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Animal Culture

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Culture can be defined as all knowledge and skills acquired through some form of social learning—learning influenced by social input—and usually transmitted across generations. Its prominent role in generating the variation in time and space in human behavior and values has long been recognized and considered unique among animals. A role for culture in animal behavior was therefore not seriously considered until the 1950s, when a monkey in Japan began washing sweet potatoes to rid them of sand and this invention was found to spread to others in her group. Now animal culture is a substantial field of study connected with research on human culture as well as with genetics and evolutionary biology.

History

Until relatively late in the 20th century, scholars studying animal learning processes regarded social influences as noise and endeavored to exclude them. The few experimental studies of social learning often focused on adults, ignoring the all-important developmental period [see [Social Learning](#)]. Moreover, the question of animal culture did not arise because geographic variation in behavior was rarely studied, and when it was studied, it was usually attributed to internal (genetic) or external (ecological) differences between populations.

Initially, evidence for animal culture was circumstantial (e.g., sweet potato washing; [Kawai, 1965](#)) and primarily based on geographic variation among primates. Typically, putative behavioral innovations were observed (behaviors that do not reliably develop in all healthy members of a given species) without obvious genetic or ecological correlates, as famously shown in chimpanzees across Africa ([Whiten et al., 1999](#)). Subsequent experiments with captive primates revealed social learning abilities and also showed culture-like spread of seeded innovations later confirmed in field experiments [see [Animal Cognition](#)]. One particularly elegant example involved great tits who had to push a door either to the left or the right to acquire food ([Aplin et al., 2015](#)). More recent experiments have shown similar abilities in invertebrates ([Bridges et al., 2023](#)). Field observations have also revealed the durability of these patterns across generations in many vertebrates—for example, the durability of migration paths in ungulates ([Jesmer et al., 2018](#)).

Fieldwork has also unexpectedly shown a role for social learning in the acquisition of universal behaviors, blurring the line between culture and nonculture; in orangutans, for instance, practically the whole diet is socially inherited ([Schuppli & Schaik, 2019](#)). In retrospect, this dependence on the social environment for the acquisition of universal behaviors was foreshadowed decades ago by experiments showing that monkeys growing up without contact to conspecifics became fearful and aggressive adults and socially incompetent mothers ([Harlow & Harlow, 1962](#)).

Core concepts

Many studies have examined the mechanisms of social learning, which is fundamentally individual learning under social influence. Social learning is best regarded as a set of decisions of when and how

closely to attend to others' actions, which subsequently trigger individual learning processes. The capabilities for social and individual learning therefore coevolved. The more complex forms of social learning involve production imitation, the copying of novel actions or action sequences, as it requires causal inference in addition to the translation of perception into action ([Subiaul, 2016](#)).

Social learning has been demonstrated in various birds and primates, but its value in nature is limited, given the required alternation with periods of individual practice. Given the risks of being injured or poisoned during unguided individual exploration, especially for those unfamiliar with the local environment (immatures or immigrants), such socially guided rediscovery is the default mode of naïve social organisms, even in many taxa, from insects to fishes, for whom lack of intergenerational continuity prevents the build-up of cultures. Adults rarely rely on social learning, other than to easily acquire useful perishable information such as the location of ripe berries. Teaching is an active form of social transmission of cultural variants. It is prominent in humans but less widespread among animals, for reasons still debated ([Kline, 2015](#)).

Documented animal culture has mostly focused on technology in large-brained birds, primates, and marine mammals, but animal cultures can include ecological skills such as food choice, techniques of prey capture, travel paths, migration routes, predator recognition, habitat choice, nest building, food-processing techniques, social skills like song dialects, alliance formation, or servicing bonds with social partners. The preference for social learning means that even the acquisition of routine skills that are not geographically variable, like mating or parenting, often depend on social influence, as this transmission method requires less time and is less risky. Accordingly, it can be said that culture is widespread and adaptive in animals and can affect selection on a variety of traits relying on genotypic coding, leading to culture–gene coevolution ([Whitehead et al., 2019](#)).

Questions, controversies, and new developments

A major unsolved problem is the taxonomic reach of culture in the animal kingdom relative to genetically grounded local adaptation. It is also unclear which kinds of social learning are most common and effective in nature. More fundamentally, the relationship between the tendency to innovate (the origin of cultural variants) versus reliance on social learning to acquire behavioral repertoires is not well understood, nor is the relationship between each of these and taxonomic affiliation.

Where culture is an important contributor to local adaptation, cultural erosion due to human disturbance or climate change may affect population viability as well as species' evolutionary potential ([Kühl et al., 2019](#)). Since it is unknown how long it takes a population to reinvent its local cultural repertoire, it is prudent to preserve cultural variation as part of conservation efforts ([Brakes et al., 2021](#)).

Broader connections

Animal culture, however pervasive, remains modest in complexity and diversity relative to human culture. Indeed, although more intelligent species pass on more complex innovations, most, though not

all, primate cultural variants are easily reinvented in captive settings if a conducive context is provided. Most animals lack curiosity (the motivation to explore), no doubt reflecting its high risk and its poor utility where causal understanding is rudimentary [see [Causal Learning](#)]. Chance opportunities are therefore thought to explain most of the origins of culture in animals. Among humans, we also see a larger role for the much vaunted necessity, which requires the need for innovation is recognized. Accordingly, most animal culture is not cumulative, in the sense that the behavior requires multiple innovation steps and, over time, leads to innovations that individuals could never invent on their own.

This complexity represents one major difference between animal and human culture (compare a stick or stone hammer to a voting machine or an electoral system). In the human lineage, cultural evolution has emerged as a second evolutionary process matching the original organic evolution in importance ([Whiten, 2005](#)). Although much research examines this critical difference, the modest variation in the degree of cultural accumulation among great apes, especially chimpanzees, is poorly understood.

In contrast, there is near-agreement on what caused the massive accumulation over hominin evolution: active transmission through teaching of increasingly complex technical skills and social institutions, linked to a new highly interdependent form of cooperative breeding or foraging, gave individuals a stake in helping others acquire cultural skills. Such a system can give rise to culture-driven coevolution of prosociality (the motivation to transmit information, increasingly through language) and intelligence (because social learning requires cognitive skills, such as attention management, causal understanding, and working memory) [see [Attention](#)] ([van Schaik & Burkart, 2011](#)). This cultural repertoire will inevitably reach a ceiling because each individual has to learn by going through the complete innovation history, even if occasional shortcuts are possible. The final step in this coevolutionary process is therefore the origin of a true division of labor: different individuals specialize in different sets of skills made possible by reciprocal exchanges of culture-based products and services.

Another likely difference between human and nonhuman animals is that human culture is highly normative, as required to sustain interdependent coordination and cooperation—a function critically dependent on language. Within-group uniformity arises by conformity, which can be spontaneous or imposed by sanctioning. That immigrants adjust to local cultures has been shown to happen in various primate species ([van de Waal, Borgeaud, & Whiten, 2013](#)). It is likely to improve social integration, but active sanctioning of deviations has so far only been documented in humans.

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