

Introduction

Culture and cumulative culture in animals

Culture has dozens of definitions and interpretations. Some ethologists consider any socially transmitted information culture (Bonner 1980), but in cultural evolutionary theory, it is widely accepted that, although there are instances of culture in nonhuman animals, many aspects of culture are restricted to humans. Before considering one of these, cumulative culture, that is central to this dissertation, we will discuss some examples of cultural variation in nonhuman animals. We will limit our discussion to behaviors that are socially transmitted, maintained over generations, and that produce population-specific variations.

Many examples of culture in animals relate to methods of acquiring food. For instance, arboreal black rats (*Rattus rattus*) in Israeli forests during a sensitive period in early life learn a particular and very efficient technique to open pine cones from their mother. Pine cone scales form a spiral – some spirals go left, others right. The technique involves finding the key scale at the bottom of the cone, identifying the direction of the spiral, and then removing each scale in turn to get to the pine nut which is hidden below it. This behavior does not appear spontaneously (Aisner & Terkel 1992). For example, naïve adult rats can open pine cones, but they do so by simply chewing a hole in its middle, and never revise their inefficient technique of obtaining the pines. Even their offspring do not improve the technique. It is assumed that at some point an especially creative rat must have come up with it on her own, but it is only maintained in the population because the technique is learned by new generations.

Other examples of culture in animals involve the usage of tools to get to food more efficiently. For example, chimpanzees stick probes into termite nests and manipulate them in a way that results in many termites getting caught on the stick (Goodall 1964). Young chimpanzees observe older individuals performing this trick and then practice it on their own. Moreover, in the Congo Basin, chimpanzees use an improved design,

brush-tipped fishing probes that are different from the simpler probe sticks of East and West Africa (Sanz et al. 2009). Even more impressively, New Caledonian crows manufacture tapered tools from narrow leaves of pandanus trees which they use to extract invertebrates from the rainforest vegetation (Hunt 1996). Although tool use and manufacture is common among crows, only those in New Caledonia (*Corvus moneduloides*) make the tapered tools. In different regions of the main island, Grande Terre, there are differences in the design of the tools, with more northerly regions containing more sophisticated tools with more steps. The geographical distributions of the different designs overlap and are independent of ecological correlates, which implies that the designs are culturally transmitted and maintained, although there is no direct evidence for this (Hunt & Gray 2003). Building increasingly sophisticated tools by improving on previous designs is indicative of cumulative cultural evolution.

Cumulative culture, although widespread in humans, is extremely rare even in birds and mammals. An obvious human example is technological evolution: as an instrument-building behavior is transmitted across generations, instruments become more and more sophisticated, each time building on the previous state, so that it reaches a point when no single individual, no matter how clever, could invent the instrument from scratch. According to Boyd & Richerson (2005), cumulative cultural evolution assumes a gradual change in the behavior over many generations and a branching pattern of descent by modification, that is, populations that are more closely related share more characteristics than populations more distantly related. This, of course, is somewhat complicated by the horizontal transmission of culture, and since good documentation only exists for human culture (language and technological changes), investigation of cumulative cultural evolution in nonhuman animals may be challenging. According to Boyd & Richerson's criteria, one of the very few examples of nonhuman cumulative cultural evolution exist in songbirds, because regional dialects exhibit such geographical relationships (Marler & Tamura 1964). However, in the absence of empirical evidence, we cannot be certain that song dialects do not represent random fluctuations in singing behavior over generations and over space (analogous to genetic drift) as opposed to directional shifts that accumulate over generations (e.g., songs becoming more and more structured over

generations), which would be more similar to what we see in human cumulative cultures. In this study, we provide the first evidence that wild-type birdsong evolves in a cumulative manner and results in behavioral variants that cannot be produced by an individual animal.

Song culture in birds

Vocal learning

The complex behavior that allows song cultures to develop is vocal learning. Songbirds, just like human infants, are born with a predisposition to learn complex vocalizations, which they do during an early stage in development by gradually modifying their vocal output to match that of adults (Immelmann 1969). This is, of course, similar to how humans learn to speak languages. Vocal learning behavior is rare: besides humans and oscine songbirds (Thorpe 1958), strong evidence only exists for parrots (Pepperberg 1999), hummingbirds (Baptista & Schuchmann 1990), and cetaceans (Reiss & McCowan 1993, Foote et al. 2006). There is some indication that bats may be vocal learners as well (Boughman 1998). Vocal learners are able to change their vocal behavior based on auditory stimuli, and they imitate adults to achieve species-typical vocal behavior. In addition, there are some characteristics of the developing vocalization that are shared among vocal learners: for example, sounds become more structured and less variable during development. In fact, the early song of young birds is sometimes referred to as babbling, because the vocal exploration involved in it is reminiscent of pre-linguistic vocalization in human infants (Doupe & Kuhl 1999).

The sensitive period

As mentioned above, vocal learners acquire their vocalizations by imitating their parents during an early stage in development. This period is called the sensitive period, the time during which the young bird is able to memorize adult sounds and by gradually changing his own vocalizations, match those sounds. In some species, like the song sparrow, the two processes (memorization and practice) are removed from each other in time, as song sparrows listen to adult males in the spring, but do not produce their own songs until the

next spring, which they do even when isolated (Marler 1964). Therefore, vocal learning in birds requires the formation of a long-lasting memory of the model song, often referred to as the ‘auditory song template’ (Konishi 1965). Vocal learning is then the gradual process of mapping the template onto a set of motor commands which becomes the acoustic signal, the song. It is thought, although without firm supporting evidence, that the mechanism of sensory-motor conversion necessary for achieving vocal imitation might be similar in birds and humans.

Song dialects

Many oscine bird species can only acquire new songs during the early sensitive period. These birds are called “age-limited” learners, and an example is the zebra finch (*Taeniopygia guttata*). However, some species can also learn new songs as adults; we refer to these as “open-ended” learners, and this group includes the canary (*Serinus canaria*). Open-ended learners often learn new songs in a seasonal pattern (Nottebohm 1987). Errors in song learning and faithful return to natal areas are thought to give rise to geographical variation in the songs of most birdsong species. The variation in song between populations is much larger than within a population (Thompson & Baker 1993), which is the basis for regional song dialects. Marler and Tamura were the first to systematically study song dialects and discovered that over large geographical distances the songs become less and less similar (Marler & Tamura 1962). Cross-fostering experiments proved that these dialects are not genetic, rather, they are an outcome of cultural transmission (Marler & Tamura 1964). Shifts in song dialects can occur when the separation between neighboring populations is sharp, often in the form of a geographical boundary (Thielcke 1969, Baker 1987). However, sometimes sharp boundaries between dialect populations do not coincide with habitat changes (Baptista 1977). Several studies demonstrated that song dialects can remain stable over many generations, probably because of bounded cultural transmission within stable populations with relatively little migration (Trainer 1983). When modifications to the dialect arise, they spread through the population by social transmission, and as more and more individuals (including the new generations) have incorporated the new inventions, the modifications become a stable part of the local dialect. This way, song dialects can evolve dynamically and

cumulatively within a population. Payne et al. (1981) recorded the songs of Village indigo buntings (*Vidua chalybeata*) in southern Michigan over a 15-year period. He found that although 80% of the young birds copied song types from neighbors when establishing territories, they also made changes and over the 15-year old study period, only a few song types persisted. However, the half-life of songs was roughly three times longer than the half-life of the individuals.

What drives the evolution of song dialects?

There are several social interactions that underlie the cultural evolution of song dialects. In some species, especially age-limited learners who grow up in the presence of their parents, juveniles often imitate from their fathers, but only slightly more than from other males (Williams 1990). Young males have been found to imitate adult males who interacted with them most, including feeding them (Mann & Slater 1994), and even from those who were more aggressive towards them (Clayton 1987). Migrating birds, who arrive at a geographical location to establish a territory, often copy neighbors (Payne 1981). Village indigo birds copied their songs more from successfully breeding males than from males who were unsuccessful (Payne 1985).

Females probably play an important role, as well. The mating preferences of female cowbirds can be measured due to their display of copulatory postures. They respond significantly more to songs of reproductively successful males (West et al. 1981). Females can influence the persistence of the local dialects, because they were shown to preferentially mate with males who sing familiar dialects (Baker and Cunningham 1985, Slabberkoorn & Smith 2002). There are ways in which females can contribute to song diversity and complexity. For example, song sparrow females have been found to show preference for males with larger repertoires (Reid et al. 2004). In addition, Okanoya's studies revealed that female selection can result in higher song complexity (2004). He studied Bengalese finches, a domesticated strain of the wild white-rumped munia, that for the last 240 years has been maintained in captivity in Japan. The song of the munia is much simpler and more stereotyped, whereas the Bengalese finch's songs are complex and variable in syntax. Okanoya and his colleagues measured estradiol levels and nesting

activity in females after stimulation with either complex domesticated or simple wild-type song, and found that both measures were higher after stimulation with complex songs. They hypothesized that a sudden elimination of predation pressures and the females' preference for complex song resulted in the complex song syntax of Bengalese finches.

Documentation of changing cultures

Although cultures, cumulative or non-cumulative, have been studied intensely in both humans and animals, the development of existing cultures has only rarely been studied. In humans, Nicaraguan Sign Language (NSL) is perhaps the only well documented example. With the foundation of a school for special education in Nicaragua in 1977 (Kegl 2001), previously isolated deaf children from across the country came together for the first time. These children communicated in home signs within their families, which varied widely between families in form and complexity. Although the education was conducted in Spanish, the children began communicating with their peers, and within a few years established a sign language that bore grammatical properties similar to other existing sign languages. The spontaneous development of NSL is a fascinating example, but it leaves many questions open, such as what is needed for the language acquisition system to be activated, whether rich lexical or grammatical input is necessary and how exactly it happens. For obvious ethical reasons, it is impossible to subject human children to experimental manipulation to answer these questions.

In animals, culture has been studied mostly in the wild, where researchers must rely on small samples of the behavior. To our knowledge no studies have been done in a laboratory setting, where the environment can be controlled over generations, as culture develops. In addition, most studies rely on a qualitative assessment of cultural change. Besides a tight experimental control, there is a need for robust quantitative methods that allow us to measure cultural evolution reliably. This study hopes to overcome this obstacle by proposing a model system to study cultural evolution in the laboratory.

Goals and rationale of this dissertation

We developed a controlled experimental setting which recreates conditions that are conducive to cultural evolutionary changes, which we have recorded and analyzed. We take advantage of the distinction between isolate and wild-type zebra finch song. As mentioned before, zebra finches are closed-end learners, which means they learn only one song early in life and then lose the ability to learn more. There is also a strong sexual dimorphism in the organization of the brain (Nottebohm & Arnold 1976), which manifests itself in behavior, because only males produce song. Young males learn their songs from older males by imitation. Zebra finches, when raised in complete acoustic and social isolation, will invent a song and will stabilize on a stereotyped song structure upon maturity and sing that song for the rest of their lives. Such improvised songs are called isolate (ISO) songs. These songs differ in several aspects from those that wild birds or birds reared in laboratory colonies produce (Price 1979, Williams 1993), which we will refer to as wild-type (WT) songs.

WT songs can be regarded as the cultured form of singing. They are the result of many generations of cultural transmission. ISO songs, on the other hand, represent the innate behavior that emerges without any social transmission or imitating. Of course, even ISO song has a learned aspect to it, because the birds make changes to it based on the auditory feedback of hearing themselves sing (Price 1979). The evidence for this is that birds deafened in early development, and therefore deprived of auditory feedback, produce a virtually “structureless” song (Nottebohm 1966), which is much more abnormal than ISO song. In fact, ISO song goes through developmental changes as does WT song, and it becomes more structured and more stable during ontogeny. The level of structure and stability is, however, lower than in WT songs. In addition, the sensitive period is also extended in ISO birds, and they are able to learn new songs or modify their songs after WT birds have already crystallized and incapable of new imitation - beyond 100 days or so (Eales 1985).

From a cultural evolutionary perspective, one would expect that, given enough time, and in appropriate conditions, ISO songs should evolve into WT songs, assuming that the wild-type birdsong culture is constrained by innate components. Therefore, by training young birds with ISO song, we may be able to create a situation where there will be strong cultural evolutionary forces, such as those that restrict local dialects, that drive the song towards the WT. We test if ISO song evolves into WT song over multiple learning generations in different social situations: either one-to-one in an impoverished social setting or in a colony. In the one-to-one setting, we establish tutoring lineages starting from ISO birds, and document how the song changes across multiple learning generations. In the rich social setting, we establish an isolated semi-natural colony with an ISO bird, and follow the song as it is imitated by the offspring that are born into the colony.

Several possible mechanisms could account for a progression towards WT-like song. We present 3 non-mutually-exclusive scenarios.

Scenario 1. Cultural evolution of songs by sexual selection

Darwinian mechanisms have been proposed to be responsible for the transmission of cultural information (Campbell 1965), and even Darwin himself claimed that acquired variation was compatible with the forces of natural selection (1874, *Descent of Man*). Memetics, put forth by Richard Dawkins (1976), claims that the units of cultural transmission, called memes (in our case, song syllables), are self-replicating and therefore analogous to genes. Clearly, there are fundamental differences between cultural and genetic transmission, one being that culture can spread horizontally but genes can only proceed vertically. Horizontal transmission is a crucial element in the evolution of culture, because it allows young animals to learn from their peers or authoritative figures besides their parents. Examples abound in human culture, but there is evidence for it even in birdsong, since siblings can be influenced by each other's imitations (Tchernichovski 1998). Nonetheless, cultural learning has been claimed to be a highly adaptive behavior because an efficient transfer of cultural information will likely make the receiver fitter

(Bonner 1980). In some cases, the adaptive advantage is obvious, as in having a more efficient method to gather food or being able to recognize other individuals in the same population. Sometimes, cultural inheritance can reduce fitness (Cavalli-Sforza and Feldman 1981) in individuals, but Henrich and Boyd (2002) maintain that at the population-level fitness-enhancing traits must be preserved in subsequent generations.

In this scenario, random “mutations” occur in the imitation of ISO song, females prefer songs that are more WT-like, and chicks imitate more from their fathers. In this case, in analogy to Darwinian evolution, the song syllables are like genes, females are like the “selecting environment”, and the male songs that “survive” are transferred to the next generation of males, eventually optimizing female choices, namely towards WT features that the females prefer. In this scenario, the WT song is encoded in female preference, which provides the engine for cultural change, whereas males imitate randomly – WT-like song just provides them with a sexual selection advantage. If the transformation of ISO song into WT is by random modification and natural selection, we expect that it will only happen in the colony setting and it will take a long time.

Scenario 2. Cultural evolution of songs by selective imitation

Selective imitation means imitating a certain action only in particular circumstances, when there is good reason to do so. It assumes that the learner applies decision rules to the cultural variants he observes (Boyd & Richerson 2005). Children do this often during development, and recently the domestic dog has been shown to possess the ability to use judgment in imitation (Range et al. 2007). This mechanism is different from natural selection in that the subsequent song imitations will not happen by random mutations, rather, by active selection, so the birds bring innate predispositions to the learning process.

In this scenario, progression towards WT occurs directly by the learners during imitation. Due to their improvised nature, ISO songs vary across ISO birds. Moreover, ISO syllables within a particular bird’s song can vary in “abnormality.” This scenario suggests

that pupils imitate selectively those tutor syllables or songs that are more WT-like. For example, if the original ISO song has 5 syllable types, one similar to WT syllables, his pupil will imitate that WT-like syllable and improvise the rest of his syllables (like an ISO bird). Such recursive process of imitating syllables that are more WT-like should eventually lead to WT songs. If these forces are at play in our experiment, we expect that any approximation of WT song will happen irrespective of the social environment, that is, in both the colony setting and the one-to-one condition. In addition, only selected syllables will be copied and improvisation rate in subsequent learning generations will be high. The progress toward WT will take many generations of learners as WT-like syllables need to be selected in every generation from improvised, ISO-like songs, which slows the rate of accumulation.

Scenario 3. Cultural evolution by biased imitation

Cultural evolutionary theory does not distinguish between selective imitation and biased imitation, because one of the prerequisites of cumulative cultural evolution is that the cultural information itself is not modified from generation to generation, but is faithfully inherited (Bonner 1980). Therefore, the question is not how to change existing cultural information, but how to copy from what is available to be more successful. Humans use innate or learned biases to selectively imitate certain individuals, for example those who are more successful or those who are imitated more frequently by their peers (Boyd and Richerson 2005). In our case, it is important to distinguish between the two, as they involve completely different strategies and have different implications, therefore biases are used in a different context here. By biases, we mean imitation biases that have a direct phenotypic effect on the learners' songs, that is, the model song is altered by the learner during imitation.

In this scenario, as in Scenario 2, the learners guide the cultural evolutionary process. The difference is that in biased imitation pupils imitate both ISO-like and WT-like syllables, but change them actively during the imitation process. Syllables are stable and inherited but with modifications that steer the song culture toward WT-like songs. The ISO

features change gradually into WT features as each generation of learners contributes to the process.

Biased imitation produces nonrandom modifications which accelerate the rate of evolution (Richerson and Boyd 2005). The birds are active participants and contributors to evolutionary changes. No improvisation is involved, as birds modify existing syllables. We may experience a slowing down in the progression towards WT which may cause some features to asymptote as the approximation of WT is more complete. This is because the innate biases the birds will employ to change the ISO-like songs will have a smaller effect when the deviation from WT song is smaller. We expect that if imitation biases act on song imitation, young males will not need the help of females, so we will see the effect in the impoverished social setting as well as in the colony. The difference between Scenario 2 and 3 is that in this scenario, all the syllables will be imitated but altered rather than some WT-like syllables being more preferentially imitated. Abnormal syllables should change more than WT-like syllables but both kinds will appear in pupils' songs.

Depending on the outcome of our experiment, we will be able to infer some of the cultural evolutionary mechanisms involved in the transfer of cultural information.