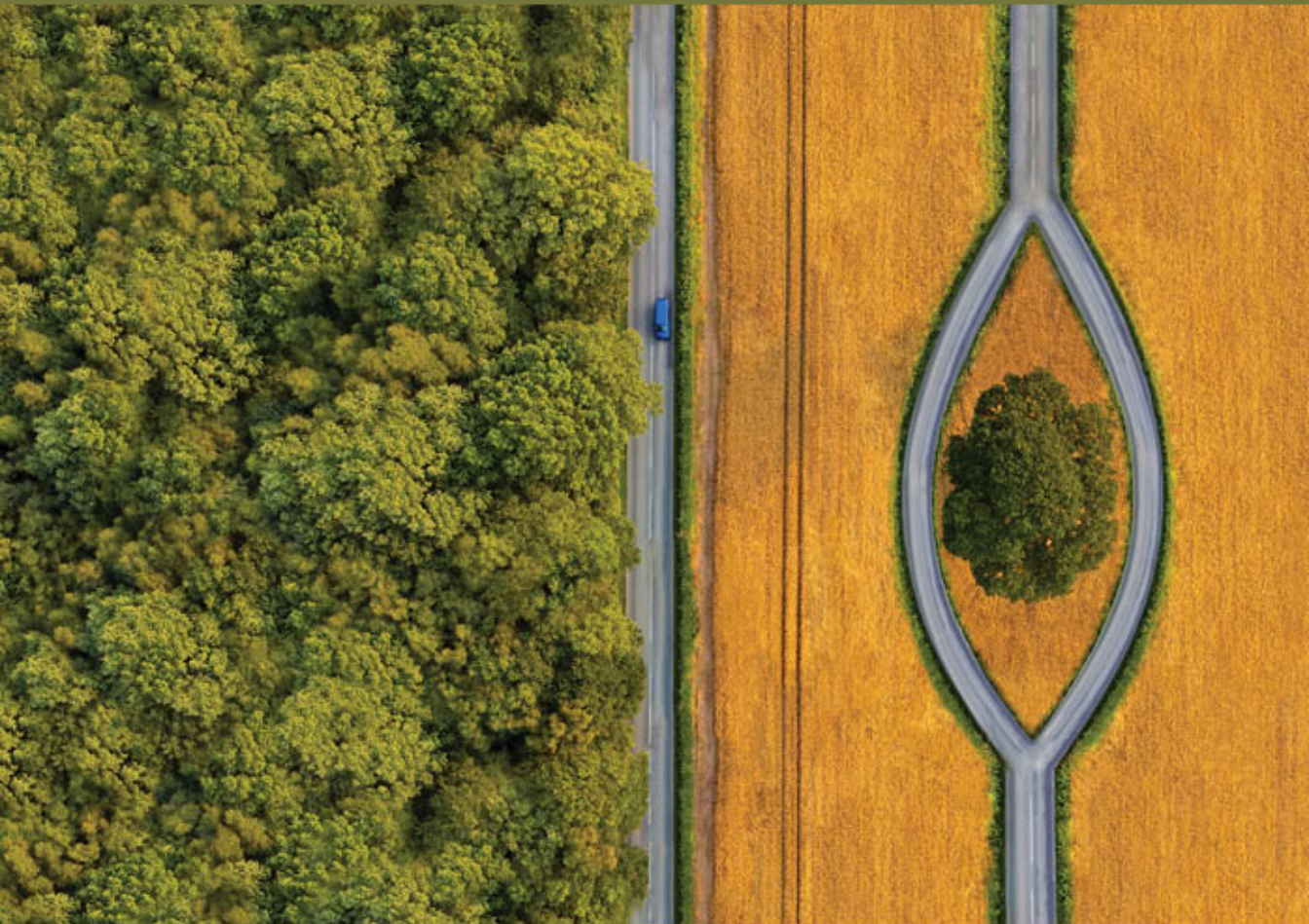


Vienna Series in Theoretical Biology

# The Evolution of Techniques

Rigidity and Flexibility in Use,  
Transmission, and Innovation



edited by Mathieu Charbonneau

## **The Evolution of Techniques**

## **Vienna Series in Theoretical Biology**

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# **The Evolution of Techniques**

## **Rigidity and Flexibility in Use, Transmission, and Innovation**

edited by Mathieu Charbonneau

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# Contents

Series Foreword	vii
Preface and Acknowledgments Mathieu Charbonneau	ix
Introduction Mathieu Charbonneau and Dan Sperber	xi
<b>I</b>	<b>TIMESCALES OF TECHNICAL RIGIDITY AND FLEXIBILITY</b>
<b>1</b>	<b>Adaptive Behavior within Technological Stability: Field Experiments with Potters from Five Cultures</b> 3 Valentine Roux, Blandine Bril, Anne-Lise Goujon, and Catherine Lara
<b>2</b>	<b>Innovation and Social Identity in Madagascar</b> 27 Rita Astuti
<b>3</b>	<b>Apprenticeship, Flexibility, and Rigidity: A Long-Term Perspective</b> 37 Bert De Munck
<b>4</b>	<b>When Rigidity Invents Flexibility to Preserve Some Stability in the Transmission of Pottery-Making during the European Middle Bronze Age</b> 55 Sébastien Manem
<b>II</b>	<b>FROM RIGID COPYING TO FLEXIBLE RECONSTRUCTION</b>
<b>5</b>	<b>Relevance-Based Emulation as a Prerequisite for Technical Innovation</b> 81 György Gergely and Ildikó Király
<b>6</b>	<b>Flexible Social Learning of Technical Skills: The Case of Action Coordination</b> 107 James W. A. Strachan, Arianna Curioni, and Luke McEllin

<b>7</b>	<b>Playing with Knives: Children’s Learning, Cultural Niche Construction, and the Evolution of Technical Flexibility</b> Adam Howell Boyette	121
<b>8</b>	<b>Stability and Change in Paleolithic Toolmaking</b> Dietrich Stout	139
<b>III</b>	<b>EXOGENOUS FACTORS OF TECHNICAL RIGIDITY AND FLEXIBILITY</b>	
<b>9</b>	<b>How Variability, Predictability, and Harshness Shape Cognitive Flexibility</b> Sarah Pope-Caldwell	161
<b>10</b>	<b>The Cultural Identity of Techniques: Rigidity and Flexibility among the Akha of Highland Laos</b> Giulio Ongaro	179
<b>11</b>	<b>Why Do Children Lack Flexibility When Making Tools? The Role of Social Learning in Innovation</b> Nicola Cutting	195
<b>12</b>	<b>A Tactful Tradition: The Role of Flexibility and Rigidity in Horse Riding and Dressage</b> Helena Miton	215
<b>13</b>	<b>Exploring Cultural Techniques in Nonhuman Animals: How Are Flexibility and Rigidity Expressed at the Individual, Group, and Population Level?</b> Sadie Tenpas, Manon Schweinfurth, and Josep Call	235
	Discussion: The Cumulative Culture Mosaic Kim Sterelny	253
	Contributors	271
	Index	273

## Series Foreword

Biology is a leading science in this century. As in all other sciences, progress in biology depends on the interrelations between empirical research, theory building, modeling, and societal context. But whereas molecular and experimental biology have evolved dramatically in recent years, generating a flood of highly detailed data, the integration of these results into useful theoretical frameworks has lagged behind. Driven largely by pragmatic and technical considerations, research in biology continues to be less guided by theory than seems indicated. By promoting the formulation and discussion of new theoretical concepts in the biosciences, this series intends to help fill important gaps in our understanding of some of the major open questions of biology, such as the origin and organization of organismal form, the relationship between development and evolution, and the biological bases of cognition and mind. Theoretical biology has important roots in the experimental tradition of early twentieth-century Vienna. Paul Weiss and Ludwig von Bertalanffy were among the first to use the term *theoretical biology* in its modern sense. In their understanding, the subject was not limited to mathematical formalization, as is often the case today, but extended to the conceptual foundations of biology. It is this commitment to a comprehensive and cross-disciplinary integration of theoretical concepts that the Vienna Series intends to emphasize. Today, theoretical biology has genetic, developmental, and evolutionary components, the central connective themes in modern biology, but it also includes relevant aspects of computational or systems biology and extends to the naturalistic philosophy of sciences. The Vienna Series grew out of theory-oriented workshops organized by the KLI, an international institute for the advanced study of natural complex systems. The KLI fosters research projects, workshops, book projects, and the journal *Biological Theory*, all devoted to aspects of theoretical biology, with an emphasis on—but not restriction to—integrating the developmental, evolutionary, and cognitive sciences. The series editors welcome suggestions for book projects in these domains.

Gerd B. Müller, Thomas Pradeu, Katrin Schäfer





## Preface and Acknowledgments

Mathieu Charbonneau

To be culturally successful, techniques must be both effective in achieving their practical goals and efficiently transmittable from one generation to the next. To secure practical efficiency, techniques should be used flexibly, whereas, to secure cultural stability, they should, it seems, be transmitted rigidly. How are these two conflicting demands reconciled? The contributions to this volume, coming from different disciplines, address the causal factors and impacts of both flexibility and rigidity in the ways techniques are used, transformed, reconstructed, modified, and diffused through time and at varying social and timescales.

To address these issues, we invited contributors from different disciplines, including anthropology, cognitive psychology, primatology, archaeology, philosophy, and history to participate in an online five-month webinar that took place from September 2020 to January 2021. There, they presented early drafts of their contributions to be discussed online by all contributors, allowing each to gain a substantial understanding of the other contributions, to get feedback on their own ideas, and to engage in critical discussions aimed at a better overall integration of the collective project. We intended as a second step to have an in-person workshop at the Central European University in Budapest, Hungary, where all contributors would present a prefinal draft of their chapter and directly interact with one another. Unfortunately, because of the COVID-19 pandemic, this event had to be canceled. Instead, completed drafts were submitted in the summer and fall of 2021, following which philosopher Kim Sterelny wrote his final discussion chapter.

This work was part of a wider project entitled “Constructing Social Minds: Coordination, Communication, and Cultural Transmission” supported by a seven-year Synergy grant of the European Research Council (ERC Seventh Framework Program, FP7/2007–2013, grant agreement no. 609819) and aimed at better integrating the study of interindividual coordination and communication and that of cultural transmission (Brintzer 2022).

This volume would not have been possible without the help, support, and hard work of several people. Tiffany Morisseau made the online webinar a reality and a success. Miriam Haidle and Pooja Venkatesh contributed to the online discussions. Cameron Brintzer edited several of the chapters, making the contributions more accessible to nonspecialist but informed readers. Andrea Jenei provided friendly and efficient administrative support. Anne-Marie Bono of the MIT Press provided guidance that was crucial in bringing this project

from promise to reality. Last but not least, special thanks to Dan Sperber, who offered invaluable support and mentorship throughout the making of the volume.

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# 13

## **Exploring Cultural Techniques in Nonhuman Animals: How Are Flexibility and Rigidity Expressed at the Individual, Group, and Population Level?**

Sadie Tenpas, Manon Schweinfurth, and Josep Call

The existence of animal culture, understood as those group-typical behavior patterns that are shared by members and that rely on socially learned and transmitted information (Laland and Hoppitt 2003), is commonly accepted today. Following over 50 years of debate, we have convincing evidence of cultural behavior in birds (Aplin 2019), cetaceans (Allen et al. 2013; Day, Kendal, and Laland 2001), and primates (Whiten and van de Waal 2017), among others (Laland and Evans 2017; Whiten 2019). Cultural traditions are distinct behavior patterns, shared by at least two members of a group, that persist over time and that new practitioners acquire, in part, through socially aided learning (Fragaszy and Perry 2003). These traditions can include techniques that produce change toward a material goal (Lamon et al. 2017). For example, chimpanzees (*Pan troglodytes*) create and use stick tools during termite-fishing (Goodall 1964). However, for the purpose of this chapter, we will extend our definition of techniques beyond cases toward material goals to include more cultural traditions, such as different manual techniques to perform a certain action. As such, we understand techniques as complex actions whose instrumental function is to produce changes in the environment, both physical and social.

The ability to ratchet up the complexity of cultural traditions, leading to both increased efficiency and productivity, is created by cumulative culture (Dean et al. 2014; Tennie, Call, and Tomasello 2009). It is a phenomenon primarily observed, and by some exclusively described, in humans (Dean et al. 2014). Although the learning of many animal species is influenced by the observation of and/or interaction with another animal or its products (Heyes 1994), there is minimal evidence of cumulative culture in animals (but see Sasaki and Biro 2017; Schofield et al. 2018). The richest evidence of animal culture comes from one of our closest living relatives, chimpanzees (Marshall-Pescini and Whiten 2008).

Long-term research on chimpanzees has provided us with extensive documentation of cultural traditions, highlighting variation between communities and distinct cultural repertoires. Most famously, Andrew Whiten and colleagues (1999) collected candidate cultural behaviors from seven long-term field sites across Africa. Using a systematic approach, known as the method of exclusion or the ethnographic method, candidate behaviors shown only to occur within some communities were determined to be cultural when the variability between groups could not be otherwise explained by ecological or genetic differences, thus leaving social learning as the remaining source of the observed variation.

While chimpanzees show a great variety of traditions, there is little evidence that these traditions are frequently updated through additional knowledge or behaviors (e.g., Gruber et al. 2009; but see Biro et al. 2003). This tendency toward stasis is especially striking considering that chimpanzees demonstrate an impressive ability to innovate solutions to novel problems (Bandini and Harrison 2020). So, while chimpanzee cultures may not reflect the same process or complexity of human cumulative culture, chimpanzee culture still undergoes cultural evolution in which a balance must be struck between the creation, variation, or application of cultural behaviors and the high degrees of similarity between individual performances, leading to stable traditions that persist across generations despite potential disruptive influences. Thus, the questions arise: Which mechanisms and factors drive chimpanzee cultures toward stasis, which drive them toward change, and how can we understand this in respect to cultural techniques?

To address these questions, we will begin by exploring the relationship between flexibility and rigidity in culture at the individual, group, and population level. Using these concepts, we will investigate how flexibility and rigidity in chimpanzee culture are currently understood and how social learning is used to explain them. In doing so, we will highlight the limitations of what we term “social learning theory”—namely, the reliance on explaining culture through high-fidelity transmission mechanisms and the inability to meaningfully incorporate the roles of ecology and genetics into cultural transmission. We will then address an alternative theory originating in the cultural evolutionary literature, “cultural attraction theory,” that sheds light on factors supporting cultural variation and stability. Further, we will discuss the limitations of cultural attraction theory. Due to its origin and use within human cultural evolution, cultural attraction theory has been critical of social learning theory, both because individual and social learning are highly intertwined in human societies and because they argue cultural evolution need not be reliant on high-fidelity transmission mechanisms. However, cultural attraction theorists still have to discuss the precise role of low-fidelity social learning mechanisms and how they might support cultural transmission. Drawing from both theoretical perspectives, we will finally propose a framework that combines these two theories to provide a more satisfactory explanation of the occurrence of flexibility and rigidity in chimpanzee techniques.

### **Defining Flexibility and Rigidity in Primate Techniques**

To fully capture the concept of cultural evolution, we will illustrate flexibility and rigidity in primate cultural techniques at the individual, group, and population level. Beginning at the individual level, we define a spectrum with *liberalism*, describing an individual’s tendency or disposition to change, on one end, and *conservatism*, describing an individual’s tendency or disposition to remain the same, on the other end (table 13.1). Note that we expect to see variation both within and between individuals along this spectrum. Further, when we consider liberal (and later flexible) behavior, we do not differentiate between behavioral changes that result in the acquisition of novel behavior and changes that result in the utilization of alternative but familiar behaviors already existing within the individual’s repertoire (cf. Pope-Caldwell, this volume, for a more thorough breakdown of these distinctions). On one level, behavioral change can occur as an opportunity, where an individual may alter their

technique through modification, variation, or invention of behavior, often improving the technique's efficiency. On a second level, some cases of behavioral change are driven by necessity, in which access to the behavioral outcome is dependent on improvement of the technique. By distinguishing the necessity for a change in an individual's behavior, or lack thereof, we can further break down liberal and conservative behavior with respect to adaptive decisions. We will do so next by considering examples of behavioral change at the individual level on the scale of distinct decisions (i.e., each moment at which the decision to change or not is made). Over larger timescales, such as days, months, and years, individuals may oscillate between behaviors or abandon behaviors for another, and this variation is expected.

To illustrate liberalism and conservatism at the individual level and the role of necessity, we use as an example chimpanzee nut-cracking behavior in response to an environmental change. Environmental changes that influence changes in behavior can occur at the individual level, within a life span, such as seasonal changes or natural disasters. At the group and population level, environmental changes occur more slowly, across generations, such as effects of climate change or other human impacts. For our example, let us imagine a scenario in which a chimpanzee uses a wooden hammer to crack open nuts. An environmental change resulted in increased hardness of the shells of the nuts used for extractive foraging such that a wooden hammer was no longer hard enough to crack the nut. Therefore, the liberal individual selects a different hammer, such as a stone, to crack the nut. Under this condition, the individual is behaving *innovatively*, responding to the necessity for change. Alternatively, if we consider an example in which the nutshell remains the same hardness yet the liberal individual switches hammers anyway, the individual is behaving *creatively* by changing behavior, despite there being no need for change. When considering the individual behaving conservatively, the same scenarios apply. If the conservative individual maintains their behavior but there is need for change, the individual is behaving *perseveringly*. If the conservative individual maintains their behavior and there is no need for change, the individual is behaving *consistently*. While the terms we have introduced highlight distinct adaptive decisions, they do not necessarily need to be considered as binary. Likely, these decisions bookend a spectrum wherein individuals might behave somewhere in between innovatively and creatively if changing the hammer material is useful but not strictly necessary. For example, imagine that the nuts become harder, where it becomes more difficult but not impossible to use the wooden hammer. In this case, switching to a stone hammer is useful but not necessary. Conversely, in this context, if the individual chooses not to change the hammer material, they would be behaving somewhere between perseveringly and consistently.

Broadening to the group level, we introduce social factors guiding behavioral change (or lack of) using the same context and framework as before to understand how groups behave as a product of their group members. As we expect individuals to vary in their tendency toward liberal and conservative behavior, so too should we expect the composition of these individuals to vary within each group, thus affecting the overall tendency of the group. In defining a spectrum at the group level, we have *flexibility*, describing a group's tendency to change a behavior, on one end, and *rigidity*, describing a group's tendency to maintain a behavior, on the other end (table 13.1). Envisioning the same nut-cracking scenario, when a flexible group needs to change their behavior and does so, this change can be described as an *advancement*. When a flexible group does not need to change their behavior but does anyway, this change can be described as a *shift*. Alternatively, when a rigid group needs to

change their behavior but does not, this lack of change can be described as *fixedness*. When a rigid group does not need to change their behavior and does not, this lack of change can be described as *stasis*. As before, these terms can be understood as the two ends of a spectrum of behavior, and we may have groups behaving at times somewhere between an advancement and a shift, or fixedness and stasis.

Expanding further, we can examine the cultural repertoire of a group to understand the population dynamics as a product of evolution. Problems arise when a group leans too far toward either end of the flexible–rigid spectrum. For example, if a group leans too far toward the flexible end, such that it is constantly creating and abandoning cultural behaviors, the group is not able to retain long-term cultural information and risks disadvantage when facing old problems again. Over evolutionary time, an overly flexible group can lead to cultural *breakdown* (table 13.1). Conversely, if a group leans too far toward the rigid end, such that it rarely acquires new cultural behaviors or modifies existing ones, then the group is unlikely to innovate new solutions or adapt to changing environments. Over evolutionary time, an overly rigid group can lead to cultural *stagnancy* (table 13.1). Therefore, there must be a balance between flexible creation, variation, and application of cultural behaviors while also maintaining relatively rigid transmission and performance, allowing cultural traditions to form and persist across generations.

One way we can understand these dynamics is through frequency-dependent evolution, which describes how the fitness of traits within a population is related to their frequency within the population (Ayala and Campbell 1974). Within social learning, traits may be subject to frequency-dependent biased transmission, specifically conformism and anti-conformism

**Table 13.1**  
Definitions of flexibility and rigidity at the individual, group, and population level

Term	Definition	Level
Liberalism	The tendency or disposition to change	Individual
Innovation	When an individual needs to change behavior and does	
Creativity	When an individual does not need to change behavior but does anyway	
Conservatism	The tendency or disposition to remain the same	Group
Perseverance	When an individual needs to change behavior but does not	
Consistency	When an individual does not need to change behavior and does not	
Flexibility	The tendency to change behavior	
Advancement	When a group needs to change behavior and does	
Shift	When a group does not need to change behavior but does anyway	
Rigidity	The tendency to maintain behavior	
Fixedness	When a group needs to change behavior but does not	Population
Stasis	When a group does not need to change behavior and does not	
Breakdown	When a group leans too far toward flexibility, such that it is constantly creating and abandoning cultural behaviors and thus is not able to retain long-term cultural information and risks disadvantage when facing old problems again; over evolutionary time, an overly flexible group can lead to cultural breakdown	
Stagnancy	When a group leans too far toward rigidity, such that it rarely acquires new cultural behaviors or updates existing ones and thus is unlikely to innovate new solutions or adapt to changing environments; over evolutionary time, an overly rigid group can lead to cultural stagnancy	

strategies. For instance, conformity is the preferential copying of the most common behavior, and anti-conformity is the preferential copying of rare behavior (Barrett, McElreath, and Perry 2017). As the frequency of cultural traits implicitly holds important information on those different traits, learners can use frequency to select locally adaptive behaviors or avoid selecting maladaptive behaviors (Nakahashi, Wakano, and Henrich 2012). Conformist learners may use the frequency of the most common trait as a cue for which behaviors to adopt and integrate, which can be adaptive in that they learn information from their group while avoiding potential errors (Nakahashi, Wakano, and Henrich 2012). This strategy has been demonstrated to work well in spatially heterogeneous environments, but without additional flexible strategies, conformity may keep more adaptive behaviors from spreading, leading to cultural stagnancy (Barrett, McElreath, and Perry 2017; Kendal, Giraldeau, and Laland 2009; Nakahashi, Wakano, and Henrich 2012). Anti-conformity may be such a flexible strategy, offering fitness value to individuals who can more flexibly adapt to their changing environment, thus introducing new behaviors. However, in a population of only anti-conformists, no cultural behavior can become stable and will eventually disappear. This highlights the interplay of conformists and anti-conformists, which are dependent on the other strategy. If there is the right frequency of both, cultural traits can emerge and persist.

When considering primate cultural techniques, comparative researchers have historically explained the relative stability through the fidelity of social learning mechanisms. A social learning mechanism of high-fidelity would allow for rigid transmission of techniques, retaining a high degree of similarity between performances of the demonstrator and observer such that the technique remains stable as it is transmitted between individuals over a long period of time and protected from disruptive influences such as miscopying or the loss of necessary information required to sustain a tradition (Charbonneau 2020). Mechanisms of lower fidelity offer less rigidity in the transmission of a technique, such that subsequent performances may differ from that of the demonstrator, being more susceptible to said disruptive influences and thus not able to retain a high degree of similarity. In this use of fidelity, comparative researchers are specifically employing “propensity fidelity” (outlined in Charbonneau 2020), focusing on the specific mechanisms involved in the transmission of a cultural trait, where certain transmission mechanisms are more or less faithful than another in perpetuating a tradition. We will illustrate these mechanisms and their associated fidelity as described by social learning theory in the next section by addressing them in chimpanzee behavior.

### **Social Learning and Cultural Fidelity in Chimpanzees**

To this day, social learning mechanisms have been the dominant source for understanding the spread and persistence of chimpanzee cultural behavior. It has been argued that high-fidelity social learning mechanisms can stabilize cultural traditions through faithful transmission from one individual to the next. Imitation, the copying of another’s actions (Tomasello 1996), and teaching, the active facilitation of another’s learning (Hoppitt and Laland 2013), are understood to result in a high degree of fidelity and play an important role in the evolution of culture (Whiten et al. 2009). Other social learning mechanisms such as emulation, copying the environmental or end-results of another’s actions (Tomasello 1996), and local and stimulus enhancement, when the actions of another draw the attention of the observer



to particular locations or stimuli, respectively (Hoppitt and Laland 2013), are thought to be of lower fidelity. In such cases, when low-fidelity mechanisms are used, the techniques performed by the demonstrator are not retained and performance can be dissimilar between episodes of transmission from one individual to the next (Hoppitt and Laland 2013).

Following the onset of research into the culture of wild chimpanzees, the idea that an ape had the ability to ape (i.e., imitate) and the existence of culture went hand in hand (Whiten et al. 2009). However, subsequent experimental research into the social learning abilities of chimpanzees questioned and critiqued this notion, reporting that unlike humans, chimpanzees are not natural imitators but rather emulators (Tomasello et al. 1987). In an experiment, chimpanzees were exposed to a demonstrator using a rake tool to acquire a food-reward (Tomasello et al. 1987). Individuals who observed the demonstrator were more likely to adopt the behavior than those who did not observe the demonstrator. However, they did not acquire the technique used by the demonstrator to obtain food from awkward positions. These results suggest a mechanism of higher fidelity than stimulus enhancement but lower fidelity than imitation, termed emulation (Tomasello 1990). Later studies reaffirmed chimpanzees' tendency to emulate end-results rather than imitate a demonstrator's actions (Call, Carpenter, and Tomasello 2005; Tomasello and Call 1997; Whiten et al. 2004; see also Whiten et al. 2009).

Many of the aforementioned studies relied on a single episode of transmission between one demonstrator and an observer, but cultural transmission requires multiple iterations of these episodes to sustain traditions. To address this discrepancy, Andrew Whiten, Victoria Horner, and Frans de Waal (2005) conducted a transmission chain experiment with chimpanzees to experimentally replicate spontaneous imitation through the transmission of a novel food-processing technique. In doing so, an "artificial fruit" that could be opened by either using a stick to lift a hook ("lift" method) or poking a stick into a trap ("poke" method) was presented to three groups of chimpanzees. For each group, one individual was selected and exposed to the artificial fruit. One was trained with the lift method, one was trained with the poke method, and another was not trained at all. The results revealed that no individual in the untrained group was able to access the food using either the lift or poke method. Importantly, individuals of both trained groups were able to learn the seeded technique through observation of group members. However, the initial technique introduced into the trained groups was not exclusively retained by all group members, nor were all individuals able to open the artificial fruit. This variation attracted criticism.

Nicolas Claidière and Dan Sperber (2010) highlighted two features of Whiten, Horner, and De Waal's (2005) results, critiquing their argument that imitation offers sufficient fidelity to explain the stability of the observed transmission. First, because not all individuals performed the demonstrated technique, stimulus enhancement by increased manipulation of the device could have led other individuals to engage with the device. Thereby, the naive individual could have explored the device individually and discovered their own technique, leading to several techniques in the group. Even if the individual were strictly adhering to imitation to solve the problem, increased interaction may still have resulted in the observing individual spontaneously discovering the alternative technique. Second, had the groups received more naturalistic exposure to the artificial fruits, such as unrestricted access for a longer period of time, one might expect that the individuals eventually perform the most efficient method, or both if equally efficient, rather than that technique initially propagated

through imitation. This outcome is illustrated by the fact that members of the lift group more often converted to the poke method than the other way around. Thus, Claidière and Sperber suggested that the social learning mechanisms demonstrated in the experiment may act as propagation mechanisms, but that complementary stabilization mechanisms, such as ecological availability, reward-based factors (that combine an ecological and a psychological aspect), content-based psychological factors, and source-based psychological factors (Sperber and Claidière 2008), must exist to explain wild observations of cultural transmission that are not being modeled in these experiments.

This criticism highlights a more fundamental problem of social learning theory that is demonstrated by the method of exclusion, which defines cultural behavior based on social learning alone (Whiten et al. 1999). Using this method, chimpanzees have been described to demonstrate at least 39 cultural traits (Whiten et al. 1999). When only considering social learning mechanisms, these group behaviors might be difficult to explain by mechanisms of lower fidelity than imitation (such as stimulus enhancement) alone. For example, variations observed in tool-use techniques like ant-dipping, in which one group uses a long wand with one hand and the ants are wiped off with the other (McGrew 1974) and another group uses a short wand and ants are transferred directly to the mouth (Nishida 1973), could use differential copying of either technique. Here, one could imagine a mix of imitation, other social learning mechanisms, and individual learning is likely at play, as was implied by previous experimental research (Whiten et al. 2004).

However, while the method of exclusion allows cataloging and identifying cultural traits, genetic and ecological factors are often difficult to entirely exclude (Laland and Hoppitt 2003; Schuppli and van Schaik 2019). For example, subsequent studies on ant-dipping techniques in chimpanzees revealed that the performed variants are influenced by the nature of the ants' behavior (Humble and Matsuzawa 2002). Techniques differ based on the abundance of ants, their aggressiveness, and the severity of their bite, such that when each of these factors were high, the chimpanzees used the long wand and hand-swiping technique. Under the method of exclusion, this ecological explanation would lead to the exclusion of ant-dipping as a cultural trait. However, we would argue that by excluding behavioral variation understood to be influenced by ecological factors, we may be overlooking the very mechanisms that support cultural variation and stability similar to those complementary mechanisms proposed by Claidière and Sperber (2010).

Ecological factors are arguably necessary to the existence of culture. For example, the use of olive oil is a cultural feature of Mediterranean Basin cuisine, which has evolved with the historic availability of olive trees (Vossen 2007). However, we would not exclude dishes involving olive oil from being cultural traditions of these regions because olives have historically not been available in other parts of the world, as one would do if employing the method of exclusion here. Rather, we understand that these recipes are created, taught, and otherwise passed down through generations and they continue to be adapted and supported by the availability of olives. While this example is most certainly oversimplified (as the Mediterranean Basin encompasses many distinct cultures and olives have since been cultivated around the globe), one can understand that such ecological features not only make culture distinct but may additionally provide a consistent feature, which maintains these cultural traditions over generations. This idea should also be applied to animal cultures. Take again the example of the ant-dipping variations, one could imagine that a distinct technique observed in one

population is propagated through the group by social learning mechanisms but is stabilized by the nature of the ant species. Unlike the transmission chain experiments, individuals interacting with more aggressive ants may be less likely to switch to or discover an alternative, potentially more efficient technique, dissuaded by the severe bites and thus maintaining the behavior over time.

Both the transmission chain experiments and the method of exclusion highlight the emphasis placed on imitation and other high-fidelity social learning mechanisms in explaining cultural variation and stability by social learning theory. In discounting the role of lower fidelity social learning mechanisms in combination with excluding influential factors such as ecology and genetics, social learning theory may be overlooking the very mechanisms supporting cultural variation and stability. In the next section, we will explore those factors outside of social learning mechanisms that may have been excluded or overlooked but that may assist in the propagation and stabilization of cultural techniques. Here, we will shift our focus to psychological and ecological factors by addressing cultural attraction theory in the realm of animal culture and later applying it to examples of chimpanzee cultural techniques.

### **Cultural Attraction Theory and Animal Culture**

Cultural attraction theory can explain how cultural traits (such as norms, beliefs, skills) change in their distribution and form over time (Buskell 2017; Scott-Phillips, Blancke, and Heintz 2018; Sperber 1985, 1996). Initially introduced to understand human culture, cultural attraction theory was intended to reconcile two observations: (1) that at the micro-level, transmission of information between humans is generally not a copying process and typically results in modifications, and (2) that at the macro-level, cultural information is relatively stable within entire populations and often remains so across generations (Claidière and Sperber 2007). These observations suggest that the micro-process of transmission is not itself faithful enough to explain macro-stability. Thus, it contrasts social learning theory in which cultural traditions are mainly based on high-fidelity social transmission (Claidière and Sperber 2007). Instead, cultural attraction theory posits that the cognitive mechanisms producing social transmission at the micro-level create *cultural chains* of causally related events. Thereby the micro- and macro-level are interconnected. Mental representations (knowledge, beliefs, intentions) allow for public productions (artifacts, behavior, speech) that influence the mental representations of others and thus both levels act as positive feedback loops (Scott-Phillips, Blancke, and Heintz 2018). Transformations in these chains are biased because they are not totally random. Hence, over time, cultural traits emerge within a population. In a system of cultural chains, *cultural attraction* is the probabilistic favoring of specific traits. *Factors of attraction* that bias cultural traits influence an individual's mental representation and thus the production of traits, which can be applied to nonhuman cultures.

Cultural attraction theory suggests that factors of attraction can be divided into three categories: reconstructive learning, motivational factors, and ecological factors (Buskell 2017). To understand factors related to reconstructive learning, we must turn to the transformative nature of transmission assumed by cultural attraction theory. As such, an individual acquiring a new cultural trait rarely strictly copies the variant(s) but instead draws

on the information transmitted in addition to personal background knowledge, inferential abilities, and interests to produce their own variant(s) (Claidière and Sperber 2007). Therefore, reconstructive learning consists of processes involved in inferential learning that are influenced by individual beliefs, emotions, judgments, and cognition (Buskell 2017). This is distinct from motivational factors that make one want to use or transmit a particular variant (Buskell 2017; Morin 2015). Finally, ecological factors encompass environmental elements influencing cultural traits. Ecological factors can range from features of the biological or physical environment, such as food and material resources, to behaviors and artifacts, including public representations used for communication (Buskell 2017; Heintz and Claidière 2015; Morin 2015; Scott-Phillips, Blanke, and Heintz 2018).

The factors of attraction outlined by cultural attraction theory contribute to a variety of items that influence cultural traits, resulting in a similar distribution of those traits between a given time step and another. This phenomenon has been termed within cultural attraction theory as hetero-impact, where one item of a population can affect the evolution of another item; for instance, item A influences the frequency of item B (Claidière, Scott-Phillips, and Sperber 2014; Sperber, pers. comm.). Conversely, homo-impact describes the impact of one item in a population on the evolution of itself; for instance, item B influences the frequency of item B (Claidière, Scott-Phillips, and Sperber 2014; Sperber, pers. comm.). Whereas “impact” describes the evolutionary relationship between items from cause to effect, “attraction” identifies attractors by viewing the same relationship from the opposite perspective, from effect to cause (Sperber, pers. comm.). Copying processes, like that of imitation, would be described as homo-attraction as propagation by high-fidelity social learning mechanisms would result in self-similar reproductions of a cultural item. Cultural attraction theory makes a point to highlight the idealization of models of cultural evolution that rely on copying processes for the reproductive success of cultural items, noting that, in the context of human cultures, it would be surprising if the success of our traditions were the product of imitation alone, given the many ways with which we can share information (Claidière, Scott-Phillips, and Sperber 2014). Rather, cultural attraction theory posits that a variety of mechanisms contribute to social learning, few of which would be of high enough fidelity to support cultural stability (Sperber, pers. comm.). Cultural attraction theory thus de-emphasizes imitation within cultural evolution, contrasting human social learning research that holds copying to be a key process, and has yet to discuss the roles of different social learning mechanisms explicitly. Therefore, while cultural attraction theory does not deny or exclude the role of social learning mechanisms contributing to cultural fidelity, its main objective has been to identify the range of processes outside of copying processes that contribute to cultural fidelity. In doing so, much of the literature on and surrounding cultural attraction theory to date has not discussed the contribution of specific low-fidelity social learning mechanisms in detail, not so dissimilar from how the literature on social learning has yet to discuss the contribution of alternative influences like ecology and genetics in more detail. Until now, these theories have developed mostly in isolation from one another; however, given their differences in focus, we believe both theories to be complementary and that when pursued jointly, they may shed light on the contributions to cultural evolution that the other has yet to explore. Therefore, in an attempt to merge the concepts of social learning theory and cultural attraction theory, we have developed a theoretical framework, which we will now detail and describe in the context of animal culture.

When considering the factors of attraction that may bias animal cultural variants, we imagine three *classes* that are separate but highly interactive: one *social*, one *individual*, and one *ecological*. These categories are similar to, but importantly distinct from, those described for cultural attraction theory, as we will attempt to incorporate the social transmission mechanisms highlighted by social learning theory into a new framework. The social class of factors of attraction are related to the social environment, including accessibility to observe conspecifics or their products and community structure, as well as social learning mechanisms. The individual class of factors of attraction are related to an individual's psychology including emotional, motivational, and sensorimotor processes, be they determined or learned. Finally, the ecological class of factors of attraction are related to ecological availability and opportunity and environmental state, ranging from climate considerations to the available vegetation and landscape features (cf. Pope-Caldwell, this volume, for a discussion on the influence of dynamic environments). As stated previously, we imagine these classes separately but recognize that they are highly interactive, influencing one another greatly. For example, when considering individual psychological mechanisms and the social environment, combinations of the two might uniquely influence cultural variants through social learning strategies such as dominance rank based social learning which occurs when chimpanzees selectively observe and copy group members of higher dominance (Kendal et al. 2015, 2018). Further, given the species, we may see that the strength of each class's ability to bias cultural traits varies, though importantly, each class will always have some influence, even if only minimal. As factors of attraction can influence across different levels, we would also expect to see variation of each class's strength both within and between individuals, which in turn guides liberal and conservative behavior. In the next section, we will illustrate how our combined approach offers new understanding toward the flexibility and rigidity of chimpanzee cultural techniques.

### Applying Cultural Attraction Theory to Chimpanzee Techniques

Techniques can be complex actions that produce changes in the environment, both physical and social. This definition can be extended to cultural traditions that include actions beyond tool use, such as specific social grooming techniques. We analyze techniques by focusing on three aspects: (1) the *function* of a target behavior, (2) the *material means* necessary to produce the target behavior, and (3) the *actions* with which the target behavior is achieved. For example, in the case of ant-dipping, extracting ants is the function; selecting the type of tool is the material means; and hand wiping the tool is the action. Between groups and subgroups, we expect variation in techniques to occur at one or more of these aspects.

We will focus on three techniques to illustrate our approach. Table 13.2 presents these techniques as candidate examples for a strong influence by each class, along with potential social learning mechanisms and other factors of attraction supporting them. Through our integrated conceptualization of social learning and cultural attraction, we will illustrate how each technique is differently influenced by the three classes and how this affects the expression of flexible and rigid behavior, with sponging demonstrating strong individual influence, ant-dipping demonstrating strong ecological influence, and hand-clasping demonstrating strong social influence (table 13.2). Crucially, even if a technique is mainly affected by one of the classes, the others are still relevant.

**Table 13.2**

Summary of three chimpanzee techniques and the proposed social learning mechanisms and factors of attraction supporting them

Behavior	Technique	Social learning mechanisms	Factors of attraction
Sponging	Insert item in mouth Chew and suck on item Insert item in hole Repeat	Local + stimulus enhancement	Chew plant material repeatedly (wadging) Insert objects/fingers in hole
Ant-dipping	Insert stick in ant nest or near trail May swirl stick Remove stick Harvest ants by two techniques: a. Direct stick to mouth b. Sweep stick with hand and pop ants from hand into the mouth Repeat	Emulation or Imitation	Aggressive ants Avoid insect bites Insert tool in hole
Hand-clasping	Grab and lift arm high in the air Hold arm against own's by two techniques: a. Interlocking hand palms b. Pressing wrists or forearms Groom armpit Switch sides	Ontogenetic ritualization or Imitation	Low branch nearby absent Prevent partner from lowering her arm Increase own arm's comfort Coordinate actions

For our three classes, we conceptualize that the stronger the influence, the more conservative the individual tends to be and, in turn, the more rigid a group may be such that when novel innovations appear, they are unlikely to diffuse within the group. Under conditions where the influence lessens, the individual can behave more liberally, leading to innovations that can be adopted and demonstrated flexibly at the group level. For any given cultural behavior, there is always influence by each class, and the strength of each class's influence interacts with the others. For example, returning to ant-dipping behavior, we might find that a given ant-dipping technique is heavily influenced by the social class; however, in environments where the ecological class also has a strong influence (i.e., the ants are very aggressive), we may find that the behavior is rigid within this context but can flexibly switch between contexts in accordance with shifting influence. This relationship between the classes' strength can be highlighted by the chimpanzees of Bossou, Guinea, who use two ant-dipping techniques that varies due to ant behavior (Humble and Matsuzawa 2002). When the ants are more aggressive, the ecological influence becomes stronger, constraining the behavior within that context despite additional strong social influences. When the strong ecological influence is lessened, an alternative technique may be employed guided by another class.

To begin discussing our candidate chimpanzee techniques, let us first consider sponging behavior, which we view as strongly influenced by the individual class. Sponging is a foraging technique in which a wad of leaves and/or other vegetation is folded and/or chewed and used to collect water, then squeezed in the mouth (Goodall 1964). Considered to be a universal behavior, sponging is not recognized as a cultural trait by the method of exclusion

(Whiten et al. 1999). Further, when captive chimpanzees have been provisioned with the materials to sponge, they spontaneously invented the technique without prior experience or observation (Kitahara-Frisch and Norikoshi 1982). Such findings suggest that given the correct environment, chimpanzees can perform sponging behavior relying predominantly on their individual dispositions—namely, two seemingly innate behaviors: wadging, which involves extracting liquid by chewing and compressing matter in the mouth (Goodall 1989; Teleki 1973), and poking fingers and objects into holes and crevices (Köhler and Winter 1925). However, a recent observation of the transmission of a novel sponging variation using moss as different material means has provided evidence for social learning and therefore suggests sponging might be a cultural trait (Hobaiter et al. 2014).

The study by Catherine Hobaiter and colleagues (2014) also made observations that highlight the potential roles of the ecological and social classes. The novel moss-sponging variation occurred under an unusual ecological context of discovering a novel clay pit that had been repeatedly flooded by the nearby river. Consequently, the clay pit attracted larger groups, which may have increased competition. In addition to individual dispositions toward sponging, the social influence of competition combined with the unusual ecological context may have fostered the initial innovation of moss-sponging, allowing space for variation in material means that could diffuse through the group through lower-fidelity social learning, such as local or stimulus enhancement.

The second candidate technique we will be considering is ant-dipping, which we believe to be strongly influenced by the ecological class. Ant-dipping is a foraging technique in which an individual selects a wand tool, inserts the wand into a nest or near a trail of ants, may move or hold the wand still to collect ants, then removes the ants by either bringing the wand directly to the mouth or by using the opposite hand to remove ants and put into the mouth (Humle 2011). In contrast to sponging, ant-dipping is only present in some chimpanzee populations, and the technique differs in terms of material means and actions (Humle and Matsuzawa 2002; Humle 2011; McGrew 1992; Whiten et al. 1999; Yamakoshi 2001). Depending on the level of aggression of the ants present, chimpanzees select wands of different length and apply different ant-gathering techniques to avoid severe bites. Under conditions with high probability for bites, the ecological influence becomes more important. The behavior is predicted to be more rigid to avoid discomfort. In a setting where ants vary in aggressiveness or show low levels of aggression, behaviors are predicted to be more flexible, allowing for more variation. Indeed, chimpanzees from sites with more aggressive ants use longer tools and collect the ants by hand wiping them from the wand whereas those from sites with less aggressive ants were dipped with shorter tools associated with the direct-to-mouth method (Schöning et al. 2008). Strikingly, the ecology can probably not exclusively explain ant-dipping techniques because chimpanzees from two sites with ants that show the same level of aggression use differently sized wands (Möbius et al. 2008). This finding suggests that social learning mechanisms, such as emulation or imitation, may play an important role in maintaining these variations (Humle 2011). In combination with social learning, individual experience of developing chimpanzees may further reinforce a group-specific technique as they encounter ant bites. Through combining strong ecological influences with social learning and individual experience, we can imagine that variation of techniques between groups is maintained.

Our third candidate technique, representing strong social influence, is not material-based but a social custom that is only present in some groups and varies between groups. Hand-clasping is a social grooming technique where two individuals clasp hands or press wrists or forearms (or other combinations of two) together overhead and groom the other with their free hand (McGrew and Tutin 1978). Because of the dyadic nature of this grooming technique, it is unlikely that variations in the actions of this behavior would arise out of, or be maintained by, individual dispositions alone. It might have originated by holding arms overhead in a comfortable manner for which branches are needed (McGrew et al. 2001), highlighting an ecological influence. Still, groups kept under the same ecological condition show different techniques, suggesting that variations are socially determined (McGrew et al. 2001; Nakamura and Uehara 2004; van Leeuwen et al. 2012). In combination with these individual and ecological influences, as well as coordination, we can speculate that high-fidelity social learning mechanisms help maintain group-specific variations. For example, mechanisms such as imitation or ontogenetic ritualization, in which two individuals shape one another's behavior through repeated interaction (Tomasello and Call 1997), may support transmission. In this context, one could imagine that the strong influences of social learning and the dyadic nature of the technique maintain group rigidity in addition to the appropriate ecological context (i.e., no available branches) and limited individual influence.

Beyond our three candidate cultural techniques, we can use our framework to examine other techniques, offering new perspectives into how they might be shaped by the influences of our three classes. For example, nut-cracking, a foraging technique in which chimpanzees place a nut on an anvil and push or pound a hammer until cracked open (Boesch et al. 1994), is one of the most well-known examples of chimpanzee cultural techniques, yet less is understood about how it emerges and persists. Through the lens of our new framework, we can speculate that nut-cracking may be strongly influenced by the ecological class. Nut-cracking is a highly complex technique that is rare among chimpanzees and varies between groups. Thus far, nut-cracking has only been described in three wild communities across two geographically distinct populations: Bossou in Guinea and Taï Forest in Côte d'Ivoire (Whiten et al. 2001) and Ebo Forest in Cameroon (Morgan and Abwe 2006, through indirect evidence). Within the Taï Forest, ecological factors such as rainfall, raw material availability, fruit production patterns, and fruit availability are understood to be similar throughout the area (Luncz, Mundry, and Boesch 2012). However, in an experimental study, it was demonstrated that between three groups living in the forest, ecological factors related to nut hardness influenced each group's technique, in which they adapted to seasonal changes in group-specific patterns (Luncz, Mundry, and Boesch 2012). Further, another study found that ecological opportunity over necessity influenced the presence or absence of nut-cracking in that despite having access to the necessary material means with which to nut-crack, low density and low distribution of high-value nuts may limit the invention and transmission of nut-cracking (Koops, McGrew, and Matsuzawa 2013). Similar to ant-dipping, nut-cracking appears to be influenced by ecological constraints combined with social learning to maintain group-specific variations. Social learning mechanisms that have been suggested to support nut-cracking include high-fidelity copying mechanisms such as imitation and teaching (Biro et al. 2003; Boesch 1996; Boesch et al. 2019). However, an experimental study investigating the individual and social learning mechanisms involved in nut-cracking found that a captive



group was unable to nut-crack spontaneously or after a stepwise demonstration (Neadle, Bandini, and Tennie 2020). The researchers suggest that their finding might indicate the presence of a sensitive period in which chimpanzees learn nut-cracking when both ecology and development allow for it (Neadle, Bandini, and Tennie 2020). Considering this evidence together, under our framework we can imagine that strong ecological influence combined with social learning mechanisms to main group-specific variation and individual development uniquely contribute to nut-cracking as a cultural trait.

In summary, we have described three classes of factors of attraction: individual, social, and ecological. Not only do these classes act together to produce specific behaviors, but their respective strengths can limit the variations and inventions an individual can produce and in turn limit how innovations spread through a group. Subjected to strong influence, fixedness occurs. Conversely, overall weaker influence produces more variability and thereby flexibility. Depending on the species, the potential impact each class exerts over the transmission and performance of techniques may vary. For example, an animal group that does not highly affiliate or cohabitate between group members may not see as strong an influence by the social class and may not have as many socially transmitted and sustained techniques. Conversely, we can imagine that humans are very strongly influenced by the social class, allowing for the use of mechanisms like teaching and the accumulation of techniques beyond the individual. Further, individual factors may more strongly influence humans allowing for a wide array of stylistic preferences liberally demonstrated. As such, an appropriate balance between the influences by each class can provide the opportunity for liberal invention and variation by individuals and flexible yet stable adoption through social learning by groups, resulting in cultural evolution.

## Conclusion

Our three-class framework combines the insights of cultural attraction and social learning theories to produce a more complete understanding of animal cultural behavior. We do not view flexibility and rigidity as a single dimension in which individuals or groups behave one way or the other. Rather, we understand the expression of flexible and rigid behavior as the outcome of the dynamic process created by the unique influence of each class in a given context. This framework helps us to unify cultural attraction theory and social learning theory by including the role of social learning mechanisms within cultural attraction theory and integrating the role of ecology and genetics within social learning theory, while discussing the contribution of low-fidelity social learning within both theories. We do not believe that the differences between each theory should represent mutually exclusive reasoning. On the contrary, when brought together, they offer solutions for understanding one another. As such, we use this combined framework to illuminate that chimpanzee populations are not strictly flexible or rigid; rather, their flexibility and rigidity arise differentially as an outcome of dynamic attraction by factors within each of our three classes. Through this lens, we understand that the traditions and techniques demonstrated in chimpanzee cultures are a product of combined social, individual, and ecological influences that have allowed for the evolution of the distinct repertoires we observe today.

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