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OVERVIEW

A NEW SENSE OF THE COMPLEXITIES OF BIRD SONG

R. HAVEN WILEY¹

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA

SINGING BIRDS are so familiar to most of us that the astounding complexity of their feats is often overlooked. Two articles in this issue of *The Auk* serve to remind us how little we understand or even recognize this complexity.

The Nightingale Wren (*Microcerculus philomela*) of Central American forests, as Leger and his colleagues (2000) make clear, needs no special pleading to qualify as a source of wonder. This species produces one of the longest regularly repeated patterns of all bird songs. Most tropical ornithologists have assumed that these birds simply produce random sequences of notes. It turns out, however, that we have just not paid enough attention, because they actually produce a stereotyped sequence of haunting tones that can last nearly 15 seconds before repeating.

A Nightingale Wren does not sing its entire song each time, but instead often interrupts its pattern. Apparently, these interruptions do not tend to occur at particular places in the sequence. Such weak links in a prolonged sequence of notes might indicate that the sequence was organized in chunks in the bird's brain in much the same way that human songs are arranged in stanzas (Hultsch and Todt 1989). By singing songs that can end in many ways and by shifting the pattern in pitch, Nightingale Wrens turn their single pattern into a large repertoire of sorts.

Despite their length, the songs of Nightin-

gale Wrens do not include an unusual number of notes, no more than 32. The record for numbers of notes in a stereotyped pattern might well go to some species of lark or longspur, or some other open-country bird whose songs often include scores of different notes.

Somewhere in the middle falls the Song Sparrow (*Melospiza melodia*). What we learn from Peters and her colleagues (2000) is that the size of an individual Song Sparrow's repertoire for both songs and notes varies among populations in a consistent manner. In two migratory populations in Pennsylvania and Maine, individuals have significantly smaller repertoires than in two sedentary populations in North Carolina and Washington, both in songs and in notes (or MUPs, minimal units of production, the term used among melospizologists). As the authors mention, the pattern of larger repertoires in sedentary than in migratory populations recurs in other North American species as well. Evidently, differences in repertoire size among populations depend more on the differences in migratory status than on probable genetic differences.

What can we make of the complexities in the structure of passerine song and of the variation in songs among individuals and populations? These complexities raise ontogenetic issues about how song is learned and evolutionary ones about how song is used in communication. On both scores, research in the past few years has reoriented our thinking about the possibilities. Here, I take the opportunity to review these developments, with emphasis on research

¹ E-mail: haven_wiley@unc.edu

published in the past few years or that, to my mind, merits more attention than currently received.

COMPLEXITIES IN THE ONTOGENY OF SONG

All oscine passerines, so far as we know, rely partially on learning to acquire their adult repertoire of songs. The final adult repertoire, however, is the result of some surprises recognized only recently. At least in some species, young birds learn far more songs early in life than they use as adults (Nelson and Marler 1994, Marler 1997). This "over-learning" is revealed in the production of song patterns during plastic song, the "babbling" that precedes full crystallization of adult songs early in the breeding season. During this relatively neglected stage of learning, young birds choose which songs to retain in their adult repertoires, often by learning which ones match songs of territorial rivals. Song learning thus involves two quite different and often temporally separate processes: instructional learning early in life, when young birds memorize patterns for subsequent imitation, and performance learning in their first breeding season, when they selectively incorporate only a fraction of these patterns into their adult repertoire.

Recognition of these two types of learning has led to the discovery of remarkable differences among populations of the same species. The different subspecies of White-crowned Sparrow (*Zonotrichia leucophrys*), it turns out, differ in the expression of these two types of learning in a consistent way. Migratory subspecies, such as those along the Pacific Northwest coast or in the Sierra Nevada, "overproduce" to a greater degree than do the sedentary populations along the California coast (Nelson et al. 1995, 1996). Perhaps greater overproduction gives young birds greater choice in finding a suitable match to neighboring rivals when natal dispersal covers greater distances. Nevertheless, the subspecies with the longest migration, subarctic *Z. l. gambelii*, has the shortest sensitive period for early learning, and each individual appears to choose its final song at random from those overproduced in their first spring, without reference to neighbors' songs (Nelson 1999). Apparently, the short breeding season at high latitudes favors short instruc-

tional and performance phases of learning and a consequent loss of sharing among neighbors.

Could something similar explain differences in repertoire size and sharing in species like the Sedge Wren (*Cistothorus platensis*)? In this species, sedentary tropical populations develop smaller repertoires, share many of their songs with neighbors, and use these shared songs for matched countersinging, whereas the nomadic temperate populations develop larger, unique repertoires with no signs of sharing or matching between rivals (Kroodsma et al. 1999a, b).

The remarkable case of the Black-capped Chickadee (*Poecile atricapilla*) provides a stark contrast. This species manages to maintain a uniform pattern of songs in nearly all populations across the breadth of North America. Like Nightingale Wrens, individual chickadees shift the pitch of this pattern but not the arrangement or timing of notes (Horn et al. 1992). Although occasional irruptions of birds in winter and attendant dispersal of young males presumably contribute to uniformity among populations (Kroodsma et al. 1999c), the continent-wide consistency nevertheless must still hold some secrets. Even irruptive dispersal in chickadees seems unlikely to prevent cultural drift across the width of a continent. Nevertheless, isolation of populations radically changes the process of song development. A few populations of Black-capped Chickadees on islands off of Massachusetts and in western mountains have song repertoires partly shared with neighbors and have distinct dialects even within small islands.

This new wealth of information on variation within and between populations shows how hard it is to find simple answers for the complexities of bird song. Wide dispersal of young birds can promote uniformity among populations as a result of performance learning early in their first breeding seasons, but perhaps only up to a point. In sedentary populations, or those with short-range migration, performance learning perhaps can maintain uniformity. In long-range migrants and nomads, like Gambel's White-crowned Sparrows, migratory Song Sparrows, and North American Sedge Wrens, the possibilities for learning have perhaps been exceeded, so birds must develop their songs by improvisation or innovation.

Within a population, an individual's repertoire is likely to be influenced by nutritional

conditions early in life during the sensitive phase for learning (Nowicki et al. 1989). Scarce food could have a direct result on the development of the brain, but it also could have an indirect one as a result of more attention to food and less to teachers. Might this source of variation in repertoires explain some of the differences between migratory and sedentary populations?

Subtle variation in each pattern influences song learning as well. We know that young birds learn more from tape recordings of naturally variable songs than from invariant ones (Nowicki et al. 1999). As Peters et al. (2000) show, individuals in migratory populations have less variation in song patterns than do those in sedentary populations, with possible consequences for learning.

All of this new information about the development of differences in repertoires across individuals and populations tends to emphasize more than ever the interaction between genetic and environmental influences on complex learning. Although individual birds accomplish almost incredible feats of learning, it is also clear that this learning is innately channeled in quite different directions in different populations. No doubt, many intricacies of this gene-environment interaction remain to be discovered.

EVOLUTION OF COMPLEXITY BY SEXUAL SELECTION

The evolutionary questions posed by all of this complexity present challenges to our current understanding of how communication evolves. The complexities of songs result from comparable complexities of syringeal and neural structure and function. It is probably not an exaggeration to propose that the complexity of adaptation for song in passerines matches or surpasses that for plumes and trains of birds-of-paradise and peacocks. Almost everyone would agree that sexual selection can explain the evolution of elaborate plumage. Is the same true for the songs of passerines? Are bird songs vocal "plumes"?

Several studies have documented that individuals with larger repertoires have higher survival or reproductive success, as we would expect if females choose high-quality mates. In what has already become a classic study, male

Great Reed Warblers (*Acrocephalus arundinaceus*) with larger repertoires obtain more extra-pair copulations and have more surviving offspring than those with smaller repertoires (Hasselquist et al. 1996). Other recent studies have shown that Song Sparrows in California are more likely to survive the winter if they have larger repertoires (Wilson et al. 2000) and that Sedge Warblers (*Acrocephalus schoenobaenus*) with larger repertoires not only mate earlier in the season, they have stronger immunological defenses against hematzoan parasites and provide more food for their young (Buchanan et al. 1999). If nutrition early in life affects adult repertoire size, as mentioned above, then a larger repertoire might indicate genes for more effective parenting or greater competitiveness.

Nevertheless, it has proven surprisingly difficult to obtain clear evidence that these differences among males directly affect female preferences. It is possible to explain the results for Great Reed Warblers, for instance, as direct consequences of higher-quality males obtaining better territories. Of course, the differences among males in mating success could result from *indirect* mate choice by females, rather than from *direct* preferences (Wiley and Poston 1996). By their preferences for particular microhabitats, females might set conditions for competition among males and thereby indirectly obtain high-quality mates.

The most compelling evidence for effects of repertoires on female preferences is from studies of captives implanted with estrogen. When presented with taped songs, females often respond more consistently with copulatory-solicitation displays to repertoires than to repetitions of a single song type. Most striking, female Common Grackles (*Quiscalus quiscula*) and Zebra Finches (*Taeniopygia guttata*) show this preference even though individual males sing but one song type (Searcy 1992, Collins 1999). This might indicate "sensory bias" in female preferences, or it might represent an adaptation to the stimulation of a colony, because Common Grackles and Zebra Finches often nest in colonies in which many individuals would easily be heard singing.

The relationship between an isolated female's behavior in a sound-attenuating compartment and her behavior in the complex natural environment where mate choice actually occurs is

problematic. I return to this point below, but it is reassuring that a recent experiment has demonstrated how sensitively this assay can reveal subtleties in a female's responses. In particular, an estrogen-implanted female Song Sparrow reveals preferences for her mate's and nearby males' songs over the songs of other males (O'Loghlen and Beecher 1999). Only two previous studies have demonstrated that females discriminate among the songs of individual males (Wiley et al. 1991, Lampe and Slagsvold 1998).

COMPONENT PROPERTIES OF COMPLEXITY

The hypothesis that complexity in song has evolved primarily to promote mate attraction assumes that the size of a repertoire or the number of notes in a song is a collective property. The relevant parameter is not so much *which* song or note a male chooses as *how many*. A difficulty with any such idea is that many passerines do not sing in a way that readily reveals their repertoires, as we might expect if the collective properties of repertoires were used for assessment or mate attraction. Why, for instance, do Nightingale Wrens spend 15 seconds producing a complete song, and more often than not fail to finish it before starting over? Why do so many birds sing with eventual variety rather than immediate variety? They seem to be hiding their talents under a bushel. If repertoires are a signal for assessment, it is hard to imagine an advantage in forcing a listener to take longer to make a decision. Listeners should demand immediate variety, and singers should comply.

The general alternative to the collective properties of repertoires is their component properties. Perhaps not only the overall variety, but the specific kinds of songs used, can make a difference. Song, in some species, has some attributes of a rudimentary "vocabulary" in that different song patterns indicate different states of the singer. For instance, many wood-warblers sing in two different modes (Spector 1992, Wiley et al. 1994). These might serve to address different recipients (e.g. potential mates and rivals), or they might serve different communicatory situations (e.g. short- and long-range interactions). The Louisiana Waterthrush (*Seiurus motacilla*) responds to territorial intrusions with a more complex song than used in

routine territorial advertisement (Smith and Smith 1996). Male Dark-eyed Juncos (*Junco hyemalis*) also have two distinct modes of singing. In juncos, these modes correlate with distance between interacting individuals, whether potential mates or rivals, rather than with the kind of interactor (Titus 1998). These alternatives for context-dependent use of songs suggest that different songs in repertoires sometimes convey different information in the sense that they correlate with different states of the signaler and thus possibly evoke different responses from listeners.

COMPLEXITIES IN RECOGNITION OF SONG

One way that complex songs might serve to transmit information over long distances is by identifying individuals. We humans tend to take individual recognition for granted. This dismissal is so thorough that no literature is devoted to human capabilities for individual recognition (in contrast to a large one on the cues used), yet surely our abilities to archive and access the identities of perhaps thousands of distinct individuals rivals our ability to master vocabulary. Our ability to track the complex relationships among many individuals rivals our grammatical abilities.

For the student of bird song, the most unfortunate consequence of the tendency to dismiss individual recognition is the widespread impression that it needs no explanation. Even many ethologists intuitively feel that there is nothing much to explain: "Of course animals recognize each other. Why wouldn't they?" Indeed, most experiments on individual recognition of mates, offspring, parents, and neighbor do not pose much of a cognitive challenge, because they ask subjects to make only binary distinctions between one individual (or set of individuals) and all others. More impressive is an ability to form distinct associations with a number of other individuals. The clearest evidence of such abilities in birds comes from demonstrations that some passerines singing complex songs can recognize more than two categories of "others," in particular their different territorial neighbors.

These experiments use playbacks of tape recordings to demonstrate that territorial birds respond less strongly to neighbors' songs, provided they are presented near the correct

boundary, than to neighbors' songs presented at incorrect boundaries. The coincidence that a "positive" result in these experiments corresponds to a decrease in response raises the possibility that location-specific habituation to neighbors' songs might provide the mechanism. Such contextual cues also might play a role in complex forms of human individual recognition. Nevertheless, at least one experiment long ago on Eastern Towhees (*Pipilo erythrophthalmus*) that had mistakenly learned another species' songs indicated that associative learning is in fact involved in birds learning their neighbors' songs (Richards 1979).

Recent experiments suggest that repertoires of modest size do not seem to impair individual recognition markedly. It seems inconceivable, however, that large repertoires would not make the task of discriminating individuals more difficult. One species with a large repertoire, the Red-eyed Vireo (*Vireo olivaceus*), so far has shown no signs of recognizing individual territorial neighbors (Godard 1994). More work remains to be done, however. A failure to show individual recognition is difficult to interpret, particularly because the "dear enemy" effect on which the experiments depend might not apply to all species equally (Godard 1994, Stoddard 1996). Although Godard found no evidence that Red-eyed Vireos are more likely to trespass on their neighbors' territories while singing than were Hooded Warblers (*Wilsonia citrina*), which do recognize individual neighbors (Godard and Wiley 1995), we need more study of this and similar species.

An advantage of recognizing the songs of rivals could arise from the possibility of tit-for-tat relationships among neighbors. Evidence suggests that neighboring males can realize mutual advantages by reducing their time spent on aggression (Beletsky and Orians 1989), one of the requirements for tit-for-tat cooperation. Another requirement, contingent behavior toward individual neighbors, has been demonstrated in Hooded Warblers in which the strength of a male's response to a neighbor near their territorial boundary depends on the immediately preceding behavior of the neighbor (Godard 1993). Encroachments simulated by playbacks within a subject's territory provoke intense reactions to the neighbor's songs near the boundary, where previously they had evoked little response. So far,

both of these requirements for tit-for-tat have yet to be demonstrated in a single species. We also need to confirm eventual "forgiveness," as would be expected following an isolated breach of trust.

Complex songs also must affect species recognition and thus the process of speciation. Of course, song patterns differ among species and often have helped systematists to recognize boundaries between morphologically similar species. Particularly among suboscines, subtle differences in songs often separate closely related species, as recently confirmed for thamnophilid antbirds (Isler et al. 1998). The complexity in songs of oscines must affect species recognition and individual recognition. For instance, in the hybrid zone between Lazuli (*Passerina amoena*) and Indigo (*P. cyanea*) buntings, a female's plumage correlates with the song of her mate, and adult females prefer conspecific songs and morphology (Baker 1996, Baker and Boylan 1999). We have yet to learn, however, whether a female's preferences result from learning songs like her father's or from channelization despite early exposure to both species' songs. Regardless of their preferences, some females evidently commit disadvantageous errors, an issue I pursue below. How song might affect gene flow between populations remains an open and crucial question.

COMPLEXITIES IN PROCESSING SONG STRUCTURE

An ability to recognize neighbors requires an ability to monitor the locations of singers by listening to them. Much recent work has confirmed that the structure of bird songs degrades in subtle but predictable ways during propagation through natural environments. Can birds put these slight changes to use? We have a reasonably clear understanding of the four possible kinds of degradation in complex sounds (decrease in overall amplitude, frequency-dependent attenuation, increase in reverberation, and increase in random amplitude fluctuations), each of which accumulates at different rates in forested versus open environments (Wiley 1991, MacGregor 1994). One of the clearest demonstrations of changes in a bird's song during propagation comes from work with Winter Wrens (*Troglodytes troglodytes*) in Eurasia (Holland et al. 1998). Some

studies of degradation during sound transmission are more difficult to interpret because they have used measures of degradation that have little relevance to the processing of sound by avian (or mammalian) ears, such as long (one-second) samples of sound (instead of durations comparable to a bird's temporal discrimination on the order of milliseconds) or general indices of degradation that conflate the four kinds of physical change in sounds.

We intuitively associate the overall attenuation of sound with distance, although we can hear the other kinds of degradation just as well. Consequently, the earliest experiments on distance discrimination controlled for overall amplitude to determine whether birds might use any of the other cues. Recent evidence shows that birds can use reverberation or frequency-dependent attenuation, in addition to overall amplitude, to range songs (Naguib 1995). Presumably, they can do best when all cues are available at once. Furthermore, birds can recalibrate these cues when the acoustic properties of their habitats change from season to season. Recently, we learned that passerines make continuous quantitative judgments of distance, not just rule-of-thumb categorizations (Naguib 1996, 1997; Nelson and Stoddard 1998; Naguib et al. 2000).

On the other hand, the suggestion that a bird must actually incorporate a song pattern into its repertoire to be able to discriminate the fine features used for ranging (Morton 1986) has not received experimental support. Even Kentucky Warblers (*Oporornis formosus*), a species in which each individual sings a single unique long-range pattern, does as well as any other species so far studied in ranging experiments (Wiley and Godard 1996). The general properties of sound degradation during propagation allow birds to range songs, at least coarsely, even when they have not heard the specific pattern before (Naguib 1997, Morton et al. 1998). Familiarity with a song pattern is, nevertheless, likely to improve performance.

Despite sophisticated capabilities for ranging, it is difficult to believe that complex repertoires of song would not impair this ability. Morton's original suggestion that birds have evolved large repertoires in part to disguise their locations while singing (Morton 1986) might still have merit, even if we reject the specific mechanism he proposed. Yet, if song

serves to attract mates or extrapair partners, how could it be advantageous to disguise the singer's location?

COMPLEXITIES IN DETECTION OF SONGS

One issue still generally neglected in studies of animal communication, including bird song, is error by receivers. Signal detection theory and decision theory, as developed some 40 years ago, have just as fundamental implications for animal communication as they do for other forms of communication (Wiley 1994). The essential conclusion is that communication in noisy conditions has some properties that differ markedly from communication in ideal noise-free conditions. In particular, receivers face inescapable tradeoffs between two kinds of errors: false alarms and missed detections. Noise in this context includes any possibility for confusion by a receiver between the occurrence or nonoccurrence of a signal (or between two different kinds of signals). It can result from degradation of signals during propagation, from background energy produced by similar species or other sources, or from limitations of a receiver's sense organs and nervous system. When noise is a factor, it is impossible for a receiver simultaneously to minimize its chances of false alarms (responding when the appropriate signal has not occurred) and missed detections (failing to respond when the appropriate signal has in fact occurred). Consequently, receivers inevitably face tradeoffs in setting their thresholds for response. The upshot is a prediction that receivers might often evolve one of two contrasting adaptations: *adaptive gullibility*, or *adaptive fastidiousness* (Wiley 1994, 2000).

Recent theoretical studies have begun to incorporate the possibility of receiver errors in strategic modeling of evolutionarily stable strategies (Johnstone 1994, 1998). So far, models have not included contingencies among the four possible outcomes of any communicatory interaction as required by adopting the full implications of signal detection. This objective remains a challenge. Perhaps new attention in the next decade to the possibilities and consequences of noise and errors in communication will spur these developments. How much do we know, for instance, about how females choose mates under the noisy conditions in na-

ture? Signal detection theory suggests that it might differ fundamentally from the way choices are expressed in ideal conditions.

CONCLUSION

The two reports on bird song in this issue of *The Auk* and other recent papers leave us with a renewed realization of the complexity of communication by singing birds and their listeners. Yet, none of the theories of the evolution of this complexity seems to provide a compelling general explanation, either for acoustic "plumes" or for "vocabularies." Are passerine songs sexually selected ornaments for assessment? Are they complex systems of information exchange? Of course, it is tempting to conclude that whatever cannot be explained in one way might be explained in the other. Complexity is inherently difficult to investigate. No doubt, however, the coming years will continue to reveal further subtleties in one of nature's true marvels.

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