

## Vocal Communication in Birds

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### Introduction

Studies of vocal behavior in birds have made central contributions to animal behavior and the neurosciences. A well-known body of research has built on the discovery that vocal production in birds, particularly songbirds, is underpinned by an elaborate, hierarchical array of song nuclei distributed throughout the brain. Elucidation of the 'song system' has proceeded apace, powered by a host of methodological advances including *in vivo* single-cell recording, *in vitro* recordings from brain slices, selective lesioning, and neuronal tracings. The specialized nature of the song system for vocal production is exemplified by two key observations: the neural morphology of the song system varies seasonally, in a manner that corresponds to variation in vocal output, and in species in which males sing but females do not, song system nuclei are comparatively reduced in females. Studies of the avian vocal system continue to provide key insights into neural mechanisms of motor control.

This entry focuses on three additional, complementary lines of research in the avian vocal system that hold particular relevance for the neurosciences:

- The vocalizations of some bird groups, including songbirds, hummingbirds, and parrots, develop through imitative learning, in a manner that parallels speech acquisition in humans. Vocal learning in songbirds is now known to be mediated by a specialized neural pathway, the anterior forebrain pathway, the development of which depends on birds' auditory experiences. A 'developmental stress' hypothesis suggests that learned song can provide a reliable indicator of a male's neural developmental history and that females may thus use vocal parameters to assess the quality of prospective mates. Experimental studies with hand-reared birds illustrate a previously unrecognized axis of plasticity in sensorimotor development, in which birds faced with physical limits on vocal model reproduction can calibrate their 'targets' of learning.
- Vocal production entails extensive use of peripheral mechanisms. The vocal acoustic source, the syrinx, is dynamically coordinated with activity of the respiratory and vocal tract motor systems. Rapid and precise modulations in breathing patterns are

required for the production of intricate vocal timing patterns, and modulation of vocal tract configuration during phonation enables birds to adjust vocal tract resonances and thus the spectral properties of song. It is not yet clear how birds manage to coordinate these multiple motor systems in vocal production, in terms of both neural control and its development. Limits on vocal performance, associated in particular with peripheral systems of vocal production, have been shown to constrain the production and evolution of certain vocal parameters.

- The biological function of birdsong has been examined with vocal playback studies, which are providing new insights into birds' perceptual and recognition abilities. Field playback tests have been conducted primarily with territorial males, in which vocal stimuli are presented to simulate territorial intrusions. Laboratory playback tests have been used to test birds' perceptual capabilities and limitations, and the preferences of females for different vocal stimulus classes. In conjunction with analyses of vocal variation, these studies are helping to specify the role of song in species recognition. 'Interactive' playback studies are helping researchers assess how birds modulate vocal output to convey varying levels of aggressive intent.

### Vocal Learning

Songbirds learn to sing using a diversity of learning strategies or 'programs.' As with human speech development, vocal imitation in birds includes sensory and sensorimotor phases. During the sensory phase, birds memorize song models to which they are exposed. The sensorimotor phase, defined by transitions of vocal output from babblelike 'subsung' to crystallized adult forms, is mediated by comparison of vocal output to memorized song models via auditory feedback. During this phase, birds develop general proficiency with the vocal apparatus, as well as proficiency in the reproduction of memorized song models.

Species vary considerably in the timing of closure of their sensitive phases of song acquisition, in innate tendencies to memorize species-specific song stimuli, and in the relative impacts of social interactions on song model development. Within-species studies have proven especially beneficial in addressing the evolutionary causes of diversification in learning programs. The most comprehensive such studies to date have focused on white-crowned sparrows. Some populations of this species engage in long-distance migrations, whereas others remain essentially sedentary

throughout the year. Migration tendencies in white-crowned sparrows have now been shown, in both laboratory and field studies, to correlate with at least three aspects of song learning programs. First, migratory birds tend to experience earlier closure of the sensory phase of song learning. Second, birds from migratory populations tend to memorize more song types than do their sedentary counterparts, as revealed in vocal output during the initial stages of sensorimotor learning. Third, migratory populations show more evidence of 'selective attrition' during the sensorimotor phase of song learning; that is, they retain only a subset of previously memorized models. Interpopulation differences in learning programs enable birds from across the spectrum of migratory tendencies to crystallize song types that are shared by neighboring territorial rivals; as such, this diversity in learning programs may facilitate aspects of song function (see the section titled 'Song function'). In addition to highlighting ecological correlates of song learning, these data raise interesting new questions about the hormonal and neural bases of diversity in song learning programs.

Another recent body of research on vocal learning in songbirds focuses on the potential impacts of phenotypic condition on song learning and development. This work is motivated in part by advances in sexual selection theory, which posits that mating signals such as bird songs should evolve to provide accurate, reliable indicators of male genetic and phenotypic quality. Female choice of mates in many animals is informed by male signaling behavior. Females presumably evolve to attend to signal features that honestly and reliably reflect male quality because of the enhanced reproductive fitness of females that choose higher-quality mates. To explain the putative link between male quality and signal evolution, evolutionary biologists often refer to the so-called 'handicap' principle, which posits that high costs in signal production or expression enforce the honest and reliable nature of signaling. In this context, a stated goal of many current studies of mating signal evolution is to elucidate their underlying metabolic, developmental, and fitness costs.

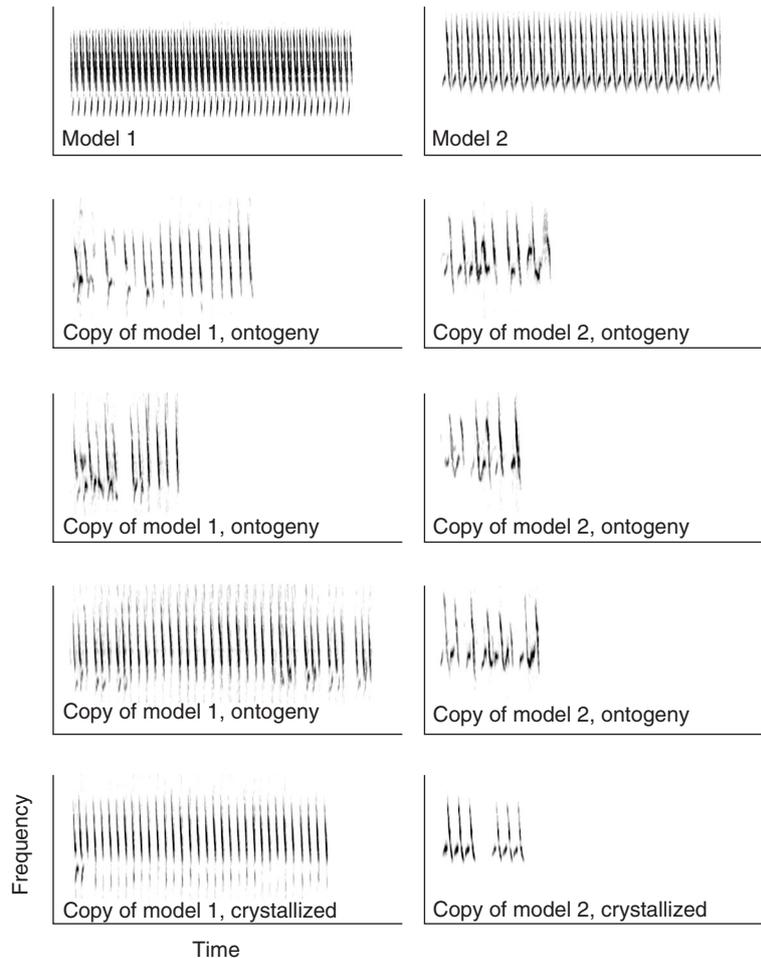
Bird vocalizations are a promising system for studies of signal costs, given the elaborate neural and motor mechanisms that underpin vocal expression and development. Available evidence suggests that vocal production in adult birds requires only minimal increases in metabolic output above and beyond basal metabolic rates. However, accumulating evidence suggests that during vocal development, birds do face significant costs associated with stresses incurred during birds' early months of life. Young birds may suffer developmental stress from numerous sources,

including insufficient nutrition, parasite infection, and trials of thermal regulation. Recent experimental work indicates that developmental stress can indeed interfere with the acquisition and expression of certain song features. Canaries infected with malaria at a young age and zebra finches reared under conditions of stress were found as adults to produce smaller song repertoires and smaller syllable repertoires, respectively. Swamp sparrows reared with restricted access to food copied song model notes less accurately than did birds reared with *ad libitum* access to food.

Degradation of vocal imitation abilities caused by developmental stress would likely be caused by subpar neural growth and development. Consistent with this hypothesis, the volume of the higher vocal center (HVC), a telencephalic song nucleus, was found to be significantly diminished in canaries reared under developmental stress compared with HVC volume in control birds. Similar results have been reported for zebra finches and swamp sparrows, although for the latter species, another song nucleus, the robust nucleus of the archistriatum (RA), suffered the greatest impact under conditions of developmental stress. These results are broadly consistent with comparative studies showing positive correlations between song nuclei size and song or syllable repertoire size. Males that suffer from only limited developmental stress would theoretically be able to devote more metabolic resources to developing larger song nuclei, and thus to developing larger song repertoires.

The evolutionary relevance of developmental stress can be tested by assessing, using song playback, the functional impact of variation in song features affected by developmental stress. In one such test, wild-caught female song sparrows were presented with songs recorded from males that had been imitated either with high accuracy or with poor accuracy. The dependent variable in this study was the copulation solicitation display, a behavioral pattern that normally precedes copulation in the wild and is thus regarded as a valid indicator of female song preferences. Subjects in this study displayed more often to playback of songs that had been learned with high accuracy. In a similar experiment, female zebra finches were shown to significantly prefer the songs of males that had been reared in a nonstressed environment over songs from males reared with nutritional stress. Available data thus provide increasingly strong support for the developmental stress hypothesis.

Studies of song learning have also revealed that birds can adjust the targets of song learning during sensorimotor development. Birds normally reproduce, with impressive accuracy, song models they had memorized previously. However, under some



**Figure 1** Sensorimotor calibration of song learning targets in swamp sparrows. Each column shows a song model (top row), a crystallized copy of the model (bottom row), and three ontogenetic intermediaries of those models produced during sensorimotor development. Song models featured trill rates manipulated to exceed natural trill rates. The bird in each example is observed to ‘experiment’ during ontogeny with potential motor solutions in reproducing manipulated song models. In the first column, the bird is seen to attempt but eventually fail to integrate the low-frequency notes of the model into the crystallized song (with the exception of the opening syllables). In the second column, the bird is seen to experiment with varying trill rates and reduced frequency bandwidths before settling on the ‘broken’ syntax that was eventually crystallized. X-axis scale, 0–2.5 s; y-axis scale, 0–8 kHz. Reproduced from Podos J, Peters S, and Nowicki S (2004) Calibration of song learning targets during vocal ontogeny in swamp sparrows. *Animal Behaviour* 68: 929–940, with permission.

circumstances, birds may face performance limitations in the reproduction of certain vocal parameters. For example, some song features may be situated near the limits of a species’ production capacities, or some birds may develop generally poor proficiency in vocal learning and reproduction because of developmental stresses. Young swamp sparrows reared with artificially manipulated song models, in which trill rates were elevated above natural rates, showed flexibility during sensorimotor learning in the reproduction of these rapid models. Memorized model targets were calibrated, over the course of sensorimotor learning, to better match birds’ motor performance capacities (Figure 1). These data support ‘active’ models of song

learning and sensorimotor development and suggest that the song-learning template retains plasticity through sensorimotor development even for birds with closed-ended memorization programs.

### Peripheral Mechanisms of Vocal Production

Research on the neural bases of vocal behavior has traditionally focused on the nature and architecture of connections that descend to the brain stem and ultimately to the syrinx, the sound source. More-recent studies have started to evaluate the contributions in vocal production of the respiratory system

and the vocal tract. Above and beyond interest in questions about vocal mechanics, this work is motivated by evidence that peripheral mechanisms can delimit the range of vocal behaviors that can be expressed and thus evolve.

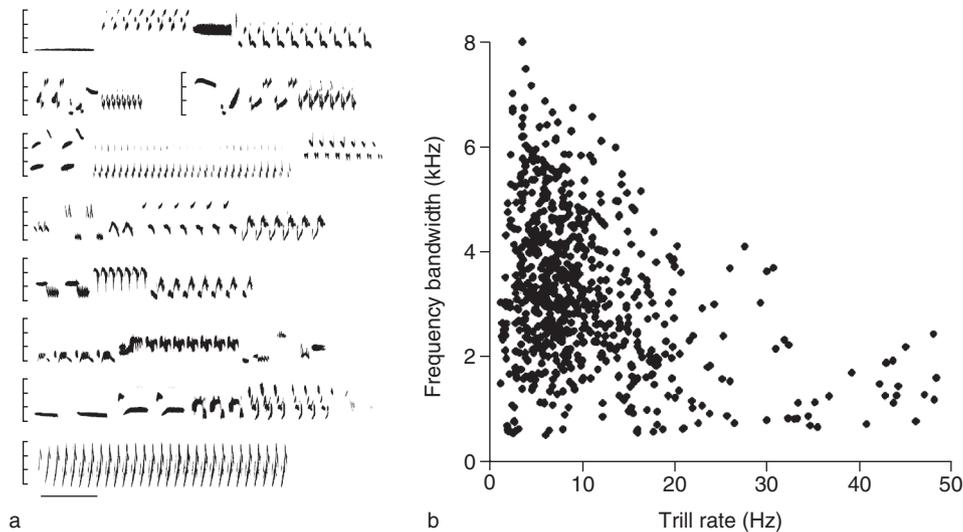
The temporal features of vocalizations can be shaped by dynamics of respiratory ventilation. In recent studies, respiratory and syringeal motor output was monitored in vocalizing birds by means of surgically implanted microbead thermistors and pressure transducers. One finding of this work is that birds vocalize almost exclusively during respiratory exhalations; by contrast, birds generally do not phonate during respiratory inspirations. As birds breathe out, airflow across the syrinx induces syringeal tissues to vibrate and thus produce sound. Patterns of breathing help define the structure of vocal trills, in which one or more notes (syllables) are repeated in rapid succession. For trills with slow to moderate rates of syllable repetition, birds employ a 'minibreath' motor strategy, with each respiratory expiration followed by a respiratory inspiration. As such, birds are able to maintain a steady tidal volume of air and thus produce trills of extended duration. For the production of more-rapid trills, however, birds appear to switch to another motor program, 'pulsatile' respiration, in which the tidal volume of the singing bird is rapidly depleted through expirations only. In a recent study, mockingbirds were presented with recordings of canary trills, with syllable repetition rates of 20 Hz and of extended duration. Mockingbirds that attempted to mimic these trills proved unable to reproduce them accurately, presumably as a result of performance limitations in their respiratory dynamics. More specifically, mockingbirds reproduced the rapid trill models using pulsatile rather than minibreath respiration, and resulting trills featured 'broken' syntax in which multisyllable segments were separated by pauses. Broken syntax had been observed previously in young swamp sparrows trained with trilled song models in which trill rates had been artificially elevated (e.g., [Figure 1](#), right column).

The vocal tract, which includes the trachea, glottis, tongue, and beak, also affects song expression. The vocal tract acts as a resonance filter of sound produced by the syrinx, as first demonstrated in a study of birds that sang in an experimental helium-enriched environment. Vocalizations produced in this environment included harmonic overtones that would not otherwise have been expressed. These results indicate that the tonal quality of song is shaped by resonance properties of the vocal tract. Recognition of an acoustic function for the vocal tract helps explain the evolution of unusually elongated trachea in a wide diversity of birds including cranes, swans, curassows, and geese.

In songbirds, song production often includes rapid reconfigurations of the vocal tract. High-speed video recordings of several species of sparrows and finches indicate that changes in beak gape co-occur with temporal changes in vocal fundamental frequency. This observation concords with a resonance model of vocal tract function: wider beak gapes effectively shorten the volume of the vocal tract, thus providing a more appropriate resonance filter for high-frequency sounds. Performance constraints in vocal tract modulation have been offered as an explanation for an observed trade-off between two vocal parameters, trill rate and frequency bandwidth, in the evolution of trills in emberizine finches and sparrows ([Figure 2](#)). Rapid trill rates require rapid vocal tract modulations, and wide frequency bandwidth production requires broad vocal tract modulations. Because of a trade-off in the rapidity versus the breadth of vocal tract modulations, trills beyond a certain rate can presumably be accompanied only by vocal tract modulations of narrow breadth. Similar trade-offs between trill rate and frequency bandwidth have now been described in other taxa, including blackbirds, wrens, and warblers.

Recognition of the beak's contribution to vocal production has suggested a previously unrecognized mechanism of vocal evolution. Birds are known for diverse adaptations of their beaks, as they have occupied diverse feeding niches. Evidence now suggests that the evolutionary diversification of beaks can invoke incidental consequences on the evolution of song structure. In particular, a 'vocal tract constraint' hypothesis predicts that birds with comparatively large beaks, adapted for crushing hard seeds, should suffer comparatively severe constraints on vocal performance because of biomechanical trade-offs between the force and speed of beak gape modulations. Support for this hypothesis comes from studies of several bird groups, including Darwin's finches of the Galápagos Islands, Ecuador. Analysis of song structure from birds with different beak morphologies, both across and within species, reveals differences in expressed 'vocal performance' that are consistent with the vocal tract constraint hypothesis ([Figure 3](#)). As birds adapt to new habitats, adaptations of the beak may thus drive secondary changes in song structure.

Because song is used in mate and species recognition, beak adaptations and subsequent evolutionary changes in song may facilitate reproductive isolation and speciation. This hypothesis is supported by field studies of a population of medium ground finches at *El Garrapatero* on Santa Cruz Island, Galápagos. This population features two discrete beak-size morphs, with small-beaked birds producing songs with consistently higher



**Figure 2** (a) Songs of eight North American Emberzine sparrows, illustrating the diversity of songs that can be expressed even among closely related species. Each of these songs contains trilled sequences, which can be characterized in part by trill rate (the rate of syllable repetition) and frequency bandwidth (the range of fundamental frequencies expressed over the course of the trill). This horizontal scale bar is 0.5 s, and y-axis spans 2–8 KHz. (b) Plot of trill rate versus frequency bandwidth for 740 trilled sequences across 34 species from the family Emberizidae. Triangular distributions evident for the family (here) as well as for individual species and genera support a vocal tract constraint hypothesis. (a, b) Reproduced from Podos J (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51: 537–551, with permission from Blackwell publishers.

levels of vocal performance. Differences in the songs of small- and large-beaked birds can be detected by both ornithologist and finch, the latter as indicated in playback studies to territorial males. Female Darwin's finches generally choose mates based primarily on song structure, and preferences for morph-specific songs in the *El Garrapatero* population presumably explain observed patterns of assortative mating and incipient genetic divergence among morph types.

## Song Function

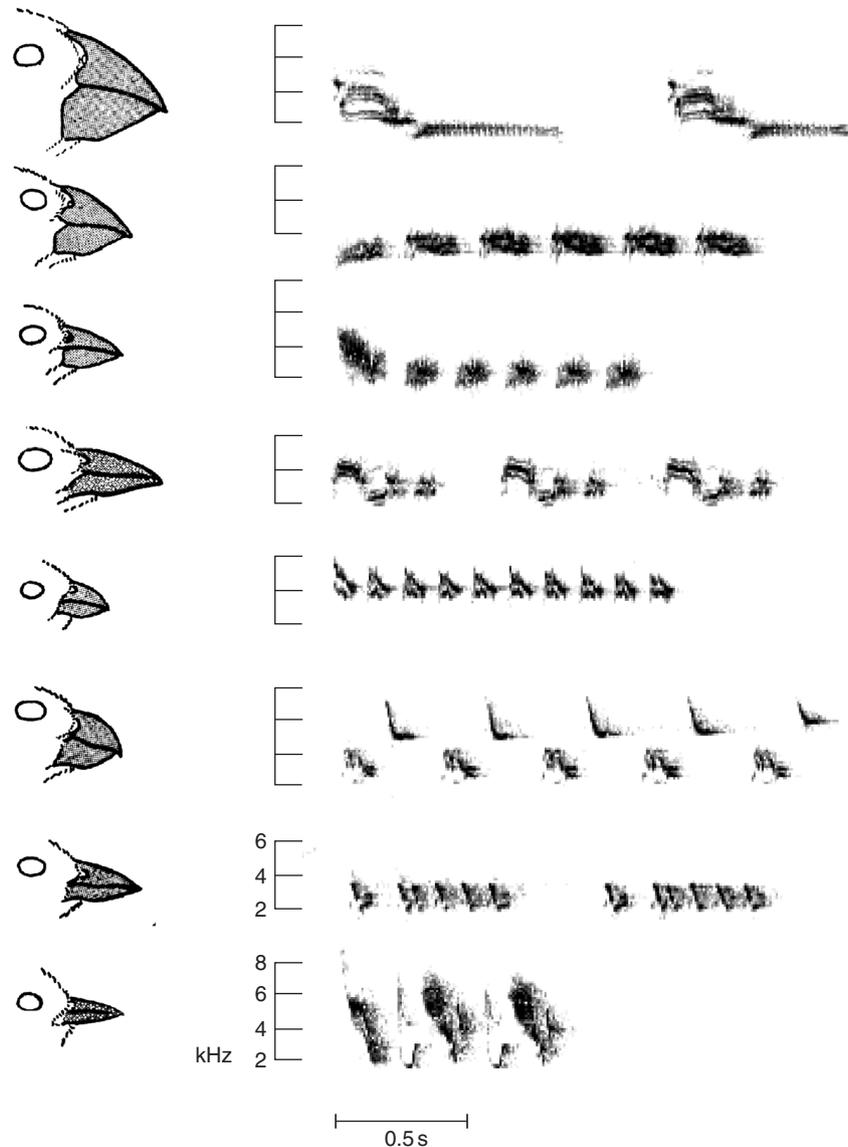
### Species Recognition

Birds sing mostly to communicate with individuals, such as potential mates or rivals, of their own species. For song to function in this way, individuals must have the ability to recognize the songs of their own species and to differentiate such songs from those produced by heterospecifics. Songs indeed have diverged markedly among species, to the extent that most species produce songs that can be considered 'species-specific.'

Interspecific divergence of songs is thought to be driven largely by selection against hybrid (cross-species) mate selection and offspring production. Males that produce species-distinctive songs, and females that are able to successfully identify conspecific songs, will be more likely to achieve conspecific matings and thus avoid costly hybrid matings. Thus the production

and recognition of species-distinctive songs should propagate along distinctive trajectories in different songbird lineages. Support for this 'sound–environment' hypothesis has been garnered from studies showing that species living in proximity, especially those that are closely related, tend to evolve songs that occupy distinct positions in 'acoustic space,' defined by dimensions of song structure. A recent study of neotropical antbird songs provides strong support for the sound–environment hypothesis. This study evaluated song similarity within nine species trios, each representing a genus of the antbird family Thamnophilidae. Each trio was comprised of a focal species, a closely related species living in sympatry (at the same location as the focal species), and a closely related species living in allopatry (at a different location from the focal species). Across all nine trios, the songs of allopatric species pairs were found to be significantly more similar than songs of sympatric species pairs. This finding suggests a recent history of independent song divergence events within sympatric species, presumably caused by selection favoring the evolution of species-specific song production and song recognition abilities.

Compared with song features that vary among individuals, song features that do not vary within a species ('invariant' features) presumably serve as reliable species identification signals. This is especially true for invariant features that are clearly distinct (i.e., have little structural overlap) from songs of



**Figure 3** Beak morphology and representative song spectrograms from eight species of Darwin's finches. Interspecific variation is evident in both morphology and song structure. Each of these songs includes trilled segments. Birds with larger beaks, for which rapid gape modulations are comparatively difficult to achieve, tend to produce trills with lower trill rates and more narrow frequency bandwidths than the trills of their smaller-beaked counterparts. Reproduced from Podos J (2001) Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409: 185–188, with permission.

sympatric species. A recent study of field sparrows tested, using a series of playback trials, the functional significance of multiple invariant song features. Playback stimuli were synthesized in which single invariant features were modified, one at a time, to values outside of the species-typical range. Territorial males were then presented with a choice of modified and control (unmanipulated) songs. Males were found to approach speakers broadcasting control songs more often than speakers broadcasting modified songs, as expected. Follow-up trials were then performed in which test stimuli expressed modifications in all possible combinations of invariant features. These

trials enabled an assessment of feature 'weighting' in the perceptual salience of field sparrow song, with song frequencies ultimately shown to be the invariant song features of the greatest import.

### Song matching

The functional consequences of variation in song structure have traditionally been assessed using 'loop' playback studies, in which song stimuli are presented according to previously determined sequences and rates, for example as recorded in advance on a cassette tape taken to the field. With the advent of portable

computers and specialized software packages, however, it is now possible to 'interact' with focal birds by selecting a specific playback song from a set of available digitized stimuli. Interactive playbacks are allowing researchers to test hypotheses that before they could investigate only through correlative analyses.

A growing number of experiments using interactive playback focus on the question of how birds signal aggressive intent. In bird species with large repertoires, neighboring individuals often share subsets of song types. In such species, males engaged in territorial skirmishes can respond to rivals with song types that are either shared or not. According to theory, the degree to which birds match the song types of rivals may reflect levels of aggressive intent. This theory has now been supported by an experiment with song sparrows that used interactive playbacks. Territorial male song sparrows were found to escalate their levels of response when they received playback of song types similar to the ones they had been singing, compared with their response to playback of non-matching song types. Matching can also occur for other vocal parameters. Black-capped chickadees were found to approach a playback speaker more closely and make more flights over the speaker when presented with songs in which the acoustic frequency of the stimulus closely matched frequencies of their songs, compared with their responses to playback of songs with different frequencies.

### **Song overlapping**

Studies of chickadees and other species have examined another type of aggressive signaling, termed 'overlapping.' Overlapping occurs when a bird begins to sing before another individual has completed its song. In some species, such as European thrushes, the efficacy of communication is more compromised in the overlapped bird than in the overrapper, given that the degree of information encoded in songs tends to increase toward the end of songs. Nightingales have shown intense responses to playbacks of overlapping song. When presented with songs from two speakers, one speaker that broadcast overlapping songs and one that did not, male nightingales responded more rapidly, more vocally, and with closer approaches to the speaker that broadcast the overlapping song. In an experiment that varied both frequency matching and overlapping, male chickadees were most agitated when presented with playback stimuli that both overlapped and matched the frequency of their songs.

### **Eavesdropping**

In most vocal interactions, individuals other than the intended receiver are able to overhear the signaling

individuals. In a series of studies on great tits, researchers showed that both males and females can use information gathered by eavesdropping to assess rivals or prospective mates. In one such study, researchers broadcast a simulated interaction of two 'virtual' individuals, unknown to the focal bird, in stereo over two speakers outside his territory. In this interaction, one of the two virtual individuals either switched song types (to match the other simulated individual or not) or continued to sing a single song type. The songs of this individual were subsequently presented to the focal bird. For the former condition, in which the virtual bird had matched song types during its earlier simulated interaction, focal birds responded more strongly than they did when virtual territorial intruders had not matched during simulated interactions. Thus it was shown that by eavesdropping, male great tits extract information about the level of perceived threat from potential rivals.

Another clever experiment addressed the topics of eavesdropping and song overlapping simultaneously by providing male great tits the opportunity to gather information from both direct and indirect interactions. Songs of a simulated intruder stranger male (X) were broadcast to focal territorial males. With the use of interactive playback, these songs were varied either to overlap or to alternate with a subject's songs. A simulated interaction between this intruder male, X, and another virtual, stranger male, Y, was then played outside the subject male's territory, with a different speaker for each bird. Male X was manipulated to either 'win' or 'lose' the interaction in terms of patterns of overlap. Finally a territorial intrusion by male Y was then simulated and the focal male's responses measured. If the subject male had been manipulated to 'beat' male X, and male X to 'beat' male Y, the subject tended to respond with less effort, fewer songs, and diminished approach to male Y, presumably because of diminished perceived threat. By contrast, in scenarios in which the threat level of male Y was ambiguous (if, for example, the subject was manipulated to 'beat' male X, but X subsequently lost to male Y) or the level of threat was high (if X beat the focal male, but Y subsequently beat X), subjects responded with significantly more songs and closer approaches to the speaker, presumably because of a comparatively elevated perceived threat.

Females presumably could also use eavesdropping to evaluate social mates or potential extrapair partners. In an experiment with great tits, focal males were presented with overlapping ('escalated') playback songs, but neighboring males were presented with de-escalated (fewer songs, with shorter phrases) playback songs. Females mated to males that

had received escalated playback (apparent 'losers') subsequently visited territories of neighboring males more often than did females whose males had received the de-escalated treatment (apparent 'winners'). This finding holds functional relevance because females might visit neighboring male territories to seek copulations from perceived higher-quality neighbors. In another experiment, female black-capped chickadees were found to engage in extrapair copulations with greater frequency if their mates had received aggressive, overlapping playbacks at an earlier time. These studies together provide new evidence of advanced perceptual and cognitive abilities in birds and suggest avenues for future studies that integrate neurobiological, psychological, and ecological perspectives.

*See also:* Animal Communication: Honesty and Deception; Bird Brain: Evolution; Bird Song Systems: Evolution; Birdsong Learning: Evolutionary, Behavioral, and Hormonal Issues; Birdsong Learning; Birdsong: The Neurobiology of Avian Vocal Learning; Signal Production and Amplification in Birds.

### Further Reading

- Beecher MD and Brenowitz EA (2006) Functional aspects of song learning in songbirds. *Trends in Ecology and Evolution* 20: 143–149.
- Huber SK, de Leon LF, Hendry AP, Bermingham E, and Podos J (2007) Reproductive isolation of sympatric morphs in a population of Darwin's finches. *Proceedings of the Royal Society B* 274: 1709–1714.
- Marler P and Slabbekoorn H (eds.) (2004) *Nature's Music: The Science of Birdsong*. San Diego, CA: Elsevier Academic Press.
- Mennill DJ and Ratcliffe LM (2004) Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour* 67: 441–450.
- Nelson DA (1988) Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* 106: 158–182.
- Nelson DA, Marler P, and Palleroni A (1995) A comparative approach to vocal learning: Intraspecific variation in the learning process. *Animal Behaviour* 50: 83–97.
- Nowicki S and Searcy WA (2005) Song and mate choice in birds: How the development of behavior helps us understand function. *Auk* 122: 1–14.
- Peake TM, Terry AMR, McGregor PK, and Dabelsteen T (2002) Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society of London B* 269: 1925–1929.
- Podos J (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51: 537–551.
- Podos J (2001) Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409: 185–188.
- Podos J, Huber SK, and Taft B (2004) Bird song: The interface of evolution and mechanism. *Annual Review of Ecology, Evolution and Systematics* 35: 55–87.
- Podos J, Peters S, and Nowicki S (2004) Calibration of song learning targets during vocal ontogeny in swamp sparrows. *Animal Behaviour* 68: 929–940.
- Searcy WA and Nowicki S (2005) *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, NJ: Princeton University Press.
- Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* 59: 200–215.
- Slater PJB (2003) Fifty years of bird song research: A case study in animal behaviour. *Animal Behaviour* 65: 633–639.
- Spencer KA, Buchanan KL, Leitner S, Goldsmith AR, and Catchpole CK (2005) Parasites affect song complexity and neural development in a songbird. *Proceedings of the Royal Society B* 272: 2037–2043.
- Suthers RA and Zollinger SA (2004) Producing song: The vocal apparatus. *Annals of the New York Academy of Sciences* 1016: 109–129.