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NEH Project:
Modeling Acoustic Adaptation in Bird Song

G. K. D. Crozier

Canada Research Chair in Environment, Culture and Values, and Assistant Professor
Department of Philosophy, Laurentian University, Sudbury, Ontario, Canada, P3C 2C6
publications11@aaai.org

Abstract

The objective of the family of models 'Singing to Neigbours' is to explore the mechanisms that may be responsible for the strong correlation between the song types and habitat types observed in populations of South American Rufous-collared Sparrows, *Zonotrichia capensis*. Formal models of this type could be used to address outstanding objections to Cultural Selection Theory, according to which Darwinian processes of blind variation, heredity, and selective retention operate directly on cultural objects. In particular, 'Singing to Neighbours' can offer a better understanding of the crucial relationship between culture and environmental selection pressures. What is vital for Darwinian evolution is that there exists a directional selection pressure – as contrasted with a system's inherent rate of change by the introduction of selectively neutral variations – and that this pressure has the effect of weeding out variations in the population that are less successful at reproducing under these conditions. The acoustic adaptation of the songs of the Rufous-collared Sparrow shows potential to serve as a such case study since it can clarify the role of environmental interaction in cultural evolution. Importantly, this system is not vacuously memetic, and there is potential to reveal the details of the selection mechanism through further investigations. One key part of this process can be played by spatial Game Theoretic models such as 'Singing to Neighbors,' which may have the resources to clarify the selective mechanisms underlying these systems.

Cultural Selection in Bird Songs

One significant obstacle facing Cultural Selection Theory lies in the challenge of characterizing the mechanism of heredity and selection that underwrite putative cases of cultural evolution (Hull 2000; Crozier 2008; 2010). In part, clarification is required with respect to the interaction between cultural systems and their purported selective environments – clarification that can only be obtained by building stronger connections between theory and empirical observations through the development of simple case studies of cultural systems that exemplify Darwinian processes of blind variation and selective retention.

One promising case study is the song of the Rufous-collared Sparrow, which is culturally transmitted and which seems to exhibit adaptations to the acoustic features of ecological habitats. Specifically, forest birds whistle while field birds trill; furthermore, it has been hypothesized that this difference has the function of minimizing signal degradation (Handford 1981; 1988; Handford and Lougheed 1991). By studying the population dynamics of song transmission through computer simulations and comparing the results to natural populations, we can clarify the causal structure of the putative selection mechanism involved and provide a 'model organism' to guide the development of selection theory in cultural evolution.

Bird 'calls' refer to signals between birds that are transmitted over short distances, whereas 'songs' refers to signals that are transmitted over long distances – such as over the distance of territory diameters. In Rufous-collared Sparrows, songs are sung only by males, and these songs serve in the defense of territories, which are crucial in terms of attracting female mates. Songs are learned by fledgling males during their first year. A young male will situate himself among the territories of a set of older males, and it will listen to their songs. In the following year, it will sing songs that it learned from among this set of 'mentors'. If one of its mentors has died, it will try to take over this newly available territory, or alternatively it will try to wedge itself among the territories of its mentors. Failing this, a group of young males who have learned

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overlapping repertoires of songs will together establish a new cluster of territories.

It has been well established that, within the range of species-specific song types that can be learned by fledglings, the characteristics of those songs tend to be functionally equivalent except insofar as song sharing is concerned. Song sharing has several important purposes in territorial defense, including facilitating ranging (estimating the distance of conspecifics) and serving as a password between neighbouring birds. Thus, when there is selection for song types, this tends to be based on frequency or density-dependent selection (Fitch 2009).

One potential exception to this is seen in the tail end (or 'coda') of the songs of the Rufous-collared Sparrows, which seem to exhibit adaptations to the acoustic conditions of the local environment. Specifically, birds in open habitats (such as fields) sing songs with trilled codas while birds in closed habitats (such as forests) sing songs with whistled codas. It has been hypothesized that these songs exemplify the veracity of the Acoustic Adaptation Hypothesis, according to which auditory signals between organisms are sometimes structured so as to minimize signal degradation relative to the local environment (Brown and Handford 1996; 2000). Specifically, it has been argued that these sparrow songs are trilled in fields and whistled in forests precisely because these song types transmit with different fidelity in different environments. It has been experimentally determined that whistled signals are transmitted with greater fidelity in forests than trills because the echos that result when the sound waves are bounced off of vegetation tend to blur the tightly-spaced elements in a trilled song; conversely, trilled signals are transmitted with greater fidelity in fields than whistles because the relative absence of redundancy in whistled signals renders them vulnerable to being distorted by the wind.

According to ornithologist Paul Handford and colleagues, the mechanism behind the observed song-type is as follows: It has been experimentally confirmed in laboratory settings that fledglings preferentially learn undegraded songs; trilled songs degrade more in forests than whistled ones, and whistled songs degrade more in fields than trilled ones; thus the sparrow songs experience acoustic selection for trills in fields and whistles in forests due to preferential copying by fledglings. Further evidence has lent credence to this hypothesized mechanism: investigations have revealed that there is no correlation between song type and genetic measures of relatedness among birds, other environmental features (such as altitude), or morphological characteristics of the birds (such as size).

However, even though a trait looks like it is the product of a Darwinian selection process, such appearances can be deceiving. Evidence of a 'fit' between a trait and its environment could, for example, be the product of rational foresight or of exaptation (that is, selection on another trait that results serendipitously in the emergence of a trait that has functionality for the organism). What is needed to protect from charges of 'Panglossian' reasoning is not only an account of how possibly the adaptation could have arisen, but further evidence that the adaptation was likely to have evolved given the conditions that actually obtained during the relevant period of time.

In the case of sparrow song, there are a range of alternative mechanisms that might be responsible for the observed correlations; including imitation based on frequency of singing by mentors, female preference, or other factors that are more closely tied with the biological fitness of the mentoring birds. By introducing formal models into this analysis, it is anticipated that we will be able to flesh out the key elements of this story and explore further the mechanisms that cause the observed distribution of song types.

The Models: 'Singing to Neighbours'

The set of models referred to as 'Singing to Neighbours' are constructed in NetLogo, with the objective of simulating the key features of song propagation in populations of South American Rufous-collared Sparrows. To date, simple toy models have been developed as a starting point. These toy models involve two kinds of habitat-type – forests and fields – represented as two kinds of patches. These toy models also involve two breeds of agents – whistling birds and trilling birds – represented as red and blue 'turtles,' respectively. The habitat-types occur in different patterns in order to test the importance of the shapes and sizes of various boundary regions in terms of differential song-type propagation. Birds are initially designated randomly as either trillers or whistlers, and they are distributed randomly across the set of patches. In each iteration of the code, the birds move through the territories in a slow meandering motion. Birds have a fixed probability of dying in each iteration of the code, and also a fixed probability of mentoring a new bird (which is represented in the model as a 'hatching' event, where the bird produces another bird of the same 'breed'). The probability that a given bird has of mentoring a new bird is determined by a combination of its song-type and the habitat-type in which it is situated: trillers have a higher probability of creating a new triller when they are in fields than in forests, and whistlers have a higher probability of creating a new whistler when they are in forests than in fields.

This set of simple toy models serves as a benchmark simulation, and 'Singing to Neighbours' needs to be extended in a variety of directions to determine the threshold sensitivities of the system, to compare it with natural populations, and to contrast some of the alternate mechanisms. But, even this simple model reveals some interesting results. First, it appears that maladaptive song types can hold out when clustered together, or on the frontier between territory types. This was found to hold especially true when the territories are divided diagonally: Because the game-space wraps around the edges, the corners of the diagonals were occasionally occupied by maladaptive song types in a manner that proved to be quite stable. This indicates that exploring different shapes in the boundaries between territories could prove to be informative because neither of the two song types has any clear competitive advantage in these regions.

There are a variety of potentially relevant variations that will be incorporated into the model in order to determine their relevance and to render the model closer to nature. One of the key extensions of the 'Singing to Neighbours' family of models will be to explore the effects of different mechanisms that might be responsible for the observed correlations between song-type and habitat-type. Additional ways in which the model could be rendered closer to what is observed in natural populations include: removing the bounding on the edges of the game-world; introducing a more realistic representation of aging, whereby older birds have a higher probability of dying than new birds; introducing a factor to represent mutation and immigration, whereby occasionally a new bird will adopt a random song type; and running simulations under a wide range of selection pressures in order to determine the threshold sensitivities of the system.

Importantly, natural populations of Rufous-collared Sparrows also exhibit trills and whistles on a continuum, and their natural environments exhibit a similar continuum between fields and forests; furthermore, the correlation between song types and habitat types is found to hold along these continuums. More complex versions of the model will incorporate the five different categories of habitat used in field studies of sparrow song distribution. Field studies have documented that the correlation in song types in natural environments holds very strongly across these five types of habitat, with songs being more trilled the more open the habitat and more whistled the more closed the habitat. Songs that are closer to the 'trill' end of the continuum include a higher number of more tightly-spaced elements (that is, notes) whereas songs that are closer to the 'whistle' end of the continuum consist of a fewer number of more widely spaced and slow elements. Thus, future versions of 'Singing to Neighbours' will represent birds, not as two discrete types, but rather as on a continuum between the extremes of trillers and whistlers.

The final and most important extension of the 'Singing to Neighbours' family of models will be to incorporate actual ornithological data into the simulation, including actual maps of sparrow territories, habitat-types, and bird song distributions. Ideally, the simulations that exemplify different mechanisms of song propagation will yield different predictions regarding the behaviour of actual bird populations under some circumstances, and that this will be useful in determining which of the mechanisms actually obtains in natural populations of South American Rufous-collared Sparrows.

Having a clear and compelling model of a set of ecological selection pressures operating on a system of cultural inheritance could provide a useful backdrop or null hypothesis for investigating deviations that might be attributable to selection pressures that are properly cultural or biological in origin. With improvements in its predictive capacity, the model could serve as a means for comparing competing theories regarding the origin of observed patterns in song types, measuring the strengths of various factors in the relevant mechanisms, and identifying the sources of various deviations from the main predictions of the model. This is not to suggest that such models might serve as substitutes for field testing when it comes to evaluating competing theories, but rather that they may offer additional resources for making such evaluations – for example by offering a means of narrowing down what sorts of field observations might be most fruitful to pursue.

Future Directions

I have argued elsewhere that high-level theoretical defenses of the viability of cultural selection theory should be suspended until further empirical observations are identified. This empirical support must include case studies that provide compelling and tractable examples of cultural adaptations by the mechanism of Darwinian selection on cultural units. In particular, these case studies must provide a better understanding of the crucial relationship between culture and environmental selection pressures. The acoustic adaptation of the songs of the Rufous-collared Sparrow shows potential to serve as a such case study since it can clarify the role of environmental interaction in cultural evolution. Importantly, spatial Game Theoretic models such as 'Singing to Neighbors' have the potential to reveal the details of the mechanisms responsible for the observed correlation between song-type and habitat-type in these natural populations.

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