that make clear predictions about gender-typical preferences for media content: Men tend to prefer action and violence-heavy genres that deal with competition and the acquisition of resources, while women are more interested in media content in the area of interpersonal relationships and qualitative partner choice.

3 Stereotype or Reality?

Regarding gender differences in the preference for certain genres (as with gender differences in general), the question arises whether such differences are actually empirically observable or “only” so-called stereotypes.

Gender stereotypes are assumptions about the experience and behavior (i.e., about abilities, attitudes, and preferences, etc.) of a typical “woman” and a typical “man” (Mealey 2000; see also Bischof-Köhler 2022). The original connotation of the term “stereotype” was exclusively negative (Lippmann 1922); nevertheless, the literature shows that stereotypes are not necessarily empirically false (Brown 2010; Hilton and von Hippel 1996; overview by Schwarz et al. 2018). The question of whether a stereotype is true or not (and if so, how much) is now rather considered an empirical question rather than an ideological one (Jussim et al. 2009).

Accordingly, the first study (Wühr et al. 2017) presented in this chapter empirically addresses the question of the size of the perceived difference in preference for film genres between women and men (“stereotype”). To verify whether these stereotypes are true, women and men were also asked how much they personally like the same film genres. By comparing the respective results, it can be assessed whether the phenomenon “men want action, women want romance” is a pure stereotype or actual gender differences. Analogous to Wühr et al. (2017), two further studies were conducted that examined gender differences and stereotypes with regard to television series genre preferences (Lange and Zahn 2021a) and video game genre preferences (Lange et al. 2021). These two studies will also be presented in the following.

3.1 Study by Wühr, Lange and Schwarz (2017): Gender Differences and Stereotypes in Preference for Film Genres

In the study (see Wühr et al. 2017 and Schwarz et al. 2018), 150 predominantly student participants (female: 75, age $M = 23.5$ years) were asked whether, in their opinion, a total of 17 film genres (adventure, action, animation, tragedies, erotica, fantasy, homeland, historical, horror, comedies, war films, crime, mystery, romance, science fiction, thriller, and western) are liked more by women or men. An 11-point scale was used for this purpose (with the endpoints "only liked by women" and "only liked by men" and the middle category "liked equally by women and men").

Gender-specific preferences for the same film genres were recorded using another, also predominantly student sample ($n = 160$, female: 80, age $M = 23.5$ years) on an also 11-point scale (from *0 = not at all* to *10 = extremely like*).

The results demonstrated numerous stereotypes about the (supposed) film taste of women and men (Hedges g in brackets): Women supposedly prefer romance films ($g = -2.74$) and homeland films ($g = -0.91$) more than men. Men supposedly prefer war films, westerns, science fiction, action, erotica, horror, adventure, thriller, and historical films more than women (according to the conventions of Cohen, 1988 with small to large differences: $g = 0.45$ to 2.38). The strength of these assumed gender differences was often remarkable. Another noteworthy result was that women and men were very similar in their assessment ($r = 0.99$), i.e., they had the same stereotypes about the preferences of typical women and men.

The survey of women and men about their actual film taste revealed a very similar pattern overall: Men prefer science fiction, war films, action, erotica, adventure, westerns, horror, fantasy, mystery, and thriller more than women (according to the conventions of Cohen, 1988 with small to large differences: $g =$ 0.41 to 1.44). Women, on the other hand, prefer romance films ($g = -1.20$) and tragedies ($g = -0.50$) more than men.

In summary, four conclusions can be drawn from these data: People can (1) correctly predict the direction of gender differences for most genres, but also (2) overestimate the size of gender differences for most genres. Women and men show (3) very similar gender stereotypes. The probably most important finding is finally (4) that assumed gender differences in film preferences do not only represent pure stereotypes, but reflect real gender-specific preferences.

3.2 Study by Lange and Zahn (2021a, b): Gender Differences and Stereotypes in Preference for Television Series Genres

Lange and Zahn (2021a; see also Lange and Zahn 2021b and Zahn 2019) investigated gender differences and stereotypes regarding preferences for television series genres, analogous to Wühr et al. (2017). Among other things, this was intended to answer the question of how generalizable the results of Wühr et al. (2017) are to other media phenomena—in this case, to television series preferences. The two core questions were accordingly: What preferences for series genres do women and men have? And what do people think about the corresponding preferences of women and men?

Similar to Wühr et al. (2017), a two-part study (each using 11-point scales) was conducted. In Study 1, the actual preferences of women and men for 17 television series genres were determined using a predominantly student sample of $N = 184$ (w: 105; age $M = 27.1$) (*0 = not at all* to *10 = very much*). For example, the question was asked: "How much do you like action series?"

In Study 2, using a non-predominantly student sample of $N = 180$ participants (w: 100; age $M = 27.63$) (see Zahn 2019), it was asked whether each of the same 17 genres is preferred more by women or men (*0 = exclusively liked by men* to *10 = exclusively liked by women*). For example, the question was asked: "What do you think: Are action series liked more by women or more by men?"

Gender differences (Study 1) and stereotypes (Study 2) were finally compared to determine the accuracy of the stereotypes.

In Study 1, various differences in genre preferences emerged. Genres that are preferred more by women (Cohen's d in brackets) are: Romance, Musical, Family, Fantasy, History, Mystery, and Drama (according to the conventions of Cohen, 1988 with small to large differences: $d = -0.22$ to -1.32). Genres that are preferred more by men are: Action, War, Western, Science Fiction, Adventure, and Animation (with small to large differences: $d = 0.41$ to 0.75). For four genres, no or only a very small gender difference ($d < 0.2$) was found: Thriller, Comedy, Horror, and Crime series. Fig. 1 (black bars) provides a visual summary of these results.

Note. The black bars show the effect size (Cohen's *d*) of the real gender difference, the white ones that of the assumed gender difference. Negative values represent a (assumed) male preference, positive ones a (assumed) female preference.

In Study 2, numerous and often strong gender stereotypes were found. Genres that are assumed to be preferred more by women are: Romance, Musical, Drama, and Family (with large differences: $d = -1.29$ to -2.18). Genres that are assumed to be preferred more by men are: War, Western, Action, Science Fiction, Adventure, Horror, Fantasy, Thriller, and Animation ($d = 0.26$ to 1.59). For the genres Comedy, Crime, History, and Mystery, no assumed gender difference was found ($d < 0.2$). Fig. 1 (white bars) provides a visual summary of these results.

By comparing both studies, the correctness or accuracy of the stereotypes was finally determined (see Fig. 1). Thirteen (out of 17) stereotypes agreed in direction with the real preferences. However, for the thirteen genres, it was found that the true gender difference was often overestimated: strong overestimation

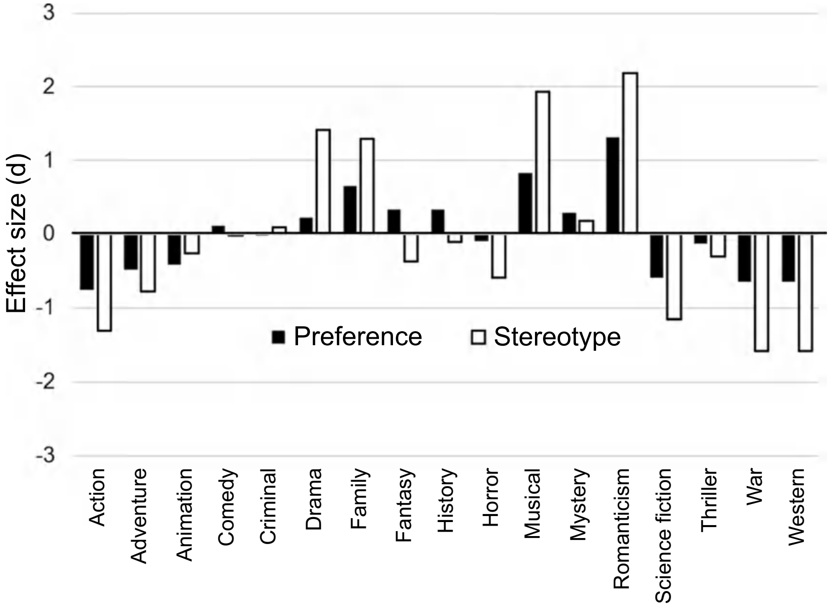

Fig. 1 Comparison between real and assumed gender differences in television series genre preferences

($d > 0.8$) for five genres, moderate overestimation ($d > 0.5$) for three genres, slight overestimation ($d > 0.2$) for two genres. A relatively correct estimate ($d < 0.2$) was found only for three genres.

3.3 Study by Lange, Wühr and Schwarz (2021): Gender Differences and Stereotypes in the Preference for Video Game Genres

Lange, Wühr and Schwarz (2021) investigated—analogous to the approach of the two empirical studies described above—the accuracy of gender stereotypes in relation to preferences for video game genres.

In Study 1, a sample of a total of $N = 484$ participants (female: 203; age $M = 23.88$) rated their preferences for 17 video game genres on a 5-point rating scale (gender differences). In Study 2, another sample of $N = 226$ participants (f: 125; age $M = 24.12$) rated, using a likewise 5-point rating scale (from *1 = rather female* to *5 = rather male*), to what extent the same genres are probably preferred by women and men (gender stereotypes). The results of both studies were then compared to determine the accuracy of the gender stereotypes.

Study 1 showed gender differences in the preference for most genres—predominantly of moderate effect size: The genres preferred by women are (Cohen's d in brackets): Music & Dance, Quiz, Learning games, Skill/Casual games, Simulations, Puzzle and Thinking games, and Jump 'n' runs (with small to medium differences: $d = -0.38$ to -0.76). Genres that are preferred more by men than by women are: First-Person Shooters and Third-Person Shooters, Western, Shoot 'em ups, Strategy, Adventure, Open-World, Sports and Role-playing games (with small to large differences: $d = 0.25$ to 1.31).

Study 2 revealed substantial gender stereotypes regarding video game genre preferences. Genres that are assumed to be preferred more by women are: Simulations, Music & Dance, Learning games, Quiz, and Puzzle and Thinking games ($d = -0.51$ to -1.17). Genres that are probably preferred more by men are: First-Person Shooters and Third-Person Shooters, Shoot 'em ups, Beat 'em ups, Western, Sports, Strategy, Adventure, Erotica, Open-World, Role-playing games and Jump 'n' runs (with small to large differences: $d = 0.39$ to 2.17).

When comparing the results from both studies, it was again shown that gender-specific stereotypes for most genres went in the right direction, but were to a certain extent inaccurate regarding the assumed size of the gender differences: For most genres, the gender stereotypes overestimated the actual gender difference with a moderate to high average effect size.

4 Conclusion and Outlook

Evolutionary psychological approaches postulate that men tend to prefer action-packed genres that revolve around competition and the acquisition and maintenance of resources, while women tend to prefer genres that focus on interpersonal relationships and qualitative partner selection. These gender-differentiated genre preferences are consistent with evolutionary psychological assumptions and empirical findings (Hennighausen and Schwab 2015a). The male preference for the action genre (Oliver et al. 2000), for example, aligns with evolutionarily assumptions about gender differences in aggression (overview by Bischof-Köhler 2022; Euler and Lange 2018). The female preference for the romance genre and generally for media content revolving around social relationships (Oliver et al. 2000) is consistent with the generally greater female interest in people and relationships (Su et al. 2009; overview by Bischof-Köhler 2022) and with the female qualitative reproductive strategy (Bischof-Köhler 2022; Euler and Lange 2018; see also Hennighausen, Lange, & Schwab, in this volume).

In this contribution, we were able to show that while there are pronounced notions about the preferences of typical women and men for the various genres, the preferences for the majority of the genres examined are accurate in direction but overestimated in magnitude.

However, the question arises to what extent the findings presented here can be generalized—for example, to older people. The participants of the studies were often students and rather young. Studies on older samples are rare. Hoffman and Schwender (2007), for example, asked over 1000 people between the ages of 50 and 91 which film genre they like to watch. They found that women preferred romance films, dramas, musicals, and homeland films more often than men, while men preferred animation films, science fiction films, action films, and westerns more often. They also found that with increasing age, both men and women increasingly preferred genres favored by women. Biological explanations for gender differences in genre preferences have already been mentioned at the beginning. Against this background, the preference of older men for genres actually preferred by women could have something to do with the decrease in testosterone levels with age (Decaroli and Rochira 2016). However, corresponding—ideally longitudinal—studies in which both film preferences and testosterone levels are collected to disentangle age and cohort effects are still pending.

It is significant that the findings obtained for film genres can be transferred to other media areas. Especially under the assumption that the gender differences presented here are evolved predisposed differences, similar patterns would always be expected—regardless of whether traditional media such as films, series, literature are considered or a rather new interactive medium like video games. If men prefer media content that revolves around competition and the acquisition of resources (e.g., action), and women prefer media content that focuses on interpersonal relationships and qualitative partner selection, these gender-specific preferences should also be transferred, for example, to the preference for certain series and video game genres. The data presented here from Lange and Zahn (2021a) and Lange, Wühr and Schwarz (2021) confirm this.

From an evolutionary psychological perspective, however, the question remains as to what the adaptive benefit of stereotypes in general could be. This could also provide a clue as to why most gender stereotypes in all three studies presented in this book chapter predominantly overestimate the actual gender differences.

The classical social psychological answer to the question of why stereotypes exist at all refers to the aspect of economy. By stereotyping people based on appearances (= putting them in "drawers" or categorizing them), the cognitive system is relieved and people can act faster and more economically (Allport 1954). However, this categorization leads to differences within categories being perceived as smaller than they really are (intragroup effect), while differences between categories are perceived as larger than they really are (interclass effect) (Tajfel and Wilkes 1963).

This explanation could already explain the effect—but only at a proximate level (mechanism of action); the question of why our mental apparatus exhibits this tendency, i.e., what the ultimate cause (mechanism of purpose) is, is not answered by this. An explanation at the ultimate level, which, as Tinbergen (1963) has already pointed out, does not compete with other explanations, but is rather to be understood as another view of the same phenomenon, begins with the observation that human information processing is aimed at increasing reproductive success (Sng et al. 2017). Humans, as "social animals" (Aronson 2007; Hennighausen et al. 2016), are particularly dependent on their social environment due to their social nature. Other people can help us survive and increase our reproductive success or hinder us and, for example, compete directly with us. It is therefore assumed that mechanisms have developed in our evolutionary past that help us identify people who represent opportunities or dangers for us. To promote survival and/or reproduction, stereotypes help to quickly assign an individual as a member of a social group and attribute certain group characteristics to this individual (Sng et al. 2017).

Why are stereotypes often made about, for example, gender? The classic social psychological answer is: the visual features are easy to recognize and cultural norms and conventions teach us that they are significant. Upon closer examination, however, this does not seem particularly convincing. Other visual cues are also easily visible and not subject to stereotyping. Moreover, this traditional view does not explain why cultural norms select gender as the basis for stereotypes. From an evolutionary psychological perspective, however, gender is diagnostically relevant information for deciding whether a danger or a reproductive opportunity exists. Because gender is diagnostically relevant (in the evolutionarily ultimate sense), it is stereotyped in this regard.

From such an evolutionary psychological perspective, it therefore also seems understandable why modern media preferences (film, television, and video games) are subject to such gender stereotypes. If this thought is pursued further, it could be that the preference for action-packed/violent content, which is attributed to men and is actually present in them, is particularly strongly overestimated because it is diagnostically relevant for one's own survival to assume that men generally prefer action and violence. Conversely, the attributed preference for romantic entertainment genres by women would increase the chance for reproduction, as romance or family themes should be relevant solely on the basis of greater parental investment (Trivers 1972) by women compared to men. Genres where the content is not diagnostically relevant for survival or reproduction (e.g., animation or possibly comedy) could not be strongly stereotyped from this logic. Therefore, this adaptive perspective could provide an explanation for why perceived gender differences (stereotypes) are more pronounced in some genres than in others.

It would therefore be expected that the extent of the overestimation of gender differences is particularly large in those domains that are significant for survival or reproduction. The data from the three studies presented here allow a first verification of this assumption. In the study by Lange et al. (2021), the true gender differences for the five video game genres Beat 'em ups (fighting/brawling game), First- and Third-Person Shooters, Shoot 'em ups (i.e., various games focusing on shooting), Sports, and Western were particularly strongly ($d > 0.8$) overestimated. All these genres are preferred more by men, but the subjects of the study assumed an even considerably larger male preference than was actually present. When considering the content of these genres, the aspects of combat, (intrasexual) competition, and status acquisition stand out. In the study by Lange and Zahn (2021a), the five series genres Drama, Musical, Romance, War, Western were particularly strongly ($d > 0.8$) overestimated (see Fig. 1). The first three go in the female direction (real female preference, but significantly overestimated perceived female preference), the last two in the male (real male preference, but significantly overestimated perceived male preference). The same can be said about the content of the two 'male' series genres as was stated above for the video game genres. The three 'female' series genres show a content-related proximity to female qualitative partner choice (Bischof-Köhler 2022) as well as possibly to the topic of family. The data from Wühr et al. (2017) and their content interpretations go in the same direction. Here, the film genres Action and Western (male) and Drama and Romance (female) were among the genres with particularly noticeable overestimation (see Wühr et al. 2017, Fig. 3).

This provides an evolutionary approach that can ultimately explain gender stereotypes and their strength in terms of overestimation, thereby meaningfully supplementing classic proximate-social psychological explanations. Above all, however, this perspective allows empirical predictions about which domains are particularly strongly overestimated (gender stereotypes significantly stronger than the real gender differences). Once again, this example shows that evolutionary psychological assumptions are not "post-hoc stories", but can provide new predictions for human experience and behavior that have not been considered without this perspective. Whether and to what extent these hypotheses are correct, however, must be further investigated empirically, rather than being viewed solely ideologically (in reference to Jussim et al. 2009).

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To What Extent is Person Perception a Psychological Adaptation? An Evolutionary Psychological Perspective on the Automatic Processing of Mate Choice Relevant Features

Lisa Klümper and Sascha Schwarz

1 Introduction

What determines the famous "first impression" when we meet a person for the first time? This is a question that not only occupies us in everyday life, for example when we are invited to a party with many unknown people and we ask ourselves how we are perceived, but also in a professional context, when it comes to job application situations.

Psychological research has already identified numerous factors that influence the first impression. Most often, the circumstances of the social situation in which an encounter takes place (e.g., private or professional context), as well as the characteristics of the perceiving person (perceiver) and the properties of the perceived person (target) are discussed (e.g., Tagiuri and Petrullo 1958).

In the past, research has particularly focussed on the importance of the appearance of targets. Various studies have shown that appearance has a significant

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influence on the first impression (e.g., Agthe, et al., 2023; Ritchie et al. 2017; Vernon et al. 2014; Weisbuch and Ambady 2011).

The face is given a very special importance, which has been at the center of research in recent years. From the features of a person's face, we can identify three dimensions in particular that contribute to the formation of the first impression (Sato et al. 2013; Sutherland et al. 2013; Todorov 2008). The relevant dimensions include characteristics of *trustworthiness/valence*, *dominance/competence* and *youthfulness and attractiveness* (e.g., Sutherland et al. 2013, 2016). From an evolutionary perspective according to Oosterhof and Todorov (2008), these dimensions are essential as they are associated with the assessment of threats to the individual. The domain of trustworthiness/valence gives an indication of whether the target might have the intention to help or harm the perceiver. The dominance/competence domain serves to assess whether the target is potentially capable of actually carrying out the pursued intention (Sutherland et al. 2013). Recognizing trustworthiness and the ability to carry out threatening intentions are also crucial for survival (Oosterhof and Todorov 2008). Features of physical attractiveness include, for example, facial symmetry, skin health and color, and averageness. They reflect information about what is broadly defined as a person's health (Thornhill and Gangestad 1999). Even though the correlations between actual health and attractiveness are rather weak and inconsistent (e.g., Henderson and Anglin 2003; Kalick et al. 1998), very high correlations are shown between the *perceived* health and the perceived physical attractiveness of targets. The more attractive a person is perceived to be, the healthier they are also estimated to be (Rhodes et al. 2007).

2 The Three Domains in the Context of Mate Selection

The three domains of trustworthiness/valence, dominance/competence, and youthfulness and attractiveness can be identified with similar connotation as central domains in mate selection. In this context, they are referred to as *trustworthiness*, *status and resources*, and *physical attractiveness and youthfulness* (Fletcher et al. 1999).

All three domains are relevant beyond the general first impression, as they provide information about the characteristics of a potential relationship partner. In the context of mate selection a high degree of trustworthiness suggests that the emotional and social support necessary for the establishment and maintenance of a family will be provided (Fletcher et al. 2004; Gangestad and Simpson 2000).

The availability of material and status-related resources ensures the survival of the family, especially of one's offspring. The physical attractiveness of a partner provides clues about the survivability of the offspring (for an overview see Rhodes 2006). In terms of developmental stability, it signals the organism's ability to defend itself against pathogens (especially diseases, toxins, parasitic infestation, etc.) during development and to produce a healthy phenotype (Little et al. 2011; Wade 2010). Thus, physical attractiveness is not only helpful in short-term interactions to determine whether someone is healthy (and thus potentially contagious) at the moment, but also in the long term in the context of mate selection regarding the health of potential offspring.

It is particularly noteworthy that in the context of mate selection, it is not necessary to observe the target multiple times to make a judgment about the characteristics of these three domains. All three domains can also be conveyed by the face (e.g., Sutherland et al. 2013). An assessment of the person before the first personal contact is thus possible.

3 The Relevance of Target and Perceiver Effects in Mate Selection

To determine the value of a person as a partner, it is not solely the expression of the target in these three domains that is decisive. An important role plays the expression of the target's characteristics in the three domains depending on the characteristics of the perceiver (Hassebrauck and Schwarz 2016). A prominent and well-studied perceiver characteristic is the gender of the target. Comparing the evaluations of potential partners between men and women, they place different value on the expression of the three domains on average. These differences can be explained from an evolutionary psychological perspective with different evolutionary costs.

Mate selection, according to the *Sexual Strategy Theory* (SST, Buss and Schmitt 1993), represents a complex set of psychological adaptations that exist to solve adaptive problems of men and women. One of these problems is the increase in individual fitness, i.e., ensuring one's own survival and the transmission of genetic material to the offspring. Therefore, mate selection is characterized by an integrated set of adaptations (= sexual strategies) that have evolved to ensure individual reproductive success (core of the SST; Buss and Schmitt 1993). These sexual strategies direct the resources and energy of the individual into specific strategies. Therefore, a mate selection strategy can manifest itself in attitudes and behavior in many ways (Gangestad and Simpson 2000). The SST describes that men and women were confronted with different adaptive problems, which are particularly due to an asymmetry of the minimum parental investment (Trivers 1972). Parental investment is the effort made for the offspring to increase their chances of survival, at the expense of further possible offspring. Due to their low minimum parental investment, men's reproductive success is primarily determined by access to fertile partners. For women, the minimum investment, purely biologically speaking, is associated with more effort and costs. They should therefore be more selective and critical in mate selection (Buss and Schmitt 1993). This results in gender differences in various attitudes and behaviors regarding mate selection.

As already explained, each domain of person perception has a specific adaptive benefit to ensure one's own survival and the survival probability of the offspring. The adaptive benefit of the target's characteristics is differently pronounced depending on the gender of the perceiver. These predictions from the SST about gender differences in the importance of the three domains can be empirically supported by results from previous research.

3.1 The Domain of Physical Attractiveness

When considering heterosexual mate selection from an evolutionary perspective to increase reproductive success, it is relevant for males to identify signs of high reproductive capability in a potential partner. Female reproductive capability is strongly associated with physical attractiveness (Symons 1979). Compared to women, men on average assign a higher relevance to the physical attractiveness of a partner (Schwarz and Hassebrauck 2012; Schwarz et al. 2020). When men have to decide what is particularly important to them in mate selection and what aspects they can neglect, they place even more emphasis on the physical attractiveness of a partner (Li and Kenrick 2006; Li et al. 2011). These preferences are evident over several decades and across different cultures (Thomas et al. 2020; Walter et al. 2020).

3.2 Status and Resources

For women, to increase their reproductive success, characteristics of a partner that signal the presence of status and resources and the partner's willingness to invest these in the woman and offspring are important. Women consistently assign more importance to characteristics of a potential partner that signal status and resources over time and across different cultures. There is an increased preference for associated characteristics such as ambition, assertiveness, intelligence, and self-confidence (Buss and Schmitt 1993; Schwarz and Hassebrauck 2012; Schwarz et al. 2020; Wang et al. 2018).

3.3 Trustworthiness

The domain of trustworthiness is associated with cooperative behavior and good parental qualities (Buckels et al. 2015). For example, individuals report that they find a highly trustworthy potential partner more attractive. Satisfaction in an existing relationship also depends on the degree of trustworthiness (Valentine et al. 2020). In contrast to the other two domains, trustworthiness is rated as equally important by both women and men (Fletcher et al. 2004). However, this domain has received less attention in empirical research relative to the other two (Fletcher et al. 1999; Valentine et al. 2020).

4 Beyond Self-Report: The Automatic Processing of Partner-Related Characteristics

The three domains of person perception and especially the importance of a long-term romantic partner are central for physical and psychological well-being (e.g., Braithwaite and Holt-Lunstad 2017) as well as survival (Holt-Lunstad et al. 2010). It is plausible that the described gender differences in partner preferences are also reflected in cognitive processes of information processing at a more basic level, adaptively in relation to aspects relevant for mate selection.

From our point of view, this perspective is of particular importance for evolutionary social sciences for two reasons. Firstly, the findings presented so far are based exclusively on self-report and therefore describe higher-order cognitive processes (partner preferences). These findings dominate the literature. However, a person’s self-report can be subject to numerous judgment biases (Paulhus and Vazire 2007). Therefore, self-report is less suitable for investigating to what extent psychological processes are modulated by cultural differences. With a more systematic investigation of the automatic processing of partner-related characteristics, we can better understand whether and how we perceive people without additional cognitive effort.

In addition, automatic processing of partner characteristics could indicate a “hard-wired” predisposition in person assessment. For example, it is known from fear research that rhesus monkeys (and other primates) have a predisposition to develop a learned fear response to snakes. This develops even if there has been no previous contact with snakes, for example, because they were either raised in the laboratory or lived in Madagascar, where there are no snakes. However, if these "laboratory primates" observe other primates showing a fear response to flowers, they do not learn this fear response (e.g., Cook and Mineka 1989). It is concluded that primates have a predisposition to learn a fear response to snakes, but not unspecifically to other stimuli. Analogously, a specific phobia of snakes is very widespread in our latitudes today. A specific phobia of cars, which are much more dangerous in our current environment, is not known ("preparedness" in the sense of Seligman 1971). Similarly, person perception could also have a domain-specific and possibly gender-specific predisposition to be processed automatically. A deeper understanding of the underlying cognitive processes could help us better understand at which levels of processing we could expect the influence of cultural differences.

4.1 The Importance of the Automaticity of Cognitive Processes

An important characteristic of cognitive processes is the degree of automaticity (e.g., Bargh 1994; Moors and De Houwer 2006; Posner and Snyder 1975), which is also discussed as a criterion for an evolutionary-psychological adaptation (for a brief discussion see Jung et al. 2012).

To characterize a cognitive process as automatic and to distinguish it from controlled processes, different criteria are proposed in the literature (Moors and de Houwer 2006). The most frequently mentioned criteria include *control or intentionality*, *awareness* and *efficiency (capacity requirement)*.

According to the characteristic of control or intentionality, an automatic process is initiated without the need for a corresponding intention and, once triggered by an appropriate stimulus, is difficult to inhibit. The characteristic of awareness describes that automatic processes can occur unconsciously, while controlled processes are always conscious. The characteristic of efficiency states that automatic processes do not require limited processing capacities (e.g., attention, working or short-term memory), while controlled processes need these limited cognitive resources (e.g., Bargh 1994; Jonides 1981; Neumann 1984; Schneider and Shiffrin 1977).

4.2 The Automatic Processing of Physical Attractiveness

There are initial empirical studies that provide evidence that the processing of characteristics from the domain of physical attractiveness is subject to an automatic process. For example, the processing is effortless, unconscious, and quick (e.g., Olson and Marshuetz 2005; Werheid et al. 2007). However, these and other studies sometimes focus only on the characteristics of the targets and neglect possible target x perceiver interactions, which are suggested by research results on mate choice. Initial indications of interaction effects show that men and women can quickly process female, but not male, physical attractiveness (Maner et al. 2003). Similarly, there is an attention bias regarding female physical attractiveness among male and female perceivers (Maner et al. 2005; Duncan et al. 2007).

Neuroscientific and cognitive psychological studies suggest gender differences in the perceiver. In men, but not in women, attractive faces activate areas in the anterior cingulate cortex (Winston et al. 2007) and only in men does activity in the orbitofrontal cortex increase when attractive faces are presented (Cloutier et al. 2008). Attractive female faces are processed in areas that are also associated with the reward system in men. These areas are not addressed in male or unattractive faces (Aharon et al. 2001).

With regard to the efficiency criterion of automaticity, so far only three empirical studies have addressed the question of whether the processing of physical attractiveness requires central attention resources. Rellecke et al. (2011) found evidence of an automatic process in male and female perceivers, whereas Jung et al. (2012) could not determine automaticity in a female sample. Both studies only considered the physical attractiveness of the target, neglecting the characteristics of the perceiver and possible interactions. In a more recent published study (Klümper et al. 2020), the inconsistent results were clarified using the *Psychological Refractory Period Paradigm* (PRP) by supplementing the predictions for capacity-free processing from the bottleneck model (Posner and Snyder 1975) with predictions about intersexual differences in the relevance of physical attractiveness in mate choice (Buss and Schmitt 1993). Accordingly, female targets are only automatically processed by male (and not female) perceivers, while male targets are not automatically processed by either male or female perceivers. This pattern of results suggests that the physical attractiveness of female targets occupies a special place in the cognitive processing of male perceivers.

4.3 The Automatic Processing of Status and Resources as well as Trustworthiness

The evidence regarding the automatic processing of characteristics related to status and resources, and trustworthiness remains inconclusive. However, results suggest that cues to status and resources as well as trustworthiness can be quickly and unconsciously read from a target's face (Todorov et al. 2009; South Palomares et al. 2018).

Studies suggest that people can quickly assess the social status of others based on their faces (South Palomares et al. 2018). Further results suggest that individuals with high status are recognized faster, receive more attention, and are better remembered (Ratcliff et al. 2011; Cheng et al. 2013; Dalmaso et al. 2012). In addition, perceivers shift their attention towards targets with high status (Dalmaso et al. 2012). In some cases, there are perceiver × target interactions, whereby both men and women direct more attention toward male targets who possess high status or high dominance (DeWall and Maner 2008; Maner et al. 2008). However, the inconsistent operationalization of the domain of status and resources (e.g., physical dominance, job position, competence or agentic traits, Carrier et al. 2014; Mattan et al. 2017) is problematic. In this domain, methodologically consistent results focusing on a representative characteristic are lacking. Moreover, there is a lack of empirical basis to speak of automatic processing (especially capacity freedom and interference) for the corresponding characteristic.

Regarding the domain of trustworthiness, studies show that the amygdala is automatically activated by differently trustworthy faces, regardless of whether the perceiver actively pays attention to these in faces (Engell et al. 2007; Winston et al. 2002). Clues to this are quickly recognized and assessed in the face (Kovács-Bálint et al. 2014; Yang et al. 2011) and spontaneously encoded in memory (Klapper et al. 2016). Judgments about trustworthiness can also be made when perceivers are presented with images of people for a very short duration (approx. 100 ms) or the perceivers are not consciously aware that the images are present (Todorov et al. 2009; De Neys et al. 2017).

An initial indication of capacity freedom is provided by findings that differences in intelligence between perceivers or the load on working memory have no effect on assessments of trustworthiness (Bonnefon et al. 2013). However, only a few studies explicitly consider the target × perceiver interactions. Especially with regard to gender, there are only a few studies that explicitly test the effects. For example, women assess the trustworthiness of a target based on the face faster and more accurately than men (Dzhelyova et al. 2012). In addition, female perceivers show typical adaptation effects (adaptation aftereffects) depending on the trustworthiness of the target, while male perceivers do not show this effect (Wincenciak et al. 2013). However, it is unclear whether women or men can be said to have an automatic or controlled processing process in terms of efficiency and interference.

5 Conclusion and Outlook

Research has been able to show on a theoretical and empirical level that the three domains of trustworthiness/valence, dominance/competence, and youthfulness and attractiveness (Sutherland et al. 2013; Sutherland et al. 2016) are relevant not only in the interpersonal context, but also in partner selection in particular (Fletcher et al. 1999).

In addition, there are temporally and interculturally robust gender differences regarding the physical attractiveness of the partner (more important for men than for women), as well as regarding the status and resources of potential partners (more important for women than for men). With regard to trustworthiness, there are no gender differences in self-report, although differences can be found at a more basic cognitive level.

Although the mutual enrichment of evolutionary psychological theories with cognitive theories for the investigation of partner choice-relevant characteristics has already been highlighted (e.g., Maner et al. 2003), there is a lack of systematic research on the more basic cognitive (e.g., perceptual) processes in the three domains of partner choice. While most findings rely on self-reports, it is equally important to investigate more basic cognitive processes to better capture and validate the patterns identified through self-report measures.

A special feature of these basic cognitive processes is the degree of automaticity, with the criterion of efficiency being particularly important. Cognitive processes that are subject to the processing of physical attractiveness are relatively well researched. Significantly fewer empirical studies investigate the processes that concern the domains of status and resources as well as trustworthiness. In all three domains, there is a lack of robust findings. Predominantly, results are only available for one criterion of automatization. Due to different methodological approaches (stimuli and implementation), there is a lack of replications and generalizations. In addition, most studies primarily focus on the properties of the targets and neglect the perceivers and the target × perceiver interactions, which are particularly relevant in the context of partner choice research. To date, no comprehensive research program systematically investigates whether and when cognitive processes underlying perceiver and target effects — including their interaction in the three domains of partner choice — operate automatically and efficiently. Such results would not only complement the findings from self-reports on a theoretical level, but would also provide feedback on the understanding of cognitive processes as an adaptive response to our social environment.

In particular for the evolutionary social sciences, a systematic research program that equally addresses the three domains of partner choice, as well as the target, perceiver, and target × perceiver interactions, could be helpful. This could lead to the hypothesis that very basic automatic cognitive processes, such as those involved in perception and attention allocation, may exhibit cultural invariance, whereas higher-order cognitive processes (e.g., self-reports) are likely to be strongly shaped by cultural influences. Furthermore, an evolutionary psychological perspective may provide new impulses for identifying environmental features that potentially regulate experience and behavior. For example, it has already been shown that for people living in regions with a high burden of disease-causing pathogens (such as a high prevalence of leprosy-causing *Mycobacterium leprae*), the appearance of potential partners is more important than for people in regions with relatively low pathogen load (Gangestad and Buss 1993; see summary Schwarz 2015). A very interesting, but open question would be whether such long-term or short-term accumulations of pathogens in different populations could also modulate the automatic processing of targets. This could give us information about whether the control of the famous first impression is culture-invariant (and perhaps rather "hard-wired") or not. Cognitive psychology certainly has the right paradigms in these (and other) cases to provide answers to such questions beyond self-report. One just has to dare to ask such questions.

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Mate Value lies in the Fitness Function of the Beholder

Alex Rieger, Annemarie Hartung and Jan de Haan

1 Background

In recent decades, modern evolutionary theory has increasingly made its way into the behavioural sciences, and evolutionary psychology has been a firmly established discipline for some time. The starting point here is that evolutionary theory can be seen as an overarching theoretical basis for the study of human behaviour (Borgstede 2020; Buss 2004; Catania 2013; Miller 2011). Although such an overarching and general theory appears highly desirable in psychological science (see Gigerenzer 2010), many concrete approaches so far have not been able to link formal evolutionary biological models to psychological theories, as these are almost never formalised, but usually exist in (colloquial) linguistic form (Stearns and Rodrigues 2020). As a consequence, there is a largely metaphorical use of evolutionary biological concepts within (evolutionary) psychology. This metaphorical use of evolutionary biological terminology leads to a loss of precision regarding their formal-theoretical meaning (see e.g. Stearns and Rodrigues (2020) and Nettle and Frankenhuis (2020) on the use of the term *life history*). Stearns and Rodrigues (2020) point out that this can be misleading and within the behavioural sciences and psychology even leads to the derivation of hypotheses

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that contradict formal models from evolutionary biology. This problem is also relevant for the evolutionary psychological term mate value.

Mate value is defined as the contribution of a person to the fitness of their reproductive partner (Howie and Pomiankowski 2018). Since this is a latent, unobservable construct, evolutionary psychological and sociological research faces the challenge of finding empirical access to it. Approaches to this either use individual characteristics, the sum of various such characteristics of a person, or a holistic self-assessment, by asking people to rate their own mate value on a scale (Edlund and Sagarin 2014). These mate value relevant characteristics include, for example, *physical attractiveness* and *physical symmetry* (e.g. Fisher et al. 2008; Walter et al. 2020), *financial status* (Walter et al. 2020; Buss 1989) or certain *personality traits* such as kindness (Miller 2007). The problem with this approach is that there is no agreement on which characteristics are of what importance for capturing mate value (Edlund and Sagarin 2014). The methodological approach also varies greatly. For example, in self-assessments, people are asked how they rate their own attractiveness (or another mate value relevant characteristic) for potential partners (Brase and Guy 2004). Other approaches capture concrete events as an indicator of mate value, such as mating success or the number of offspring (Edlund and Sagarin 2014).

Strictly speaking, the various operationalizations define different characteristics and thus suggest that various characteristics (physical properties, self-assessments, etc.) are summarised under the theoretical concept of *mate value*. This leads to an ambiguity in the theoretical embedding of mate value and possibly contradictory empirical results. These become apparent, for example, when the characteristic-based approach to mate value (mate value is considered a personality trait here) is used to search for underlying dimensions on which to project the many different characteristics. Following a dimension-reductionist approach, various models were established using factor and principal component analyses (Buss and Barnes 1986; Flechter et al. 1999; Goodwin and Tang 1991; Kenrick et al. 1990; Regan and Joshi 2003; Shackelford et al. 2005; Simpson and Gangstad 1992). These models differ in both the number and type of dimensions of partner preferences. For example, Simpson and Gangestad (1992) found only two dimensions, while Buss and Barnes (1986) found nine dimensions. Most researchers assumed independent dimensions (Buss and Barnes 1986; Goodwin and Tang 1991; Kenrick et al. 1990; Regan and Joshi 2003; Simpson and Gangstad 1992). Only Shackelford et al. (2005) and Flechter et al. (1999) suggested solutions with dependent dimensions. Especially considering that all preferences refer to properties that should serve as indicators for mate value, the finding of independent dimensions is surprising, as it should be assumed that the properties of mate value should all be related to fitness (Howie and Pomiankowski 2018).

Based on newly proposed formal models of behavioural selection (Borgstede and Eggert 2021; Borgstede 2020), the theoretical embedding of the term mate value or its scope can be achieved. In these models, the selection of behaviour within recurring contexts is formally and theoretically embedded in natural selection and thus theoretically integrated. As a result, these models offer an alternative approach to the concept of mate value and consequently to mate choice (in humans) in general. The following presents the *Multilevel Model of Behavioral Selection* (MLBS) used by Borgstede and Eggert (2021) (see also Borgstede and Simon in this volume), and two examples illustrating how empirical phenomena can be represented and explained by the model.

2 Model

The theoretical basis for the MLBS is *Price's Equation* (Price 1970), with which selection processes, especially natural selection, can be formally modelled.

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E(w_i \Delta z_i) \tag{1}$$

Eq. 1 describes the average change of a feature z ($\Delta\overline{z}$), weighted by the average fitness $\overline{w}$, in a population of n individuals (index i = 1,2,…,n). This change is described as the sum of the linear relationship between fitness and feature, as well as the expected value of the product of fitness and change in feature. The linear relationship on the right side of the equation is modeled by the covariance of feature value z_i and fitness w_i of the individuals. The covariance term ($Cov(\ldots)$) can be interpreted as the influence of natural selection on the average change in feature value in the population (from one time step to the next) (Price 1970). The expectation term ($E(\ldots)$) then describes all other influences that cannot be attributed to natural selection.

What is interesting about *Price s Equation* is that the expected value term on the right side of the equation has a formal similarity to the term on the left side of the equation. This makes it possible to define the equation for multiple levels of selection and to nest these recursively into each other (Frank and Godsoe 2020). For an additional level of selection, which is indexed by j, Eq. (2) results.

$$\overline{w}\Delta\overline{z} = Cov(w_i, z_i) + E\left(Cov\left(w_{ji}, z_{ji}\right) + E_j\left(w_{ji}\Delta z_{ji}\right)\right) \tag{2}$$

In the expected value term on the right side of the equation, *Price s Equation* for the additional level of selection is included. For modelling behavioural selection, a two-level *Price Equation* as in Eq. (2) is required. The two levels are interpreted as natural selection over generations (phylogenesis) and *behavioural selection* over behavioural episodes (ontogenesis) (Borgstede and Eggert 2021). As a result, a version of Eq. (2) is obtained for which the considered characteristic z is a specific behaviour b (e.g., measured as behaviour rate). This is possible because the behaviour of an organism is also a phenotypic feature. Eq. (3) follows from Eq. (2) by appropriate substitution.

$$\overline{w}\Delta\overline{b} = Cov(w_i, b_i) + E\left(Cov\left(w_{ji}, b_{ji}\right) + E_j\left(w_{ji}\Delta b_{ji}\right)\right) \tag{3}$$

Analogous to Eq. (2), Eq. (3) describes the average behaviour change. By assuming linear fitness predictors, which are substituted for fitness in the model and serve organisms to anticipate fitness consequences, the *Covariance-based law of effect* (CLOE),[1] which describes the behaviour change, results in Eq. (4) (Borgstede and Eggert 2021). Fitness predictors (in Eq. (4) referred to as p) are possible consequences of behaviour, which are statistically correlated with the fitness of the organism.

$$w_i\Delta b_i = \gamma_p\beta_{pb}Var\left(b_{ij}\right) + \delta \tag{4}$$

Here, δ denotes a residual term. The central pieces of the CLOE are the covariances of behaviour and fitness predictors, as well as the fitness predictors and fitness. These statistical relationships between fitness predictor and fitness or behaviour and fitness predictor are represented in the CLOE by the regression weights γ_p and β_{pb}. It is assumed that the organism approximates fitness through the fitness predictor *linearly*. Also, a linear approximation of the relationship between fitness predictors and behavior is assumed. Based on these considerations, it is possible to formulate the CLOE in the form of a covariance structure model (more precisely a path model; see Weiber and Mühlhaus 2014), so that the regression coefficients can be both theoretically interpreted and possibly empirically estimated.

To show this initially abstract and detached from concrete examples, a possible specification of such a covariance structure model is shown in Fig. 1.

In this exemplary specification of the model, there are three different alternative behaviors (b_1, b_2, b_3), each with different statistical relationships (represented by the regression weights β_{11}, β_{21}, …) to the four possible fitness predictors here (p_1, p_2, …). These four fitness predictors in turn each have different statistical relationships (represented by the regression weights γ_1, γ_2, …) with fitness (w). It

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[1] For details on the derivation, see the appendix of Borgstede and Eggert (2021).

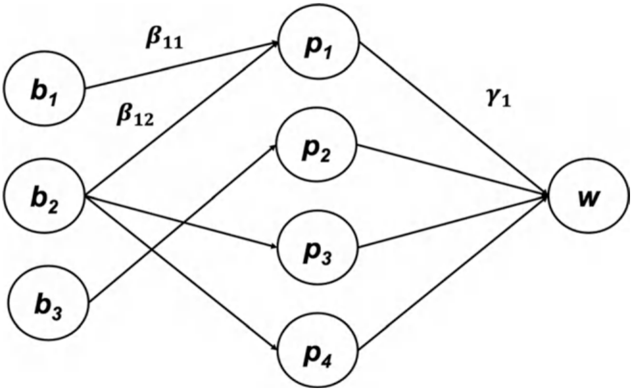

Fig. 1 A possible specification of the path model as in Borgstede and Eggert (2021). Three behavioural alternatives b_1, b_2, b_3, with respective relationships β_{jl} ($j = 1,2,3$, $l = 1,2,3,4$) to the four fitness predictors p_l ($l = 1,2,3,4$), which in turn each have a relationship γ_l ($l = 1,2,3,4$) to fitness w.

is important to note that some paths in this exemplary specification were explicitly removed or the corresponding regression weights were set to zero. On the other hand, it should be noted that for better clarity in the chosen representation, measurement errors are not taken into account for now in order to better illustrate the conceptual idea.[2]

In addition to the graphical representation as a path model, it is also possible to formulate the model in matrix form as a system of equations (Weiber and Mühlhaus 2014). This will be shown for the case in Fig. 1 in the following. For this, the individual regression equations are first written separately for the fitness predictors (5) and for the fitness (6):

$$\begin{bmatrix} p_1 \\ p_2 \\ p_3 \\ p_4 \end{bmatrix} = \begin{bmatrix} \beta_{11} & \beta_{12} & 0 \\ 0 & 0 & \beta_{23} \\ 0 & \beta_{32} & 0 \\ 0 & \beta_{42} & 0 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} \tag{5}$$

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[2] Of course, measurement errors can easily be integrated into the model and could be inserted both in the fitness predictors and in the fitness itself, depending on the specific application case.

$$w = \begin{bmatrix} \gamma_1 \\ \gamma_2 \\ \gamma_3 \\ \gamma_4 \end{bmatrix}^T \begin{bmatrix} p_1 \\ p_2 \\ p_3 \\ p_4 \end{bmatrix} \tag{6}$$

Overall, by substituting (5) into (6), equation (7) results:

$$w = \begin{bmatrix} \gamma_1 \\ \gamma_2 \\ \gamma_3 \\ \gamma_4 \end{bmatrix}^T \begin{bmatrix} \beta_{11} & \beta_{12} & 0 \\ 0 & 0 & \beta_{23} \\ 0 & \beta_{32} & 0 \\ 0 & \beta_{42} & 0 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} \tag{7}$$

The model can be formulated even more compactly in matrix algebraic shorthand:

$$w = \overrightarrow{\gamma}^T \boldsymbol{\beta} \overrightarrow{b} \tag{8}$$

In (8), $\overrightarrow{\gamma}^T$ denotes a four-dimensional vector of fitness predictors, $\boldsymbol{\beta}$ the matrix of regression coefficients, and $\overrightarrow{b}$ the behaviour vector, which in this case is three-dimensional. The matrix $\boldsymbol{\beta}$ describes the relationship of behaviours with the fitness predicting consequences. This is usually referred to as *contingency structure* in behavioural theory. For a specific (e.g., empirically determined) behaviour vector, the predicted fitness results as a linear function of the behavioural distribution (on different alternatives, which correspond to the elements of the behavior vector $\overrightarrow{b}$) described by this vector.

3 Applications of the Model

For the application of the model in an example case, the behaviour vector $\overrightarrow{b}$ is of central importance, as it describes the distribution of the organism's behaviour at any given time (a temporal trajectory of this vector can then be interpreted as behavioural adaptation; Borgstede and Luque 2021).

The assumed environmental context for these examples is supposed to be a nightclub. Two alternative behaviours of a person are considered. Here, b_1 represents the behaviour of approaching a person, while b_2 represents the behavior of dancing with a person. Then, the linear relationships (described by the regression

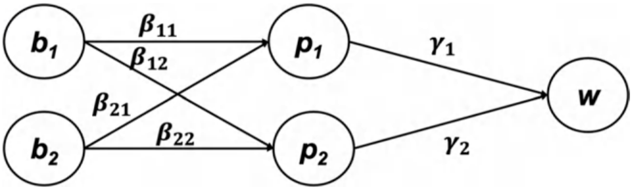

Fig. 2 Displayed is a specific application of the model for two behavioural alternatives b_1, b_2 and two fitness predictors p_1, p_2, as well as the respective relationships represented by the parameters β_{jl} ($j = 1{,}2$) and γ_l ($l = 1{,}2$) relating to the prediction of fitness w.

weights β_{11}, β_{12}, …) with the two fitness predictors of going home with the person (p_1), or arranging to meet the person again (p_2), which then also have different linear relationships (described by the regression weights, γ_1 and γ_2) with fitness are considered (Fig. 2).

For this example, we assume that speaking to a person is more likely to lead to another date than dancing with a person. Formally, this is expressed in the constraint that the regression coefficients are: $\beta_{21} > \beta_{22}$. We also assume for this example that dancing with a person is more likely to result in going home with that person, than is speaking to that person. This is expressed in another constraint for the regression coefficients, here: $\beta_{12} > \beta_{11}$. The regression weights γ_1 and γ_2 each describe the fitness prediction, which results from the consequence of going home with the person or arranging to meet the person again.

Now we consider a second case of the example to illustrate dynamic changes in the context conditions. Let's assume that the *Sex Ratio* in the nightclub changes. Specifically, we consider here the occurrence of an additional person competing for mating partners (hereinafter referred to as *rival*). This results in a change in the coefficient matrix of the model, which describes the change in the contingency structure (Fig. 3).

The rival (here denoted by *R*) influences, for the assumed example, how the relationships of the behaviour of talking to a person are with the respective fitness predictors, e.g., because the rival interferes in a conversation. We initially assume for the example that it is easier to physically keep the rival at a distance while dancing, for instance, by positioning oneself between the rival and the potential partner. This could be interpreted as *Mate Guarding* (Arnocky et al. 2014). Formally, this is expressed through changed regression coefficients β'_{11} and β'_{12}, which include the respective influence of the rival on the corresponding behavioural alternatives. We assume that the influence of the rival, as described above,

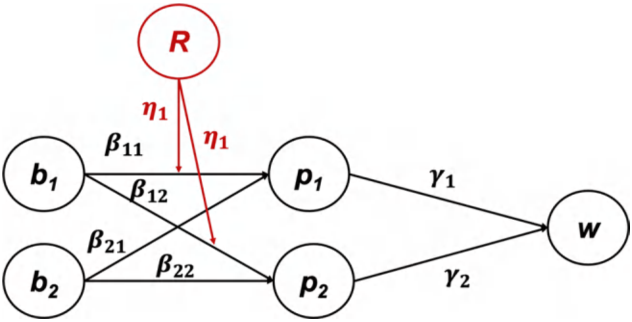

Fig. 3 Again shown is a specific application of the model for two behavioral alternatives b_1, b_2 and two fitness predictors p_1, p_2, where here the relationships of the behaviours with the fitness predictors are modified by the influence of a rival R (represented by the parameters η_1 and η_2).

leads to the behaviour of r talking to a person having a lower correlation with the fitness predictors. This is formally expressed by $\beta'_{11} < \beta_{11}$ and $\beta'_{12} < \beta_{12}$.

This example shows how changes in the contingency structure formally result in changes to the coefficient matrix $\boldsymbol{\beta}$, which represents the relationships between behaviour and the fitness predictors.

4 Outlook

The modeling approach presented here is based on the *Multilevel Model of Behavioural Selection* (*MLBS*), which describes behavioral selection at various levels. The *MLBS* provides a new theoretical framework for the consideration of mate selection behaviour. This approach dispenses the assumption of a latent and theoretically not precisely defined construct of *mate value*. The model presented explicitly (i.e., formally-mathematically) establishes a connection to evolutionary biology, which in previous evolutionary psychological considerations is often only of a metaphorical nature (see Eggert and Holzhauser in this volume).

Looking at the approach presented here, it becomes clear that the assumption of a static *mate value* (in the sense of a psychological property) is of limited explanatory potential: The *mate value* of a specific person can be fully formulated as fitness consequences for a specific other person. Specifically, the behavioural distribution of a person results in an expected fitness consequence (as a weighted sum of the respective fitness predictors and the behaviour distribution). Interestingly, these expected fitness consequences can change dynamically. Formally, this is expressed by the fact that the coefficient matrix $\boldsymbol{\beta}$ and the coefficient vector $\vec{\gamma}$ can be changed over time by various influencing factors and could be explicitly parameterized with a corresponding parameter t. Therefore, the *mate value* or a comparable, assumed to be static, construct cannot provide a meaningful explanation. It is appropriate to explicitly consider changes due to, for example, different (potential) partners. For this, it is necessary to construct such a path model for each person, whereby the same paths can have different regression coefficients for different people. Accordingly, it is possible that addressing a certain person provides different fitness predictions for different people. This is not compatible with the idea of a fixed *mate value* of the person to be addressed.

At the same time, this modeling approach allows a more precise explanation of behaviour compared to the often imprecise, verbal idea that potential partners have a different expression of a characteristic named mate value and are differentially approached with mate attraction behaviour depending on this.

It can be assumed that this model will enable the description of various special cases in the future. This allows for a quantitative description and a more precise theoretical clarification of existing approaches, such as the distinction between "short-term" vs. "long-term" mate choice strategies (Buss and Schmitt 1993). An example of a phenomenon that has so far only been described empirically, but has not yet been embedded in a theory, is the *closing time phenomenon*, which was studied in the context of bars. This refers to the fact that people of the opposite sex are perceived as more attractive the later it gets. The ratings are particularly high when the bar is about to close (closing time; Gladue and Delaney 1990). This corresponds to a lowering of the standards for the physical attractiveness of potential partners. In our model, this could be translated into the behaviours of addressing people with cues of high physical attractiveness (e.g., Waist-Hip Ratio; Singh et al. 2010) and addressing people who lack these cues. While at the beginning of an evening the behaviour of addressing people with cues of high physical attractiveness can still have a relatively high correlation with fitness predictors, such as a one-night stand, this changes over the course of the evening as more and more potential mating partners become unavailable because they have already left the bar (alone or with someone else). This change in context leads to the behaviour of addressing a person who has fewer cues of physical attractiveness now having a significantly higher correlation with the fitness predictor of having a one-night stand.

In addition, this model can not only investigate individual effects, but also integrate the dependency structures of individual terms (behavioural alternatives, fitness predictors, fitness) into a model. It also shows that existing mate value definitions correspond to different terms of the formal model, pointing to the already mentioned lack of precision of the theoretical construct *mate value*. This can simultaneously offer approaches to integrating the existing empirical findings into a new theory of behaviour.

Thus, the clarification of the relationship between mate choice and partner value expands the *theory-net* (Borgstede and Luque 2021) surrounding the MLBS to include mate choice.

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Evolutionarily Stable Reviewing Strategies and Scientific Paradigm Dominance

Georg P. Müller

1 Introduction and Research Question

The *peer-reviewing* of academic papers is an important standard procedure of modern science (Daniel 1993, Chap. 1). Those who as authors successfully overcome this hurdle and thus can publish in respected journals, have better chances of surviving in the long term in the university system and, based on their own research experience, becoming a *reviewer* themselves (Shatz 2004, pp. 128 ff.). *Monoparadigmatic reviewing,* which strongly orientates the acceptance/rejection of works on a single *dominant* paradigm, therefore has a certain conservative tendency towards self-perpetuation (Shatz 2004, Chap. 3; Moosa 2018, Sect. 7.3 and 7.4). To what extent this represents an evolutionarily stable strategy in the sense of Maynard Smith (1996), which prevents the penetration of new, alternative paradigms into a scientific field, will be clarified in this work.

For this purpose, the author has conceptualised science dynamics as an *evolutionary game* of two competing "species" of scientists, who represent the dominant old, resp. a new paradigm and are active both as *reviewers* and as scientific authors (Mueller 2017). The publication success of the two paradigmatic groups corresponds to their *evolutionary fitness,* because the long-term survival in academia depends on successful publishing in journals. According to the Darwinian

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This chapter is a substantially revised version of a work that the author published in English a few years ago with Springer-Verlag. See Mueller (2017).

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principle of the *survival of the fittest*, the population growth of the two groups can therefore be formalized as an evolutionary game (Weibull 1997).[1] The development of the size of the two paradigmatic groups depends, among other things, on their representation in the *board of reviewers,* their openness to other (foreign) paradigms, and the scientific depletion of the two paradigms. The last two parameters are central analytical variables of this work (see Figs. 5 and 6).

Due to the relatively high complexity of the aforementioned relationships, computer simulations are the method of choice to analyze the population dynamics of the two "species" of paradigm representatives for different parameter values and scenarios. The simulations based on an *EXCEL spreadsheet* start with the "invasion" of a new paradigm, which is supported by 5% of the entire academic population in the short term and then continue over 200 time steps. With this methodological approach, it can be analyzed whether and for how long the old paradigm can regain its original 100% dominance, whether it disappears completely in the long term or is still represented asymptotically by a certain population share.

Such simulations can bring the central research questions of this work closer to an answer: Under what conditions is monoparadigmatic *peer-reviewing* an evolutionarily stable strategy, which, however, also prevents a scientific field from adapting to new methods, theories, and questions? Under what circumstances and with what delay does the opposite happen, i.e., a complete adaptation to changed environmental conditions through a revolutionary paradigm shift in the sense of Thomas Kuhn (1962, Chap. ix), by which the old paradigm definitely and completely disappears? And finally: Under what conditions occurs a stable coexistence of paradigms, which is so characteristic for the humanities and social sciences and through which the old paradigm survives in a more or less large ecological niche?

2 A Model of Paradigm Competition

The simulation model presented below assumes the existence of two disjoint "species" of scientists, of which a population share Pa exclusively represents an initially still dominant old paradigm and a complementary population share

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[1] For more on evolutionary game theory, see also the contribution by Diekmann in this volume.

Pn (= 1 - Pa) exclusively represents a new paradigm. Proportional to these population shares, the two "species" are also active as reviewers in the review committees of scientific journals. When they review an *intra-paradigmatic* work, which corresponds to their own paradigm, the average *acceptance probability is Ai.* When reviewing an *extra-paradigmatic* work, which represents a paradigm foreign to them, the average *acceptance probability is Ae.* It is likely that Ai > Ae, because the reviewers are convinced of their own paradigm. Under the assumption of random matching of author and reviewer, Table 1 shows for works based on the *old* paradigm, a *total acceptance probability*

$$\mathrm{Pa} * \mathrm{Ai} + \mathrm{Pn} * \mathrm{Ae} \tag{1a}$$

and for works based on the *new* paradigm, a *total acceptance probability*

$$\mathrm{Pa} * \mathrm{Ae} + \mathrm{Pn} * \mathrm{Ai} \tag{1b}$$

The publication success of a paradigm naturally depends not only on the total probability of acceptance by the review committees, but also on the *simplicity of discovering Ea,* resp. *En* with the *old,* resp. the *new* paradigm: New paradigms initially offer many easy-to-solve scientific problems, which is much less the case with old, depleted paradigms (Kuhn, 1962, Chaps. 6 and 7). In Table1 it is

Table 1 The fitness Fa and Fn of the representatives of the old/new paradigm

	Author represents	
	Old Paradigm	New Paradigm
Population share	Pa	Pn = 1 - Pa
Acceptance by old paradigm	Ai	Ae
Acceptance by new paradigm	Ae	Ai
Total acceptance probability	Pa * Ai + Pn * Ae	Pa * Ae + Pn * Ai
Ease of discovery	Ea	En
Publication success = Fitness	Fa = Ea * (Pa * Ai + Pn * Ae)	Fn = En * (Pa * Ae + Pn * Ai)

Legend: Ai = Acceptance of intra-paradigmatic works; Ae = Acceptance of extra-paradigmatic works; Pa = Share of old paradigm in population of authors and reviewers; Pn = Share of new paradigm in population of authors and reviewers; Ea = Ease of discovery with the old paradigm; En = Ease of discovery with the new paradigm; Fa = Fitness of the representatives of the old paradigm; Fn = Fitness of the representatives of the new paradigm therefore postulated that the publication success of the *old* paradigm, referred to as fitness, equals

$$\mathrm{Fa} = \mathrm{Ea} * (\mathrm{Pa} * \mathrm{Ai} + \mathrm{Pn} * \mathrm{Ae}) \tag{2a}$$

and the publication success, resp. the fitness of the *new* paradigm is equal to

$$\mathrm{Fn} = \mathrm{En} * (\mathrm{Pa} * \mathrm{Ae} + \mathrm{Pn} * \mathrm{Ai}) \tag{2b}$$

The term *fitness* reflects the ability of the paradigm representatives to survive in academia in the long term according to the principle of *publish or perish* (Moosa 2018, Sect. 1.1).[2] Since the number of academic positions is limited, there is paradigm competition in the *survival of the fittest* (Darwin 2014, Chap. 4; Spencer 1974, p. 78). The populations of the paradigm representatives grow according to the fitness difference between the two "species". Thus we hypothesise that

$$\Delta Pa = \delta * (\mathrm{Fa} - \mathrm{Fn}), \text{ if } 0 < \mathrm{Pa} < 1, \text{ else } \Delta Pa = 0 \tag{3a}$$

and

$$\Delta Pn = \delta * (\mathrm{Fn} - \mathrm{Fa}), \text{ if } 0 < \mathrm{Pn} < 1, \text{ else } \Delta Pn = 0 \tag{3b}$$

where δ is the *length of the time step considered* and ΔPa and ΔPn are the *growth* of the *old,* resp. *new* paradigm. This growth is controlled not only by arrivals and departures of scientists, but also by social *imitation learning* (Bandura 1971, pp. 6 ff.), through which a portion of the scientists pragmatically converts to the paradigm with the higher fitness.

According to the two equations (2a) and (2b), the fitness of a paradigmatic "species" also depends on the simplicity of discoveries Ea, resp. En with the corresponding paradigm. Since paradigms are depleting by the collective solving of scientific "puzzles" (Kuhn 1962, Chap. iv), Ea and En are not constants, but change over time: The larger the share Pa, resp. Pn of the researching representatives of a paradigm and the greater their publication success Fa, resp. Fn, the more the stock of such "puzzles" dwindles and the more difficult the remaining scientific problems are to solve. Accordingly, in this work it is assumed that Ea and En change according to the following difference equations:

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[2] For the concept of biological/evolutionary fitness, see also the contribution by Willführ in this volume.

$$\begin{aligned}&\mathit{\Delta En} = -\delta * \mathrm{Fn} * \mathrm{Pn},\ \text{if En} > 0,\ \text{else}\ \mathit{\Delta En} = 0,\\ &\text{with standardised start value En} = 1\ \text{and constant time interval}\ \delta\end{aligned} \tag{4a}$$

$$\begin{aligned}&\mathit{\Delta Ea} = -\delta * \mathrm{Fa} * \mathrm{Pa},\ \text{if Ea} > 0,\ \text{otherwise}\ \mathit{\Delta En} = 0,\\ &\text{with ``aged" start value Ea} < \text{En} = 1\ \text{and constant time interval}\ \delta\end{aligned} \tag{4b}$$

The overall model discussed in the following sections of this work consists of the equations (2a, 2b), (3a, 3b) and (4a, 4b). It has been empirically tested in a previous work of the author (Mueller 2017), by analysing the competition between the old paradigm of the simulation technique of *systems dynamics modelling* and the newer approach of *agent based modelling* (Gilbert and Troitzsch 1999, Chaps. 3 and 8). By comparison with the number of publications that appeared between 1993 and 2012 and which were recorded in Google Scholar (2014), the model could be empirically well confirmed (see Mueller 2017, Fig. 4).

3 A Typology of Paradigm Dynamics

To explore the previously described model of paradigm dynamics, the share of the representatives of the new paradigm is increased from 0 to 5% at the start of the simulations. Subsequently, the population dynamics of the two paradigms under investigation are analyzed over 200 time steps, with a particular interest in the occurrence and duration of the evolutionary stability of the *old* paradigm. In qualitative terms, four types of paradigm dynamics can be distinguished:

a) The *permanent evolutionary stability* of the old paradigm, which successfully defends its dominance and repels the "invasion" of the new paradigm: See Fig. 1. Science becomes a quasi-religious dogma, for which, however, there are few examples. The political economy of Marxism-Leninism probably belongs to this. As Fig. 1 shows, such paradigms survive even when their fitness Fa and their scientific productivity asymptotically approach the level zero.

b) The *temporary evolutionary stability* of the old paradigm: See Fig. 2. With parameter values that are only slightly changed compared to Fig. 1, the old paradigm is still stable for a certain period of time, but is eventually completely replaced by the new paradigm. Typically, the new paradigm represents scientific ideas, for which the time is not yet "ripe", such as the heliocentric cosmology of Copernicus that only later established itself as the dominant new

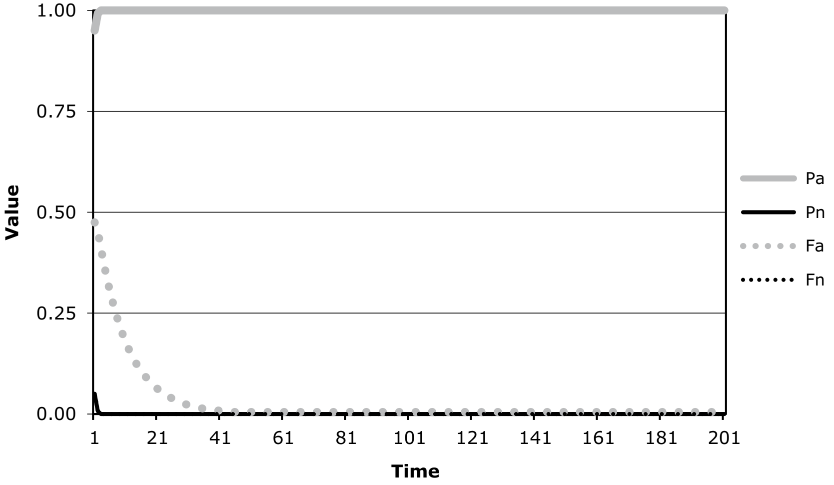

Fig. 1 Permanent stability of the old paradigm
Legend to the values on the vertical axis: Pa: Population share of the old paradigm; Pn: Population share of the new paradigm; Fa: Fitness of the representatives of the old paradigm; Fn: Fitness of the representatives of the new paradigm, here invisible due to overlay by Pn. *Parameter values*: Acceptance Ae = 0; Acceptance Ai = 1.0; Simplicity Ea = 0.5; Simplicity En = 1.0; Time interval δ = 0.1

paradigm in spite of the resistance of the Catholic Church. The central descriptive parameter here is thus the time between the "invasion" of the new paradigm and the beginning of the decay of the old.

c) The *lack of evolutionary stability* of the old paradigm: See Fig. 3. Here, the old paradigm is unable to repel the "invasion" of the new one and disappears after a short time *completely* and *definitively.* This dynamic is typical for scientific revolutions in the sense of Thomas Kuhn (1962), e.g. for the transition from Newtonian to relativistic mechanics at the beginning of the 20th century. In the model discussed here, Kuhn's scientific revolution is thus only one possible case among other science dynamics, which are described under (a), (b) and (d).

d) The *Renaissance* of the old paradigm: See Fig. 4, which shows how the old paradigm is initially displaced by the new one, but then experiences a renaissance in a more or less large niche. The asymptotically long-term population

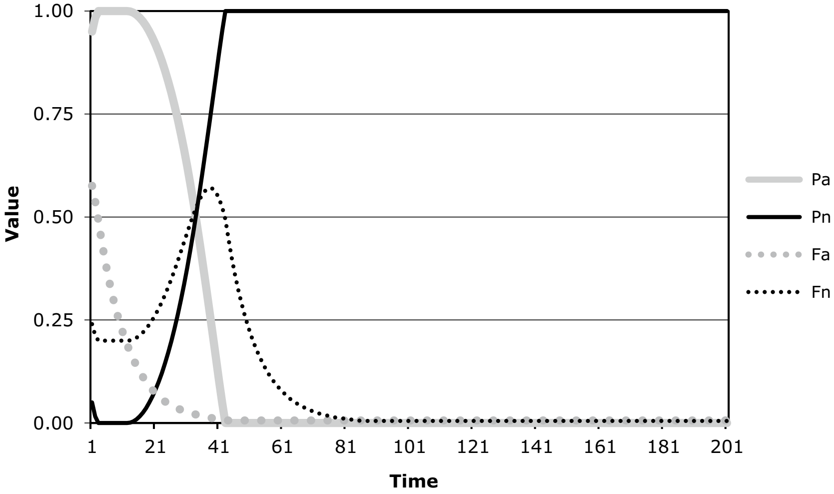

Fig. 2 Temporary stability of the old paradigm
Legend to the values on the vertical axis: Pa: Population share of the old paradigm; Pn: Population share of the new paradigm; Fa: Fitness of the representatives of the old paradigm; Fn: Fitness of the representatives of the new paradigm. *Parameter values*: Acceptance Ae = 0.2; Acceptance Ai = 1.0; Simplicity Ea = 0.6; Simplicity En = 1.0; Time interval δ = 0.1

share of the old paradigm is an important descriptive parameter for describing the size of the niche in this situation. The current revival of non-evidence-based "pre-school medicine" is a typical example of the renaissance of an old paradigm and the resulting multiparadigmatic science.

4 Conditions for the Evolutionary Stability of the old Paradigm

Computer simulations show that the science dynamics discussed in the last section depend on the one hand on the acceptance Ae of external paradigms by the representatives of the old and new paradigms. The present model *simplifyingly* assumes that all reviewers—regardless of their paradigmatic orientation—have the same acceptance value Ae. On the other hand, the depletion of the old paradigm, which is complementary to the simplicity Ea, must also be taken into

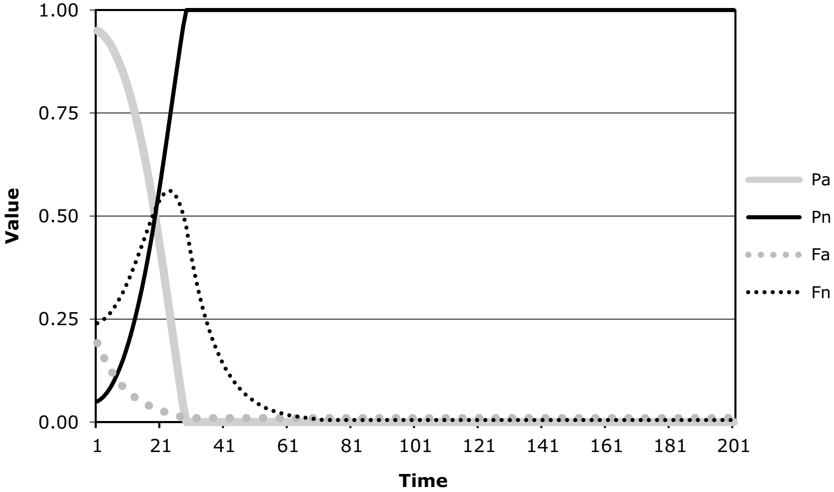

Fig. 3 Lack of stability of the old paradigm
Legend to the values on the vertical axis: Pa: Population share of the old paradigm; Pn: Population share of the new paradigm; Fa: Fitness of the representatives of the old paradigm; Fn: Fitness of the representatives of the new paradigm. *Parameter values*: Acceptance Ae = 0.2; Acceptance Ai = 1.0; Simplicity Ea = 0.2; Simplicity En = 1.0; Time interval δ = 0.1

account for the paradigmatic development. By varying these two parameters, it can be determined how *long* the old paradigm remains stable after the appearance of 5% of scientists representing the new one (see Fig. 5) and what *asymptotic value* the population share Pa has 200 time steps after this event (see Fig. 6).

Permanent evolutionary stability of the old paradigm only exists according to Fig. 5 if the acceptance Ae for external paradigms is zero and the old paradigm is not completely depleted, i.e. if Ea > 0. This in turn requires a monopolistic, or dictatorial control of the scientific journal market by the representatives of the old paradigm, which is difficult to achieve in an open society. In practice, Ae is likely to always be greater than zero. As Fig. 5 shows, the old paradigm remains dominant for a certain period of time for 0 < Ae ≤ 0.20, until it is sufficiently depleted. After that, however, it collapses and disappears definitively (see Fig. 6). The lifespan of the old paradigm is the greater the higher its *initial* simplicity of discovery Ea is. However, the lifespan can also be *zero* (see Fig. 5, e.g. Ae = Ea = 0.20).

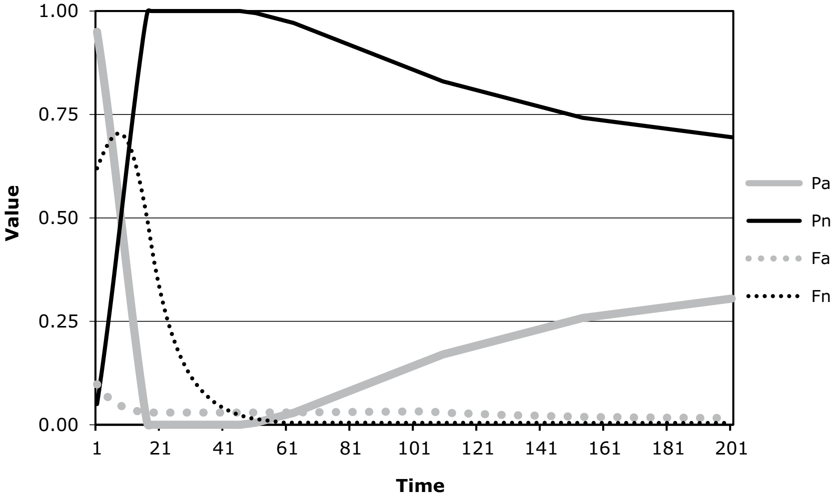

Fig. 4 Renaissance of the old paradigm
Legend to the values on the vertical axis: Pa: Population share of the old paradigm; Pn: Population share of the new paradigm; Fa: Fitness of the representatives of the old paradigm; Fn: Fitness of the representatives of the new paradigm. *Parameter values*: Acceptance Ae = 0.6; Acceptance Ai = 1.0; Simplicity Ea = 0.1; Simplicity En = 1.0; Time interval δ = 0.1

Then a scientific revolution, as described by Thomas Kuhn, occurs *immediately* after the appearance of the new paradigm.

If the acceptance of external paradigms is further increased, so that Ae ≥ 0.30, the collapse of the old paradigm either occurs immediately or with a certain delay, followed by its *renaissance*. It survives in a more or less large niche, but is no longer dominant: Two paradigms tolerate each other in this situation, resulting in a *multiparadigmatic* situation. Thus, not only a very low, but also a high acceptance of foreign paradigms is a good survival strategy for the followers of the old paradigm. This "live and let live" in the sense of Paul Feyerabend's "*Anything goes*" (1976) seems to be a typical evolutionary strategy of the various currents in the humanities and social sciences. The so-called *hard sciences*, on the other hand, tend to lean towards the first strategy of low acceptance of external paradigms, which often led to that sequence of monoparadigmatic stages in the history of these sciences that Thomas Kuhn (1962) also described.

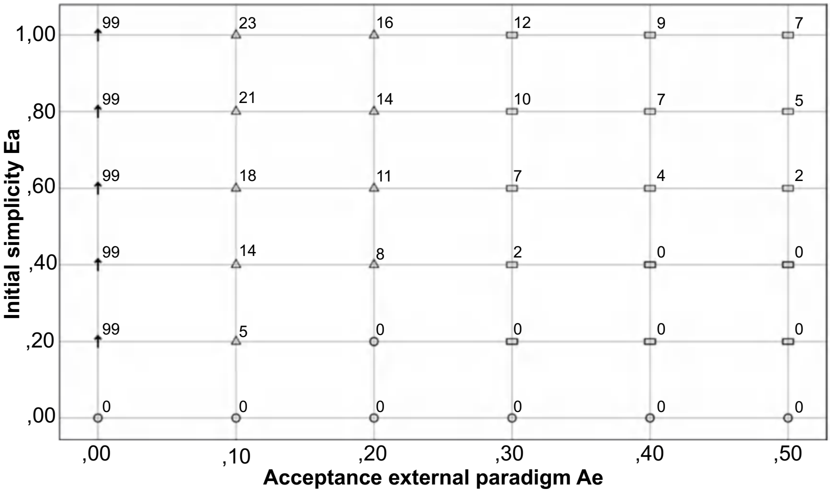

Fig. 5 Duration of the stability of the old paradigm
Legend: 0–98: Finite duration of stability in simulated time units; 99: Infinite duration; Ae: Acceptance of external paradigm; Ea: Initial simplicity of discovery with the old paradigm; Arrow: Permanent stability; Triangle: Temporary stability; Circle: Lack of stability; Rectangle: Renaissance of old paradigm. *Initial parameter values*: Acceptance Ai = 1.0; Simplicity En = 1.0; Population Pn = 0.05; Time interval $\delta = 0.1$

5 Summary and Outlook

Based on the analyses in the preceding subchapter, the variable Ea for describing the depletion of the old paradigm is only of secondary importance insofar as it primarily influences the moment in *time,* when the old paradigm begins to lose significance. The actual key variable for the dynamics of the old paradigm is the acceptance Ae of external paradigms: For Ae = 0, an infinite perpetuation of the old paradigm results. For medium, but non-zero acceptance values Ae < 0.30, the old paradigm is sooner or later irreversibly replaced by a new one, as is relatively frequently observed in the natural sciences. For even higher acceptance values Ae ≥ 0.30, on the other hand, a renaissance of the old paradigm occurs, which ultimately leads to a multiparadigmatic situation, as is quite typical for the humanities and social sciences.

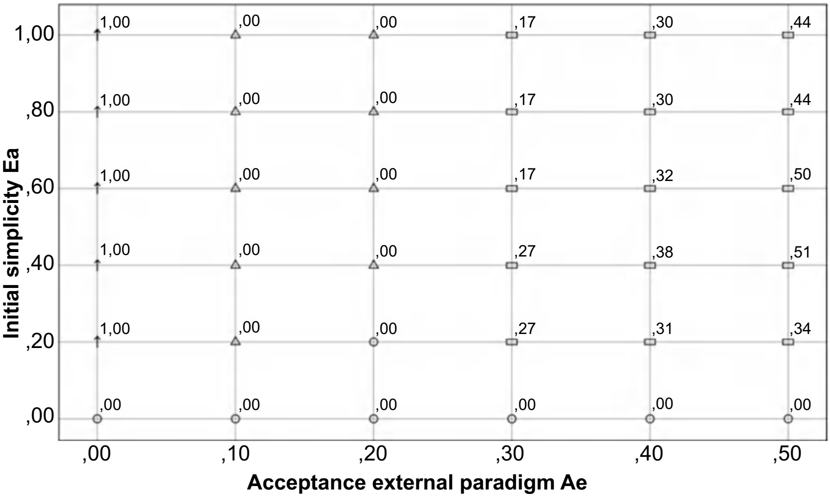

Fig. 6 Population share of the old paradigm after 200 time units
Legend: 0.00–1.00: Population share, equivalent to 0–100%; Ae: Acceptance of external paradigm; Ea: Initial simplicity of discovery with the old paradigm; Arrow: Permanent stability; Triangle: Temporary stability; Circle: Lack of stability; Rectangle: Renaissance of old paradigm. *Initial parameter values*: As in Fig. 5

This work largely leaves open the *explanation* of the *discipline-specific* differences regarding the acceptance Ae and the resulting consequences for the evolution of the respective sciences. Do natural sciences generally have rather low Ae values because these so-called *hard sciences* have highly elaborated paradigms and standards that allow little deviation? Is the absence of such rigid standards in scientific "truth finding" the reason why social sciences are much more tolerant of foreign paradigms and therefore multiparadigmatic? What role does the "therapeutic success" play in applied sciences such as economics, engineering, or medicine, which can pragmatically legitimize any deviations from the standard paradigm and thus should be conducive to the acceptance of new, foreign paradigms? These and similar questions are currently still open and are to be answered in a continuation of this work.

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Evolution of Artifacts? On Evolutionist Premises in Prehistoric Archaeology and Their Consequences for the Social Historical Interpretation of Goods.

Matthias Jung

1 Oscar Montelius' "Typological Method" and its Evolutionary Theoretical Premises

To this day, research on the Central European Bronze Age (approx. 2200–800 BC) is subtly influenced by a nineteenth-century assumption of evolutionary mechanisms in the development of material culture. One of the founding figures of prehistoric archaeology[1] was the Swedish archaeologist Oscar Montelius (1843–1921), who sought to establish its theoretical-methodological foundation and developed the "typological method", which aimed to trace the development of goods over time, beyond mere classification by similarity and dissimilarity. The resulting order of the material was not only a prerequisite for its socio-historical interpretation, but also preformed it in terms of content. There is much to suggest that the reference to Darwin was primarily for strategic reasons—prehistoric research, previously a domain of amateurs and laymen, wanted to underpin

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[1] When "archaeology" is mentioned in the following, it always refers to prehistoric archaeology.

This text follows on from earlier considerations of innovations in prehistoric societies (Jung 2015; de Zilva and Jung 2017).

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its claim to scientific status with this theoretical borrowing, and the established and practiced practice thus experienced a post-rationalization. Montelius claimed a purely Darwinian basis for his method (Montelius 1899, pp. 267 f.), even though the claimed analogy between type development and species development was primarily illustrative (Gräslund 1987, p. 105).

Above all, the transfer of two evolutionary theoretical theorems to the development of objects (and to cultural development in general)[2] is problematic: the evolution by branching and the gradualism. Montelius explains the evolution by branching using the metaphor of the tree and compares the development of typological series with "a many-branched oak, or a genealogical family tree" (Montelius 1903, p. 20). This image is suggestive, but misleading, because it excludes the crucial possibility of the cultural development of the absorption of external influences not sprung from the trunk. It also carries the risk of wanting to bring convergence phenomena into a developmental historical context. Gradualism, a development taking place in small steps without jumps, is articulated as follows:

> "The similarity of two members [of the chain of a typological series, M.J.] immediately adjoining each other can often be so great that an untrained eye can hardly notice any difference between them." (Montelius 1903, p. 16)
>
> "The development can proceed slowly or quickly, but man is always obliged to obey the same laws of development when creating new forms, which apply to the rest of nature." (Montelius 1903, p. 20)

In relation to artefacts, this assumption is incorrect, as their development can not only proceed linearly, but also dialectically, for example in the form of radical counter-designs to the existing, and jumps are also made possible here by external influences. The Darwinian basis of the method was codified by Nils Åberg in the entry "Typology" in the "Reallexikon der Vorgeschichte" published in 1929: "Typology is the application of Darwinism to the products of human labor" (Åberg 1929, p. 508). This is based even more clearly than with Montelius on an essentialist understanding of types. Typology is not supposed to be a classification imposed on the material from the outside, but a tracing of a living development: "The antiquities develop as if they were living organisms, the individual objects are individuals, a type series represents the development of a species and a group of type series in turn a development that branches into different species and forms a family" (Åberg 1929, p. 508).

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[2] See also the contribution by Brandl, Micheletti and Mace in this volume.

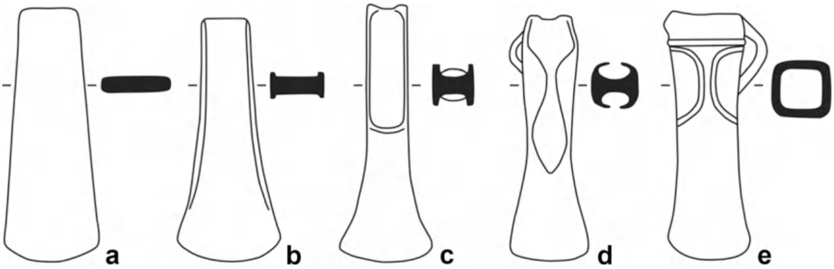

Fig. 1 Bronze Age axe blades. Graphic B. Voss

2 Case Study: The Typological Development of Bronze Age Axe Blades

This thinking is to be illustrated using a prominent example, the typological development of Bronze Age axe blades.[3] These blades are cast and then reworked by forging.

The traditional interpretation of the typological series shown in Fig. 1 can be paraphrased as follows:

At the beginning are the so-called flat axes (a), which were initially made of copper and then of bronze and morphologically correspond to their predecessors made of rock. In line drawings, without knowledge of the material, it would often be impossible to decide whether it is stone or copper or bronze. The blades were inserted into the forked split end of a shaft, which was then wrapped with a string made of plant fibers or leather. The typological development of the blades was determined by the optimization of their fixation in the shaft. Thus, flat axe blades were followed by those with lateral ridges (b), which provide a better fit in the hafting ("flanged axes"). The "palstaves" (c) additionally received an approximately centrally running cross ridge, which prevents the blade from being driven into the shaft during use. Then the marginal ridges enlarged and gradually became lobe-like extensions (d), which enclose the prongs of the hafting fork ("winged axes"). The final stage of development consisted of a perfection of the hollow shape already hinted at in the winged axes in the form of a closed socket,

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[3] The merely illustrative character of the following explanations should be emphasized; for an introduction to the topic, see e.g. Aner 1962; Eggert 2012, pp. 196–202; Harrison 1926a; Kunst 1982; Sangmeister 1967, pp. 204–210; Sprockhoff 1941, pp. 103–123.

which is slipped onto a hafting spike (e). The hafting is now inside the axe blade, not outside as in a fork hafting. The continuous-gradualistic development of the axe blades is attested by functionless indications of hafting winges in the emerging socketed axes, which Montelius, like equally functionless, inherited features in biological evolution, referred to as "rudiments", as "parts of an object, which once had a function, but gradually lost their practical significance" (Montelius 1903, p. 17). Comparable rudiments were shown in the North European Bronze Age, in which the socketed axes followed the palstaves and were therefore provided with functionless ridges.

So far the usual interpretation, committed to gradualism and evolution through branching, of the development of the axe blades.

3 Interpretive Topoi and Metanarratives of Bronze Age Research

The thinking originating from the time of the academic formation of prehistoric archaeology, in the logic of phylogenetic trees and gradualisms, influenced not only the treatment of detailed typological questions, but also the socio-historical interpretations of the Bronze Age as an epoch. The idea of a common origin and a continuity in the development of artifacts have solidified into background certainties and also determine the metanarratives about the Bronze Age. Two interpretive topoi[4] are fundamental: The first topos consists in the assumption of a pan-European Bronze Age ecumene, within which the regions are culturally independent, but they share a common, specifically Bronze Age deep structure, which goes back to a common origin and establishes the unmistakable unity of the epoch. Differences between the Aegean and Near Eastern Bronze Age on the one hand and the Central and Northern European on the other are therefore only understood as gradual, and forms of social, economic and political organization of the eastern high cultures are also transferred to Central and Northern Europe. The Near Eastern forms of rule and economy were conveyed to Europe via the Mycenaean world, the societies were aristocratically constituted, and their elites shared lifestyle and mindset over long distances. This aristocracy is presented as a "leadership layer that recognizes each other over long distances by their signs

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[4] The research historical backgrounds and implications of these topoi cannot be discussed here, and a third interpretive topos, that of a pronouncedly warlike character of the Bronze Age, is to be neglected in the given context; see Jung 2018, 2021.

and values each other as like-minded and equal in these signs" (Hänsel 1998, p. 21). Despite all differences in detail, not only a common root of regional cultures and individual artifact genres is assumed, but also a continuity of uses and meanings of artifacts across spaces and times. The second topos understands the Bronze Age as a formative period for the further course of European history, and this formative character is also conveyed via the Mycenaean culture, because through it "our continent receives its first civilizational and cultural contours, which it will never lose again" (Hänsel 1988, p. 62). In their combination, the two topoi construct a unified historical space, which corresponds to a narrative that is linear, open and expansive: a narrative of progress. The underlying idea of evolution through branching resembles less an actual tree than Alfred L. Kroeber's "tree of cultural evolution" (Kroeber 1948, p. 260; Fig. 18), in which the branches and twigs can reunite through growth and then form new branches. But even this modified tree metaphor is not sufficient for an understanding of the evolution of artifacts. It concedes a certain exchange between the branches, which, however, still spring from a common trunk, so there is no exchange between different trees. The theorem of gradualism also remains untouched. In the common interpretations of the Bronze Age as a prehistoric epoch, ideas of evolution through branching and gradualism are copied from the level of typological assignments to that of universal history, without the Darwinian prerequisites of these interpretations being discussed, except in research historical contexts. The importance of aspects of pragmatics in representation should not be underestimated, as borrowing from evolutionary theory in the context of describing cultural and historical processes provides a "red thread" and a certain narrative flexibility. Nevertheless, these theorems are unsuitable for explaining the peculiarities of social, cultural and technical innovations. Donald Campbell (1965) writes: "The stringent restrictions against cross-lineage borrowing in organic evolution is necessitated by the rigid chromosome-gene preservation system, and becomes unnecessary in the social evolution of particular social groups. (…) This removes the requirement that advanced (complex) forms be achieved only by a complete set of viable intermediate forms in each specific cultural group" (Campbell 1965, p. 42).

4 Mechanisms of Artifact Development: Recursion, Insertion, Restabilization

What mechanisms are then crucial for the development of artifacts? These are *recursion* and *insertion*. Recursion refers to the reinsertion of known and proven components, while insertion refers to the inclusion of those that are not derived from the artifact's development line and therefore represent a variation. This distinction is not absolute, as insertion will normally represent recursion insofar as the inserted originates from the technically available of a culture, but has not yet been part of the artifact to be produced. Whether an element is understood as recursion or insertion is a question of the level of observation: something that represents recursion in relation to the material culture of a society is an insertion in relation to a specific artifact. Moreover, under the conditions of pre-industrial device production, complete recursion represents a borderline case, as small, gradual variations can always occur in the manufacturing process, which may have significant consequences for the further development of an object type. Recursion and insertion are thus to be understood as poles of a spectrum, and specific elements of artifacts are to be evaluated according to their respective recursive and insertive components. As early as the 1920s, Herbert S. Harrison (1926b, 1930) proposed a similar concept. Variation in his view means an innovation that continuously emerges from the known through recursion, while mutation emphasizes the aspect of discontinuity, and what he referred to as "cross mutation" corresponds to the transfer of an element originating from another object, which is understood here as insertion. Harrison's terminology is somewhat unfortunate because it provokes misunderstandings with the biological concept of mutation.

Variation primarily occurs through a recombination of the existing—in line with Schumpeter's view (1961, p. 91), according to which innovation means any kind of "doing differently" and does not require an "invention". The dominance of recursion has another reason. For a selected variation in a technical artifact to become a permanent structural change, a balancing with the existing and retained components is necessary, a process following variation and selection, which Niklas Luhmann (1997, pp. 426–428) refers to as *restabilization* following Campbell. The necessity of integrating the new into the existing sets limits to the extent and frequency of variations. Just as, freely after Wittgenstein (1984, p. 186), doubt is only possible against the background of certainties, one can in principle doubt everything, but not everything at once, so the possibilities for variation are limitless, but the restabilization of the new requires a balancing with the existing, which is why typically recursive elements outweigh insertive ones. Using the example of Edison's development of an electric lighting system, George Basalla (1988, pp. 46–49) described how it adopted parameters of gas lighting (central supply stations and underground lines), which was not technically necessary, but was necessary for restabilization. On the one hand, a too restrictive retention mechanism prevents innovations, on the other hand, too much variation endangers restabilization, and therefore “some kind of a compromise” (Campbell 1975, p. 1108) between the two must be achieved.[5]

The prerequisite for the production of devices and tools is the human-specific cognitive ability for recursion. While non-human primates use and prepare tools (McGrew 1992), such as stripping branches to fish termites out of their mound, humans manufacture tools with which they make other tools, with which they in turn make other tools, and so on. Thus, “a significant difference to artifacts of animals (…) lies in the fact that tools are used for their production, which are artifacts themselves” (Feest and Janata 1999, p. 3). Even if animal artifacts can exhibit elementary recursion, the “recursive depth” of human artifacts is much higher. Recursion in the sense of “productive detour actions” (Popitz 1995, p. 19) is therefore the central mechanism for the cumulative upgrading of human technology.[6] In relation to tool use, this not only refers to an additive integration of elements taking place in the mode of restabilization, but above all to a variant of recursion described by Davor Löffler as “process-emulative”, which he describes using the example of the hammer:

> “The performance of modular culture (hammering with stone tools) reappears as an abstracted process in composite culture (hammer equipped with a handle) and is *emulated* therein: The handle increases the degree of indirectness of the action and *mediates* the original process as an instrumental medium. Thus, the *entire* former assembly, without a handle, is imagined *into* the handle: *The process form as a whole is abstracted and reintroduced emulatively.*” (Löffler 2019, p. 200; emphasis in the original, M.J.)

The significance of recursion for technology can also be studied using the so-called simple machines. These either shift the point of application and/or the direction of a force (rod, rope, pulley) or work with the ratio of effort and distance covered (lever, inclined plane). All (work) machines consist of the recursive reinsertion of these simple machines, and even some traditionally counted among them prove to be composite upon closer inspection, such as the wedge (two inclined planes), the wheel (pulley and lever), or the screw (inclined plane and

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[5] Even technically simple innovations, which seem to offer obvious improvements, can lead to a multitude of unforeseen action problems that endanger restabilization. An instructive example of this are the resistances that forest workers opposed to the replacement of the felling axe by the saw (see Radkau and Schäfer 1987, pp. 11–14).

[6] See Corballis 2013, pp. 204–206; Haidle et al. 2015; Tennie et al. 2009 on this.

lever).[7] Marx rightly criticized the theory of simple machines, arguing that their explanatory value is low without “the historical element” (Marx 1962, p. 392); conversely, however, the examination of the historically concrete forms of human devices and tools only becomes informative when they are understood as recursive combinations of the universal simple machines.

5 The Development of Bronze Age Axe Blades in the Light of These Mechanisms

If we apply this model to the interpretation of the typological series[8] of axe blades, the following picture emerges:

In the case of the flat axes (a), the insertion consists of the new material (copper or bronze), while the shape, which largely corresponds to that of axe blades made of rock, is recursive. This conservative shaping is traditionally explained by a lack of knowledge of the material properties, which prevented the manufacturers from fully exploiting the possibilities inherent in the new material. However, metallographic analyses, which allow conclusions to be drawn about the manufacturing knowledge incorporated into the blades, have shown that this was already very complex, and that the peculiarities of the material and the requirements for its treatment were known (Kienlin 2008, p. 108). Contrasting shapes to the stone axe morphology would have been possible, but were initially avoided for reasons of restabilization. The lateral ridges of the flanged axes (b) represent the insertion of something new, which, to my knowledge, was not adopted by any other contemporary device or tool, but proved to be a close possibility for better fixation of the blade in the practice of hafting.[9] The cross ridge of the palstaves (c) can be understood as recursive, because it is based on a similar principle as the edge ridges, it is insertive insofar as it is not located laterally and

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[7] Ernst Kapp’s (1877, pp. 29–39) principle of “organ projection” also describes a recursive mechanism.

[8] Of course, this series is highly artificial: While representatives of the types are present in large numbers, it is not known for reasons of the peculiarity of archaeological finds how many and which variants there were where a restabilization did not succeed. Moreover, the discussion primarily refers to morphological and not to technological and functional aspects.

[9] The great variety of shapes of the flanged axes with regard to the design of the cutting edge, which can take on a wide and arcuate shape, is neglected here because only the changes that affect the attachment of the blade to the shaft are dealt with as examples.

longitudinally, but centrally and transversely on the blade and therefore represents a variation. In the case of the winged axes (d), there are specimens where it is hardly possible to decide whether the marginal extensions are to be referred to as enlarged edge ridges or as hafting winges. But even if these pieces are morphologically *intermediate* forms, which can be described by weighting their recursive and insertive components, this does not justify a gradualistic interpretation as *transitional* forms. In the case of the socketed axes (e), the insertive character of the socket is evident. Their comparatively late appearance in Central Europe is remarkable, as the hafting socket had been in use for centuries in spearheads. The insertion of the socket significantly changed the shape of the axe blade, so a restabilization required a balance with recursive elements, and these consisted in the hints of flanges on the sockets. They are not rudiments in the sense of "dragged along" functionless features—although they have no function in the hafting of the blade, as recursive reintroductions of the known into an object with a strong insertive variation they have an important function in restabilization.[10] The same applies to the socketed axes with indicated shoulders.

6 Outlook

What could a conceptual alternative to the common interpretive topoi and narratives look like, which leaves behind the notions of continuity and contiguity that underpin them and instead takes into account aspects of recursion, insertion, and restabilization? Regarding the Bronze Age and other prehistoric epochs, a promising candidate would be a model that focuses on questions of cultural appropriation (Hahn 2011). As a counter-model to concepts of acculturation and assimilation, which are based on the assumption of a continuity of meaning of objects and practices in processes of cultural transfer and imply cultural

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[10] Harrison also argues similarly: A gradualistic interpretation would have to presuppose axes in which the winges form a closed double socket with a partition, "but the winged celt shows little signs of real progress towards a complete double socket, whilst the socketed celt makes its appearance fully-formed" (Harrison 1926a, p. 217). The sudden appearance of the socketed axe contradicts the assumption of a continuous process, it rather arose "by an application of the socket-idea, introduced from outside" (Harrison 1926a, p. 217), and the pseudo- winges attached to the socketed axes also testify to the attempt to moderate the suddenness of the transition. They are an expression of the "tendency of man to pay propitiatory tribute to the past" (Harrison 1926a, p. 217), which aptly describes the necessities in the course of a restabilization.

homogenization, this approach considers how the new is integrated into the existing and what changes in meaning it may undergo in the process, in other words: what the respective processes of restabilization are like.[11] Also in terms of the principle of parsimony, this approach would be preferable because it requires fewer basic assumptions. However, since the interpretive topoi are deeply embedded in the self-conception of research, this would amount to a paradigm shift that would have to overcome considerable resistance.[12]

Even though the proposed approach has only been exemplified here using a very specific object, it nevertheless claims to be generally applicable to processes of cultural evolution. From this perspective, a critique of meme theory could also be formulated, which on the one hand postulates close analogies to the Darwinian paradigm like Montelius' method, while on the other hand the concept of the meme is stretched to the point of being shapeless. In other words, this concept always requires a content specification, but once this has been provided, the concept of the meme has become superfluous, because it, unlike a reconstruction of the interplay of the mechanisms of recursion, insertion, and restabilization, could not reveal anything beyond this specification. Also, from the perspective of meme theory, cultural appropriation in the described understanding can only be a special case of imitation, not the normal case of cultural evolution.[13]

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[11] For a case study on this using the example of Mediterranean imported goods in the early Central European Iron Age, see Jung 2007.

[12] See the contribution by Müller in this volume.

[13] It would be tempting to reformulate the case example of the evolution of the basket presented by Susan Blackmore (Blackmore 2001, pp. 243–245) in terms of recursion, insertion, and restabilization; for a pointed critique of the concept of imitation central to meme theory, see Millikan 2003.

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