ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Cultural Evolution in Animals

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Annu. Rev. Ecol. Evol. Syst. 2019. 50:1–22

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110218-025040

Keywords

social learning, tradition, culture, innovation, natural selection, adaptation

Abstract

In recent decades, a burgeoning literature has documented the cultural transmission of behavior through social learning in numerous vertebrate and invertebrate species. One meaning of "cultural evolution in animals" refers to these discoveries, and I present an overview of key findings. I then address the other meaning of the term focused on cultural changes within a lineage. Such changes in humans, described as "cumulative cultural evolution," have been spectacular, but relatively little attention has yet been paid to the topic in nonhuman animals, other than asserting that the process is unique to humans. A variety of evidence including both controlled experiments and field observations has begun to challenge this view, and in some behavioral domains, notably birdsong, cultural evolution has been studied for many years. In this review, I dissect concepts of cultural evolution and cumulative culture and appraise the accumulating evidence bearing on their nature and significance for evolutionary biology at large.

INTRODUCTION

The scope of animal culture discussed in this review is best introduced by stepwise unpacking of its key constituents. First is an essential underlying process, social learning, defined as learning from others, not only from their actions but also from consequences of their actions, such as toolmaking (Heyes 1994). Social learning thus contrasts with individual learning based on personal discovery. One reason that such social learning is of major interest to biologists is that it provides a second inheritance system (Whiten 2005, 2017) supplementary to, and interacting with, the primary system of genetic inheritance in living organisms. Traditions are phenomena that have come to be shared by a community through this process of social learning and are sustained over time, either within or across biological generations. Not all social learning eventuates in traditions, for some things that are socially learned are quite ephemeral, like currently optimal foraging sites. Phenomena classed as traditional in the animal literature commonly refer to behavioral patterns and artefacts like tools and nests, extending in the literature on human culture to phenomena such as attitudes and beliefs. Culture is defined minimally by some authors as the existence of a tradition, but other authors utilize more demanding criteria. Whiten & van Schaik (2007), for example, suggest the term culture be applied to the totality of traditions characterizing a community, as when we distinguish different regional human cultures by multiple traditions such as dress and social customs. “Cultural transmission” refers to the various processes of social learning through which individuals may acquire traditions by learning from existing practitioners.

If an individual learns from others but incorporates changes, as when a songbird modifies the songs it heard during the learning process or extends the migratory pathway learned from its parents, such changes may become incorporated into subsequent cultural transmission and the second inheritance system has thence given rise to a second form of evolution, cultural evolution. The analogy with organic evolution was already well recognized by Darwin in such cases as the evolution of human languages, in which present-day forms display the results of descent by modification from earlier forms (Darwin 1859, 1871; Schleicher 1869). Nowadays, studies of such language evolution draw on sophisticated numerical methods developed in biology (Gray & Atkinson 2003). Cultural evolution is not necessarily dependent on further organic evolution and can happen relatively fast compared with organic evolution (e.g., the evolution of digital technologies over recent decades). However, over the longer term it may have organic evolutionary effects, such as selection for neural changes that promote cultural learning, in cases where this enhances fitness (Whiten 2017, Whiten et al. 2017).

DISSECTING THE SCOPE OF CULTURAL EVOLUTION IN ANIMALS

The concept of evolution in the organic, biological sphere will be familiar to readers, but what might the concept entail when applied to culture? We can first distinguish two main senses in which culture evolves (Whiten et al. 2011; see **Figure 1**). The first sense refers to the emergence and shaping of cultural capacities (notably including not only different forms of social learning but also other capacities such as powers of behavioral innovation) and their consequences in the manifestations of traditions, as they have developed across diverse biological taxa (**Figure 1**). For example, cultural transmission through social learning has been identified in all classes of vertebrates, where it sometimes performs different functions in different species. Social learning is well established in at least some invertebrates, too, notably insects, although the extent to which it generates cultural traditions remains little researched by contrast. An overview of what we have learned of this first sense of cultural evolution follows in the section titled Diverse and Convergent Evidence for Widespread Animal Culture.

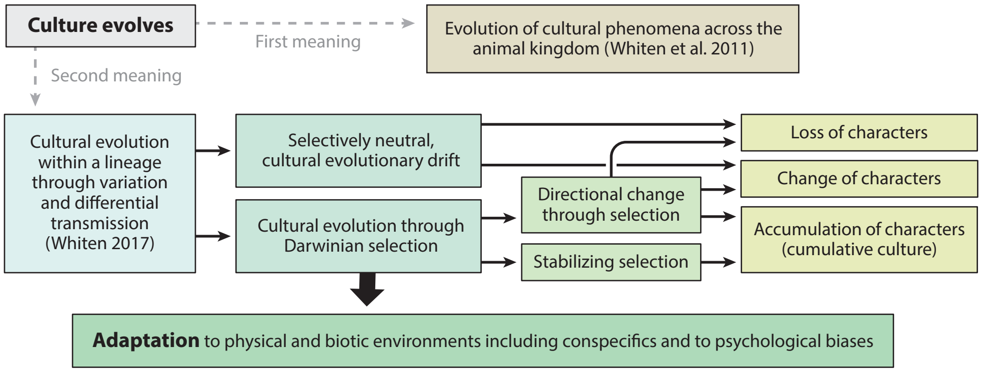

Figure 1

A hierarchical dissection of the term cultural evolution, its meanings, and variant forms. Solid arrows indicate relationships between categories and subcategories. Gray dashed arrows indicate two alternative meanings. The thick arrow indicates a causal link.

Once some form of culture is manifested in a species, cultural entities like socially transmitted behavior patterns and artefacts may themselves evolve, through the second inheritance system provided by social learning (Whiten 2005). This is the second sense of cultural evolution distinguished in **Figure 1**. Introducing a recent authoritative volume surveying human cultural evolution, Richerson & Christiansen (2013) stated that "cultural evolution is fundamentally just the change of culture over time" (p. 3).

I further divide such intraspecies cultural evolution into two categories. The first includes changes that are selectively neutral, the counterpart to the well-established phenomenon of genetic drift in organic evolution (Futuyma 2013). Here, through such effects as imperfect inheritance over long periods and/or geographic dispersion, characters such as behavior patterns gradually diverge from their ancestral forms, which may lead to them becoming regionally differentiated (**Figure 1**). I label this cultural evolutionary drift. Other culturally transmitted behaviors may instead become subject to selection, in ways that are analogous to Darwinian natural selection and sexual selection, thus driving adaptation to the sources of the selective forces involved. These thus constitute Darwinian cultural evolution (Boyd & Richerson 1985, Mesoudi et al. 2006). On the one hand, such selection may act to stabilize characters where this is beneficial (stabilizing cultural selection), thus contrasting with drift. On the other hand, it can be directional, actively selecting for evolutionary change (directional cultural selection). In turn, such changes may accumulate over longer periods, with successive additions building on earlier ones (cumulative cultural evolution), or instead act to select against and possibly eliminate some cultural entity—one can make an analogy between such changes and the organic selection that led to the loss of limbs in snakes, for example (**Figure 1**). Cumulative cultural evolution may include changes that increase the complexity and/or efficiency of the behavioral phenomena involved.

To illustrate such principal distinctions in the realm of culture, I turn to a recent study of birdsong. Field studies of birdsong began decades ago (e.g., Marler & Tamura 1964), so audio recordings now make it possible to trace change over long periods, and following Slater & Ince (1979), more birdsong papers have come to boast "cultural evolution" in their titles than in any other field of animal behavior (see **Supplemental Table 1** for listings). One such study suggests that aspects of three main evolutionary effects are discernable in the songs of the Savannah sparrow, tracked for 30 years (Williams et al. 2013; for some potential parallels in cetaceans, see Murray et al. 2018). The song includes a sequence of three main parts, with particular patterning within

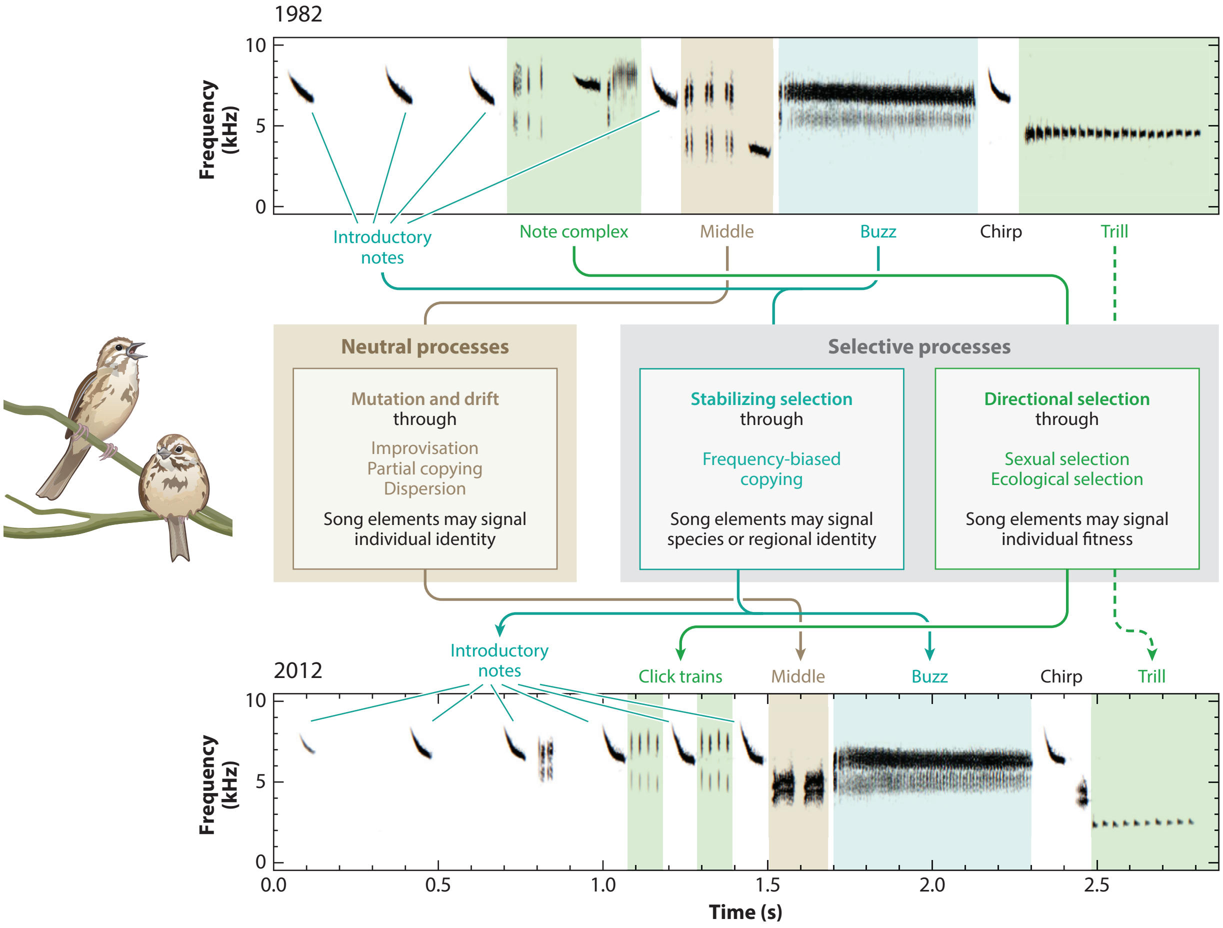

Figure 2

Evolution of Savannah sparrow song over a 30-year study (Williams et al. 2013). Representative sonograms are shown for 1982 (*top*) and 2012 (*bottom*), with elements ascribed to three different types of evolutionary change marked.

each part (**Figure 2**). Over the 30-year study, the terminal section (the trill) became substantially lower pitched and the average trill length halved. This latter difference in trill length was shown to affect fitness, with males emitting the shorter trill lengths having as many as 1.9 more fledglings per year. The authors accordingly suggest this is either a case of cultural evolution under directional selection, perhaps sexual selection operating through female choice, or the accruing of some competitive advantage to males with shorter trills.

The middle section of the song includes distinct notes that distinguish four major types within this segment. The identity of the most commonly expressed type was found to change substantially from year to year, as did the ordering of the notes, such as the dash note (**Figure 2**). However, these changes did not proceed in any consistent direction, nor were such differences associated with reproductive success. The authors accordingly concluded that changes in these elements were selectively neutral and that their turnover and distribution were, unlike the trills described above, shaped by such factors as mutation (changes or corruption in the copying of song elements), immigration, and drift.

By contrast, the loud, descending introductory notes remained stable over the 30-year study period. The authors suggest that this may be a species-specific marker that draws conspecifics' attention to the other parts of the song that follow, with the variable middle section marking individual identity and the descending trill carrying information about a male's relative fitness. The story is yet more complex, because intercalated between the otherwise stable introductory notes were other, softer notes including trains of clicks that, like terminal trills, changed progressively and substantially over the study period, with some notes that were initially minimal gradually increasing to be sung by 90% of males. These differences were also associated with variance in reproductive success and thus were attributed to directional selection (**Figures 1** and **2**).

I shall use the distinctions made in this birdsong example and in **Figure 1** to structure the part of the review farther below titled Cultural Evolution Within Cultural Lineages. But first, I return to the first sense of cultural evolution distinguished in **Figure 1** by offering in the next section an overview of the extensive body of evidence that culture has evolved across a broad array of species and behavioral domains (Hoppitt & Laland 2013, Whiten 2017). Establishing just what forms of social learning and culture exist among animals occupies the greatest bulk of research to date, and the findings are now voluminous (Hoppitt & Laland 2013, Whiten 2017), so my overview must perforce be selective. However, it is important to appreciate the scope of animal culture that has been discovered, in order to approach the questions about intraspecies cultural evolution tackled farther below, a relatively new endeavor. This review is the first to tackle these questions directly in any comprehensive way.

DIVERSE AND CONVERGENT EVIDENCE FOR WIDESPREAD ANIMAL CULTURE

The first significant empirical evidence for animal culture emerged around the middle of the last century, notably including the identification of birdsong dialects (Marler & Tamura 1964), complementary laboratory experiments demonstrating social learning of birdsong (Thorpe 1958), the spread of milk-bottle-top opening by tits (Fisher & Hinde 1949), and the identification of novel food processing behavior by Japanese macaques (Kawai 1965). Since then, evidence has accumulated exponentially, culminating in an explosion of findings in the present century (Hoppitt & Laland 2013, Galef & Whiten 2017, Whiten 2017).

This progress has been facilitated by a range of factors including the buildup of long-term data spanning multiple generations and a growing diversity of methodological innovations. In some cases, these have provided complementary insights, as when wide-ranging field studies and laboratory experimentation have married the ecological validity of the former with the power of the latter to rigorously demonstrate that social learning is playing an essential causal role. In what follows, I aim to illustrate the range and scope of these methods and of the animal taxa and modes of behavior involved.

Convergent Evidence and Triangulation on Animal Culture: An Ape Example

Two taxon-related forms of behavior have particularly benefitted from complementary field studies to identify putative traditions in nature and laboratory experimentation to rigorously confirm capacities for social learning: birdsong and the behavioral repertoires of apes. Birdsong is featured in a later section of this review; here, I use the case of ape cultures to illustrate how diverse forms of evidence can converge on compelling conclusions about social learning and culture in animals.

1. *Large-scale geographic surveys*. Systematic surveys of behavior patterns, found to be common at some research sites yet absent at others without evident ecological or genetic explanations,

identified 39 putative cultural traditions across Africa for chimpanzees, spanning foraging techniques, tool use, social behaviors, and sexual gambits (Whiten et al. 1999). Similar studies and findings followed for orangutans (van Schaik et al. 2003; 24 traditions) and gorillas (Robbins et al. 2016; 22 traditions).

2. *Comparisons of neighboring communities.* Differences identified between neighboring groups of chimpanzees, such as seasonal preferences for stone versus wooden tools for nut cracking, more compellingly exclude both genetic and ecological explanations, isolating social transmission as the explanation (Luncz & Boesch 2014).
3. *Detailed ecological comparisons.* The above findings were further refined by detailed comparisons of key ecological variables, such as specific prey types accessed through tool use, revealing increasingly fine-grained cultural differences between communities (Möbius et al. 2008, Schöning et al. 2008).
4. *Comparisons of captive communities.* Rescued chimpanzees randomly allocated to neighboring enclosures in African sanctuaries have been found to develop specific local traditions in grooming (van Leeuwen et al. 2012), food processing (Rawlings et al. 2014), and even personal adornment (van Leeuwen et al. 2014).
5. *Developmental studies.* Lonsdorf et al. (2004) showed that young female chimpanzees were much more assiduous than their male peers in attending to the termite-fishing skills of their mothers, later mastering the technique themselves a year ahead of the males.
6. *Tracking diffusion of innovations.* A new form of mopping water by masticating moss into a sponge was shown to diffuse via chimpanzees' associates in their social network, implicating social learning (Hobaiter et al. 2014).
7. *Dyadic experiments in captivity.* Exposing individuals to models using different manipulative techniques to deal with the same problem, such as opening an artificial fruit, has shown that the observed alternative tends to be the one acquired (Galef & Whiten 2017).
8. *Cultural diffusion experiments.* Likewise, experiments in which alternative techniques are seeded in models belonging to different groups (Whiten et al. 2005), or in the first of a chain of models and observers (A-B, B-C, C-D, etc.) (Horner et al. 2006), demonstrated that behaviors will diffuse across a group and even between groups (Whiten et al. 2007) to generate incipient traditions.
9. *Field experiments*. When faced with an opportunity to extract honey from a hole bored in a log, chimpanzees in a community that habitually uses stick tools applied such tools to the task, and those who use sponges (but not sticks) applied sponges, a much less effective approach (Gruber et al. 2009, 2011). The authors attributed these responses to ingrained differences in the cultural cognition of the two communities.
10. *Archaeology.* Excavations have revealed evidence of nut cracking dating back at least 4,300 years at a location where chimpanzees continue to crack nuts today, implicating a capacity to sustain long-term traditions (Mercader et al. 2007).

Mufano & Smith (2018) have advocated that solutions to recent concerns about replicability in scientific studies, which have particularly plagued the behavioral sciences, should extend to the power of triangulation, in which results are not merely tested by repeating the same methods but variant methodologies are focused on the same core problems to check for confirmatory conclusions. I suggest that the above ten methodological approaches to social learning and culture, here illustrated for chimpanzees, offer an encouraging example of such triangulation in practice. This approach remains to be applied across the board in studies of animal culture, but there are many other such cases for some taxa at least.

As we turn to survey other taxa, it becomes evident that culture may span some quite different domains of behavior in different species. Two domains shown to be important in both cetaceans and birds are long-distance migration and communication through complex vocal repertoires. Neither are significant in primates, the taxon that has tended to dominate the animal culture literature historically (Whiten 2012).

Migration and Navigation

Approximately 2,000 or so species of birds are migratory. Many migrate more than halfway across the globe, between seasonal breeding and feeding grounds. Among naïve juveniles that have been tracked, many accompany their parents and/or local community members on their first, and in some cases later, migratory flights, subsequently becoming highly committed to the established pathways (Palacín et al. 2011). This finding provides circumstantial evidence for cultural transmission of such routes. However, in some species, juveniles migrate separately from their parents, notably in cuckoos, suggesting these birds must have other means of establishing their migratory routes. Migratory co-flying in itself therefore offers only suggestive evidence that the acquired routes are culturally transmitted. However, experimental evidence that converges on this latter interpretation has emerged from conservation measures that imprint young birds such as swans and cranes on microlite aircraft. The young follow these surrogate parents over migratory pathways, establishing routes they adopt in later years (Mueller et al. 2013).

Juvenile humpback and right whales likewise travel initially alongside their mothers on long-distance migrations, adopting these migratory pathways for the rest of their lives, again providing circumstantial evidence of cultural transmission of these routes (Baker et al. 1990, Valenzuela et al. 2009). Many ungulates also migrate substantial distances, with juveniles making their first journey along with their mothers in herds of various sizes. Bighorn sheep, for example, when translocated to new areas initially cease their prior habit of surfing green waves of high-quality forage in spring from low to high elevations. Eventually such migrations begin again and progressively extend generation by generation, thus implicating cultural transmission as this sequence proceeds (Jesmer et al. 2018). We shall revisit this study below when addressing cultural evolution specifically.

On a smaller scale, cultural transmission of travel routes has been shown in fish both in the laboratory (Laland & Williams 1997) and on reefs in the wild (Helfman & Schultz 1984, Warner 1988) where traditional routes may show fidelity across many generations spanning at least a decade. Culture may have a special role to play in relatively short-distance travel routes, where little scope exists for genetically based route knowledge of the kind that is known for some long-distance migrants.

Communication: Bird and Whale Vocal Repertoires

Some of the earliest evidence for cultural transmission in animals arose in the twin discoveries that birds in different regions may display different song dialects (Marler & Tamura 1964) and that songbirds in laboratory experiments learn particularities of their songs from others (Thorpe 1958). A rich corpus of studies replicating and extending these findings over the intervening decades indicates that such cultural phenomena are widespread in songbirds, of which approximately 4,000 species exist: The reference list of the most recent book-length review of birdsong research (Catchpole & Slater 2008) lists as many as 84 studies of different songbirds displaying vocal dialects, and experimental studies of the acquisition processes are no less extensive (Riebel et al. 2015). Farther below, I address the question of how songs not only come to vary geographically but also change over time in ways described as cultural evolution in this literature (Catchpole & Slater 2008, Aplin 2019).

The experiments so elegantly dissecting the ontogenetic acquisition of birdsong in the laboratory are not so feasible with whales. However, whale songs are clearly culturally transmitted because songs change, sometimes quite dramatically, over periods of years, yet new song types spread across large populations, thus implicating social learning (e.g., Payne et al. 1983, Tervo et al. 2011; see Whitehead & Rendell 2015, for a book-length review of cetacean culture). The most drastic song changes have been described as revolutions rather than evolution (Noad et al. 2000), and analysis of song change and hybridization during such revolutions provides deeper understanding of acquisition processes in lieu of laboratory experimentation (Garland et al. 2017).

Less evidence is available for vocal or other forms of communication being culturally transmitted in other groups of animals, but in some birds (Bartlett & Slater 1999), chimpanzees (Watson et al. 2015), marmosets, and other primates (Snowdon 2009), immigrants entering new groups have exhibited a convergence of their vocalizations to culturally conform to those of the community they have joined.

Diet, Foraging, Hunting, and Food Processing

Evidence for cultural transmission in aspects of diet and foraging spans a large and growing range of species and has been provided by a diversity of methodologies. Evidence of dietary traditions, for example, comes from records of sympatric clans of killer whales specializing in hunting either seals or fish (Reisch et al. 2012, Whitehead & Rendell 2015); orangutan juveniles matching maternal dietary profiles, with both differing from those of neighbors (Bastian et al. 2010, Jaeggi et al. 2010); and cross fostering (through egg-swapping experiments) between differently sized species of tits leading the young to match the dietary preferences of the foster parents (Slagsvold & Wiebe 2011).

Some foraging innovations have been recorded close to their inception and their spread then recorded. Evidence of transmission through networks of affiliates provides compelling evidence of social transmission, as in a new form of sponging tool use in chimpanzees (Hobaiter et al. 2014) and lob-tail feeding on fish schools by whales, which spread to more than 600 humpbacks—one-third of the population—over 26 years (Allen et al. 2013). Numerous experiments demonstrating social learning in mammals, birds, fish, and insects have involved artificial foraging tasks, including artificial fruits designed to mimic sequences of manipulation required in the wild (Whiten 2012; van de Waal et al. 2013, 2015; Gunhold et al. 2014; Galef & Whiten 2017). Most relevant to our present topic are cultural transmission experiments, in which different techniques are seeded in initial models in different groups and the differential spread of the alternatives are then tracked (Whiten et al. 2005, Aplin et al. 2015). A review of 30 such studies in 2009–2015 reported evidence of cultural spread of foraging techniques in mammals, birds, fish, and insects (Whiten et al. 2016), adding to an earlier corpus of 33 such experiments in 1972–2008 (Whiten & Mesoudi 2008). Some studies simply seed a technique that is copied by others yet rarely or never achieved by individuals acting alone; in one compelling example, the unusual skill of pulling string to access food in an artificial flower was seeded in individual bumble bees and then tracked as the skill subsequently spread via observational learning across the hive, simulating transmission from bee to bee across four such cultural generations (Alem et al. 2016).

Predator Avoidance

It has long been known that both primates (Mineka & Cook 1988) and birds (Curio et al. 1978) will acquire fear of quite random objects when experimentally exposed to adults showing alarm behavior in association with these objects. In the wild, such social learning has obvious benefits in comparison to trial and error discovery. Curio et al. (1978) extended this discovery to a cultural transmission experiment in which a starling first developed an avoidance response (alarm calling) to an arbitrary object like a plastic bottle and then in turn became the model for the next learner. Such aversive responses were transmitted along a chain of six individuals, simulating cultural generations.

Mate Choice

Mate choice copying was first shown in guppy experiments, wherein a female fish would later prefer to mate with a male she had witnessed mating with another female (Dugatkin & Godin 1993). Such findings were recently extended to fruit flies in cultural transmission experiments (Danchin et al. 2018). Virgin females first witnessed six different displays of females preferentially mating with a male dusted pink rather than other males dusted green (or the reverse, in a counterbalancing condition). These observers then displayed their acquired preferences for males of a certain color in their own mating, and the females who watched these displays became models for others, and so on. Preferences for the originally favored color of male passed along as many as eight such cultural generations, facilitated by a bias to conform to observed majority preferences, which the authors suggest is important to very short-lived animals that must make quick but optimal decisions about locally adaptive behavior. Supplementary modeling further predicted that, in the larger populations occurring in the wild, transmission would pass with fidelity over many more generations.

Social Customs

McGrew & Tutin (1978) reported the first social custom in animals: a grooming handclasp performed customarily by chimpanzees in the Mahale Mountains National Park in Tanzania, yet not by those farther along the lakeshore in the Gombe Stream National Park. Similar differences have been documented in captive chimpanzees in the United States (Bonnie & de Waal 2006) and others in adjacent enclosures in an African sanctuary (van Leeuwen et al. 2012). White-faced capuchins also showed social behavior described as social customs in which a habit of putting one's fingers in others' mouths, noses, and even eyes (or putting the other's finger into one's own) diffused across certain groups, existing for a few years before fading away again (Perry et al. 2003).

The above survey represents only a selective subset of the many findings in this burgeoning area of research. I have aimed to indicate the range of methodologies, animal taxa, and forms of behavior across which cultural transmission has been documented as occurring. Whiten & van de Waal (2018) describe primate culture as "pervading" across behavioral domains and across primate lifetimes, and Whitehead & Rendell (2015, p. 6) conclude that "culture … is a major part of what the whales are."

CULTURAL EVOLUTION WITHIN CULTURAL LINEAGES

I now address this topic (meaning 2 in **Figure 1**) by reference to the further distinctions made within **Figure 1**. This section discriminates the underlying processes of cultural change, ranging from drift to the effects of Darwinian selection.

Cultural Evolutionary Drift

As noted above, changes in the middle section of Savanna sparrow songs were attributed to selectively neutral drift because they showed no persistent directionality and were not predictive of reproductive success. The causes might include inaccuracies in song copying, or personal modification of the song, over time creating relatively random differences between early and later songs, like those shown in **Figure 2**.

In the birdsong literature this is suspected to be a widespread phenomenon, at work both in creating cross-generational changes and dialect differences between geographically spaced subpopulations. I note that birdsong studies that advertise "cultural evolution" in their titles (**Supplemental Table 1**) are based on cross-generational or other long-term but local studies rather than regional dialect studies, perhaps just because long-term historical song recordings are available for particular locations. It would be illuminating if this could be replicated to trace the evolutionary phylogenies of regional dialects in the vocal repertoires of both birds and whales.

Drift effects might often be quite difficult to establish in a compelling fashion, for they require determining that no selective advantage accrues to the change at stake, and proving the negative is always scientifically challenging. Arguably this difficulty is best tackled by making controlled comparisons, such as those made in the study of Williams et al. (2013), who discriminated between song elements that were, or were not, linked to reproductive success, the latter being ascribed to drift. Similar approaches in the studies listed in **Supplemental Table 1** include those by Nelson et al. (2004) and Byers et al. (2010), where changes in simple syllables and accented songs, respectively, appear consistent with stabilizing selection, whereas changes in relatively complex syllables and unaccented-ending songs seem more consistent with drift. Despite being defined by their selective neutrality, such effects can have important consequences for other subsequent evolutionary changes: For example, it can become difficult for members of one community of a species in which communities have drifted apart in their songs (and indeed in other aspects of courtship behavior) to successfully court and mate with members of the other community, creating incipient speciation (Grant & Grant 2002).

Like birdsong, the songs of cetaceans like humpback whales can change across generations and vary geographically (Payne et al. 1983). As these differences have not been shown to have selective advantages or disadvantages, they may likewise reflect effects best characterized as drift. However, this is largely a default assumption pending direct evidence concerning selection effects, which for cetaceans unsurprisingly lags behind the richness of knowledge that has accumulated from the long-term studies of birdsong (Murray et al. 2018).

Drift may also be at work in many other forms of cultural transmission in varied groups of animals, such as traditions (or regional differences), which appear to have at best trivial implications for fitness. For example, once their locally provisioned food ration is consumed, free-living Japanese monkeys routinely gather a set of small stones and manipulate them in various ways such as rubbing on the ground or clacking them together (stone handling; Huffman et al. 2010). Leca et al. (2007) have identified as many as 39 variants of this behavior, and the particular array of such variants differs across communities, consistent with diffusion by drift. In chimpanzees, the first social custom to be described, the grooming handclasp, involves pairs of grooming chimpanzees each holding up one arm, holding hands above them, and using the other hand to groom each other—a pattern commonly seen at one field site in Tanzania yet never at another along the same lakeshore (McGrew & Tutin 1978). Later research at Mahale showed that neighboring communities displayed different handclasp variants, either clasping hands or juxtaposing wrists, likely due to drift as the habit passed between communities (Nakamura & Uehara 2004). Note that, although such cultural differences resulting from drift may not imply differences in fitness, this does not necessarily mean the behaviors themselves are functionless. In selectively neutral drift, which cultural variant a particular community displays does not matter for fitness, but fitness may be lowered for individuals that fail to sufficiently competently display the alternative that is locally common—for example, in a chimpanzee community where handclasp grooming is customary or in a community where a particular avian or cetacean song is sung by the majority.

Cultural Evolution Through Darwinian Selection

Varied literature has discussed the extent to which cultural evolution parallels organic evolution in being shaped by the Darwinian processes of variation, inheritance, and selection, which together engineer adaptation to a community's ecological niche. Perhaps most controversial has been Dawkins's (1976) suggestion that one may recognize cultural units, which he dubbed memes and proposed were analogous to genes (e.g., Aunger 2000). Mesoudi et al. (2004) argued that because Darwin knew nothing of genes, one can sidestep these possibly sterile meme debates by appealing instead to the fundamental principles espoused in *On the Origin of Species by Means of Natural Selection* (Darwin 1859). Mesoudi et al. (2004, 2006) appraised the extent to which seven such core features of Darwin's theory—variation, inheritance, competitive selection, adaptation, geographical differentiation, convergent evolution, and changes of function—are reflected in human cultural evolution. Evidence was adduced for each.

Building on this approach, Whiten (2017) suggested that evidence is available for each of the seven features listed above for animal cultures, too, although the evidence is sparse as yet compared with that concerning the baroque forms of cultural evolution exhibited by humans. Cultural transmission is also significant for evolutionary biology because it creates new forms of evolution, notably (*a*) going beyond vertical transmission between parent and offspring to include horizontal and oblique transmission between unrelated individuals and (*b*) fine-tuning transmission biases such as "copy the successful" or "copy the majority" (Kendal et al. 2018), allowing continued adjustment to ecological contingencies that genes cannot match.

Aplin (2019) has further built on these explorations of cultural evolution in animals, reviewing the corresponding evidence for birds specifically in relation to the seven features of Darwinian evolution addressed by Mesoudi et al. (2004) and Whiten (2017). Aplin's survey is accordingly a timely complement to the present review.

In what follows, I focus on the first four of the Darwinian features, the core of the Darwinian engine of evolutionary change. First is the trio of variation, differential selection, and inheritance that forms the Darwinian algorithm (Dennett 1995) that makes things evolve. Adaptation to an ecological niche is then the resulting, fourth diagnostic element. The other three features mentioned earlier—geographic differences, convergence, and changes of function—are outcomes that may or may not follow.

Differential selection and adaptation can be regarded as two sides of the same coin, as it is the features of the animal's ecology, in the broadest sense, that provide the selection pressures that shape adaptation. What might be the scope of selection pressures in the case of cultural evolution? Most commonly, we think of adaptation to a niche characterized by the external environment, including physical features like the local climate selecting culturally for nest or burrow making, and by biotic features, such as potential foods and predators, the latter selecting culturally for evasion tactics, for example. But an animal's biotic environment also includes conspecifics, such as group-mates in social species, to which adaptive change may be shaped by selection—for example, cultural selection may create local cultural communication conventions like birdsong dialects. Also in this category is sexual selection—for example, when female preferences shape male courtship behavior, again illustrated by the example of birdsong, like the trill sections of Savannah sparrow song. However, sexual selection is a special category, because daughters may (perhaps culturally) inherit their mothers' preferences and sons (culturally) inherit their fathers' songs, a potentially runaway evolutionary scenario.

Cultural inheritance requires the brain of a cultural descendant to actively assimilate what it perceives in others, so this can also be a component of selection, where the adaptation is to the neural preferences of the receiver's brain. In human cultural evolutionary studies, this has been discussed in attractor theory, in which the hypothesis is that certain cultural variants are selected for because of a fundamental attraction between those variants and the assimilation preferences of human brains (Sperber 1996, Claidière & Sperber 2010, Claidière et al. 2014), as when some tunes spread culturally simply because they are catchy to the brains of listeners. Analogous processes may operate not only in birdsong but also in every aspect of cultural transmission, in part through adaptive biases in social learning (Kendal et al. 2018, Aplin 2019). The landscape of adaptation in the case of cultural evolution is accordingly expected to be multifaceted indeed, including adaptation to features of the physical, social, and sexual environments and the neural environments of social learners. Elements of behavior that evolve culturally under such selection regimes may do so independently of any effects on individuals' reproductive success and fitness, as measured at the level of genetic change.

In **Figure 1**, cultural evolution through Darwinian selection is envisaged to take two main forms, each defined by departure from selectively neutral drift (as in Savannah sparrow song): (*a*) directional change departing from the random nature of drift and (*b*) stabilizing selection constraining change to lower levels than expected. We can survey evidence for each in turn.

Directional Change Through Selection

Figure 1 distinguishes the main forms this may take: change or addition of characters versus loss of characters. These may be linked in episodes of replacement: For example, changes in birdsong like those already discussed may involve the loss of some elements, replaced by the addition of others. Even so, loss of elements is explicitly labeled here, first to acknowledge that cases of loss are evolutionary processes, just as in organic evolution, and second to highlight a contrast with the final category in **Figure 1**, the accumulation of characters. The latter occurs when new characters such as behavioral variations build on those already in existence, the equivalent process in organic evolution having resulted in the vast diversity of life-forms on our planet that evolved from simple primordial origins.

In the case of culture, this phenomenon is termed cumulative culture, a topic of intense interest because according to many authors in the field of cultural evolutionary studies, it is what distinguishes human culture from all the rest (e.g., Tomasello et al. 1993, Tennie et al. 2009, Henrich 2015, Henrich & Tennie 2018; see **Supplemental Table 2** for specific examples). Recent animal studies have challenged this, as we shall see below. However, the evidence is often too tentative to allow clear distinctions between cultural loss, change, addition, or accumulation. Instead, I structure the following text in relation to forms of evidence: first experimental, then observational. Each has its strengths and limitations, but they hold the promise of ultimately complementing each other.

Experimental studies. Arguably the most compelling evidence for cumulative social transmission in an animal (and the first permitted by reviewers to have "cumulative culture" in the title) comes from an experimental study of pigeon homing (Sasaki & Biro 2017). A pair of pigeons were first allowed to make multiple homing flights together, the pathway tracked by GPS. One bird was then replaced by a naïve one, and this pair flew more flights together. The more experienced of the two was then similarly replaced and the process repeated, such that later pairs were entirely different from those earlier in this transmission chain; nevertheless, homing tracks became progressively more efficient over time. This implies some process of cumulative cultural transmission over the successive steps of the cultural generations of flying pairs of birds.

In Whiten (2017), I noted an earlier transmission chain experiment completed before cumulative culture became topical. Menzel et al. (1972) exposed three juvenile chimpanzees to two novel objects that initially none dared approach. There were then 17 repeated replacements of the most experienced youngster by a naïve one. Thus, after every three steps the makeup of the group was entirely changed. In the middle of this sequence, stepwise increases in approaches to the two objects occurred over these transitions, so that in later generations, approaches reached nearly 100%. As in the pigeon homing experiment, there was cumulative cultural evolution of a simple and adaptive response, in this case approaching and exploring certain novel objects that were in fact harmless.

A very different experimental paradigm was pioneered by Claidière et al. (2014), echoing transmission chain experiments that present human subjects with simple artificial languages (Kirby et al. 2008). These studies find that the languages become progressively simplified and more systematically structured, facilitating participants' memorization. In a transmission chain experiment in which baboons had to remember where perceptual stimuli appeared in a grid, Claidière et al. (2014) reported three effects that at a certain level of comparison echo those found in human cultural evolution, namely: (*a*) emergence of systematic structure in what is transmitted, (*b*) a progressive increase in successful memorization and transmission, and (*c*) lineage specificity in the particular cultural differences perpetuated.

All three experiments offer rigorous demonstrations of cultural evolution and, indeed, of cumulative culture. However, each shows cumulative progress in relation to what we may think of as a single variable, like navigational efficiency, habituation, and memorization, respectively. Human cumulative cultures additionally include many cases where quite different elements are combined. This aspect was the focus of a study by Vale et al. (2017), in which chimpanzees were offered a variety of potential tools to help extract juice from a container outside their enclosure. Tools included sticks that could be dipped into the juice and short straws, but only one complex tool procured all the juice as its level dropped. This long bendy tube had to be uncoiled from its initial configuration and a valve opened at one end so it could be used as a long straw to suck up all the juice. Researchers found that if knowledge of this procedure was seeded in a single individual, it spread to others in their group, unlike in unseeded control groups. However, after prolonged exposure, exploratory manipulation led an individual in one control group to open the valve but without realizing that it became an effective straw. A second individual then used it as a straw. Later, this second individual observed the valve manipulator and thence attained the whole skill of unbending the tube, opening the valve, and sucking; conversely, the first individual observed and assimilated the sucking element and thence also mastered the whole sequence, which once invented spread to others. Accordingly, this is an elementary case of cumulative buildup involving the integration of two different actions following observational learning. Such results of collective intelligence in a community may perhaps be considered an analogy of recombination in genetic evolution.

Observational field studies. The experimental studies can rigorously identify a causal role for social learning. Observational field studies are often less robust in this respect but are vital to any understanding of cultural evolution's role in the natural lives of animals. They often present a richer picture of the nature of such processes.

An example echoed by the experiment of Vale et al. (2017) outlined above comes from studies of wild chimpanzees. Chimpanzees in many parts of Africa use stems as tools to extract termites from their mounds, but Sanz et al. (2009) described a more elaborate version of this. Members of a community in central Africa first used a stout stick to make a tunnel up to half a meter deep into a subterranean nest, stripped the end of a long stem they brought to the site, giving it a brush tip, and then carefully threaded this down the tunnel. Termites bit the brush tip and were delicately drawn up on the stem and eaten. The complexity of these techniques, coupled with the lack of affordances at the site for individual discovery of deep underground nests and effective techniques to access them, suggests the existing techniques may be the result of a long process of cumulative cultural evolution, from normal termite fishing aboveground to deep subterranean harvesting. As we have no historical records to test this interpretation, experimental studies like that of Vale and colleagues (2017) provide important complementary evidence that such cumulative processes can operate in this species. Various other forms of complex tool use in chimpanzees were interpreted as similar candidates for cumulative culture in a survey by Boesch (2012).

An example that corresponds instead with the experiments on pigeon navigation concerns migratory behavior. Jesmer et al. (2018) studied populations of bighorn sheep translocated to areas where they were earlier extirpated, finding that although these animals normally migrate in the spring to benefit from the green wave of high-quality forage propagating from valleys up into the mountains, the translocated groups initially ceased to migrate. Over decades and several generations, individuals progressively gained knowledge about how to surf the green wave, as evidenced in their increasing ability to track these waves of nutritious forage up mountainsides and in their migration from low-elevation wintering areas to high-elevation summer pastures. The authors concluded that their results "demonstrate that ungulates accumulate knowledge of local phenological patterns over time via the 'ratcheting effect,' wherein each generation augments culturally transmitted information with information gained from its own experience, a process known as cumulative cultural evolution. Cultural transmission therefore acts as a second (nongenetic) inheritance system for ungulates, shaping their foraging and migratory behavior and ultimately providing the primary mechanism by which their migrations have evolved" (Jesmer et al. 2018, p. 1024). A wide-ranging review of migratory culture spanning fish, birds, mammals, and insects concurred, concluding that "we find signatures not only of culture, but of cumulative culture, in the development and maintenance of animal travel routes" (Berdahl et al. 2018, p. 10).

As noted earlier, Williams et al. (2013) reported directional change in certain elements of the Savannah sparrow songs studied over a 30-year period, and given their linkage with reproductive success, the authors described this as cultural evolution, most likely attributable to sexual selection. Likewise, Gibbs (1990) (see also **Supplemental Table 1**) reported cultural evolution in ground finches attributed to both direct selection, where males with less common songs survived longer and the frequency of their songs rose in the population, and indirect selection, because these males grew larger, and larger males have more yearling offspring.

Another well-established directional effect has been identified in adaptive rises in birdsong vocal frequency that adapt to transmit better against a background of human urban noise. For example, Luther & Derryberry (2012) showed that from 1969 to 2005, white-crowned sparrow song in San Francisco progressively increased in minimum frequency, coincident with rising traffic noise; moreover, current males responded most strongly to recordings of the recent as opposed to early songs, implying selection for more effective communication.

The songs of whales such as humpbacks have also been described as evolving over time; however, every few years, populations in the South Pacific instead display cultural revolutions in which a whole new song is sung, rapidly spreading to all males within a population (Noad et al. 2000; Garland et al. 2011, 2017). Allen et al. (2018) examined several measures of complexity within the multiple-level structure of these songs sung by the population in east Australia and showed that in periods described as cultural evolution, complexity rose from year to year, but when revolutions occurred, complexity fell (**Figure 3**). The authors suggest that this recurring cyclical pattern may, by analogy with evidence of higher reproductive success associated with more complex songs in several avian species (e.g., Woodgate et al. 2012; and see Creanza et al. 2016), reflect sexual selection driving cultural evolution of song complexity, but that the fall in complexity during revolutions reflects a limit in males' capacity for social learning of novel vocal material.

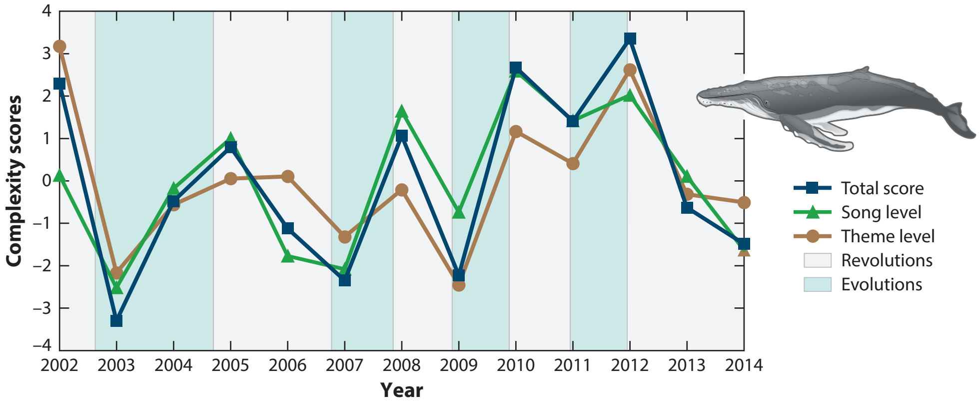

Figure 3

Cyclical rise and fall of complexity in humpback whale song. Three different measures of complexity in the multilevel structures of songs rise steadily during phases described as cultural evolution then drop during phases of cultural revolution, in which new songs are adopted. Figure adapted with permission from Allen et al. (2018).

The literature on animal culture has accumulated a variety of other studies proposed to imply directional selection and even cumulative culture, but a variety of limitations mean they are best regarded as interesting explorations that beg further rigorous testing. For example, the geographic distribution of simple and more complex forms of *Pandanus* leaf tools used by New Caledonian crows suggests cumulative evolution of the complex varieties (Hunt & Gray 2003), but whether this species learns by observation about tool or other object manipulation remains yet unproven (Kenward et al. 2005, Logan 2016). Schofield et al. (2018) describe a suggestive suite of ways in which the famous sweet potato washing of Japanese monkeys has been elaborated over decades, but again the role of social learning in many of the transitions remains untested.

Stabilizing Selection

Stabilizing selection is a recognized phenomenon in organic evolution (Futuyma 2013) but has received relatively little attention in animal culture studies. As we saw earlier, Williams et al. (2013) inferred that it must have been involved in the marked stability of elements of Savannah sparrow song over decades, perhaps because these features mark out a population's identity to potential mates. Nelson et al. (2004) and Byers et al. (2010) reported parallel effects in other species (see also **Supplemental Table 1**). Lachlan et al. (2018) reported that some swamp sparrow song syllables are copied with errors of less than 2%, associated with a conformist copying bias. Further modeling by these authors predicted that syllable types may persist for more than 500 years—vocal traditions whose stability, in the authors' words, "rivals those of humans" (Lachlan et al. 2018, p. 2417). Such effects merit more attention in other cultural domains and species.

GENE–CULTURE COEVOLUTION

Gene–culture coevolution is a well-established phenomenon in humans. The best-known example is lactose tolerance characterizing dairy-based cultures and not others, but different cases are increasingly revealed as genomic data accumulate (Laland et al. 2010, Richerson et al. 2010). The evidence for similar interactions in animals is as yet more meager but has begun to accumulate—its current scope surveyed in a review complementary to this one (Whitehead et al. 2019). The expression "gene–culture coevolution" implies that the two systems of inheritance evolve in tandem, which is very plausible given present evidence, but the implied two-way causality of the expression lacks much direct evidence, even in the human case. Most of the inferred effects, whether human or animal, concern how culture may shape genetically based evolution (e.g., Carroll et al. 2015). For example, comparative studies of primates have revealed associations between measures of cultural complexity, encephalization, and the duration of the juvenile period, suggesting that selection has favored such adaptations to facilitate a species' reliance on acquiring extensive cultural information (Reader & Laland 2002, Street et al. 2017). Such changes could in turn facilitate yet more pervasive cultural behavior, creating a spiraling coevolution of genes and culture, but this remains a plausible hypothesis rather than a clearly supported finding.

A similar state of affairs exists for other effects reviewed by Whitehead et al. (2019) such as culture shaping geographic distributions of genes, selecting for functional genes, reducing genetic diversity, and creating incipient speciation. The kinds of cultural evolution surveyed in the bulk of this review could possibly play a significant role in all of these effects, but these possibilities are highlighted here principally as potential future research targets.

CONCLUDING DISCUSSION

Dean et al. (2014) surveyed the literature and concluded that "presently there is no evidence that any species, except humans, have cumulative culture" (p. 299). This is a common assertion in the literature, including the articles cited above (see **Supplemental Table 2** for examples). Much of such discussion is focused on the concept of cumulative culture, with cultural evolution either not mentioned or treated as a synonym, and the eight birdsong papers with cultural evolution in their titles are not discussed in this literature (c.f. Boyd & Richerson 1996).

I submit that a different picture emerges from the literature reviewed here, much of it quite recent. Together, these studies suggest that both cumulative culture and the more inclusive concept of cultural evolution set out in **Figure 1** may be common in nature. For example, if the bighorn sheep studies (Jesmer et al. 2018) are representative, it could even be thought surprising if the multitude of migratory species did not cumulatively extend their relevant knowledge through cycles of cultural transmission and individual exploration (Whiten 2018). Similar cycles might operate as more sedentary species progressively rack up their ecological know-how across generations. The observational and experimental studies reviewed suggest productive ways to gain more robust understanding of such processes.

Some authors, noting that the outcomes of human cumulative culture are often beyond a single individual to generate, suggest this should be a criterion for the attribution of cumulative culture (Tennie et al. 2009, Henrich 2015). Cases such as isolated songbirds failing to sing recognizable songs and translocated bighorn sheep giving up migration seem to confirm this effect, but making this such a high ascriptional bar seems unhelpful when we are interested in the evolution of such outcomes from simpler origins. It also ignores contexts in which some individuals might be capable in principle of inventing the behavior pattern of interest but at such a cost in, for example, time or energy, that this is prohibitive (seriously depressing fitness) in the wild. Accordingly, in line with Mesoudi & Thornton's (2018) suggestion of adopting basic, core criteria and then further investigating variable outcomes, I favor the most basic definition—culture that is cumulative—leaving as an empirical question when this may eventuate in such outcomes as exceeding what individual learning can achieve.

The new discoveries about animal culture and cultural evolution have profound implications, both when looking narrowly toward better understanding of cumulative culture in humans through a more refined analysis of what separates it from the closest phenomena in other species

(Whiten 2018), and when looking more broadly to the role that culture plays in evolutionary biology across the animal kingdom (Whiten 2017, Whiten et al. 2017). Finally, implications of these same discoveries for animal conservation have now been recognized, with productive new synergies between scientific research on animal culture and conservation practices progressively explored—a most gratifying development (United Nations Env. Programme 2018, Brakes et al. 2019).

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I am grateful to Jenny Allen, Andrew Berdahl, Dora Biro, Ellen Garland, Brett Jesmer, Rob Lachlan, Luke Rendell, Peter Slater, Claudio Tennie, and Heather Williams for comments on drafts of this paper. Special thanks to Heather Williams and Jenny Allen for actively collaborating in creating **Figures 2** and **3**, respectively.

LITERATURE CITED

Alem S, Perry CJ, Zhu X, Loukola OJ, Ingraham T, et al. 2016. Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLOS Biol.* 14:e1002564

Allen J, Garland EC, Dunlop RA, Noad MJ. 2018. Cultural revolutions reduce complexity in the songs of humpback whales. *Proc. R. Soc. B* 285:20182088

Allen J, Weinrich M, Hoppitt W, Rendell L. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science* 340:485–88

Aplin LM. 2019. Culture and cultural evolution in birds: a review of the evidence. *Anim. Behav.* 147:179–87

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518:538–41

Aunger R, ed. 2000. *Darwinizing Culture: The Status of Memetics as a Science*. Oxford, UK: Oxford Univ. Press

Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidies J, O'Brien SJ. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344:238–40

Bartlett P, Slater PJB. 1999. The effect of new recruits on the flock specific call of budgerigars (*Melopsittacus undulatus*). *Ethol. Ecol. Evol.* 11:139–147

Bastian M, Zweifel N, Vogel ER, Wich SA, van Schaik CP. 2010. Diet traditions in wild orangutans. *Am. J. Phys. Anthropol.* 143:175–87

Berdahl AM, Kao AB, Flack A, Wetley PAH, Codling EA, et al. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Phil. Trans. R. Soc. B* 373:20170009

Boesch C. 2012. *Wild Cultures*. Cambridge, UK: Cambridge Univ. Press

Bonnie KE, de Waal FBM. 2006. Affiliation promotes the transmission of a social custom: hand-clasp grooming among captive chimpanzees. *Primates* 47:27–34

Boyd R, Richerson PJ. 1985. *Culture and the Evolutionary Process*. Chicago: Univ. Chicago Press

Boyd R, Richerson PJ. 1996. Why culture is common, but cultural evolution is rare. *Proc. Brit. Acad.* 88:77–93

Brakes P, Dall SRX, Aplin LM, Bearhop S, Carroll EL, et al. 2019. Animal cultures matter for conservation. *Science* 363:1032–34

Byers BE, Belinsky KL, Bentley RA. 2010. Independent cultural evolution of two song traditions in the chestnut-sided warbler. *Amer. Nat.* 176:4760489

Carroll EL, Baker CS, Watson M, Alderman R, Bannister J, et al. 2015. Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. *Sci. Rep.* 5:16182

Catchpole CK, Slater PJB. 2008. *Bird Song: Biological Themes and Variations*. Cambridge, UK: Cambridge Univ. Press. 2nd Ed.

Claidière N, Scott-Phillips TC, Sperber D. 2014. How Darwinian is cultural evolution? *Philos. Trans. R. Soc. B* 369:20130368

Claidière N, Smith K, Kirby S, Fagot J. 2014. Cultural evolution of systematically structured behaviour in a non-human primate. *Proc. R. Soc. B* 281:20141541

Claidière N, Sperber D. 2010. Imitation explains the propagation, not the stability of animal culture. *Proc. R. Soc. B* 277:651–59

Creanza N, Fogarty L, Feldman MW. 2016. Cultural niche construction of repertoire size and learning strategies in songbirds. *Evol. Ecol.* 30:285–305

Curio E, Ernst U, Vieth W. 1978. Cultural transmission of enemy recognition: one function of mobbing. *Science* 202:899–901

Danchin E, Nobel S, Pochville A, Dageef A-C, Demay L, et al. 2018. Cultural flies: conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* 362:1025–30

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection*. London: Murray

Darwin C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray

Dawkins R. 1976. *The Selfish Gene*. Oxford, UK: Oxford Univ. Press

Dean LG, Vale GL, Laland KN, Flynn E, Kendal RL. 2014. Human cumulative culture: a comparative perspective. *Biol. Rev.* 89:284–301

Dennett D. 1995. *Darwin's Dangerous Idea*. New York: Touchstone Books

Dugatkin LA, Godin JGJ. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav. Ecol.* 4:289–292

Fisher J, Hinde RA. 1949. The opening of milk bottles by birds. *Brit. Birds* 42:347–57

Futuyma DJ. 2013. *Evolution*. Sunderland, MA: Sinauer Associates. 3rd Ed.

Galef BG Jr., Whiten A. 2017. The comparative psychology of social learning. In *APA Handbook of Comparative Psychology*, ed. J Call. Washington, DC: Amer. Psycholog. Assoc.

Garland EC, Goldizen AW, Rekdah ML, Constantine R, Garrigue C, et al. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr. Biol.* 21:687–91

Garland EC, Rendell L, Lamoni L, Poole MM, Noad MJ. 2017. Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. *PNAS* 114:7822–29

Gibbs HL. 1990. Cultural evolution of male song types in Darwin's medium ground finches, *Geospiza fortis*. *Anim. Behav*. 39:253–63

Grant BR, Grant PR. 2002. Simulating secondary contact in allopatric speciation: an empirical test of premating isolation. *Biol. J. Linn. Soc.* 76:545–56

Gray RD, Atkinson QD. 2003. Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature* 426:435–39

Gruber T, Muller MN, Reynolds V, Wrangham R, Zuberbühler K. 2011. Community-specific evaluation of tool affordances in wild chimpanzees. *Sci. Rep.* 1:1038/srep00128

Gruber T, Muller MN, Strimling P, Wrangham R, Zuberbühler K. 2009. Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr. Biol.* 19:1846–52

Gunhold T, Whiten A, Bugnyar T. 2014. Video demonstrations seed alternative problem-solving techniques in wild common marmosets. *Biol. Lett.* 10:20140439

Helfman GS, Schultz ET. 1984. Social transmission of behavioural traditions in a coral reef fish. *Anim. Behav.* 32:379–84

Henrich J. 2015. *The Secret of Our Success: How Culture is Driving Human Evolution, Domesticating Our Species and Making Us Smarter*. Princeton, NJ: Princeton Univ. Press

Henrich J, Tennie C. 2018. Cultural evolution in chimpanzees and humans. In *Chimpanzees and Human Evolution*, ed. MN Muller, RW Wrangham, DR Pilbeam. Cambridge, MA: Harvard Univ. Press

Heyes CM. 1994. Social learning in animals: categories and mechanisms. *Biol. Rev.* 69:207–31

Hobaiter C, Poiset T, Zuberbühler K, Hoppitt W, Gruber T. 2014. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS Biol.* 12:e1001960

Hoppitt WJE, Laland KN. 2013. *Social Learning: An Introduction to Mechanisms, Methods and Models*. Princeton, NJ: Princeton Univ. Press

Horner V, Whiten A, Flynn E, de Waal FBM. 2006. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *PNAS* 103:13878–83

Huffman MA, Leca JB, Nahallage CAD. 2010. Cultured Japanese macaques: a multidisciplinary approach to stone handling behavior and its implications for the evolution of behavioral traditions in nonhuman primates. In *The Japanese Macaques*, ed. N Nakagawa M Nakamichi, H Sugiura. Tokyo: Springer

Hunt GR, Gray RD. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. B* 270:867–74

Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Primatol.* 72:62–71

Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Courtemanche AB, et al. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* 361:1023–25

Kawai M. 1965. New acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima Islet. *Primates* 2:1–30

Kendal R, Boogert NJ, Rendell L, Laland KN, Webster M, Jones L. 2018. Social learning strategies: bridge-building between disciplines. *Trends Ecol. Evol.* 22:651–55

Kenward B, Weir A, Rutz C, Kacelnik A. 2005. Tool manufacture by naïve juvenile crows. *Nature* 433:12

Kirby S, Cornish H, Smith K. 2008. Cumulative cultural evolution in the laboratory: an experimental approach to the origins of structure in human language. *PNAS* 105:10681–86

Lachlan RF, Ratmann O, Nowicki S. 2018. Cultural conformity generates extremely stable traditions in bird song. *Nat. Comm.* 9:2417

Laland KN, Odling-Smee J, Myles S. 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Gen.* 11:137–48

Laland KN, Williams K. 1997. Shoaling generates social learning of foraging information in guppies. *Anim. Behav.* 53:1161–69

Leca J-B, Gunst N, Huffman MA. 2007. Japanese macaque cultures: inter- and intra-troop behavioral variability of stone-handling patterns across 10 groups. *Behaviour* 144:251–81

Logan CJ. 2016. How far will a behaviourally flexible invasive bird go to innovate? *R. Soc. Open Sci.* 3:160247

Lonsdorf EV, Pusey EA, Eberly L. 2004. Sex differences in learning in chimpanzees. *Nature* 428:715–16

Luncz LV, Boesch C. 2014. Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behaviour despite frequent immigration of adult females. *Am. J. Primatol.* 76:649–57

Luther DA, Derryberry EP. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. *Anim. Behav.* 83:1059–66

Marler P, Tamura M. 1964. Song "dialects" in three populations of white-crowned sparrows. *Science* 146:1483–86

McGrew WC, Tutin CG. 1978. Evidence for a social custom in wild chimpanzees? *Man* 13:234–51

Menzel EW, Davonport RK, Rogers CM. 1972. Protocultural aspects of chimpanzees' responsiveness to novel objects. *Folia Primatol.* 17:161–70

Mercader J, Barton H, Gillisepie J, Harris S, Kuhn S, et al. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *PNAS* 104:3043–48

Mesoudi A, Thornton A. 2018. What is cumulative cultural evolution? *Proc. R. Soc. B* 285:20180712

Mesoudi A, Whiten A, Laland KN. 2004. Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*. *Evolution* 58:1–11

Mesoudi A, Whiten A, Laland KN. 2006. Towards a unified science of cultural evolution. *Behav. Brain Sci.* 29:329–83

Mineka S, Cook M. 1988. Social learning and the acquisition of snake fear in monkeys. In *Social Learning: Psychological and Biological Perspectives*, ed. BG Galef Jr., T Zentall, pp. 51–73. Hillsdale, NJ: Lawrence Erlbaum

Möbius Y, Boesch C, Koops K, Matsuzawa T, Humle T. 2008. Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Anim. Behav.* 76:37–45

Mueller T, O'Hara RB, Converse SJ, Urbanek RP, Fagan WF. 2013. Social learning of migratory performance. *Science* 341:999–1002

Mufano MR, Smith GD. 2018. Repeating experiments is not enough. *Nature* 553:399–401

Murray A, Dunlop RA, Noad MJ, Goldizen AW. 2018. Stereotypic and complex phrase types provide structural evidence for a multi-message display in humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Amer.* 143:980–94

Nakamura M, Uehara S. 2004. Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social customs. *Curr. Anthropol.* 45:108–14

Nelson DA, Halberg KI, Soha JA. 2004. Cultural evolution of Puget Sound white-crowned sparrow song dialects. *Ethology* 110:879–908

Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KCS. 2000. Cultural revolution in whale songs. *Nature* 408:537

Palacín C, Alonso JC, Alonso JA, Magaña M, Martin CA. 2011. Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. *J. Avian. Biol*. 42:301–8

Payne K, Tyack P, Payne R. 1983. Progressive changes in the songs of humpback whales: a detailed analysis of two seasons in Hawaii. In *Communication and Behavior of Whales*, ed. R Payne, pp. 9–57. Boulder, CO: Westview Press

Perry S, Baker M, Fedigan L, Gros-Luis J, Jack K, et al. 2003. Social conventions in white-face capuchins monkeys: evidence for behavioral traditions in a neotropical primate. *Curr. Anthropol.* 44:241–68

Rawlings B, Davila-Ross M, Boysen ST. 2014. Semi-wild chimpanzees open hard-shelled fruits differently across communities. *Anim. Cogn.* 17:891–99

Reader S, Laland KN. 2002. Social intelligence, innovation and enhanced brain size in primates. *PNAS* 99:4436–41

Reisch R, Barrett-Lenard LG, Ellis GM, Ford JKB, Deecke VB. 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales. *Biol. J. Linn. Soc.* 106:1–17

Richerson PJ, Boyd R, Henrich J. 2010. Gene-culture co-evolution in the age of genomics. *PNAS* 107(Suppl. 2):8985–92

Richerson PJ, Christiansen MH. 2013. Introduction. In *Cultural Evolution: Society, Technology, Language and Religion*, ed. PJ Richerson, MH Christiansen, pp. 1–21. Cambridge, MA: MIT Press

Riebel K, Lachlan RF, Slater PJB. 2015. Learning and cultural transmission in chaffinch song. *In Advances in the Study of Behavior*, Vol. 47, ed. HJ Brockmann, J Mitani, L Simmons, L Barrett, SD Healy, P Slater, pp. 181–227. Cambridge, MA: Academic

Robbins MM, Ando C, Fawcett KA, Gruiter CC, Hedwig D, et al. 2016. Behavioural variation in gorillas: evidence of potential cultural traits. *PLOS ONE* 11:e0160483

Sanz C, Call J, Morgan D. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* 5:293–96

Sasaki T, Biro D. 2017. Cumulative culture can emerge from collective intelligence in animal groups. *Nat. Comm.* 8:15049

Schleicher A. 1869. *Darwin Tested by the Science of Language*. London: JC Hoten

Schofield DP, McGrew WC, Takahashi A, Hirata S. 2018. Cumulative culture in non-humans: overlooked findings from Japanese monkeys? *Primates* 59:113–22

Schöning C, Humle T, Möbius Y, McGrew WC. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J. Hum. Evol.* 55:48–59

Slagsvold T, Wiebe KL. 2011. Social learning in birds and its role in shaping foraging niches. *Philos. Trans. R. Soc. B* 366:969–77

Slater PJB, Ince SA. 1979. Cultural evolution in chaffinch song. *Behaviour* 71:146–66

Snowdon CT. 2009. Plasticity of communication in nonhuman primates. In *Advances in the Study of Behavior*, Vol. 40, ed. M Naguib, K Zuberbühler, NS Clayton, VM Janik, pp. 239–76. Cambridge, MA: Academic

Sperber D. 1996. *Explaining Culture: A Naturalistic Approach*. New York: Blackwell

Street SE, Navarette AF, Reader SM, Laland KN. 2017. Coevolution of cultural intelligence, extended life history, sociality and brain size in primates. *PNAS* 114:7908–14

Tennie C, Call J, Tomasello M. 2009. Ratchetting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. R. Soc. B* 364:2405–15

Tervo OM, Parks SE, Christoffersen MF, Miller LA, Kristensen RM. 2011. Annual changes in the winter song of bowhead whales (*Balaena mysticitus*) in Disko Bay, Western Greenland. *Mar. Mamm. Sci.* 27:e241–52

Thorpe WH. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch. *Ibis* 100:535–70

Tomasello M, Kruger AE, Ratner H. 1993. Cultural learning. *Behav. Brain Sci.* 16:595–652

United Nations Env. Programme. 2018. *Report of the CMS workshop on conservation implications of animal culture and social complexity*. Convention on the Conservation of Migratory Species of Wild Animals, Bonn, Ger., May 29. **https://www.cms.int/en/document/report-cms-workshop-conservation-implications-animal-culture-and-social-complexity**

Vale GL, Davis SJ, Lambeth SP, Schapiro SJ, Whiten A. 2017. Acquisition of a socially learned tool use sequence in chimpanzees: Implications for cumulative culture. *Evol. Hum. Behav.* 38:635–44

Valenzuela LO, Sironi M, Rowntree VJ, Seger J. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Mol. Ecol.* 18:782–91

van de Waal E, Borgeaud C, Whiten A. 2013. Potent social learning and conformity shape a wild primate's foraging decisions. *Science* 340:483–85

van de Waal E, Claidière N, Whiten A. 2015. Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Anim. Cog.* 18:617–27

van Leeuwen EJC, Cronin KA, Haun SBM. 2014. A group specific arbitrary tradition in chimpanzees. *Anim. Cogn.* 17:1421–25

van Leeuwen EJC, Cronin KA, Haun SBM, Mundry R, Bodamer MD. 2012. Neighbouring chimpanzee communities show different preferences for social grooming. *Proc. R. Soc. Lond. B* 279:4362–67

van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, et al. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102–5

Warner RR. 1988. Traditionality of mating-site preferences in a coral fish. *Nature* 335:719–21

Watson SK, Townsend SW, Schel AM, Wilke C, Wallace EK, et al. 2015. Vocal learning in the functionally referential food grunts of chimpanzees. *Curr. Biol.* 25:495–99

Whitehead H, Laland KN, Rendell L, Thorogood R, Whiten A. 2019. The reach of gene–culture coevolution in animals. *Nature Commun*. 10:2405

Whitehead H, Rendell L. 2015. *The Cultural Lives of Whales and Dolphins*. Chicago: Chicago Univ. Press

Whiten A. 2005. The second inheritance system of chimpanzees and humans. *Nature* 437:52–55

Whiten A. 2012. Social learning, traditions and culture. In *The Evolution of Primate Societies*, ed. J Mitani, J Call, P Kappeler, R Palombit, J Silk, pp. 681–99. Chicago: Chicago Univ. Press

Whiten A. 2017. A second inheritance system: the extension of biology through culture. *Interface Focus* 7:20160142

Whiten A. 2018. Foraging skills develop over generations in the wild. *Nature* 562:198–200

Whiten A, Ayala FJ, Feldman MW, Laland KN. 2017. The extension of biology through culture. *PNAS* 114:7775–81

Whiten A, Caldwell CA, Mesoudi A. 2016. Cultural diffusion in humans and other animals. *Curr. Opin. Psychol.* 8:15–21

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, et al. 1999. Cultures in chimpanzees. *Nature* 399:682–85

Whiten A, Hinde RA, Stringer CB, Laland KN. 2011. Culture evolves. *Philos. Trans. R. Soc. B* 366:938–48

Whiten A, Horner V, de Waal FBM. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437:737–40

Whiten A, Mesoudi A. 2008. An experimental science of culture: animal social diffusion experiments. *Philos. Trans. R. Soc. B* 363:3477–88

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, et al. 2007. Transmission of multiple traditions within and between chimpanzee groups. *Curr. Biol.* 17:1038–43

Whiten A, van de Waal E. 2018. The pervasive role of social learning in primate lifetime development. *Behav. Ecol. Sociobiol.* 72:80

Whiten A, van Schaik CP. 2007. The evolution of animal 'cultures' and social intelligence. *Philos. Trans. R. Soc. B* 362:603–20

Williams H, Levin II, Norris DR, Newman AEM, Wheelwright NT. 2013. Three decades of cultural evolution in Savannah sparrow songs. *Anim. Behav.* 85:213–23

Woodgate JL, Mariette MM, Bennett ATD, Griffith SC, Buchanan KL. 2012. Male song structure predicts reproductive success in a wild zebra finch population. *Anim. Behav.* 83:773–81