# The extension of biology through culture

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Biology is the study of life. How our understanding of the nature and evolution of living systems is being enriched and extended through new discoveries about social learning and culture in human and nonhuman animals is the subject of the collection of articles we introduce here.

Recent decades have revealed that social learning and the transmission of cultural traditions are much more widespread in the animal kingdom than earlier suspected, affecting numerous forms of functional behavior and creating a secondary form of evolution, built onto the better-known primary, genetically based form. New scientific approaches to the study of human cultural evolution have also emerged and become productive. However, these developments in the study of cultural phenomena in both human and nonhuman animals have yet to be seriously integrated into mainstream evolutionary biology. Here we offer an introductory overview of the background and scope of a collection of articles that report recent progress in these fields, and outline their proposed significance for biology at large.

The theoretical backbone of the life sciences, its central organizing principle, is of course evolution, by now rich in both theory and empirical support (1–3). The great synthesis of Darwin's and Wallace's evolutionary insights and early 20th century understanding of genetics that became known as the "Modern Synthesis" was achieved by a brilliant set of biologists mainly in the period 1938–1946 (4), and its principles have provided the core of evolutionary theory since that time (5). Thus, contemporary texts on "evolution" focus on such topics as mutation, genetically based inheritance, population genetics, genomics, and the natural and sexual selection pressures that shape gene frequencies, genotypes, and phenotypes (1, 2, 6, 7). Genes and their role in inheritance have come to be celebrated as the pivotal elements in evolution (8).

However, a second form of evolution was also recognized long ago, in the ways that cultural phenomena have changed in the course of human history, through a different form of inheritance: that in which people learn from others (social learning), including from previous generations. Darwin himself recognized the parallels between the evolution of culturally inherited languages and organic evolution (9, 10); indeed, evolutionary family trees of languages proposed by philologists long predated the *Origin of Species*, although they were further spurred by its publication (11–13).

During the 1970s and 1980s, first by Cavalli-Sforza and Feldman (14–16) and then Boyd and Richerson (17), the implications of the existence of the two forms of evolution, organic and cultural, was at last explored systematically and formally, through conceptual and mathematical modeling that formed a foundation for later empirical investigations. The present collection of papers opens with a contribution by Creanza et al. (18) that offers an overview of both the foundational studies in (human) cultural evolution and major developments in the period since. The early body of 20th century work laid out some of the ways in which cultural evolution: (*i*) echoes many core principles of organic evolution, yet (*ii*) also differs from it in dramatic ways that change evolutionary dynamics, and (*iii*) interacts with the genetically based phenomena to create new complexities ("gene–culture coevolution"). We return to discuss these further, below. From a somewhat different perspective Maynard-Smith and Szathmary (19) distinguished a series of major transitions in the nature of evolution, such as the emergence of multicellularity and of sex, the most recent major transition being the emergence of (human) culture; and Dawkins (20) gave a name to cultural elements suggested to be the analogs of genetic replicators—"memes"—which has been assimilated into popular culture. Other authors suggested "semes" (21), echoing semiotics, the study of signs and symbols.

We shall discuss such developments and subsequent related scientific progress further below, but for

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the moment we make one observation: all of these writings on culture were focused on a single species, our own. That other species might exhibit the core properties of cultural transmission, and that this was worthy of scientific investigation, began to be recognized in a number of different lines of animal behavior research only around the middle of the last century. Moreover, evidence for animal social learning and tradition started to become substantial only in the most recent decades, and thus was not only unremarked in the Modern Synthesis but gained only minimal mention in the foundational works of cultural evolution (14, 17). The earliest reports for nonhuman animals (henceforth "animals") were of novel traditions arising and spreading, notably bottle-top opening to drink milk by titmice (22) and washing food items in the sea by Japanese monkeys, referred to conservatively at the time as "pre-cultures" (23). An additional revelation was the discovery of bird song learning and the existence of local song dialects (24). Since these foundational studies, there has been a proliferation of studies documenting social learning and traditions in animals (25, 26), often referred to as "animal culture" (27).

## The Discovery of Widespread Animal Culture

Research over the last half-century has led to the revelation that learning from others (social learning) is widespread in the animal kingdom and spans a great range of important functional contexts, including diet, feeding techniques, travel route selection, predator avoidance, vocal communication, migration, and mate and breeding site choices (26, 28). Hundreds of laboratory experimental studies have demonstrated social learning and transmission in a wide variety of animals. Social learning is now extensively documented in mammals (29), with a particular intensity of research studies in primates (30–33) and cetaceans (34–37), in birds (38–41), in fish (42), and in insects (43, 44). The fact that social learning has been shown to play important roles spanning multiple functional contexts (25–28) suggests that many animals are not simply acquiring one or a few behavioral patterns socially, but rather that social learning is central to their acquisition of adaptive behavior.

Social learning may lead to the spread of a behavior to other individuals, which is what defines cultural transmission, and the establishment of traditions that come to characterize whole groups, subgroups, or populations. However, social learning may also be transient, and lead to no such substantial population-level effects; for example, a monkey may learn from others that a particular tree is in fruit or that a snake is in a particular bush, which shape its behavior for only a short period thereafter. Evidence for social learning, so widespread in animals, is thus not sufficient to demonstrate the larger phenomena of traditions and culture. Nevertheless, cultural diffusion has been further documented not only in all of the vertebrate research reviews listed above, but also in insects, at least in the laboratory. For example, Alem et al. (45) trained demonstrator bumble bees to pull a small piece of string to access an artificial flower providing food, and experiments then showed that many other bees that observed them acquired the novel technique, with this learning not shown by control bees that had no model from which to learn. Moreover, other bees learned from the earliest learners, and transmission across several such "cultural generations" was demonstrated. The extent to which this kind of transmission occurs in the wild is now a question that demands focused study.

In vertebrates, plentiful evidence exists that such cultural transmission occurs in nature, with substantial and indeed striking impact. For example, archaeological excavations have shown remains of nut-cracking materials dated to 4,300 y below the surface of the Taï Forest, where modern chimpanzees continue this practice, absent in most parts of Africa (31, 46); 27 y of observations have documented the spread from a few to over 600 humpback whales of a new form of hunting technique, lob-tail fishing (47); and new humpback songs have been found to emerge, spread quickly to whole populations, and pass in waves across the Pacific in consecutive years (36, 37).

That it has taken so long to begin to discover the broad scope of animal culture has several possible explanations. One important source of the progress made has been the achievement of long-term field studies. For example, just a half-century ago researchers knew next to nothing about the behavior of our closest primate relatives in the wild, but in recent times it has been possible to assemble data on each of several species from multiple, decades-long field studies to discover putative cultural differences amenable to more focused study, as now achieved for different genera of the great apes (31). The example of the long-term observations that identified the spread of the lob-tail hunting technique in humpback whales has already been mentioned (47). That study also illustrates the application of increasingly sophisticated statistical analyses to identify social learning through the way in which a novel behavior spreads along the lines of social networks [network-based diffusion analysis (26)], an approach now applied in other contexts, such as tool use in chimpanzees (48). This is one among a growing armory of such statistical approaches bearing fruit in the discipline (26).

The most compelling evidence of social learning comes from experiments, the most basic (but powerful) forms of which involve comparing an experimental condition in which animals have witnessed a trained model complete some novel task, with a control condition lacking a model, or comparing two experimental conditions in which models display different task solutions. Dyadic studies of this kind have a century-long history, but in recent decades modifications have been made to allow testing for the more culturally relevant phenomenon of the diffusion of behaviors across multiple individuals or even between groups. Several different experimental designs have since identified diffusion through social learning, both in laboratory and field conditions, and in an accelerating number and diversity of mammalian, avian, piscine, and insect species (49, 50).

However, this growing array of widespread cultural phenomena in animals appears to have gone largely unrecognized in mainstream texts on evolution (e.g., refs. 1, 6, 7, 19) or receives only minimal mention (2). One major goal of the present PNAS issue is to illustrate the scope of the findings on animal culture that now merit integration into evolutionary biology at large.

Building on a recent book-length review making the case that culture pervades numerous aspects of the life of whales and dolphins (34), two papers in the present collection describe recent progress in studies of these cetaceans. Garland et al. (37) focus on the transmission of complex song in humpback whales, presenting a painstaking and highly illuminating analysis of the process of song hybridization during the remarkable periods of "cultural revolution" found in this species. Behavioral hybridization has often been highlighted as a phenomenon differentiating cultural from genetically based evolution, although hybridization is far from unknown at the species level and recent research increasingly suggests that it has been much more common than previously suspected at the level of genetic transfer (51). The new humpback data reveal two different, specific ways in which hybridization occurs, involving the application of systematic structural rules that the authors propose are similar to—and provide additional insights into—those identified in both birdsong and human language. Whitehead (35) goes on to review the evidence for gene–culture coevolution in both whales and dolphins, appraising the evidence that matrilineal cultural inheritance has been particularly influential in creating ecologically specialized communities in species, such as killer whales, in turn explaining low diversity in matrilineal mitochondrial DNA and regional variation in mitochondrial DNA haplotype distribution. We return to this study in addressing the issue of gene–culture coevolution further below.

Cultural transmission has long been recognized in the sphere of birdsong (24, 38) but birds have tended to be seen as "one-trick (cultural) ponies" in this respect. However, recent studies have identified cultural transmission across a much broader span of behavior (39, 40, 52, 53). A striking case is the high-fidelity spread of alternative foraging behaviors experimentally seeded in substantial communities of great tits (40). Here, Aplin et al. (41) show that these behaviors will evolve adaptively as payoffs change, and the authors present evidence that this occurs through an intriguing combination of conformist social learning and payoff-sensitive individual learning.

Recent evidence that insects also show not only social learning, but a capacity for cultural transmission spreading across communities, is reviewed here by Leadbeater and Dawson (44), leading them to appraise the potential consequences for the evolution of learning processes and the brain. The authors conclude that "Social insects are distant relatives of vertebrate social learners, but the research we describe highlights routes by which natural selection could coopt similar cognitive raw material within the animal kingdom."

Primates have long been at the forefront in research on animal culture (27). In the present collection Whiten (31) reviews the diversity of complementary observational and experimental evidence for social learning and multiple-tradition cultures in the great apes. Although ape (and other nonhuman) culture does not encompass the elaborate levels of cultural evolution evident in humans, Whiten concludes that the accumulated evidence now exists for the principal implications of culture for evolutionary biology alluded to earlier: cultural evolution displays a number of properties evident in genetic evolution but through the different means of social learning. The interactions of genetic and cultural transmission are evolutionarily consequential.

Cultural evolution rests upon the complementary processes of innovation and selective transmission, but concentration of research to date on testing primates' capacity for transmission has arguably resulted in neglect of the innovation ("mutation") element, which is less susceptible to experimental manipulation in the laboratory, and challenging to record in the wild. Here Perry et al. (33) report on 10 y of observations of over 200 capuchin monkeys (*Cebus capucinus*) in 10 groups, with research explicitly focused on innovations as well as their transmission. Distinguishing four main functional categories of behavior, these researchers report 17 innovations in foraging and drinking, 9 in hygienic and other self-directed behaviors, 53 classed as investigative, and 49 as social behaviors. Just 21% of these large totals were picked up by others, indicating marked selectivity, which these authors dissect further. This research begins to identify the Darwinian processes of variation and selective transmission underlying cultural transmission in nonhuman species. As noted above, these processes can continue throughout life, contrasting with the genetic package transmitted at conception; this is the focus of a third primate study, on a different genus of capuchin monkey (*Sapajus libidinosus*) renowned for their tool-assisted nut-cracking behavior. Fragaszy et al. (32) trace the acquisition of this skill through the course of development over the several years needed to acquire competence, revealing the complex cycles of practice and attention to experts' nut-cracking, with adults' behavior helping to focus attention on rare elements of the skill that are critical to success.

## Human Culture Is Special

The present issue includes several papers on a single species: our own. This focus clearly does not correspond with any proper proportional representation among animal species; the explanation is simply that the scope and penetration of culture is exceptional in humans (54–57), and because of this, human culture extends biology in many additional and extraordinary ways. Indeed, some of the consequences of human culture, like the destruction of other species' habitats, climate change, and pollution, are already having (and in many cases have already had) major effects on the evolution, distribution, and extinction of major segments of the world's biota (58, 59).

Studies of human cultures have been pursued by an even greater diversity of approaches than those sketched for animal culture above. There is of course a whole discipline of social and cultural anthropology for which, as the name implies, the target of study is culture, and this has often striven for forms of participant observation extending to self-immersion in different cultures, an approach actively avoided by most students of primate behavior, and often not even thinkable for more distantly related species. In contrast to common approaches in cultural anthropology, those working within the field of cultural evolution have created an array of different approaches and methods that are often more conventionally scientific. These include a greater emphasis on such elements as formal and mathematical modeling, quantification and statistical analysis of numerical data, hypothesis testing, and systematic experimentation (18, 25, 56, 60–63). There is not the space here to offer anything like a comprehensive review of the resulting discoveries, but we can outline something of their range, with selected illustrations.

Those studies that examine the earliest evidence for human culture have shown a continuing trend for markers of change to be found at ever earlier dates. For example, the earliest evidence of stone tool use has recently been pushed back from 2.6 to 3.4 million y ago (64), roughly the half-way point since our shared ancestry with *Pan*. Here, Stout and Hecht (65) develop models of early lithic culture that integrate its distinctive human elements and primate foundations, both behavioral and neural. Similarly, the beginnings of what has been labeled "symbolic culture," indexed by such features as decorative items, like beads, has been pushed back from the previous "cave art" dates of around 30 ka to closer to 100 ka, or in the case of some elements like ochre, to even earlier dates, through a diversity of striking archaeological finds (66). Here, d'Errico et al. (67) provide a rich and detailed account of the ways in which cultural repertoires and their associated ecological niches differentiated and evolved in these periods.

Within historical times, the records of human culture have become amenable to some of the systematic and quantitative methods developed within evolutionary biology to reconstruct phylogenetic relationships at scales ranging from macroevolution to finer-grained speciation patterns (68). Such approaches have been particularly powerfully applied to the differentiation and evolution of language groups (68, 69), but also to such diverse topics as the evolution of socio-political organization (70) and folk tales (71). Here, Gray and Watts (60) apply this approach to the evolution of religion, using this example to explore the analysis of cultural macroevolution.

As in the capuchin study of Fragaszy et al. (32), the psychological and social processes that allow human culture to be so distinctive need to be examined as individuals' life histories unfold, and the affordances of the culture in which they develop are selectively assimilated and further modified. On the one hand, these processes are part of our species' biology, their properties shaped during the millennia of evolutionary time over which our ancestors became increasingly and intensively dependent on cumulative cultural inheritance (54, 56, 57). In turn, these unique cultural processes operating in humans generate forms of life not hitherto witnessed in the natural world. To highlight and dissect some of these special cultural phenomena, we include in this issue four contributions that share a focus on ontogenetic development.

Legare (72) provides an overview of core features of human development that facilitate the adaptive transmission and refinement of culture, including the concept of "natural pedagogy," whereby adults provide active support to cultural assimilation and children are predisposed to recognize and respond to this in particular ways, such as selective and discriminating copying (for example with respect to alternative cultural models), conformity, including the recognition of norms, and innovative flexibility. Other, complementary contributions in the present collection focus on more specific topics, including the active role that children come to play in recognizing their ignorance, as well as their knowledge, and systematically seek information to remedy this (73); the ways in which related hypothesis testing changes through the long period of human development in relation to the stage of cognitive development and socio-ecological context (74); and the significance of language as both a product and medium of culture, illustrated by the linguistic labels and generics that provide special forms of both the transmission fidelity and affordance for innovation that permit cumulative culture (75).

## How Culture Extends Biology

How the existence of culture extends our understanding of the scope and nature of living systems and their evolution was initially analyzed in three major respects (14, 15, 17). First, cultural phenomena provide a second inheritance system (76) built on the foundations of the primary, genetically based system, and this can generate a second form of evolution in the sphere of culturally transmitted behaviors and artifacts. Second, because cultural transmission is mechanically different from genetic transmission in particular ways, such as horizontal diffusion among nonrelatives, it can have new and drastically different evolutionary consequences (62). Third, the two systems may interact in complex ways, the phenomenon of gene–culture coevolution (16, 56, 77, 78). To these three we can now add two other important dimensions. One is that the accumulating evidence that social learning and cultural transmission are much more widespread and consequential across the animal kingdom than earlier suspected, extends much more broadly the implications of the three effects outlined above, which were originally conceived with a focus on human culture. A second is that studies increasingly dissect and delineate the richness of the consequences of cultural evolution, and resulting diversification of life forms. Examples of recent such discoveries range from the elucidation of functional forms of teaching in nonhuman animals (79) to "rational imitation" (80) and "overimitation" (81) in children. The contributions to this issue address all of these prospects conceptually and empirically in diverse and important ways. Here, we offer a brief introductory overview of the background foundations to these new explorations and updated reviews.

***Cultural Phenomena Create a New Form of Evolution.*** The core of adaptive evolution through natural selection involves the triad of variation in characters, competitive selection of the best adapted to current circumstances among them ("survival of the fittest," although relative reproductive success is what ultimately counts), and inheritance of those selected characters by descendants (82). Interwoven in cycles of these processes are three additional principles, notably the refinement of adaptations suited to the properties of ecological niches, the accumulation of complexes of these, and differentiation of descendant populations where they are sufficiently separated, for example by geography, ultimately leading to speciation. The latter three effects are manifested in the picture of organic evolution with which we are familiar, involving a broadly progressive complexification in life—from early bacteria to the sophisticated animals of today—and a vast diversity of living species, all displaying a remarkable fit to the ecological niche they so successfully inhabit. Current thinking in cultural evolution suggests that all these principles are active also in human cultural evolution (14, 16, 56, 61). Social learning and transmission provide the inheritance element and human invention the variants, the most successful of which are transmitted to future generations, generating cultural adaptations to environments around the world; and progressive, cumulative cultures show immense regional differentiation. Empirical evidence in support of these contentions has accumulated over recent decades, reviewed for example in refs. 61, 62, 78, 83, and 84, and is pursued further in the present collection (18, 63).

Such questions about cultural evolution have remained little studied in the animal culture literature, which has instead been focused on the more fundamental matter of establishing what cultural phenomena exist in a diversity of species, and what transmission processes underpin these (25, 27, 34). Initial explorations of Darwinian dynamics in the case of animal culture (53) have taken the list of eight key properties extracted from the *Origin of Species* (9) for testing with human data [the six listed above, plus changes of function and convergent evolution (83)] and through examining studies of animal culture, concluded there is evidence for all of them (although minimal and slow-developing compared with the most recent, cumulative cultures of humans). However, there is evidence that animal traditions with suboptimal payoffs are sometimes, although seemingly not always (85), vulnerable to decay (41), implying the working of the core Darwinian triad, and it seems likely that those animals for which there is now evidence of multiple-tradition cultures are the descendants of lines of ancestors among whom these traditions were progressively added, surviving through their success, as in the case of over 4,300-y-old nut-cracking in chimpanzees, mentioned earlier (46). Nonetheless, experimental studies, for example, of mate-choice copying, show that animal social transmission can be evolutionarily consequential, even if short lived (86).

In any case, it is becoming apparent that cultural phenomena play an important role in shaping many species' adjustment to and exploitation of their environments, with likely significant evolutionary consequences that are the focus of current research.

***Cultural Evolution Includes Characteristics Absent in Genetically Based Evolution.*** Cultural evolution may display analogs of organic evolution outlined above, but it is also different in many fundamental respects, further extending the scope of the evolutionary processes that shape biological systems (14, 17). Notably, transmission is not only vertical, as in genetic inheritance from parent to offspring, but can be horizontal, between unrelated peers, or oblique, from unrelated individuals in the parental generation (14); moreover, because this involves neurally based learning rather than genetic change, such transmission can be quite rapid, as well illustrated by the case of "revolutions" in the songs of humpback whales, which may change annually yet quickly come to be sung by whole populations (37), and in a variety of human and animal cases further explored in this issue.

Furthermore, unlike the genetically packaged adaptive information inherited at conception, social information may be gathered throughout ontogeny and indeed across the lifespan, and in interaction with individual learning and practice, it can thus permit iterative and flexible forms of adaptation as circumstances change. Here, this is illustrated in analyses of extended ontogeny of difficult skills, like nut-cracking in primates (32, 48). Moreover, even innovations, the analog of mutations that become subject to selective adoption and further transmission to others, may be far from random; instead, they are often immediately functional, most clearly in the example of intelligent, goal-oriented human inventions, but also in the closest animal counterparts.

The social transmission process may itself be adaptively shaped by different biases in what is selectively assimilated, variously referred to as transmission biases (17) or social learning strategies (87). Examples include biases to copy behavioral routines, where there is evidence they are successful, conformist copying of the majority (exploiting "the wisdom of the crowd"), and indirect biases, such as copying individuals on the basis of their reputation or group identity. Evidence for an array of such biases has accumulated in studies of both human and animal cultural transmission (88) and are further addressed in this collection (48, 72, 73).

***Gene–Culture Coevolution.*** Empirical evidence for cultural practices creating selection pressures that feed back to affect biological evolution have been known for some time in the human case (17). Such ideas reach back further to the Baldwin effect, which proposed that a measure of plasticity in animals' adjustment to their worlds during their lifetimes, including by learning, could create selection pressures for corresponding organic change (89), as well as to later notions of "behavioral drive" and "cultural drive" (90, 91) and niche construction (92). However, these ideas are becoming much refined and supported by extensive data in the age of genomics (93, 94).

Using a diversity of evidence from archaeology to neuroscientific investigations, Stout and Hecht (65) analyze how the cultures of the Stone Age shaped brain size and structure to create the cognitive and manual skills required for the evolution of greater sophistication in tool making. This kind of feedback may have been in existence for a very long time. Following a comparative phylogenetic analysis of primate brain and behavior data, Street et al. (95) conclude that cultural processes may have generated such selective feedback (see also ref. 31). Their analyses suggest that both brain expansion and high reliance on culturally transmitted behavior coevolved with sociality and extended lifespan in primates. This coevolution is consistent with the hypothesis that the evolution of large brains, sociality, and long lifespans has promoted reliance on culture, with reliance on culture in turn driving additional increases in brain volume, cognitive abilities, and lifespans in some primate lineages. Lotem et al. (96) further describe an explicit model that accommodates the shaping of cognition by culture, from basic building blocks of learning and data acquisition to phenomena such as language and tool use. The authors illustrate how learning and cognition will evolve in response to human cultural activities.

It has been proposed that cultural differentiation between groups can have knock-on effects on genetic differences, in the case of birdsong leading to segregated communities between which courtship and mating break down, ultimately leading to speciation (97). The most comprehensive analyses of such effects in cultural evolution among animals have been in whales and dolphins (34, 35). In some species, different migratory routes appear to be culturally transmitted from mothers to calves, thence reflected in diverging genetic make-ups. Most striking is the case of the differentiation of killer whale ecotypes characterized by alternative hunting strategies (targeted at seals vs. salmon and other fish, for example), song types, and residence patterns, that are proposed to be responsible for anatomical changes, such as different jaw types suited to alternative prey (35, 98).

## The Present Issue: The Extension of Biology Through Culture

The papers that follow in this collection address the multiple topics alluded to in the introduction above. Papers in the earlier parts of the collection have a predominant focus on studies of animals, and the remainder a focus on the human case. These are sandwiched between an opening paper coauthored by one of the founders of the subject of cultural evolution, that offers an overview of core cultural evolution theory and empirical findings across human demography, population dynamics, and ecology (18), and a final complementary overview appraising progress made and prospects for the future of these endeavors (63).

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