THE SECOND INHERITANCE: CULTURAL EVOLUTION

LA SEGUNDA HERENCIA: EVOLUCIÓN CULTURAL

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Abstract

Social learning allows individuals to acquire information from others, facilitating the spread of behaviors that can form stable traditions and animal cultures. This review examines the mechanisms and evolutionary consequences of cultural transmission in non-human animals, focusing primarily on primates, cetaceans, and birds. We analyze evidence across diverse biological contexts, including foraging strategies in orcas, migratory routes in cranes and whales, and vocal learning in songbirds and parrots. These examples demonstrate that behaviors previously attributed solely to instinct are often shaped by social inheritance. Furthermore, we explore how cultural evolution interacts with genetic evolution. Case studies, such as genomic adaptations in distinct orca ecotypes and accelerated speciation rates in vocal-learning bird lineages, suggest that culture can act as a selective pressure driving morphological and genetic divergence. We conclude that cultural transmission constitutes a secondary inheritance system complementary to genetics. Recognizing this dual inheritance model is essential for a comprehensive understanding of animal behavior, adaptation, and speciation.

Keywords: Animal culture, cultural evolution, cultural transmission, non-genetic inheritance, gene-culture coevolution, social learning.

Resumen

El aprendizaje social permite a los individuos adquirir información de otros, lo que facilita la propagación de comportamientos que pueden formar tradiciones estables y culturas animales. Esta revisión examina los mecanismos y las consecuencias evolutivas de la transmisión cultural en animales no humanos, con énfasis en primates, cetáceos y aves. Analizamos evidencia en diversos contextos biológicos, incluidas las estrategias de forrajeo en orcas, las rutas migratorias de grullas y ballenas y el aprendizaje vocal en aves cantoras y loros. Estos ejemplos demuestran que comportamientos previamente atribuidos únicamente al instinto con frecuencia se moldean por la herencia social. Además, exploramos cómo la evolución cultural interactúa con la evolución genética. Estudios de caso, como las adaptaciones genómicas en distintos ecotipos de orcas y las tasas de especiación aceleradas en linajes de aves con aprendizaje vocal, sugieren que la cultura puede actuar como una presión selectiva que impulsa la divergencia morfológica y genética. Concluimos que la transmisión cultural constituye un sistema de herencia secundario complementario a la genética. Reconocer este modelo de herencia dual es esencial para una comprensión integral del comportamiento animal, la adaptación y la especiación.

Palabras clave: Aprendizaje social, coevolución gen-cultura, cultura animal, evolución cultural, herencia no genética, transmisión cultural.

Introduction

Social learning is a process in which individuals learn from the actions and consequences of others (Heyes, 1994) and transmit behaviors across individuals, populations, and even generations (Heyes & Galef, 1996). This allows organisms to expand their behavioral repertoire by introducing new information (Dukas, 2013), helping them adapt to local environmental conditions (Snell-Rood, 2013). By sharing information and skills, social learning enables individuals to draw on others' prior experiences to improve their biological fitness (Slagsvold & Wiebe, 2011). This contrasts with individual learning, which relies on personal trial and error (Whiten, 2019). Studies suggest that innovations, such as specific whale songs (Garland et al., 2011) or foraging techniques in primates, birds, and cetaceans (Kawai, 1965; Allen et al., 2013; Aplin et al., 2014) can spread rapidly through populations. Furthermore, sharing this information over long periods may lead to the formation of animal culture (Laland & Hoppitt, 2003; Whiten, 2011; Aplin, 2016), which acts as an inheritance system complementary to genetics (Whiten, 2005, 2017a; Mesoudi, 2015).

But how is culture defined? Some authors define it simply as the existence of a tradition, while others describe culture as socially transmitted information, whether it be beliefs, skills, thoughts, or knowledge (Mesoudi, 2015; Whiten, 2019). However, Mundinger (1980) proposed a consensus definition based on definitions used in various disciplines: “culture is a set of populations that, through learning, are replicated generation after generation: an open population of functionally related, shared and imitable behavioral patterns (and any material products), and, simultaneously, a closed population of acquired neural codes for these behaviors.” In this definition, the concept of population follows the framework suggested by White (1959) regarding non-genetic inheritance. Therefore, it refers not to groups of living organisms but rather to a population of ideas or neural codes, and the associated motor patterns that operate as behavioral models (Mundinger, 1980). In addition, Mundinger (1980) proposed a specific definition for tradition: “a tradition is a complex of learned behaviors shared by individuals within a population of organisms, appearing and persisting in their behavioral repertoire generation after generation”.

Therefore, "cultural transmission" can be defined as the various social learning processes through which individuals acquire traditions. These traditions can be highly stable; for instance, Pipek et al. (2016) suggest that the Yellowhammer (*Emberiza citrinella*) -a bird- has maintained its song for centuries. Similarly, Haslam et al. (2009) highlight a behavior in chimpanzees that has persisted for thousands of years: the use of stone tools. However, if an individual modifies a behavior while learning it, and these changes are subsequently passed on to others via cultural transmission, a second form of evolution can emerge (Whiten, 2019).

Cultural evolution can be categorized into two main processes: cultural evolutionary drift and Darwinian cultural evolution (Whiten, 2019). Cultural evolutionary drift is analogous to genetic drift in organic evolution, involving changes that are selectively neutral (Futuyma, 2013). Conversely, some culturally transmitted behaviors may be subject to selection, adapting to specific selective pressures; this process corresponds to Darwinian cultural evolution (Boyd & Richerson, 1985; Mesoudi et al., 2006). Darwinian cultural evolution can stabilize beneficial traits or be directional, actively driving evolutionary change. These changes may accumulate or disappear over long periods, potentially increasing the complexity and efficiency of the behaviors involved (Whiten, 2019). Therefore, cultures are not static; their components can change over time, altering their form, function, or frequency. Notably, this wide range of cultural practices can significantly influence the life, survival, and biological fitness of organisms (Galef & Whiten, 2017; Whiten, 2017b).

It is widely established that cultural transmission and social learning occur across a diverse array of behaviors and animal species, spanning from insects and birds to mammals (Mundinger, 1980; Heyes, 2012; Aplin, 2016; Whiten, 2019). However, given the volume of existing evidence, three primary groups have emerged as the focus of animal culture research: primates (Whiten, 2017c), cetaceans (Rendell & Whitehead, 2001), and birds (Podos & Warren, 2007). In the following sections, we will examine specific taxa for which social learning and cultural inheritance have been suggested, as well as the specific contexts in which these inherited behaviors occur.

Cultural inheritance across diverse contexts and species

As previously noted, social learning is widespread across various taxa of the animal kingdom and occurs in a variety of contexts. In primates, examples include tool use and grooming practices (Biro et al., 2003; Whiten et al., 1999), while in whales, there is evidence of migratory routes learning (Baker et al., 1990; Valenzuela et al., 2009). Similarly, birds exhibit behaviors such as predator recognition (Curio et al., 1978), courtship (White, 2004), and foraging (Norton-Griffiths, 1967).

Foraging

Orcas (*Orcinus orca*), also known as killer whales, have a wide distribution range, extending from the Antarctic to the Arctic, and a diet that includes birds, fish, mammals, and reptiles. However, they form groups or "ecotypes" with specialized diets and distinct hunting traditions (Beans, 2017). Some groups specialize in salmon, others in mammals, and others in penguins. Furthermore, even among groups that feed on seals, hunting practices differ significantly: some generate waves to wash seals off ice floes, whereas others intentionally beach themselves to grab seals and drag them back into the water (Foote et al., 2016).

Riesch et al. (2012) present an example of cultural limitation in orcas; they describe three orcas from a mammal-eating specialist group that, after being captured and held in captivity, refused fish when offered as food. However, this fish was known to be nutritious for the species, as it constitutes the primary food source for other orca populations. Because of refusing the fish, one individual died of starvation. In contrast, within just 24 hours, the other two individuals adapted to the established culture of the group into which they were integrated and began feeding on fish. This suggests that culture can drastically influence orca behavior, potentially leading to disastrous consequences.

Migration

Both birds and cetaceans are taxonomic groups well known for their migratory behaviors. Among birds, approximately 2,000 species are migratory, and for some, evidence suggests that migratory routes may be transmitted via social learning. For instance, in the Great Bustard (*Otis tarda*), one of the heaviest flying birds, research indicates that juveniles undertake their first migration (and occasionally subsequent ones) alongside their parents or members of their local community. They subsequently follow the routes acquired during these initial journeys (Palacín et al., 2011). Such findings suggest that collective migration provides evidence that these acquired routes are culturally transmitted.

Further evidence supporting the social learning of migratory routes comes from experimental studies. For example, Sladen et al. (2002) successfully taught a migratory route to Canada Geese (*Branta canadensis*) by leading them with an ultralight aircraft. Remarkably, 83% of these birds returned independently to the training site the following spring, whereas individuals transported by ground in enclosed trucks failed to return. Similar results were reported by Lishman et al. (1997), who used the same method to teach a migratory route to Sandhill Cranes (*Grus canadensis*); the majority of these birds also successfully returned to their training grounds.

Mueller et al. (2013) offer another example involving the Whooping Crane (*Grus americana*). Their results suggest that young birds learning migratory routes by flying with "expert" individuals deviate 34% less from the route than juveniles that do not travel with such guides. These findings indicate that migratory skills in this species develop over several years and that cultural transmission via experienced birds yields progressive improvements in the migratory performance of younger individuals.

Similarly, evidence supports the social learning of migratory routes in cetaceans. These highly conserved movements between breeding and feeding grounds are typically transmitted from mother to calves. Such migratory behaviors have been documented in Southern Right Whales (*Eubalaena australis*, Valenzuela et al., 2009), Humpback Whales (*Megaptera novaeangliae*, Whitehead, 2010), and Belugas (*Delphinapterus leucas*, Colbeck et al., 2013). This transmission of information is critical, as locating novel feeding and breeding grounds without prior knowledge can be extremely costly and lead to high mortality rates (Whitehead, 2007, 2010). Conversely, these ingrained traditions may prevent whales from exploring new areas in response to habitat degradation caused by climate change. This cultural conservatism can lead to maladaptive behavioral choices within their established ranges, potentially driving populations toward collapse (Whitehead & Richerson, 2009).

Vocalization

Bird songs are often used for mate identification as well as for territorial defense (Searcy & Andersson, 1986). In birds of the suborder Passeri (songbirds), vocal development is influenced by imitative learning, allowing for wide variation in learning patterns (Beecher & Brenowitz, 2005). One of the primary advantages of song learning may be the formation of dialects, which has been suggested to promote genetic adaptation to local environmental conditions (Nottebohm, 1972). Nottebohm (1972) proposes that males learn the dialect of their natal area because local females develop a preference for these dialects; consequently, females select males capable of singing the local dialect.

Female preference for more elaborate songs is another proposed advantage, driving males to incorporate acoustic elements from other individuals into their vocal repertoire. For instance, in Zebra Finches (*Taeniopygia guttata*), it has been suggested that female preference for complex songs correlates with higher male quality (Woodgate et al., 2012).

Humpback Whales (*Megaptera novaeangliae*) learn their vocalizations, which are often highly elaborate. Much like bird songs, these calls have been suggested to serve the functions of attracting mates and repelling rivals (Tyack, 1981). In contrast, Bottlenose Dolphins (*Tursiops truncatus*) possess simple, yet unique vocalizations known as "signature whistles." These are typically emitted when individuals become separated from close group members, suggesting they facilitate social cohesion by enabling the identification and localization of distant individuals (Caldwell & Caldwell, 1965; Janik & Slater, 1998; King & Janik, 2013).

Strikingly, a similar strategy is found in some parrots. These birds also utilize short, simple, yet individual-specific vocalizations to promote social cohesion, serving primarily to attract individuals to foraging flocks and to identify mates (Balsby & Adams, 2011; Berg et al., 2011; Farabaugh et al., 1994). Some parrots, such as the Australian Cockatoo (*Cacatua galerita*), modify their contact calls to match diverse groups, suggesting an advantage in mediating the fission-fusion dynamics characteristic of many parrot species (Scarl & Bradbury, 2009).

Primates

Primates have been extensively studied in both field and laboratory settings, providing comprehensive evidence of their culture and behaviors. Consequently, more than 39 traditions have been identified in Chimpanzees (*Pan troglodytes*) across Africa, ranging from foraging techniques and tool use to social behaviors and sexual habits (Whiten et al., 1999). A wide variety of traditions has also been reported for other primates, including 24 for Orangutans (genus *Pongo*; van Schaik et al., 2003) and 22 for gorillas (genus *Gorilla*; Robbins et al., 2016).

Chimpanzees demonstrate distinct preferences in nut-cracking tools; some populations prefer wooden tools, while others utilize stone tools (Luncz & Boesch, 2014). Furthermore, archaeological excavations have revealed that this behaviour dates back at least 4,300 years, indicating that this tradition has persisted for a significant period (Mercader et al., 2007).

Additionally, McGrew and Tutin (1978) reported the first social custom observed in a non-human animal: the "grooming handclasp". This behavior is performed exclusively by a chimpanzee population in a national park in Tanzania, and was not observed even in a nearby group inhabiting a different national park within the same country.

Can cultural inheritance drive genetic divergence?

Currently, animal populations are recognized as possessing two distinct streams of information: genetic and cultural. Cultural information is inherited as individuals learn behaviors from mothers, fathers, mates, or unrelated individuals. But how do these two information streams interact? A prominent example in humans is the production of lactase in adulthood within European populations. This trait co-evolved with the cultural practice of dairy farming, selecting individuals with the LP allele, which allows for the continuous production of the enzyme throughout adult life (Itan et al., 2009).

Furthermore, current research suggests that culture can directly influence trait evolution and the divergence of populations toward speciation. Just as variations in morphological traits allow some individuals to survive or reproduce more effectively than others, cultural innovations — such as tools or predator avoidance tactics — can also enhance an individual's survival and reproductive success (Beans, 2017). Consequently, culture can drive selection for adapted morphology to these behaviors, such as arms better suited for tool manipulation, or selection for cognitive traits, like the ability to acquire tool use through imitation (Galef & Whiten, 2017).

Although obtaining evidence for these phenomena is challenging, the research on orcas provides substantial support for this theory of cultural selection. Foote et al. (2016) examined the genomic consequences of specialized hunting cultures in 48 orcas across five distinct ecotypes. They aimed to determine if these groups were truly isolated and if their cultures were linked to unique genomic changes. The results revealed genetically distinct groups, even among those inhabiting the same geographic areas with overlapping distribution ranges. Furthermore, they identified genetic variants associated with adaptations to the specific hunting traditions of each ecotype. For instance, mammal-eating ecotypes were associated with variants in the metabolism of the methionine-regulating gene, an essential amino acid found in high concentrations in their prey. Conversely, groups inhabiting the extreme cold of the Antarctic showed variants in genes related to adipose tissue development, providing necessary thermal protection. Despite these significant findings, the authors note that not all groups will necessarily diverge into separate species, suggesting that full speciation has not occurred in the past, given that their common ancestor is relatively recent.

Further evidence can be found in bird songs, which are innate in some species but require social learning in others. In both cases, the song evolves over time and across generations. Mason et al. (2017) suggest that culture plays a crucial role in this evolutionary process. They analyzed the songs of nearly 600 bird species from two families: *Thraupidae* (Tanagers), which learn their songs, and *Furnariidae* (Ovenbirds), which possess innate vocalizations. The researchers estimated how quickly songs evolved within different branches of the family tree; high rates of evolution were inferred where songs differed significantly between closely related species. Subsequently, they combined this acoustic dataset with genetic data indicating speciation rates to identify relationships between acoustic change and species divergence. When the rate of song evolution increased in a phylogenetic branch, the rate of speciation also increased. Notably, songs evolved 1.4 times faster in *Thraupidae* — the song-learning family — compared to *Furnariidae*, which relies on innate vocalizations. The authors suggest that while song may diverge before the species in some instances, and vice versa in others, a clear pattern emerges: the faster the song evolves, the faster the species diverges. This leads to the conclusion that rapid song evolution — facilitated by cultural transmission — can contribute to speciation.

Conclusions

The discussion of the existence of culture in non-human animals dates to the 1950s, yet lacks the attention it merits, and few studies attempt to link the influence of cultural phenomena to genetic, morphological, and even ecological research. Nevertheless, the studies reviewed in this article highlight the importance of social learning and culture in behaviors previously attributed to the simplest explanation: instinct. Key examples include the learning of migratory routes in birds and cetaceans, and individual recognition in dolphins and parrots.

On the other hand, few studies conclusively demonstrate genetic, morphological, or ecological changes resulting from cultural evolution. Even in humans — the most studied species — examples remain scarce, with lactase persistence in European populations standing out as a classic case. Consequently, a primary objective for researchers should be to determine whether cultural evolution influences the genetic, morphological, and perhaps ecological variations observed across taxa.

In an era of accelerated scientific discovery, we can no longer afford to ignore cultural evolution as a potential explanation for these phenomena. It must be recognized that, alongside genetics, a secondary form of inheritance plays a substantial role in the lives of many organisms: cultural inheritance.

References

Allen, J., Weinrich, M., Hoppitt, W., Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science, 340 (6131), 485–488. https://doi.org/10.1126/science.1231976

Aplin, L. (2016). Understanding the multiple factors governing social learning and the diffusion of innovations. Current Opinion in Behavioral Sciences, 12, 59–65. https://doi.org/10.1016/J.COBEHA.2016.09.003

Aplin, LM., Farine, DR., Morand-Ferron, J., Cockburn, A., Thornton, A., Sheldon, BC. (2014). Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature, 518, 538. https://doi.org/10.1038/nature13998

Baker, CS., Palumbi, SR., Lambertsen, RH., Weinrich, MT., Calambokidis, J., O'Brien, SJ. (1990). Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature, 344 (6263), 238–240. https://doi.org/10.1038/344238a0

Balsby, TJS., Adams, DM. (2011). Vocal similarity and familiarity determine response to potential flock mates in orange-fronted conures (Psittacidae). Animal Behaviour, 81(5), 983–991. https://doi.org/10.1016/J.ANBEHAV.2011.01.034

Beans, C. (2017). Can animal culture drive evolution? Proceedings of the National Academy of Sciences, 114 (30), 7734–7737. https://doi.org/10.1073/pnas.1709475114

Beecher, MD., Brenowitz, EA. (2005). Functional aspects of song learning in songbirds. Trends in Ecology & Evolution, 20 (3), 143–149. https://doi.org/10.1016/J.TREE.2005.01.004

Berg, KS., Delgado, S., Okawa, R., Beissinger, SR., Bradbury, JW. (2011). Contact calls are used for individual mate recognition in free-ranging green-rumped parrotlets,Forpus passerinus. Animal Behaviour, 81 (1), 241–248. https://doi.org/10.1016/J.ANBEHAV.2010.10.012

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. Animal Cognition, 6(4), 213–223. https://doi.org/10.1007/s10071-003-0183-x

Boyd, R., Richerson, PJ. (1985). Culture and the evolutionary process. University of Chicago Press.

Caldwell, MC., Caldwell, DK. (1965). Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). Nature, 207(4995), 434–435. https://doi.org/10.1038/207434a0

Colbeck, GJ., Duchesne, P., Postma, LD., Lesage, V., Hammill, MO., Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. Proceedings of the Royal Society B: Biological Sciences, 280 (1752), 20122552. https://doi.org/10.1098/rspb.2012.2552

Curio, E., Ernst, U., Vieth, W. (1978). Cultural transmission of enemy recognition: One function of mobbing. Science, 202 (4370), 899–901. https://doi.org/10.1126/science.202.4370.899

Dukas, R. (2013). Effects of learning on evolution: Robustness, innovation and speciation. Animal Behaviour, 85 (5), 1023–1030. https://doi.org/10.1016/J.ANBEHAV.2012.12.030

Farabaugh, SM., Linzenbold, A., Dooling, RJ. (1994). Vocal plasticity in budgerigars (Melopsittacus undulatus): Evidence for social factors in the learning of contact calls. Journal of Comparative Psychology, 108 (1), 81–92.

Foote, AD., Vijay, N., Ávila-Arcos, MC., Baird, RW., Durban, JW., Fumagalli, M., Gibbs, RA., Hanson, MB., Korneliussen, TS., Martin, MD., Robertson, KM., Sousa, VC., Vieira, FG., Vinar, T., Wade, P., Worley, KC., Excoffier, L., Morin, PA., Gilbert, MTP., Wolf, JBW. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. Nature Communications, 7, 11693. https://doi.org/10.1038/ncomms11693

Futuyma, DJ. (2013). Evolution (3rd ed.). Sinauer Associates Inc.

Galef, BG., Whiten, A. (2017). The comparative psychology of social learning, in: J. Call, GM. Burghardt, IM. Pepperberg, CT. Snowdon, T. Zentall (Eds.), A handbook of comparative psychology: Perception, learning, and cognition (pp. 411–439). American Psychological Association. https://doi.org/10.1037/0000012-019

Garland, EC., Goldizen, AW., Rekdahl, ML., Constantine, R., Garrigue, C., Hauser, ND., Poole, MM., Robbins, J., Noad, MJ. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Current Biology, 21 (8), 687–691. https://doi.org/10.1016/J.CUB.2011.03.019

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R. (2009). Primate archaeology. Nature, 460 (7253), 339–344. https://doi.org/10.1038/nature08188

Heyes, CM. (2012). What's social about social learning? Journal of Comparative Psychology, 126 (2), 193–202. https://doi.org/10.1037/a0025180

Heyes, CM. (1994). Social learning in animals: Categories and mechanisms. Biological Reviews of the Cambridge Philosophical Society, 69 (2), 207–231.

Heyes, CM., Galef Jr, BG. (1996). Social learning in animals: The roots of culture. Academic Press.

Itan, Y., Powell, A., Beaumont, MA., Burger, J., Thomas, MG. (2009). The origins of lactase persistence in Europe. PLoS Computational Biology, 5 (8), e1000491. https://doi.org/10.1371/journal.pcbi.1000491

Janik, VM., Slater, PJB. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour, 56 (4), 829–838. https://doi.org/10.1006/ANBE.1998.0881

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. Primates, 6 (1), 1–30.

King, SL., Janik, VM. (2013). Bottlenose dolphins can use learned vocal labels to address each other. Proceedings of the National Academy of Sciences, 110(32), 13216–13221. https://doi.org/10.1073/pnas.1304459110

Laland, KN., Hoppitt, W. (2003). Do animals have culture? Evolutionary Anthropology: Issues, News, and Reviews, 12 (3), 150–159. https://doi.org/10.1002/evan.10111

Lishman, WA., Teets, T., Duff, JW., Sladen, WJL., Shire, GG., Goolsby, KM., Bezner, KWA., and Urbanek. RP. (1997) A reintroduction technique for migratory birds: leading Canada geese and isolation-reared sandhill cranes with ultralight aircraft, en: Urbanek RP, Stahlecker DW, eds. (1997). Proceedings of the Seventh North American Crane Workshop, 1996 Jan 10-13, Biloxi, Mississippi. Grand Island, NE: North American Crane Working Group. pp. 96-104.

Luncz, LV., Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. American Journal of Primatology, 76 (7), 649–657. https://doi.org/10.1002/ajp.22259

Mason, NA., Burns, KJ., Tobias, JA., Claramunt, S., Seddon, N., Derryberry, EP. (2017). Song evolution, speciation, and vocal learning in passerine birds. Evolution, 71 (3), 786–796. https://doi.org/10.1111/evo.13159

McGrew, WC., Tutin, CEG. (1978). Evidence for a social custom in wild chimpanzees? Man, 13 (2), 234–251.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C. (2007). 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proceedings of the National Academy of Sciences, 104(9), 3043–3048. https://doi.org/10.1073/pnas.0607909104

Mesoudi, A. (2015). Cultural evolution: A review of theory, findings and controversies. Evolutionary Biology, 43(4), 481–497. https://doi.org/10.1007/s11692-015-9320-0

Mesoudi, A., Whiten, A., Laland, KN. (2006). Towards a unified science of cultural evolution. The Behavioral and Brain Sciences, 29 (4), 329–383. https://doi.org/10.1017/S0140525X06009083

Mueller, T., O'Hara, RB., Converse, SJ., Urbanek, RP., Fagan, WF. (2013). Social learning of migratory performance. Science, 341(6149), 999–1002. https://doi.org/10.1126/science.1237139

Mundinger, PC. (1980). Animal cultures and a general theory of cultural evolution. Ethology and Sociobiology,1 (3), 183–223 https://doi.org/10.1016/0162-3095(80)90008-4

Norton-Griffiths, M. (1967). Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. Ibis, 109(3), 412–424. https://doi.org/10.1111/j.1474-919X.1967.tb04014.x

Nottebohm, F. (1972). The origins of vocal learning. The American Naturalist, 106 (947), 116–140.

Palacín, C., Alonso, JC., Alonso, JA., Magaña, M., Martín, CA. (2011). Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. Journal of Avian Biology, 42(4), 301–308. https://doi.org/10.1111/j.1600-048X.2011.05395.x

Pipek, P., Petrusková, T., Petrusek, A., Diblíková, L., Eaton, MA., Pyšek, P. (2016). Dialects of an invasive songbird are preserved in its invaded but not native source range. Ecography, 41(2), 245–254. https://doi.org/10.1111/ecog.02779

Podos, J., Warren, PS. (2007). The evolution of geographic variation in birdsong. Advances in the Study of Behavior, 37, 403–458. https://doi.org/10.1016/S0065-3454(07)37009-5

Rendell, L., Whitehead, H. (2001). Culture in whales and dolphins. Behavioral and Brain Sciences, 24, 309–382.

Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B., Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: Ecological speciation in killer whales? Biological Journal of the Linnean Society, 106 (1), 1–17. https://doi.org/10.1111/j.1095-8312.2012.01872.x

Robbins, MM., Ando, C., Fawcett, KA., Grueter, CC., Hedwig, D., Iwata, Y., Lodwick, JL., Masi, S., Salmi, R., Stoinski, TS., Todd, A., Vercellio, V., Yamagiwa, J. (2016). Behavioral variation in gorillas: Evidence of potential cultural traits. PLOS ONE, 11(9), e0160483. https://doi.org/10.1371/journal.pone.0160483

Scarl, J. C., Bradbury, J. W. (2009). Rapid vocal convergence in an Australian cockatoo, the galah Eolophus roseicapillus. Animal Behaviour, 77(5), 1019–1026. https://doi.org/10.1016/J.ANBEHAV.2008.11.024

Searcy, W. A., Andersson, M. (1986). Sexual selection and the evolution of song. Annual Review of Ecology and Systematics, 17 (1), 507–533. https://doi.org/10.1146/annurev.es.17.110186.002451

Sladen, WJL., Lishman, WA., Ellis, DH., Shire, GG., Rininger, DL. (2002). Teaching migration routes to Canada geese and Trumpeter swans using ultralight aircraft, 1990-2001. Proceedings of the North American Crane Workshop, 25.

Slagsvold, T., Wiebe, KL. (2011). Social learning in birds and its role in shaping a foraging niche. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1567), 969–977. https://doi.org/10.1098/rstb.2010.0343

Snell-Rood, EC. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour, 85 (5), 1004–1011. https://doi.org/10.1016/J.ANBEHAV.2012.12.031

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology, 8 (2), 105–116. https://doi.org/10.1007/BF00300822

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*). Molecular Ecology, 18(5), 782–791. https://doi.org/10.1111/j.1365-294X.2008.04069.x

van Schaik, CP., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, CD., Singleton, I., Suzuki, A., Utami, SS., Merrill, M. (2003). Orangutan cultures and the evolution of material culture. Science, 299 (5603), 102–105. https://doi.org/10.1126/science.1078004

White, D. J. (2004). Influences of social learning on mate-choice decisions. Learning and Behavior, 32 (1), 105–113.

White, L. A. (1959). The concept of culture. American Anthropologist, 61 (2), 227–251.

Whitehead, H. (2007). Learning, climate and the evolution of cultural capacity. Journal of Theoretical Biology, 245 (2), 341–350. https://doi.org/10.1016/J.JTBI.2006.10.001

Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. Learning Behavior, 38 (3), 329–336. https://doi.org/10.3758/LB.38.3.329

Whitehead, H., Richerson, P. J. (2009). The evolution of conformist social learning can cause population collapse in realistically variable environments. Evolution and Human Behavior, 30(4), 261–273. https://doi.org/10.1016/J.EVOLHUMBEHAV.2009.02.003

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. Nature, 437(7055), 52–55. https://doi.org/10.1038/nature04023

Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1567), 997–1007. https://doi.org/10.1098/rstb.2010.0334

Whiten, A. (2017a). A second inheritance system: The extension of biology through culture. Interface Focus, 7 (5), 20160142. https://doi.org/10.1098/rsfs.2016.0142

Whiten, A. (2017b). Culture extends the scope of evolutionary biology in the great apes. Proceedings of the National Academy of Sciences, 114(30), 7790–7797. https://doi.org/10.1073/pnas.1620733114

Whiten, A. (2019). Cultural evolution in animals. Annual Review of Ecology, Evolution, and Systematics, 50, 1–22. https://doi.org/10.1146/annurev-ecolsys-110218-025040

Whiten, A., Goodall, J., McGrew, WC., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. EG., Wrangham, RW., Boesch, C. (1999). Cultures in chimpanzees. Nature, 399 (6737), 682–685. https://doi.org/10.1038/21415

Woodgate, JL., Mariette, MM., Bennett, ATD., Griffith, SC., Buchanan, K. L. (2012). Male song structure predicts reproductive success in a wild zebra finch population. Animal Behaviour, 83 (3), 773–781. https://doi.org/10.1016/J.ANBEHAV.2011.12.027