

REVIEW SUMMARY

ANIMAL CULTURE

The burgeoning reach of animal culture

Andrew Whiten

BACKGROUND: Culture—the inheritance of an array of behavioral traditions through social learning from others—was once thought specific to humans. Recent and accumulating evidence has shown that, to the contrary, culture permeates the lives of a great diversity of animals, with far-reaching implications for evolutionary biology, anthropology, and conservation. Early evidence for animal culture emerged in the mid-20th century in the discovery of regional birdsong dialects and the spread of provisioned sweet potato washing in Japanese monkeys. Stimulated by these discoveries, long-term studies of wild chimpanzees and orangutans later in the century revealed complex cultures composed of multiple traditions spanning diverse aspects of apes' lives, from tool use to social and sexual behavior.

In part through the accumulation of further long-term field studies, the present century

has witnessed an explosion in discoveries about social learning and culture, not only in primates but also in a rapidly growing range of animal species, from cetaceans to a diverse array of birds, fish, and even invertebrates.

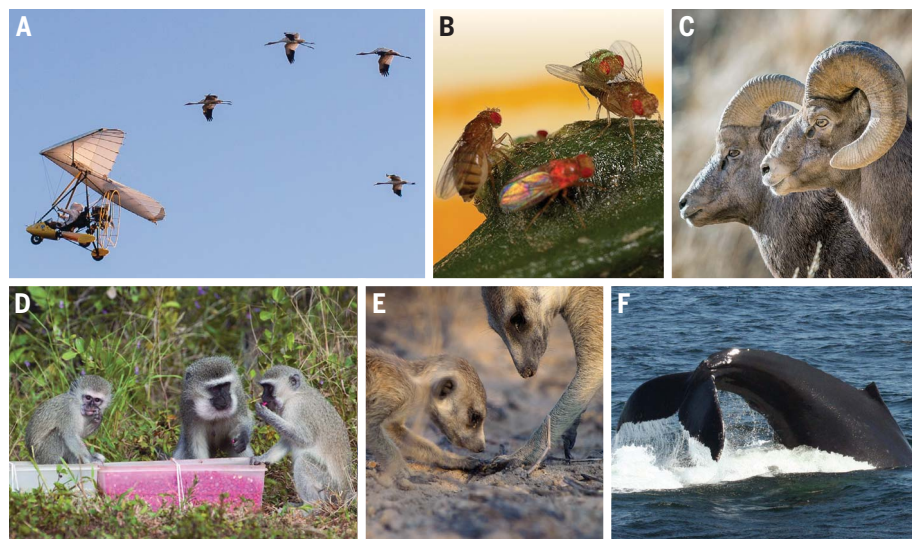
ADVANCES: Novel experimental designs have rigorously demonstrated the cultural transmission and spread of behavioral innovations introduced by researchers, both in the wild and in labs. New statistical methods have detected the signatures of behavioral innovations as they spread through social networks, identifying culture in species (e.g., whales) for which experiments are impractical. Through these and other methodological advances, the reach of cultural learning is now known to encompass an unexpected range of species, with surprising new discoveries extending even to insects, from bees to fruit flies.

The reach of culture has similarly been discovered to span diversity in behavioral domains, including foraging techniques, tool use, vocal communication, social customs and preferences for particular prey, migratory pathways, nesting sites, and mates. The revelation that cultural inheritance permeates many species' lives is increasingly recognized to have profound implications for evolutionary biology at large, because it provides a second form of inheritance that builds on the primary genetic inheritance system, facilitating cultural evolution. The two inheritance systems may generate rich interactive effects, as they have in humans.

A plethora of innovative experiments has further identified an array of cognitive processes involved in learning from others, ranging from simple and ubiquitous forms to specialized ones such as imitation and teaching. These forms of social learning have been shown to be further refined through a variety of selective biases, such as conforming to majorities or copying particularly skilled elders.

OUTLOOK: United Nations bodies operating under the aegis of international conventions have recently recognized the importance of all that has been discovered about animal cultures, for conservation policies and practices. Among sperm whales and chimpanzees, specific cultural entities, as opposed to genetically defined units, have been recognized as meriting conservation in their own right. This finding, in turn, urges a greater focus on understanding cultural phenomena in the wild. The task of rigorously identifying social learning has relied heavily on controlled experiments in captivity, but field experiments are increasingly carried out. These and other innovative methods to identify and trace animal cultures in the wild deserve to be developed and applied further to wild populations.

The wealth of methodological advances and empirical discoveries about animal cultures in the present century provides an exciting foundation from which to explore deeper questions. Do animal cultures evolve, cumulatively, as human cultures have done so impressively over past millennia? How profoundly does the lifetime reach of culture in animals' lives reshape our understanding of behavioral ecology and the fundamentals of evolution at large? How close are human and animal cultures now perceived to be, and where do the principal differences remain? ■



Diversity in cultural species and behavioral domains. (A) After filial imprinting on the costumed human pilot of a microflight aircraft, young cranes followed the flight path of this surrogate parent, adopting it as a traditional migratory route. (B) Female fruit flies (left) that witness a male marked with one of two colors mating (top right) later prefer to mate with similarly colored males. This behavior is further copied by others, initiating a tradition. (C) Bighorn sheep translocated to unfamiliar locations were initially sedentary, but spring migration and skill in reaching higher-altitude grazing grounds expanded over decades, implicating intergenerational cultural transmission. (D) Groups of vervet monkeys were trained to avoid bitter-tasting corn of one color and to prefer the other. Later, when offered these options with no distasteful additive, both naive infants and immigrating adult males adopted the experimentally created local group preference. (E) Young meerkats learn scorpion predation because adults initially supply live prey with stingers removed and later provide unmodified prey as the young meerkats mature. (F) A humpback whale innovation of slapping the sea surface to refine predation, known as "lobtail feeding," spread over two decades to create a new tradition in hundreds of other humpbacks. For reference citations, see the full article.

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Culture can be defined as all that is learned from others and is repeatedly transmitted in this way, forming traditions that may be inherited by successive generations. This cultural form of inheritance was once thought specific to humans, but research over the past 70 years has instead revealed it to be widespread in nature, permeating the lives of a diversity of animals, including all major classes of vertebrates. Recent studies suggest that culture's reach may extend also to invertebrates—notably, insects. In the present century, the reach of animal culture has been found to extend across many different behavioral domains and to rest on a suite of social learning processes facilitated by a variety of selective biases that enhance the efficiency and adaptiveness of learning. Far-reaching implications, for disciplines from evolutionary biology to anthropology and conservation policies, are increasingly being explored.

Culture shapes our human lives profoundly, so much so that what it means to be human (our behavioral repertoires, for example) differs enormously between, and sometimes within, the many different regions of the planet occupied by our species, as well as across human history. In the past, it was thought that humans' ability to have culture separates us from the rest of living systems and the dynamic evolutionary forces that shape them. Yet, a broader perspective recognizes that culture is intimately embedded in evolutionary biology because it incorporates a second inheritance system (social learning, or learning from others) built on the foundations of the primary, genetically based inheritance system (1, 2). Moreover, as recognized by Darwin himself (3) and addressed in more recent theoretical and empirical works (4–7), this can in turn engender an elaborated manifestation of evolution: cumulative cultural evolution, the results of which we see in our technologies, languages, customs, and virtually all aspects of human life (8).

Interactions between these two evolutionary systems create the complexities of spiraling gene–culture coevolution (5, 6), the effects of which have become increasingly apparent as the fields of human genomics and cultural evolution have progressed (9, 10).

The discovery of animal cultures: An endeavor spanning seven decades

Though all of these manifestations of culture have historically been thought specific to our species, research in recent decades has revealed that, in varied guises, they are shared with a plethora of species and span a growing range of behavioral domains (2, 7).

Evidence of culture in nonhuman animals (henceforth “animals”) first emerged from three

mid-20th-century discoveries. First, the innovation in titmice of tearing milk bottle tops to drink the cream beneath was tracked from a small number of initial UK centers as it diffused across the country over the next decade (11). Second, novel foraging behaviors in Japanese macaque monkeys were likewise tracked as they spread through kin networks (12). Finally, the discovery of regionally varying birdsong dialects was coupled with laboratory experiments to confirm the necessity of learning from existing models, thus providing early evidence of vocal cultures in animals (13). These beginnings were followed by a steady stream of other examples in the 20th century, some based on naturalistic recordings in nature and others on experiments with captive populations, demonstrating social learning and the diffusion of new traditions, principally in a diversity of mammals, birds, and fishes (2, 7, 14).

These studies typically demonstrated a single tradition, as in the three examples outlined above. Research on chimpanzees, by contrast, accumulated evidence during the latter part of the century that communities differed in multiple traditions, spanning a variety of behavior patterns such as tool use, grooming styles, and foraging techniques. By the turn of the century, systematic collation of these records revealed as many as 39 such cultural variants, with different communities identifiable by distinctive arrays of traditions (15), echoing the way human cultures are distinguished by arrays of technologies, social customs, and diets. This was soon followed by similar reports of multiple-tradition cultures in orangutans (16) and cetaceans [whales and dolphins (17)].

A rapidly expanding research literature in the present century has revealed cultural phenomena in a widening diversity of both the species involved and the range of behavioral domains implicated. Many such advances

have followed the accumulation of long-term field records. For example, a humpback whale foraging innovation called lobtail feeding was traced from its origins in just 1 or 2 individuals to more than 600 others, through the collation of 27 years of consecutive records (18). Experimental designs that earlier typically focused only on what one individual might socially learn from another have been extended to identify transmission chains in which a behavior spreads between multiple individuals, a core criterion for culture (19, 20) (Fig. 1). Such “diffusion” experiments have naturally been easier to engineer with captive subjects than in the wild, but their power in reliably identifying a role for social learning has increasingly been applied in the field. For example, introduction into wild populations of pairs of great tits trained to use either of two alternative foraging techniques demonstrated high fidelity spread of whichever technique was seeded, continuing into a subsequent season (21). An alternative to training initial models to perform novel behaviors has been to cross-foster young, an approach particularly suited to birds, as eggs can simply be swapped. The adoptive species then provides natural models who behave differently from what is normal for the adopted chick species. Such cross-fostering remains rare but has demonstrated social learning of dietary preferences by blue tits fostered by great tits and vice versa (22). In cases for which diffusion experiments of these different kinds are impractical (as, for example, with whales), a range of sophisticated statistical techniques have been developed (14). In the lobtail feeding example outlined above, cultural transmission was revealed because the behavior could be shown specifically to spread along social networks, as a social learning hypothesis predicts (18).

The burgeoning reach of culture across animal taxa and behavioral domains

Figure 2 offers illustrations of the reach of animal culture across both animal taxa and behavioral domains (23–38), adding to those shown on the summary page (18, 39–43).

Identifying cultural transmission depends on establishing a critical role for social learning, and controlled experiments arguably offer the most compelling option in scientists' toolbox to clarify this issue of causality. If we thus first consider diffusion experiments of the kind illustrated in Fig. 1, we find, in a survey of the 34 such efforts published by 2008, that the focus on primates and birds evident in the field's mid-20th-century origins persisted (19). These experiments provided evidence of cultural transmission of behavior in chimpanzees, baboons, vervet monkeys, macaques, colobus monkeys, pigeons, blackbirds, magpie-jays, cowbirds, keas, and chickens (19). There was also positive evidence from two species of fish:

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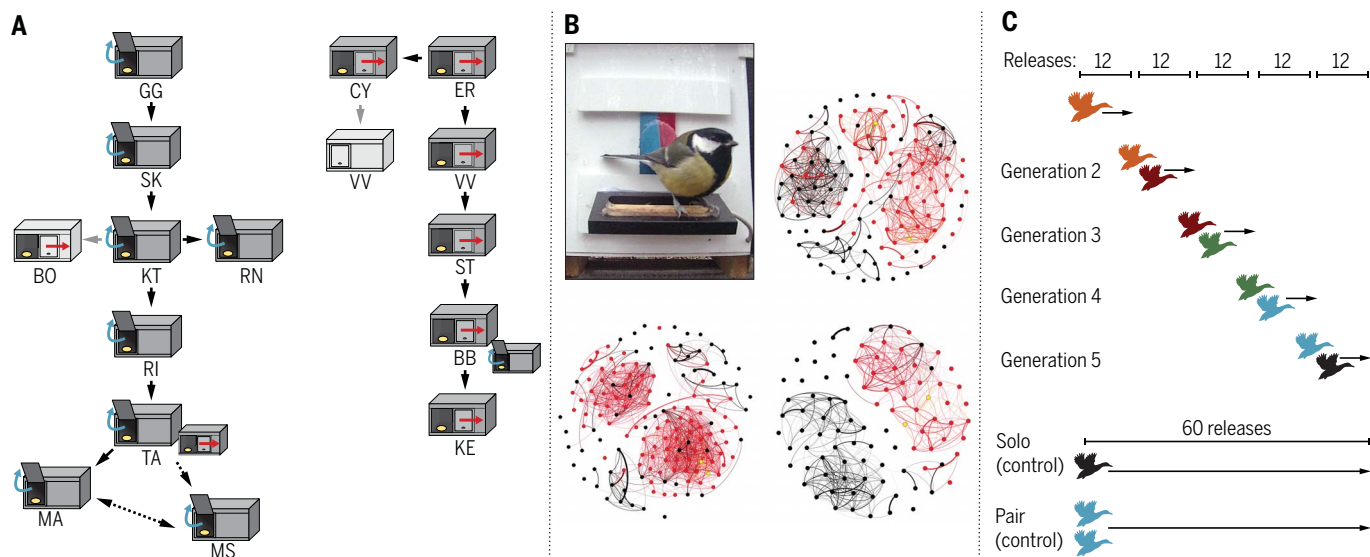


Fig. 1. Cultural diffusion experiments. Three alternative designs are illustrated. **(A)** Transmission chain. One individual is allowed to observe an initial model trained to perform either of two alternative behaviors. After testing, that observer becomes the model for a third individual, and so on, simulating potential intergenerational transmission (each two-letter identifier represents an individual chimpanzee). In this experiment, the first chimpanzee (GG or ER) learned to open an “artificial fruit” box by either lifting a hatch (left chain; blue arrows) or sliding it to one side (right chain; red arrows) (91). After four or five transitions, fidelity remained at 100% for each alternative (although BB performed a hatch-lift action in 5% of trials). Such an approach has challenges—for instance, VV was intimidated by CY so was allowed to learn from ER instead. Solid black arrows represent each individual’s progression from observer to model. Dashed black arrows indicate that MS observed both TA and MA (and the two-headed arrow indicates that MA, in turn, observed MS). Gray arrows denote that the experiment

failed to progress, owing to the behavior of a particular individual. **(B)** Open diffusion (here, “open” refers to how any learning spreads in a population). In this example, populations of wild great tits were exposed to two models trained to push a small door to either the blue or red side of an artificial feeder (21). Each option spread with high fidelity to others. The diagrams represent social networks for three subpopulations, with original models marked by yellow circles, those learning the local technique marked by red circles, and naïve individuals marked by black circles. Red connecting lines represent diffusion across social networks; black connecting lines represent other social networks. [Photo: Lucy Aplin] **(C)** Replacement design. One individual is replaced by a naïve individual after each transmission, so after multiple transmissions the population is entirely different from the original. In this example, pigeons homed repeatedly in pairs before each replacement (77). Homing efficiency increased over time, demonstrating a cumulative aspect to the implicated cultural transmission.

guppies and platyfish. However, only 2 of these 34 studies (both on birds) pioneered such experiments in the wild. To these 34 studies from the first 60 years of the field, a further 30 diffusion studies could be added over just the next 8 years (20), highlighting accelerating discoveries. By this point, 13 of these experiments were extended to wild populations. The first experiments to demonstrate cultural diffusion in insects were also included, with fruit flies being shown to adopt the preferences for alternative egg-laying substrates of conspecifics (36).

Such controlled experiments are unlikely with species such as whales, but alternative routes to identifying social learning have emerged. When new humpback songs appear frequently and records show their rapid spread across populations, neither genetic nor environmental explanations can account for this phenomenon, and these occurrences have been aptly described as “cultural revolutions” (31). Cetaceans have contributed substantial evidence of cultural transmission across these and multiple other behavioral domains, with a recent review (25) able to cite as many as 70 publications reporting evidence for social learning or cultural

transmission. Similarly, since helping to lay the foundation for animal culture study 70 years ago, birdsong research has confirmed regional dialects in more than 80 species (31), so the phenomenon may well be common across many of the ~4000 species of songbirds.

Surveying the field more broadly, we find that social learning has been identified in choices of diet, prey types, nest sites, migratory pathways, and mates, as well as in shaping foraging techniques, tool use, vocal repertoires, courtship displays, predator recognition, circadian rhythms, allogrooming patterns, social customs, and even play patterns (2, 14, 37, 44, 45) (Fig. 2).

The reach of culture through the lifetime

A recent review distinguished three main phases of social learning that occur across many primates (46): (i) an infant’s initial intimate relationship with its mother, (ii) the later progressive expansion of a juvenile’s social network, and (iii) adult dispersal to new groups and ranges. A field experiment with wild vervet monkeys illustrates both the first and third phases (42). Whereas most social learning experiments begin by allowing an

observer to watch a trained model, van de Waal *et al.* (42) first trained four whole groups of vervet monkeys to avoid either pink- or blue-stained corn provisions (Fig. 2), by making one unpalatable at a stage after the birth season when infants were not taking solid food. When later tested with no unpalatable additive in either color, all 27 weaning infants, naïve to the corn, matched their mother’s color choice, ignoring the (now equally palatable) alternative. This illustrates phase one, in which a parent (typically the mother in primates and many other mammals) provides the principal model for what the infant learns. In birds, both parents more often share this initial role, and the prevalence of this phase will clearly depend on the extent of parental care in the species studied.

The vervet experiment additionally found that dispersing adult males quickly adopted the local preference of the group they entered, even when an opposite preference had been habitual in the group from which they came, a result attributed to a tendency to conform to the behavioral profiles of a majority of one’s companions (42). This illustrates phase three, when dispersal creates a new role for social

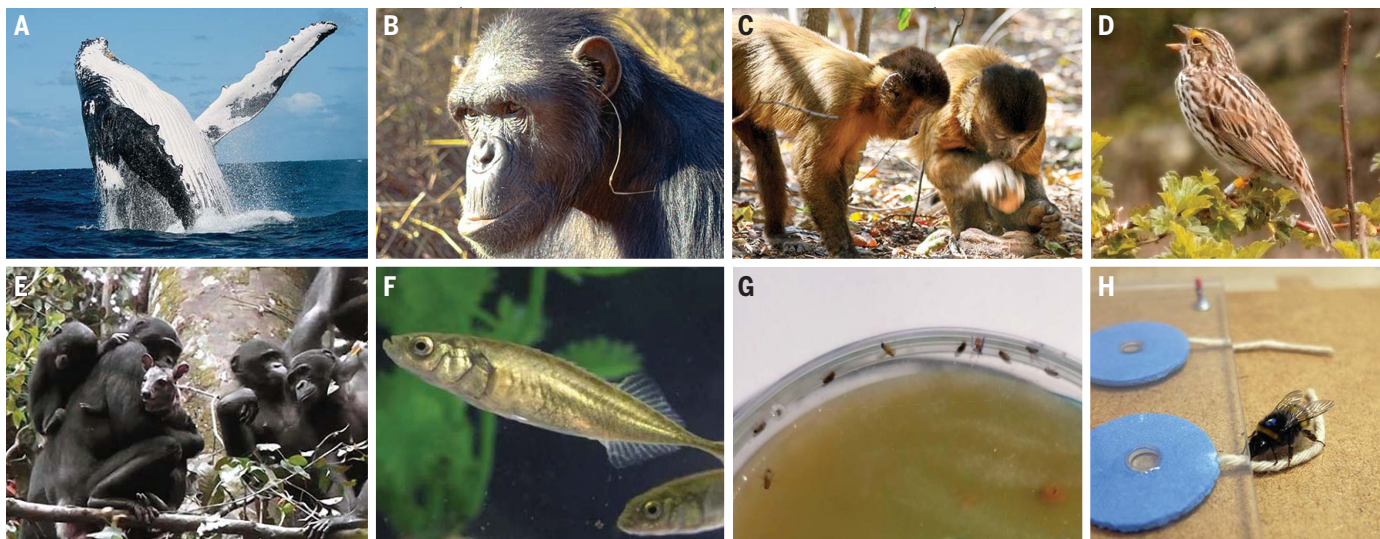


Fig. 2. Illustrations of diversity in cultural phenomena across species and behavioral domains. (A) Vocal and migratory traditions. In humpback whales, new songs arise intermittently and spread rapidly across large populations (23), including eastward drift across the Pacific basin over several years (24). Juveniles follow mothers on annual migrations between breeding and feeding grounds, assimilating these traditional routes (25). [Photo: Jennifer Allen] (B) Arbitrary and social customs. The arbitrary custom of placing a grass blade in one ear spread from the innovator to other chimpanzees in just one among four sanctuary enclosures (26) [Photo: Edwin van Leeuwen]. In capuchins, social customs—such as mutual placing of fingers in mouths, nostrils, and eyes—spread and may last several years (27). (C) Tool use. Young capuchin monkeys selectively attend to the best nut-crackers in regions where stone tools are so used (28) [Photo: Tiago Falótico]. Similarly, young New Caledonian crows attend closely to complex parental tool use (29). Diffusion experiments with apes demonstrate that tool use techniques spread through social learning (19, 20). (D) Vocal dialects. Local birdsong dialects persist for decades but also show evolutionary change, as recognized in savanna sparrows (30) [Photo: Heather Williams]. Scores of studies document such dialects in many avian species (31), in some cases creating

the conditions for incipient speciation (32). (E) Prey selection. Neighboring communities of bonobos display different preferences for prey animals, even in areas of large overlap between adjacent ranges, excluding ecological explanations for the differences (33) [Photo: Kokolopori Bonobo Research Project]. Ecotype clans of killer whales display quite different hunting traditions, such as specializing in seal versus fish prey (25, 34). (F) Predator recognition. Sticklebacks and minnows developed fear responses to pike by learning from conspecifics and, in turn, passed this disposition on to others (35) [Photo: Mike Webster]. In birds, experiments that seed fear of arbitrary objects have demonstrated cultural transmission along chains of individuals (19). (G) Breeding sites. Preferences of fruit flies for specific egg-laying substrates have been shown experimentally to be adopted by others, from whom yet others learn (36) [Photo: Frederic Mery]. There is evidence of similar effects in birds, leading to traditionally favored breeding sites (37). (H) Foraging techniques. A bumble bee trained to pull string to access an artificial food source was copied by other bees, who were subsequently copied by others, initiating a tradition (38) [Photo: Lars Chittka]. Experiments with primates have shown that alternative techniques may spread differentially in the groups seeded (19, 20).

learning about an animal's new habitat and the local social dynamics, drawing on the accumulated knowledge of the local residents.

Phase two describes a common (but variable) pattern in primates for the early relationship with the mother to be supplemented by a widening social network, providing opportunities to learn from others with different knowledge and skill sets. Primate examples include male juveniles apprenticing themselves to adult males to learn about sex-typical foraging options (47) or tool use (28) (Fig. 2).

A recent study has argued, controversially, that the scope of all that is learned through such phases has been underestimated by research to date, which has typically relied on enumerating behavioral differences between communities where genetic and environmental explanations can reasonably be discounted (15, 16). As Schuppli and van Schaik (48) correctly note, this neglects cultural adaptation to local ecologies, as well as cultural universals. In an earlier study in wild orangutans, these authors established that a behavior known as

“peering,” which involves close and sustained visual attention to another's actions, confirmed nine different predictions consistent with the implication of social learning, with juveniles repeating acts they had just witnessed, from foraging to nesting. It was found that such peering occurred in as many as 125 and 195 different contexts in two communities studied. This led the authors to conclude that “when looking closely at great ape skill acquisition, it seems that immatures learn virtually all of their skills socially” (48). Whether every instance of peering truly indexes social learning may be debatable, but this study presents a welcome challenge to critically test similar measures in this and other species in the future.

The psychological reach of culture: An array of cognitive adaptations

A reliance on cultural transmission requires associated cognitive capacities. Most fundamental are forms of social learning that have been dissected conceptually and experimentally for more than a century (49), predating

the serious study of the larger topic of culture. More recently, attention has additionally turned to what are variously termed “transmission biases” or “social learning strategies” that refine the targeting of social learning processes according to cues such as those provided by particularly successful or high-ranking individuals (50). Finally, heavy reliance on cultural acquisitions requires appropriate storage capacity in the brain. Our human reliance on culture delivers a vast volume of information that taxes our memory banks, but arrays of cultural knowledge may have important neural requirements in animals, particularly long-lived species (51, 52).

Social learning has been discovered to show a range of different forms among animals. Dissections of these forms over recent decades have themselves evolved along with empirical findings (53, 54). The most recent reviews differ in details but converge in distinguishing ~10 principal categories (55, 56). Those illustrated in Fig. 3 differentiate what is socially learned, with the associated cognitive

requirements varying from those generally regarded as relatively simple to the relatively complex. There is not enough space here to offer a comprehensive analysis of these processes; instead I offer examples from either end of the array. At the more elementary end, stimulus enhancement occurs when an observer witnesses a model that focuses on particular objects and subsequently adopts the same focus. For example, bumble bees that observed model bees on green or orange flowers later visited those with the color they had seen preferred (57). Such effects would appear to require only the kind of associative learning that is common across the animal

kingdom, but with the added factor of learning not from associations of events and reinforcements in relation to one's own behavior, but instead from those perceived in others' actions. This may be the most widespread form of social learning across numerous species and behavioral contexts.

At the other end of the scale is the copying of relatively complex behavioral routines, as demonstrated in transmission chain experiments with chimpanzees (58, 59). A recent study discovered that each of 10 different wild chimpanzee communities is characterized by a distinctive combination of action elements used locally to fish for termites from

aboveground mounds and subterranean nests, the latter involving a tool set. A thick stick is first used to make a long tunnel underground, with a finer stem—its end first fashioned into a more effective brush tip—then inserted to fish out termites (60). The authors judged that ecological factors could not explain the alternative methods adopted locally, and because these involved specific bodily postures, it was concluded that relatively high-fidelity bodily imitation was implicated. This finding is consistent with experimental studies showing that chimpanzees may copy specific alternative sequences of component actions that they witness (61) (Fig. 4). Nevertheless, the distribution of such forms of social learning among animals has been, and continues to be, a focus of debate in this field (56, 62, 63). Even bees have been shown to be sophisticated in their social learning. In one study, instead of simply copying a demonstrator's movement of an object to a target, the bees flexibly created an improved version of this action (64). This topic is ripe for imaginative and taxonomically diverse studies to provide greater clarity in the coming years.

The forms of social learning detailed in Fig. 3 have been found to be supplemented by a further range of modulating biases that can refine their adaptive power. For example, evidence of conforming to an option that most members of a population have already adopted (and thus likely tested already), itself taking several different forms (65), comes from birds (21), primates (42), and insects (40). A recent review of such modulating influences [i.e., transmission biases or social learning strategies (50)] enumerates as many as 25 variants, which include, as major categories, those that are state based (e.g., copy when uncertain), frequency dependent (e.g., copy majority, as above), model based (e.g., copy high-rankers), or content based (e.g., copy behavior seen to earn highest payoff). Evidence has also accumulated

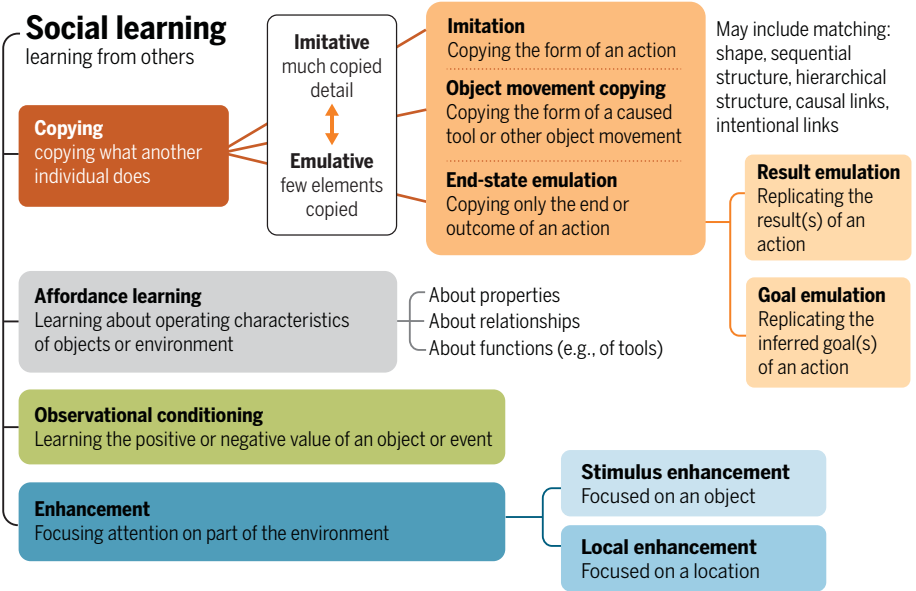


Fig. 3. A taxonomy of social learning processes. In each example, something new is learned from one or more individuals. The primary distinctions concern what is learned in this manner [for detailed dissections of this and related taxonomies, see (14, 53–56)]. The array portrayed here displays an approximate gradation from processes with low cognitive requirements at the bottom to those with higher requirements above (see main text for further discussion).

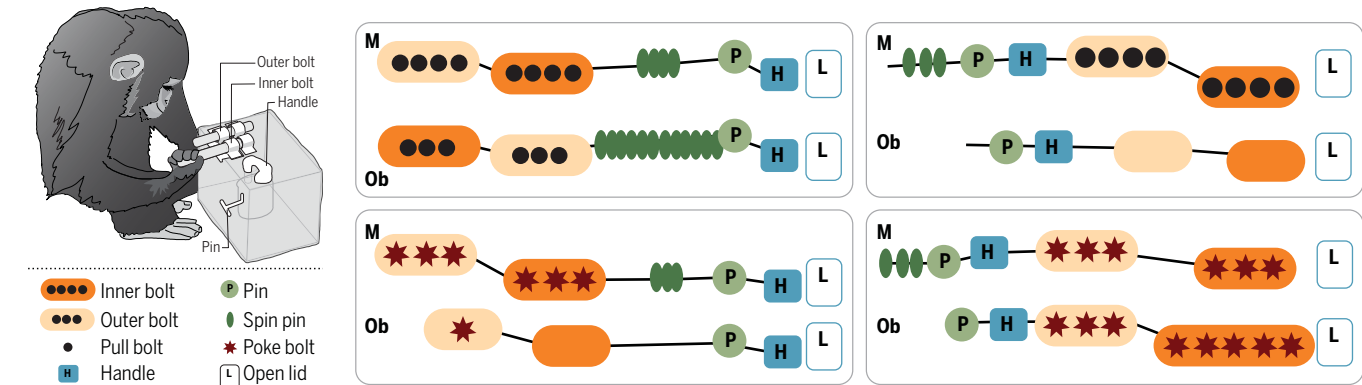


Fig. 4. Experimental evidence for copying of behavioral sequences by four chimpanzees. A human model (M; upper graphic in each pair of sequences) opened an “artificial fruit” box, removing bolts and a pin, which then allowed the model to disable a handle, after which a lid could be opened to gain a reward. The model displayed different sequences composed of alternative forms of action, each of which were matched by chimpanzee observers (Ob; lower graphic in each pair) beyond chance levels (61).

from both birds and mammals for active support of parents and others to juveniles' social learning, a phenomenon conceptualized as “teaching” but defined in functional rather than the intentional terms familiar in human contexts (66, 67).

Implications for anthropology: The evolution of human culture

With regard to evolutionary anthropology, the broadest implication of the discovery of widespread social learning and culture in animals is that human culture did not spring up out of nowhere but instead has ancient evolutionary foundations. Further, the comparative method can be applied to use studies of humans' living relatives, particularly primates, to reconstruct key ancestral cultural foundations. Such work has by now generated a substantial research literature reviewed elsewhere (68–70), any serious treatment of which is beyond the scope of this brief review. An illustrative example is that identification of cultural commonalities in great apes (including humans), and hence attributed to their common ancestry, includes the patterning of multiple and diverse traditions in time and space (15, 16), a “portfolio” of social learning capacities (48, 56) facilitating the spread and maintenance of traditions (58, 59), and cultural contents such as tool use (68).

Research on cultural phenomena in more distantly related species may also cast light on principles that underlie convergent evolution. For example, teaching, as defined in functional terms above, appears particularly common in long-lived and predatory species, in which the young have to vault from suckling to skillful hunting and killing (43, 66, 67). Similarly, extended juvenility and a heavy reliance on hunting were key innovations in hominin evolution (71).

Animal culture expands the scope of evolutionary biology

Social learning provides a second inheritance system built on the more widespread foundations of genetic inheritance. In turn, this creates the potential for a second form of evolu-

tion: cultural evolution (1–7, 45, 62, 63, 72, 73) (Fig. 5).

In organic evolution, selectively neutral genetic drift occurs as mutational changes in DNA are coupled with dispersion of populations across time and space (74). In the cultural counterpart, “mutation” may occur through imperfect copying of others, coupled with similar kinds of dispersion patterns (72, 73). Long-term field studies may be required to detect such changes, and these are progressively accumulating. For example, a study of changes in the song repertoires of Savannah sparrows over 30 years identified a subset of elements that showed no consistent directionality in their changes and were not associated with variations in reproductive success (whereas some other elements were linked to reproductive success and thus fit other categories in Fig. 5, as discussed below) (30). Birdsong research provides many more such examples (31), and similar processes are thought to exist in the diffusion of whale songs (24). These sorts of effects may be more common in such communication patterns than in behavior such as foraging, for which an ecological optimum may exist.

A similar methodological challenge is likely to exist when we turn to the other major category in Fig. 5: cultural evolution through Darwinian selection processes. Here the Darwinian triumvirate of elements will be in play—inheritance (through social learning), variation (in culturally transmitted behavioral elements), and selection according to the relative fitness of these elements—hence shaping more optimal adaptation in the repertoires of descendant generations (1–7, 45, 72, 73). The time frames for such changes may often be longer than the lifetimes of human scientists: Archaeological excavations have found evidence of western chimpanzees' use of stone hammers to crack nuts extending over 4300 years, with no indications of change (75). Yet this behavior must have evolved over some longer time frame. Some such changes may occur only in response to very intermittent or long-term ecological perturbations. In contrast to the chimpanzee nut-cracking

data, sampling of capuchin monkey nut-cracking artifacts from an archaeological record of 3000 years indicates four different phases—distinguished by size, use-wear, degree of percussive battering, and use of stone versus wooden anvils—that the authors suggest must reflect adaptations to the food types exploited (76). Capuchin stone tool use has thus evolved over these millennia. In the case of the Savannah sparrow study noted above, 30 years was sufficient to detect changes in song elements, some of which showed both an association with enhanced reproductive success and consistent directional change, in line with Darwinian natural or sexual selection (30).

All of the above examples appear to express evolutionary change rather than the kind of progressive advancement in features such as complexity and efficiency that characterizes human cultural evolution, often known as cumulative culture and suggested to be exclusive to our species (62). However, experimental evidence for such cumulative cultural buildup has begun to appear in diverse species and contexts that range from pigeon homing (77) (Fig. 1) through pattern recognition in baboons (78) to exploration and tool use in chimpanzees (79, 80). In all of these cases, it has been possible to record cumulative change over short periods, given the experimental manipulations involved.

Long-term field studies have also revealed evidence of forms of cumulative culture among animals. For example, bighorn sheep translocated to areas of the US in which they had previously been extirpated were initially sedentary, but over many decades and multiple generations they became progressively migratory in the spring, developing an enhanced skill in arriving at higher-altitude pastures at an optimal time (41). The authors conclude that this represents cycles of exploration and transmission of accumulated knowledge to subsequent generations. Similar effects may await confirmation in other migratory species and other behavioral contexts (81).

Culture presents more than an echo of organic evolution, however, precisely because it operates through radically different processes. Two examples are particularly notable. One is that, unlike genetic inheritance that occurs between parents and offspring only (“vertically”), social transmission may occur between related and unrelated individuals in the same temporal generation (“horizontally”) as well as between generations (“obliquely”) (5). Individuals may thus have multiple “cultural parents” from whom they learn. A second is that, unlike the genetic inheritance received in a single “package” at conception, social learning can fine-tune adaptive responses to environmental changes throughout a lifetime. Together, these characteristics generate more

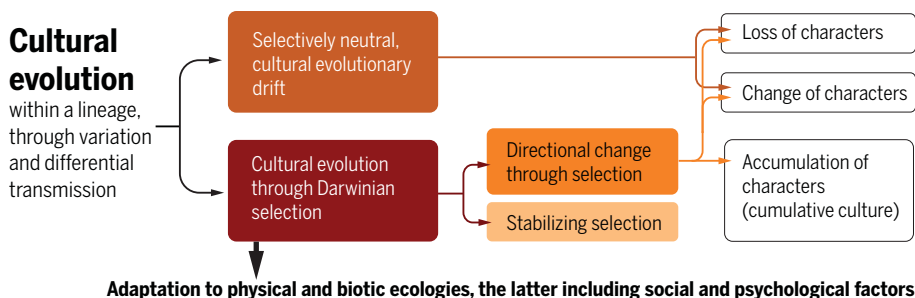


Fig. 5. A dissection of forms of cultural evolution. For elaboration and discussion, see the main text. [Based on figure 1 of (72)]

elaborate dynamics in animals' adaptive potentials, including the possibility of much faster and more nimble adaptive change than would occur via gene-based evolution (37).

Gene–culture coevolution

A further major implication of animal culture for evolutionary biology arises from coevolutionary dynamics between cultural systems and genetic inheritance (37), numerous expressions of which are well known for humans (9, 10). Whitehead (82) pioneered the further exploration of such phenomena in cetaceans. A more recent survey encompassing diverse avian and mammalian taxa examined the evidence relating to six major types of coevolutionary dynamics (83), as follows.

First, cultural differences may exert selection pressures on functional genes. For example, culturally based killer whale ecotypes differentiated by radically different prey choices (e.g., seals versus salmon) have evolved associated differences in anatomy and physiology, including the methionine cycle of their digestive systems (34).

Second, selection may favor organic adaptations that support culture. In primates, a study spanning 55 genera and 184 species has shown that cultural propensities are correlated with greater encephalization and longer juvenile and reproductive life spans (84). This and other evidence have been adduced in support of a “cultural intelligence hypothesis” for the evolution of large brains and intelligence in primates (51, 52). This hypothesis could apply to other species that are particularly reliant on a richly cultural behavioral repertoire.

Third, culture may affect coevolution between species. For example, in great tits, controlled experiments that involve simulated prey have shown that social learning from the disgust reactions of others to aposematic prey lead to a switch from this prey type to more cryptic alternatives. This behavior imposes changing selection pressures on prey and their respective defense mechanisms (85).

Fourth, culture may shape even neutral genetic diversity in space. For example, a subset of dolphin families off the coast of Australia use sponges placed over their rostrums to hunt fish in deep water. These dolphins have developed substantially different maternally transmitted mitochondrial haplotypes from those of their nearby non-tool-using neighbors (86).

Fifth, culture may reduce genetic diversity, as is thought to be the case for the minimal mitochondrial variation among sperm whales and other cetaceans that display matrilineal social structures. In these structures, daughters remain with their mothers, and hence a daughter is restricted to inheriting both her mother's genes and the distinctive culture of her mother's clan, a process dubbed “cultural

hitchhiking” (87). Over time, the more successful surviving cultures will thence contain unusually limited genetic variation.

Sixth and finally, cultural variation may drive the incipient phases of speciation. Birdsong provides a well-researched case. As songs differentiate between populations, it becomes increasingly difficult for successful courtship and mating to occur between them. For example, a study of more than 4000 song recordings from 581 species of two major avian clades (tanagers and ovenbirds) revealed associations between macroevolutionary bursts in vocal evolution and speciation, with faster rates of vocal evolution predicted by the extent of reliance on song learning (32).

Outlook

The United Nations Environment Programme has recently recognized the potential importance of all that has been discovered about animal cultures for conservation policies and practices, for migratory and nonmigratory species alike. An expert working group has made initial recommendations and a summary *Science* Policy Forum article ensued (88), later joined by other new approaches to the issues so raised (89, 90).

A core goal of conservation policies is to maintain heritable variation and adaptive evolvability in natural populations, so the range of discoveries outlined above begs an urgent integration of the cultural components of heritable variation into conservation planning. Notable examples include the increasing recognition that different cultural variants of the same species may require differing management approaches, that individuals such as matriarchs merit special preservation as cultural repositories, and that animals reintroduced into the wild may lack critical cultural knowledge for which conservation efforts must compensate (88).

Recognition of such practical implications of the reach of animal culture, along with the implications for the broad range of scientific disciplines discussed above, should help assure a bright future for research in this field. A new generation of scientists will now surely pursue the wider reaches of culture in animals' lives, aided by the substantial armory of methodological advances developed over the past two decades.

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The burgeoning reach of animal culture

Andrew Whiten

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We are not alone

Before the mid-20th century, it was generally assumed that culture, behavior learned from others, was specific to humans. However, starting with identification in a few species, evidence that animals can learn and transmit behaviors has accumulated at an ever-increasing pace. Today, there is no doubt that culture is widespread among animal species, both vertebrates and invertebrates, marine and terrestrial. Whiten reviews evidence for animal culture and elaborates on the wide array of forms that such culture takes. Recognizing that other species have complex and varied culture has implications for conservation and welfare and for understanding the evolution of this essential component of animal societies, including our own.

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