

**Culture in songbirds and its contribution toward the evolution of new species**

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## Introduction

The human ego has had a two-sided relationship with science. On the one hand, the scientific method has enabled us to understand the natural world in ways previously inconceivable, and to make inventions that would have astounded our ancestors. On the other, the history of science is one of breaking down the ways in which we had previously thought we were special: the Earth is not the center of the universe, our anatomy is similar to that of other primates, our behavior shares many similarities with diverse groups of animals, and some other types of animals have intelligence and emotional awareness that approach our own. Thus the results produced by the scientific method have gradually moved us toward an integration of fields that were previously considered separate: the natural sciences and the humanities. The study of one phenomenon widely considered to be unique to humans, culture, is no exception.

Like other phenomena originally conceived by humans to be unique to humans, culture has experienced a tumultuous definitional history. Originally used in an agricultural sense to refer to the cultivation or improvement of soil, plants, or animals, the term was eventually applied in a similarly value-laden way to human societies (Kroeber et al. 1952). In the 18<sup>th</sup> and 19<sup>th</sup> centuries, the term often was used in a subjective way to refer to the “best” or “ideal” traditions that a society can have (Kroeber et al. 1952). Recently, the term has taken on a variety of less value-laden meanings, referring in general to socially learned behavior; most dictionaries define “culture” as a property of humans alone:

“the sum total of ways of living built up by a group of human beings and transmitted from one generation to another.” – Random House Webster’s Unabridged Dictionary, second edition. 1999. Random House: New York.

“the total set of beliefs, values, customs, and behavior patterns that characterizes a human population; the noninstinctive manner in which humans interact with or manipulate their environment” – Academic Press Dictionary of Science and Technology. 1992. Academic Press: San Diego, California.

“the customs, civilization, and achievements of a particular time or people” – The Oxford Dictionary and Thesaurus, American Edition. 1996. Oxford University Press: New York.

“the totality of socially transmitted behavior patterns, arts, beliefs, institutions, and all other products of human work and thought.” – [www.thefreedictionary.com](http://www.thefreedictionary.com)

From a biologist’s perspective, the references to a single species in the above definitions are somewhat humorous; these definitions seem as absurd as the following:

“Flight: the propelled movement through the air of Townsend’s big-eared bats.”

“Song: a vocal signal given by yellow-rumped warblers to defend their territories and attract mates.”

Defining a phenomenon as existing solely in a single species greatly limits use of the comparative method, a fundamentally important technique in the biological sciences. If we want to understand the origin and evolution of a trait in a single species, we can gain great insight by comparing that trait among multiple species. This approach has allowed us to identify the functions of human genes by studying related genes in fruit flies and mice, and to understand human behavior by studying such behavior in a broad range of species and observing common patterns. Thus, defining culture as a feature of humans alone can prevent us from making progress in understanding the origins and evolution of culture.

In fact, there is considerable evidence that cultural phenomena are common in the biological world. Here I define culture broadly by simply taking the words “human” or “people” out of the above definitions: by “culture” I essentially mean “socially learned behavior that can grow and change through time.” By this standard it is clear that many non-human species have culture. This is not to say, however, that the culture of other species approaches human culture in terms of its complexity or richness. Clearly, humans are unusual among species in terms of the extent to which culture has affected our ecology and evolution, as well as our impact on the other species with whom we share our planet.

In this chapter, I first briefly review the evidence for culture in non-humans and propose birdsong as an excellent system for the study of culture. I then discuss the ways that genetics and learning can be jointly involved in cultural evolution, through a process of gene-culture coevolution (Feldman and Laland 1996). I consider the role that culture can play in the evolution of new species and propose a model of how sexual selection can drive gene-culture coevolution along different trajectories in separated populations. I finish with some comments on the lessons of birdsong research for the study of culture in humans and other primates.

Note that I approach the topic of culture as a bit of an outsider: my training is as an evolutionary biologist who uses birds as a model system for the study of how multiple species evolve from one (i.e. the process of speciation). My work on bird song has gradually led toward a general interest in the evolution of learned behaviors. The literature on birdsong commonly refers to birdsong as a form of culture, thus it was surprising to me to read the definitions that limit that term to humans, as well as the arguments among primate biologists as to whether other primates have culture.

### Culture in non-humans

From my perspective, it is clear that many species have culture. Convincing examples from primates include chimpanzees (Whiten et al. 1999, 2001; Lycett et al. 2007), orangutans (van Schaik et al. 2003), and capuchin monkeys (Perry et al. 2003). Cetaceans also provide clear examples (Rendell and Whitehead 2001) such as songs of humpback

whales (Noad et al. 2001), calls of killer whales (Yurk et al. 2002), and tool use of bottlenose dolphins (Krützen et al. 2005).

Culture is especially common in birds. These include feeding methods in such birds as ravens and crows (Marzluff and Angell 2007), and singing behavior in songbirds (Catchpole and Slater 1995). Migratory behavior in some species that migrate in groups is a particularly compelling example: young geese, ducks and cranes typically migrate with older individuals, learning the route as they go. Remarkably, humans have used ultralight aircraft to teach young birds a new migratory route to a new wintering area (e.g. with the endangered whooping cranes *Grus americana*; see [www.operationmigration.org](http://www.operationmigration.org)). This socially learned behavior has then been passed down by experienced birds to younger birds, providing an example of a new socially-transmitted tradition. Such cross-species transfers of behavior provide particularly clear examples of the abilities of other species to transmit culture. Singing behavior provides another clear example of socially transmitted behavior (Catchpole and Slater 1995; Price 2008). A role for social learning in the development of an individual's singing behavior has been demonstrated in at least three major groups of birds: oscine passerines (known informally as the "songbirds"), parrots, and hummingbirds.

Examples of culture in animals are not without controversy (reviewed by Laland and Janik 2006). Ironically, though, the amount of skepticism regarding demonstrations of non-human culture seems to be highest with regard to that group that is closest to humans, the non-human primates, and moderately high with regard to cetaceans as well (Laland and Janik 2006). In contrast, there is wide agreement among ornithologists that bird song, when socially learned, can be viewed as a form of culture (Price 2008). The extreme skepticism encountered by primatologists who claim that non-human primates have culture simply has not occurred in relation to similar claims of culture in birds. This reluctance to accept culture in our closest relatives is probably related to the ongoing human desire to keep humans separate from other species (Corbey 2005).

#### Birdsong: a combination of genetics and learning

In the vast majority of bird species, vocal signals play a vital role in survival and reproduction (Catchpole and Slater 1995; Collins 2004). Vocal signals can be divided broadly into two categories: calls, which are signals used in a variety of contexts by both sexes throughout the year, and songs, which are sung primarily by males (with some exceptions, notably in the tropics) mainly during the breeding season. Songs are often much longer and more complex than calls, and in many species songs are highly influenced by learning, whereas most calls are not. Songs usually have a role in both mate attraction and territory defense (Collins 2004). In many species, each male defends a small territory—his songs tend to repel other males (unless they decide to challenge his ownership of the territory), while females choose mates partly based on song, often preferring songs that are longer, more complex, or otherwise more elaborate in some way. Songs often differ dramatically between closely related species or even between different populations of the same species, suggesting that they can evolve quickly (Price 2008).

In the literature on culture in humans and other primates, learning and genetics are sometimes viewed as competing or antagonistic influences on traits (i.e. the “nature vs. nurture” debate). In primatology, this view is encapsulated in the so-called “ethnographic method” (reviewed by Laland and Janik 2006), which holds that to demonstrate culture, the influence of genetic and ecological variation on the behaviors being studied must be ruled out. In the birdsong literature, a more complex view emerged some time ago: song is influenced by genes, learning, and environmental characteristics, all of which interact in complex, often synergistic, ways both in the development of an individual’s song and in the evolution of song within and between species (reviewed by Marler 2004).

This view is supported by considerable experimental and observational evidence (Marler 2004; Price 2008). In some of the earliest experiments, Thorpe (1961) showed that young chaffinches (*Fringilla coelebs*) that were raised in isolation did develop songs, but they sounded very rudimentary compared to wild song. Others were raised while hearing recordings of adult chaffinch songs, and these developed songs similar to those they had heard. Yet others were raised while being exposed only to a variety of artificially created sounds or songs of other species, but these did not learn to produce those sounds. The one exception was tree pipit (*Anthus trivialis*) song, which has a tonal quality similar to the chaffinch; the chaffinches were able to learn this song perfectly. Thorpe concluded that the young chaffinches have an innate tendency to learn songs that are similar to a crude template, but that to develop the correct wild song they must hear it first. Another good example is provided by Marler and Sherman’s (1985) work on song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*). When reared in isolation, individuals from each species sing rudimentary songs, much simpler and at a slower tempo than wild songs. Yet the songs of isolates differ between species in a way that is similar to the way wild songs differ between species, with song sparrows having a more complex song structure (Fig. 1). This experiment clearly shows that the two species have innate (i.e. genetic) tendencies to sing different songs, yet the full wild song needs to be heard to be learned.

#### An excellent system for the study of cultural evolution

A number of characteristics of birdsong make it particularly well suited for the study of cultural evolution. Song is an easily recorded behavior; with a portable microphone and recorder, a researcher can record song while having little impact on the subject. Song can be analyzed by converting the recording into song spectrograms; these can be compared visually, and a variety of measurements can be made. Songs of many bird species can be categorized into distinct song unit types, allowing a quantification of song variability and a comparison of repertoires between individuals (e.g. Lynch and Baker 1993, 1994; Irwin 2000). By recording songs of all individuals in a population, researchers can determine from which of many possible song tutors a young bird learned its song (it is often not the father). These patterns can be compared to patterns of genetic inheritance, when relationships between relatives have been determined (Grant and Grant 1998). Playback experiments can be used to test how birds respond to a variety of recordings; such experiments have been used to test recognition of songs from a different population (e.g.,

Irwin et al. 2001). Much is known about the neurological and physiological basis of song, providing background knowledge that assists in the understanding of singing behavior (Jarvis 2004). It is relatively easy to sample large numbers of individual birds so that genetic, morphological, and environmental variation can be compared with song variation (e.g., Irwin et al. 2008). Lastly, the large number of songbird species (roughly 4000) provides a wide variety of research systems that can be studied in a comparative framework.

Evolution, or change in the traits of a population over time, only requires two things: variation and inheritance. Due to random sampling from generation to generation, the frequencies of traits in a population will change stochastically over time, a process known as drift. But for evolution to be driven in a particular direction, a third factor is required: selection, meaning that variants that differ in some trait have different average survival and reproduction.

Like all cultural phenomena, the evolution of birdsong can be studied from two complementary angles in terms of selection. First, we can consider how variation in singing behavior affects the fitness of individual birds that display that behavior. Using this approach, many experimental and observational studies have shown that, in most species examined, female birds choose mates partly based on the way that they sing (reviewed by Collins 2004). Studies have also demonstrated that song plays a role in male-male territorial interactions, and that different singing behaviors function better or worse in this context (Collins 2004). These two selective forces on song are both forms of sexual selection: individuals with some variants of song survive and reproduce more than those with other variants, due to their differential ability to compete for mates. Hence genetic variants that influence singing behavior in favorable ways tend to increase each generation.

Second, rather than focusing on the fitness of organisms that display partially learned behavior, we can examine the fitness of learned behaviors themselves. In other words, we can view a particular learned song as a “meme” (Dawkins 1976; Lynch and Baker 1993) that can be transferred from one individual to another, just as a gene can be passed from parent to offspring. Some memes may be particularly good at being transferred (i.e. have high fitness), because they transmit well through the environment, are easily learned, or confer greater survival on the individuals that carry them, and therefore get repeated more and are transmitted to more individuals. Because songs of individual birds or populations can often be categorized into distinct song types, it is possible to generate libraries that illustrate the “meme pool” of a population (e.g., Payne 1996). A number of studies have examined song divergence between populations in a “population memetics” framework, using theory originally designed for population genetics. Most applications of this theory so far have looked for evidence of “memetic drift,” or the divergence of songs between populations that are not driven by selection. For example, songs of chaffinches on a number of Atlantic Islands show more differentiation from each other than do populations on the mainland, an observation consistent with memetic drift due to population bottlenecks and lower migration rates during the colonization of the islands

(Lynch and Baker 1994), although Price (2008) notes these patterns are also consistent with selection on song due to environmental differences on the islands.

### Genes and memes: a single coevolving system

How do we make sense of these two aspects of the evolution of birdsong—the fitness of genetic variants and the fitness of memetic variants? Biologists have developed two concepts that aid in understanding how these aspects interact.

The first is the concept of gene-culture coevolution (reviewed by Feldman and Laland 1996). Rather than genes and learning being competing influences on song, the two are in fact different components of a single coevolving system:

The two transmission systems [genetic inheritance and cultural learning] cannot be treated independently, both because what an individual learns may depend on its genotype, and also because the selection acting on the genetic system may be generated or modified by the spread of a cultural trait. (Feldman and Laland 1996)

Thus genetic variation influences the types of memes that are preferentially learned by individuals, and memetic variation influences the form of selection on genes.

The second concept is “genetic assimilation” (Waddington 1961; Price 2008). This is the idea that a socially learned behavior can eventually become genetically based. Imagine a newly learned behavior that causes high fitness, such as a new feeding method. Initially, individuals learn the behavior from each other, and it spreads through the population. Those who can learn the behavior most quickly or efficiently benefit most from the new behavior. This exposes to selection any genetic variation that influences how quickly the behavior is learned. Over the generations, individuals become better and better at learning the behavior. Eventually, a few individuals may have so many of the genes for efficient learning of the behavior that they simply exhibit the behavior without having to observe it—they exhibit the behavior without learning. In this way, the learned behavior has become genetically assimilated.

Genetic assimilation is expected to occur with song evolution because a population of birds is under constant selection for efficient learning of its population-specific song. Thus song may evolve through a process of memetic evolution, but genetic variants that enable efficient learning of that song are constantly favored by selection. In this way, the genetic instinct to learn song of certain characteristics constantly tracks the evolving songs of the population. While genetic assimilation is constantly occurring, there may still be forces driving song evolution (e.g. sexual selection) and thereby maintaining a benefit of some degree of song learning. Thus cultural evolution and genetic assimilation can occur at the same time.

### An example: the greenish warblers

For a number of years, my colleagues and I have been studying song and other variation in greenish warblers (*Phylloscopus trochiloides*), a group of songbirds that breeds in the temperate forests of Asia (Irwin 2000; Irwin et al. 2001, 2005, 2008). The greenish warblers provide a good illustration of many of the aspects of song research discussed above. Moreover, they provide an example in which cultural evolution may have contributed to the splitting of a single species into two.

Greenish warblers are a rare example of a “ring species,” a phenomenon that is particularly illustrative for the study of how two species evolve from one (Wake 2001): Two northern forms, one in west Siberia (known by the subspecies name *Phylloscopus trochiloides viridanus*) and one in east Siberia (*Phylloscopus [trochiloides] plumbeitarsus*), do not interbreed and are genetically distinct where they meet, effectively making them distinct species; yet these forms are connected by a long chain of interbreeding populations encircling the Tibetan Plateau to the south through which genes, body size and shape, plumage patterns, and vocalizations change gradually (Fig. 2; Ticehurst 1938; Irwin 2000; Irwin et al. 2001, 2005, 2008). These patterns have supported the hypothesis that a single ancestral species once occurred in the southern part of the current ring and then expanded northward along two pathways, northwestward and northeastward, into Siberia (Ticehurst 1938). During these expansions, vocalizations, plumage patterns, and genes gradually diverged, such that western and eastern Siberian populations did not interbreed when they finally came into contact in central Siberia.

Geographic variation in song around the ring is especially remarkable. In all locations, songs are constructed out of short “song units” that are highly distinct; each individual has a limited repertoire of song units and constructs songs by joining together song units in various ways (Irwin 2000). But the characteristics of song units and the rules by which they are joined together into complete songs differ dramatically between populations (Fig. 2). In the south (e.g. in the Himalayas), song units are short and simple, and entire songs are constructed by simply repeating a single unit four to six times. Moving from the western Himalayas northward into western Siberia, song units gradually increase in length and in frequency range, such that each unit becomes more complex. Entire songs are constructed by joining together (usually two to five) different units, resulting in songs that are much longer and more complex than those in the south. By contrast, moving from the eastern Himalayas northward into eastern Siberia, songs again become more complex but in a different way than in the west: units become only slightly longer, but songs are constructed out of a much larger unit repertoire per bird, unit repetition goes down, and more units are used to construct each songs. In both west and east Siberia, songs are much longer and more complex songs than those in the south. But the form of complexity differs between the two Siberian forms (Fig. 2b); the birds recognize this difference, as demonstrated by playback experiments (Irwin et al. 2001). Where the two forms meet in the north, their songs are completely different, even though change in songs is gradual around the ring.



To explain this intriguing pattern, we have postulated that the intensity of sexual selection on male song based on female choice has increased during the northward expansions into Siberia (Irwin 2000; Irwin et al. 2008). There is much evidence in a variety of songbird species that females tend to prefer song that is more complex or otherwise more elaborate in some way (Collins 2004). It is likely that the dramatic shifts in various ecological factors (e.g. food abundance, time on the breeding grounds, population density, forest density, day length, temperature at night) have shifted the balance of selective forces on song in a direction that amplifies the impact of female choice for complex song (see Irwin 2000 for some ideas of exactly why this may have occurred). This could have then driven the evolution of long and complex songs during the two expansions into Siberia. This scenario is supported by the parallel increases in a number of characteristics related to the intensity of singing behavior (e.g. time spent singing, repertoire length, song length, and unit switching rate; Irwin 2000).

Assume for the moment that the above scenario is correct: there has been parallel selection for greater song complexity and length during the two northward expansions. An interesting question arises: by what mechanism has song evolution occurred? What are the relative roles of genetic evolution and memetic evolution? Could this be an example of cultural evolution contributing to the evolution of two species from one? To address these questions, we need to first examine whether there is evidence for learning being involved.

A number of observations support the hypothesis that learning is involved in greenish warbler song. First, greenish warblers are members of the oscine passerine evolutionary group (the “songbirds”), in which song learning is common (Catchpole and Slater 1995; Price 2008). Second, it is difficult to imagine that the pattern of song variation would arise without some role for learning: a bird’s entire repertoire consists of a highly complex series of sounds that are organized into discrete units; it is reasonable to think that the detailed structure of each unit was learned from other individuals. Third, there are clear examples of different individuals singing the same unit, except for minor differences. These differences most likely correspond to cultural mutations. In some cases, there are clear insertions or deletions, in which it appears that an individual simply repeated a syllable or two in the middle of a unit, or conversely that an individual dropped a syllable to two from the unit. In other cases, two units in one individual’s song are fused as a single unit in another individual’s song. In yet other cases, there are small changes to the detailed structure of a unit in different individuals’ songs. Fourth, one unusual individual from central Siberia sings songs that consist of some syllables characteristic of west Siberian *viridanus* and some syllables characteristic of east Siberian *plumbeitarsus* (Fig. 3). This individual had the syntax of a typical *viridanus*, grouping the *plumbeitarsus* syllables into long song units rather than the shorter units typical of *plumbeitarsus*. Unfortunately, we were unable to capture this individual and cannot test its genetic identity, but the singing pattern strongly suggests that it was *viridanus* that learned some elements of *plumbeitarsus* song.

While the evidence for song learning is strong, it is also likely that genes influence variation in greenish warbler song. Genome-wide genetic signatures differ dramatically

around the ring, with *viridanus* and *plumbeitarsus* being at the extremes, suggesting it is quite plausible that many genes that influence the propensity to learn certain kinds of songs vary around the ring. As with many other species (e.g. the song sparrows and swamp sparrows discussed above), it is likely that greenish warblers have an innate tendency to learn a particular type of song; this innate template likely differs around the ring. This idea is supported by the unusual *viridanus* that learned some *plumbeitarsus* song but then organized it into a unit length typical of *viridanus* (Fig. 3). It is as if the general acoustic structure of *plumbeitarsus* units was acceptable to this *viridanus*, but the unit length and repetitive structure was not. So it learned the details of the units, but converted the syntax (the pace and rules by which units are put together into songs) to conform to its own genetically-encoded template.

#### A simplified model of gene-culture coevolution driven by sexual selection

The above observations suggest a greatly simplified model for greenish warbler song evolution: song units are learned, whereas song syntax is genetically coded. This model, like most, is certainly a great simplification compared to reality and is not intended as a fully precise description of the mechanics of song evolution in greenish warblers. In fact, both units and syntax are likely influenced by both genes and learning, to varying degrees. But considering this simplified model for the moment may nonetheless allow us to gain real insight into how greenish warbler song evolves. Adopting this model, we see that greenish warbler song evolution can be seen as a form of gene-culture coevolution (Feldman and Laland 1996): syntax is controlled by genes, whereas song units are memes. The genes that encode syntax influence the selective environment for memes: the memes that a bird learns (and therefore have high fitness) are those that conform best to the bird's genetic template for syntax (i.e. the right length and frequency range). Conversely, memes influence the selective environment for genes: the genes with highest fitness are those that allow efficient learning of memes that convey fitness benefits to individual birds. In this way, genes and memes coevolve.

Now, we can add sexual selection to the model. We postulate that females prefer males that sing longer and more complex songs, and that the ecological conditions have changed in a way that amplifies the strength of this sexual selection based on female choice or, conversely, relaxes opposing selection against elaborate singing. For example, perhaps a shift toward greater food availability has enabled birds to sing more (Irwin 2000). There are many types of changes in song that would increase length and complexity, and hence be preferred by females. In terms of memes, longer song units, greater song unit diversity per bird, and song units with more internal complexity may all be favored. In terms of genes, any genetic variation that causes birds to preferentially learn longer or more complex song units, a larger number of song units, and to sing with more complex syntax (e.g. switching more between song units) may be favored. Sexual selection is thus driving both memes and genes to evolve, and changes in memes cause selection on genes, and vice versa. This feedback loop, with memes and genes causing change in each other, enhances the effectiveness of sexual selection in driving evolution of song (Fig. 4).

In this coevolutionary process, small changes in initial conditions have the potential to cause huge changes in the eventual outcome. To demonstrate this, imagine taking a single population of birds and separating it into two groups, and then applying greater sexual selection for song complexity to each. In one population, the first genetic mutation to become fixed (that is, the first to spread through the population due to selection) may be one that favors the learning of longer song units. This then exposes the population of song units to selection for greater length. This in turn favors another genetic mutation that favors learning of even longer memes. The population eventually has songs that consist of very long, internally complex song units (such as those of west Siberian *viridanus*).

Imagine that in the second population, the first genetic mutation to become fixed is one that favors the learning of large numbers of song units and using many song units per song. This exposes the population of song units to selection favoring relatively short and easily learned units. This in turn causes selection for genetic variants that cause the learning of even larger numbers of song units and perhaps lowering the repetition rate because it is advantageous to display the large song unit repertoire. Eventually, each bird in this population has a large repertoire of song units and sings long songs that consist of many short units that are repeated little (such as those of east Siberian *plumbeitarsus*).

In these two populations, the initial form of sexual selection was identical, but the different initial mutations were magnified by the coevolutionary interaction of genes and memes, increasing the propensity of the populations to head off on different evolutionary trajectories. Thus gene-culture coevolution is a highly stochastic process, because of the strong influence of random events (mutations) on the outcome. The process can quite easily lead to the divergence of two populations even when the form of selection acting on each is initially the same. While such divergence can occur in response to parallel selection without gene-culture coevolution (Price 2008), the influence of memes and genes on each other's selective environment, as well as the high mutation rate of memes, creates especially high potential for divergence.

Now, let us add a bit more complexity to the model: the evolution of female preference. Mate preference, like singing itself, is a behavior that has strong fitness consequences and can therefore evolve in response to changing conditions (Price 2008). The coevolving gene-culture system that shapes the male songs of a population also changes the selective environment for female mate preference; the optimal preference function will depend on the distribution of song types in the population and the association of those song types with other traits that influence male survival and reproduction. Thus, in addition to the feedback interactions that occur between genes and memes in relation to song, there is feedback between male song and female preference for song. Complicating things further, there is much evidence that female mate choice in many species is shaped partially by learning: females sexually imprint on the songs of their fathers, and generalize from that song when considering potential mates (Irwin and Price 1999). Hence like song, female song preference can be shaped by both genes and learning. Furthermore, sexual imprinting, like any learning-based behavior, can lead to genetic assimilation: females initially learn to recognize a novel male song variant through sexual imprinting, but this exposes to natural selection any genetic variation in the ability to

learn to recognize that novel variant. In this way, female recognition and preference for song can track the changing male song.

These many coevolutionary interactions, between memes and genes for song, between male songs and female preferences, and between memes and genes for female preferences, as well as all the higher-order interactions between these factors, clearly lead to a highly complex coevolutionary system, even in the comparatively simple world of bird song. It is clear that the evolutionary pathway of such a system will be highly contingent on stochastic factors such as mutation, and that two populations with identical starting conditions will rapidly diverge. If the two populations then come back into contact, it is possible that male songs and female preferences have diverged to a degree that the two populations do not interbreed. In this case, the process of gene-culture coevolution has led to complete speciation: the evolution of two species from one.

While the above model was inspired by the greenish warblers, the essential components of the model are likely quite common. Sexual selection for elaborate signals (e.g. song, mating dances) is common throughout the animal world. Learning of mating signals and/or preferences are also common in many groups of animals. And some genetic control of learning is likely universal (how could it not be?). Thus the central dynamic in this model, of sexual selection driving rapid gene-culture coevolution, could be quite important in the evolution and diversification of much of life.

#### Lessons from birdsong for the study of culture in other animals

After this close look at the details of bird song evolution, we can now take a step back and ask about the lessons from bird song for the study of culture in general. One lesson is that culture is most easily studied in taxonomic groups that are amenable to study through a variety of experimental and observational methods. For reasons described above, birds are especially suitable for such study compared to groups (e.g. non-human primates) in which it is more difficult to conduct experiments and observational studies because of various ethical and logistical constraints.

Another important lesson is that culture and genes are not competing or opposing influences on the behavior of a species. Rather, memes and genes together comprise a single coevolving system; “learning” can be thought of as the process by which genes and memes interact to produce the behavior of an individual. This view contrasts with that common in the literature on culture of primates, that to demonstrate that behavioral variation is cultural one must first exclude any possible influence of genetic variation (or ecological variation) on that behavior (the so-called “ethnographic method” mentioned above). This view is flawed in two ways: (1) it ignores the fact that genetic evolution (and ecological shifts) can promote the evolution of culture through gene-meme coevolution, and (2) absence of genetic variation in a sample of genetic markers does not allow one to rule out a role for genetic variation in causing behavior; there could still be some small part of the genome that causes the behavior in question.

Lastly, we can consider the above points in relation to that most interesting of cultural species, humans. For historical and social reasons, there is sometimes a reluctance to take conclusions from the animal behavioral sciences and apply them in the humanities. In particular, there is a reluctance to accept a role for genetics in the evolution of culture, especially those aspects of culture that seem most intellectual, such as language and arts. But there is in fact clear evidence that gene-culture coevolution does occur in humans. One of the clearest examples is the interaction between the practice of dairy farming and the genetically-encoded ability for adult humans to digest lactose (Holden and Mace, 1997; Hollox 2005; Burger et al. 2007). There is evidence that the genetic variants responsible for this ability have undergone strong natural selection during the last 10,000 years, when dairy farming developed in some societies. Thus a cultural change (the drinking of milk as adults) caused selection on genetic variants that allow the efficient digestion of lactose. Conversely, it is clear that genes for milk tolerance influence culture: the culture of adult milk drinking has not spread easily to parts of the world where the genes for lactose digestion in adulthood are rare.

It is quite likely that such interactions between culture and genes are not limited to such obvious traits as culinary traditions and genes for digestive enzymes. Any behavior that is jointly influenced by learning and genetics must be influenced to some degree by a process of gene-culture coevolution. The conditions for gene-culture coevolution are too simple for this not to be the case. Thus one area of likely progress in the integration of the sciences and the humanities is in applying gene-culture coevolutionary theory to the full range of human cultural traits.

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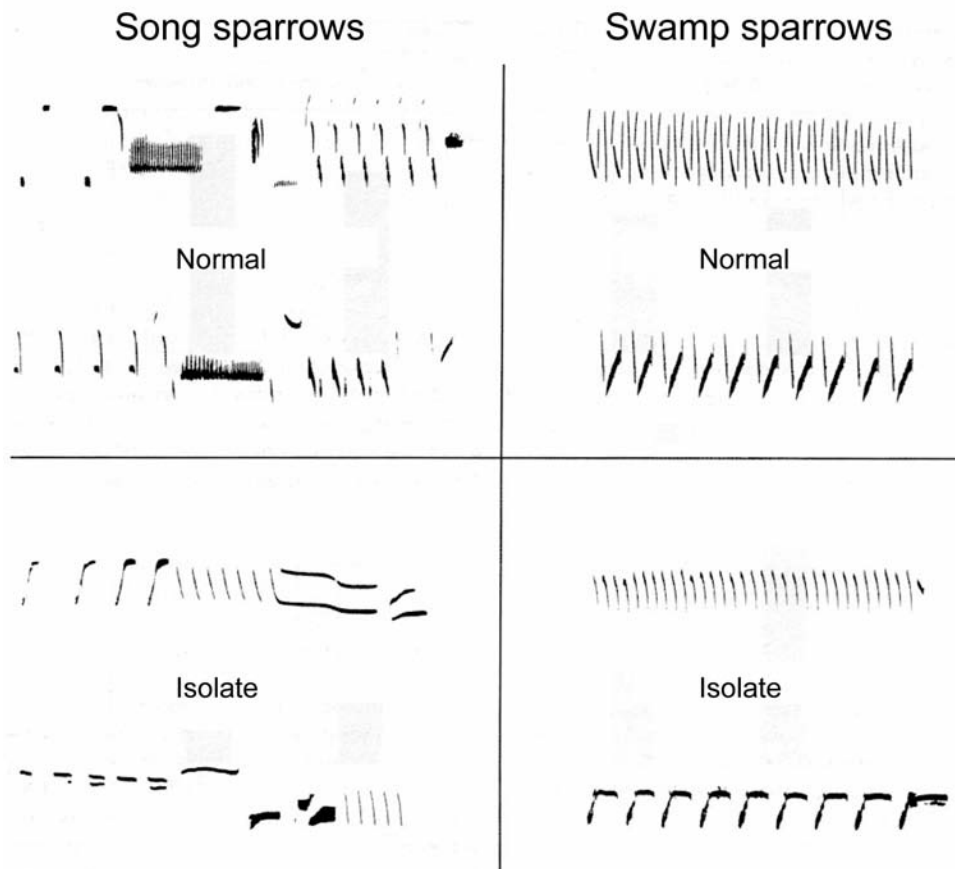


Figure 1: Example song spectrograms of song sparrows (left) and swamp sparrows (right) from wild birds (top) and birds raised in isolation (bottom; in each case, songs of two individuals are shown). Song spectrograms illustrate time along the horizontal axis and frequency along the vertical axis, with the darkness representing amplitude of sound at each frequency and time. Isolate songs are simpler than wild song, illustrating a role for learning in development of wild song. Isolate songs differ between species in a way consistent with wild song, illustrating a genetic difference in instinctive song development. Adapted from Marler (2004), after Marler and Sherman (1983).

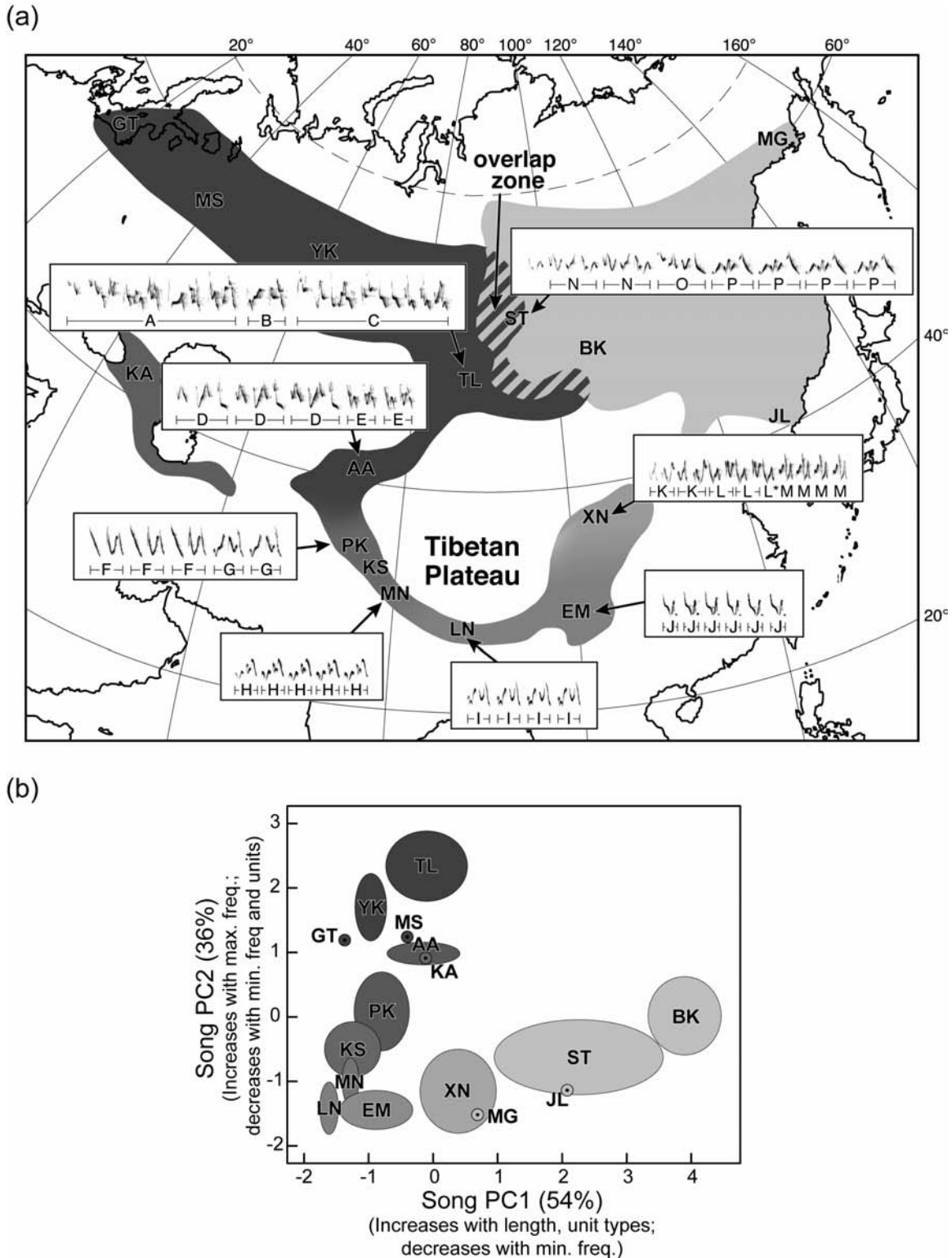
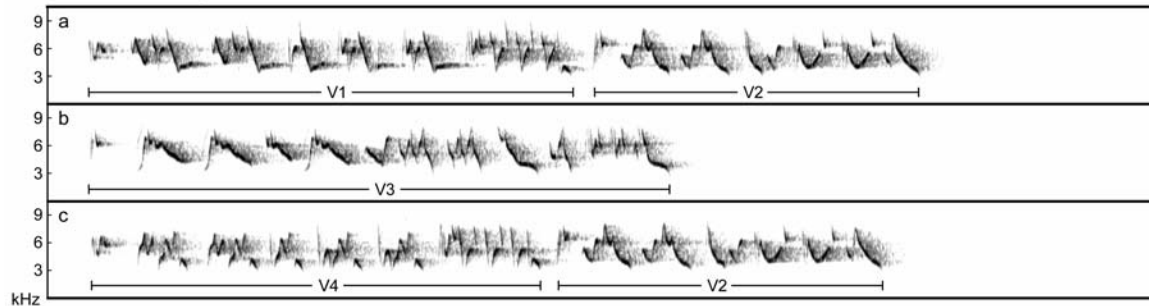


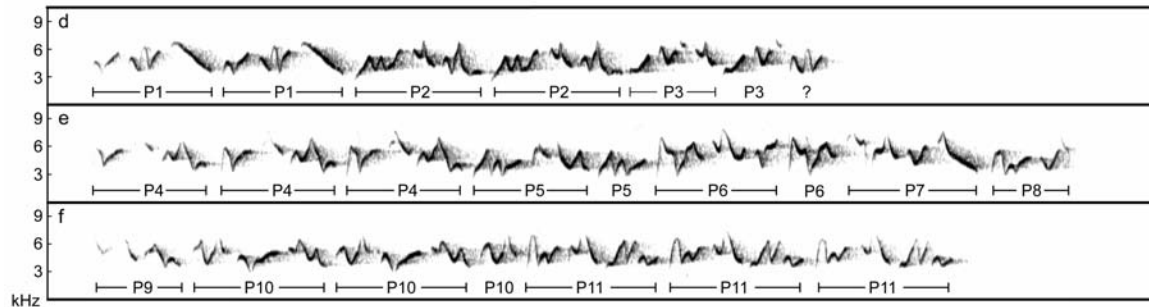
Figure 2: Geographic variation in song of greenish warblers, illustrated using (a) spectrograms on a map of Asia and (b) a plot of two composite axes of variation in song, produced using principal components analysis. Research sites are indicated by two-letter codes. On the spectrograms in (a), distinct song units are represented by letters. Various

shades of grey represent genetic characteristics of greenish warbler populations, with the grey areas in (a) representing breeding ranges and in (b) representing song variation (population means and standard deviations for two principal components of song variation; small circles with dots indicate sites where only a single bird was recorded and hence no standard deviation can be estimated). West Siberian *viridanus* (dark grey) and east Siberian *plumbeitarsus* (light grey) differ strongly in genetics and song. These traits change gradually between these extremes through a ring of populations to the south. Moving north from the Himalayas (e.g. research site LN, in Langtang, Nepal), songs become longer and more complex, along both western and eastern pathways into Siberia, but in different ways. Adapted from (a) Irwin and Irwin (2004) and (b) Irwin et al. (2008).

*viridanus*, Yekaterinburg:



*plumbeitarsus*, Lake Baikal:



mixed singer with *viridanus* syntax but some *plumbeitarsus* syllables, Stolbi:

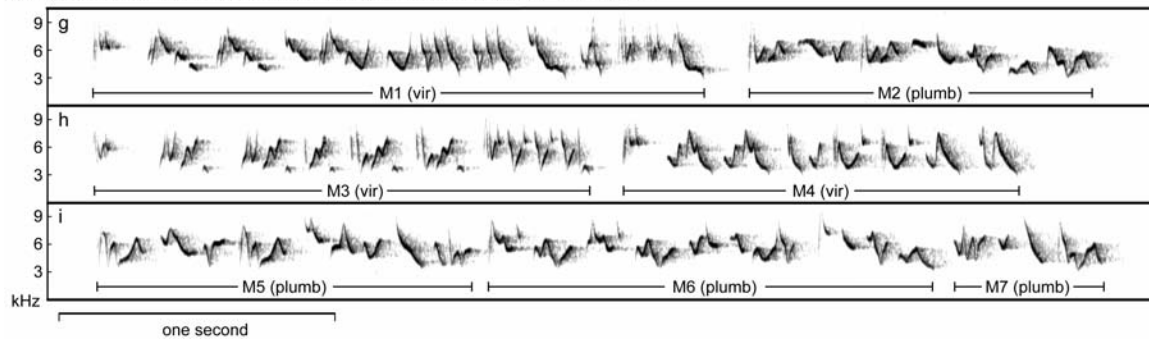


Figure 3: Example song spectrograms from (a-c) a single *viridanus* in west Siberia (Yekaterinburg, site YK in Fig. 2), (d-f) a single *plumbeitarsus* in east Siberia (Lake Baikal, site BK), and (g-i) an unusual bird in central Siberia (Stolbi National Park, site ST, recorded in June or July 1998) with songs that combine the syntax of *viridanus* (e.g. long song units, without repetition) with song elements from both *viridanus* and *plumbeitarsus*. For each individual, the three songs shown (one per line) were sung consecutively. Song units are indicated with brackets and names under the spectrograms, and in the case of the mixed singer “vir” and “plumb” indicate the match of the syllables to other *viridanus* or *plumbeitarsus* songs. For example, for *viridanus* song units compare units M1 and V3, units M3 and V4, and M4 to V2. For an example of *plumbeitarsus* parts of song, compare unit M5 with units P6 and P7. Many other parts of the mixed singer’s song match units in other recorded *plumbeitarsus* individuals (not shown), but in this mixed singer the short *plumbeitarsus* units are grouped into much longer units, consistent with normal *viridanus* syntax.

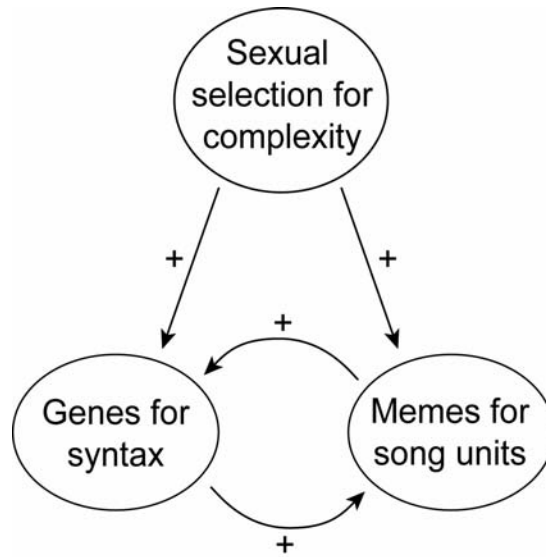


Figure 4: Diagram showing simple model for how sexual selection for more complex song can drive both genetic and memetic evolution. In turn, evolution of genes causes selection on memes, and evolution of memes causes selection on genes. This feedback loop causes the overall path of evolution to be highly depend on initial conditions and on random events during evolution, such as mutation. While we can predict that more complex song will evolve, the form of that complex song is highly unpredictable. Note the diagram could be made much more complicated, with many more feedback loops, if we were to add the genetics and learning (i.e. sexual imprinting) of female preference for song.