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Functional aspects of song learning in songbirds

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The oscine passerines, or 'songbirds', are one of the few animal taxa in which individuals learn their vocal signals. Recent comparative studies reveal a remarkable diversity of song-learning strategies in the songbirds. Here, we discuss recent studies that shed light on the possible functional basis of different song-learning programs. We argue that further insights into the evolution and ecology of song learning will require that comparative data and functional hypotheses be analyzed in a phylogenetic context, and we review recent studies that we feel might be the first steps in this process.

Songs are complex species-specific signals given by animals of many taxa in mating and intrasexual contexts, most commonly by males to attract females and to repel rival males [1]. In most animal taxa, these species-specific vocal signals develop without significant environmental input, but in a few taxa, including humans, cetaceans, some bats, and three orders of birds, they are learned. Vocal learning has been best studied in the oscine passerines or 'songbirds', a taxon defined in part by its highly developed vocal system. Particularly striking is the comparison of the oscine passerines and the closely related suboscine passerines for, although song functions in much the same way in both groups, song is learned in the oscines but not in the suboscines [2]. An extensive body of research on the underlying neural mechanisms of song has bolstered the concept of song learning as a complex biological adaptation, and has established the oscine song control system as a major model system in the neurobiology of learning (Box 1 [2–9]).

Evolutionary questions about song learning in songbirds originally focused on the adaptive advantages of learning song versus not learning song (i.e. on the origin of song learning in the oscine line [10]). As comparative studies of songbirds have accumulated, however, the focus has shifted to the evolution of different song-learning programs within the oscines [2]. Songbird species differ as to whether they: (i) learn songs in the first few months of life, over the first year, or throughout their lifetimes; (ii) learn a single song or a repertoire of songs; (iii) develop their song repertoires by imitating external models, by improvising on tutor songs, or by inventing songs with minimal reference to the external models; (iv) require early exposure to conspecific song or can develop species-typical song even when raised in isolation; and (v) copy only tutor songs that fit tightly constrained species-specific parameters or copy essentially anything they hear. These differences must reflect, at least in part, differences in the underlying song-learning programs (see Glossary).

We begin by reviewing the diversity of song-learning strategies revealed by comparative studies. We then take two approaches to analyzing this diversity. First, we discuss recent theory and data relating to the adaptive value of different song-learning programs in present-day species. We contrast two classes of hypotheses that make different predictions concerning the optimal characteristics of a song-learning program. Second, we argue that a

Glossary

Closed-ended learner: a bird that does not modify its repertoire after the first year. Also known as age-limited learner.
Imitation: a song that is a good copy of a tutor song.
Improvisation: a song that resembles a tutor song, but which is substantially different in certain respects.
Invention: a song that cannot be traced to a tutor song.
Mimicry: copying of sounds other than conspecific song, typically heterospecific song, but sometimes non-avian or even non-animal sounds.
Open-ended learner: the bird modifies its song repertoire after its first calendar year.
Repertoire matching: replying to a song with a different song from the repertoire of the bird that matches a song that the stimulus bird has in its own repertoire.
Sensitive period: a relatively short period early in life when a bird is receptive to song memorization.
Sensorimotor phase: phase during which a bird sings and tries to match its output to earlier-memorized songs; follows or overlaps the sensory phase.
Sensory phase: phase of song learning during which the bird memorizes the tutor song.
Song: a relatively complex vocalization used in interactions with males and/or female conspecifics. A single song (or strophe) is usually relatively short (usually 2–4 sec) and is separated by a longer period of silence before the next song. In some cases, birds sing more continuously and individual songs can be quite long (e.g. 20 sec or more in sedge warblers).
Song dialect: song similarity over a larger geographic area (i.e. on the scale of kilometers).
Song element: a song is composed of a series of contrasting elements, arranged in the same order each time (e.g. in song sparrows and great tits) or in unique orders every time it sings (e.g. in sedge warblers).
Song-learning program: the genetic-developmental program thought to underlie song learning in a species (or a race or population of a species).
Song matching: replying to a song with a similar song. Pertains to cases where bird has a song repertoire and can select a song type that is similar to the stimulus song.
Song repertoire: defined in terms of song types or elements. Most birds form song elements into stable song types, but others (e.g. sedge warblers) improvise songs from their repertoire of song elements.
Song sharing: song similarity within neighborhoods or groups.
Song type: song types can be categorized; that is, there is less variation within song types than between them. Also defined by singing pattern of bird when it sings songs of one song type consecutively within a bout (e.g. AAACCCBBBDDD…) or sings its song types with immediate variety but in a stereotyped order (e.g. ABCDEABCDEA …).

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Box 1. The neural control of birdsong

Song learning and production in songbirds are regulated by a discrete network of hormone-sensitive brain nuclei [54]. This brain network has been observed in each of the 60+ oscine species in ten families examined thus far, but is lacking in seven species in three suboscine families that have been investigated [55]. Traits that are widely distributed within the branches of a monophyletic lineage such as the oscines are likely to have evolved early in the phylogeny of that lineage. Following this reasoning, the song system appears to have arisen early in the evolution of the songbird lineage. It is intriguing to speculate that the initial development of this hormone-sensitive neural system was a definitive event in the evolutionary origin of the songbirds [56].

Inspection of the song system in different oscine taxa shows that this neural system is uniform in morphology and chemical properties across taxa. However, there is extreme diversity within and between taxa in different aspects of song learning. Three attributes of the song system might enable the production of extreme behavioral diversity by this highly conserved network of brain nuclei [56]: (i) The network appears to function exclusively in controlling song-related behavior. Devotion of the song system to song behavior enables more flexibility for the evolutionary modification of factors such as neuron number and developmental timing of the brain circuits than might occur if this network also functioned in contexts other than song; (ii) Steroid hormones have pronounced influences on the development and activation of these circuits. Patterns of hormone secretion and metabolism show extensive diversity across avian taxa in aspects such as developmental timing, seasonality, and sex [57]. This diversity implies that hormone secretion and metabolism are evolutionarily flexible traits. Relatively small changes in hormone release and metabolism, in turn, can have large effects on song control networks and behavior; (iii) Song is a learned behavior and is thus subject to rapid modification via cultural evolution. These three attributes together might provide the plasticity that has enabled the diverse expression of song learning across groups.

phylogenetic approach is crucial to analyzing the diversity of song-learning programs. A phylogenetic perspective addresses the possibility that the different song-learning strategies are not responses to different functional problems, but are alternative approaches to the same functional problem; that is, different species could have responded differently to the same selection pressure because they were constrained by the earlier adaptive solutions of their ancestors. We describe several recent phylogenetic studies of bird song to illustrate the approach that we think could be fruitfully applied to the comparative data available on song-learning strategies.

Comparative studies reveal a diversity of song-learning strategies

The prevalent model of song learning is based on the classic studies by Marler on the white-crowned sparrow *Zonotrichia leucophrys* [11]. During the sensory or memorization phase, a young bird must hear a tutor song and, during the sensorimotor phase, it attempts to match its vocal output to the songs memorized previously. Learning can be demonstrated by isolating the bird during the sensory phase, or by deafening it just before the sensorimotor phase; both typically produce a bird that sings abnormal song. Isolation and deafening are extreme manipulations, and their outcomes are generally considered to be obvious. Consequently, song learning is usually demonstrated by showing that the bird develops songs that closely resemble those that it was tutored on; this method is unambiguous so long as song learning takes the form of simple imitation (copying) of tutor songs (but, as we will see, it does not always do so).

In spite of the uniformity suggested by the outline of song learning just given, it has been long known that songbird species show many variations on this theme. We argue here that the diversity of oscine song-learning programs (reviewed in [3,12]) is more extreme than is generally appreciated, and varies along at least the following five dimensions:

When song is learned (or how long the song repertoire is modified)

The period during which birds can learn songs ranges widely, from a brief sensitive period during the first few months of life (white-crowned sparrow), to the entire first year (chaffinch *Fringilla coelebs* and indigo bunting *Passerina cyanea* [13,14]) to throughout the lifetime (village indigobird *Vidua chalybeata*, great tit *Parus major*, pied flycatcher *Ficedula hypoleuca* and willow warbler *Phylloscopus trochilus* [13,15–17]). Species in which birds add songs to their song repertoires after the first calendar year are referred to as open-ended learners, species in which they do not as closed-ended (or age-limited) learners.

Although closed-ended learning has generally been the default assumption, in most cases there is no evidence to support this: song-learning experiments typically are not extended beyond the first year, and longitudinal field data are rarely gathered. Thus, species that we assume to be closed-ended learners might, on closer inspection, prove to be open-ended learners, as, for example, McGregor and Krebs discovered for great tits [15]. It is harder to prove that learning is closed-ended than that it is not, for it takes only one bird to make the point that learning can occur beyond the first year, but many more to make the point that it cannot [18].

How many songs a bird learns

In ~70% of songbird species studied, males sing multiple song types. These song repertoires range in size from small (e.g. chaffinch, great tit and swamp sparrow *Melospiza Georgiana*; all less than five) to moderate (e.g. song sparrow *Melospiza melodia* and western meadowlark *Sturnella neglecta*; ten or so) to large (e.g. western marsh wren *Cistothorus palustris* and common nightingale *Luscinia megarhynchos*; >100) to huge (e.g. brown thrasher *Toxostoma rufum*, >1000). Small- to moderate-sized repertoires are most common. Several experiments in which species (song sparrows versus swamp sparrows) or subspecies (eastern versus western marsh wrens) with different repertoire sizes were raised in a common environment established that differences in repertoire size in these cases were due to genetically based differences in the underlying song-learning programs [19,20].

Copying fidelity

Although imitation is the hallmark of bird song learning (typically it is the criterion by which song learning is assessed), birds do not always copy tutor songs precisely. In different species (and sometimes in different populations of a species), song learners appear to vary along a continuum, ranging from imitation (faithful copying of tutor song), to improvisation (variations on the tutor material) to invention (develops species-typical songs that bear no obvious relation to the tutor material, and which might or might not even require song tutoring). One typical consequence of the imitation strategy is song sharing, whereby territorial neighbors or members of the group have similar songs (Figure 1).

Role of early song experience

Because bird song learning was first demonstrated by showing that songbirds raised in isolation develop abnormal song, there has been a tendency to assume that isolation rearing will always have this effect and, hence, isolation conditions are usually omitted from song-learning experiments. But isolation does not always produce abnormal song. Two recently discovered examples are the grey catbird *Dumetella carolinensis* and sedge warbler *Acrocephalus schoenobaenus*: these birds generate large, normal song repertoires when raised in song-isolation conditions [21,22]. These birds probably need to hear themselves sing to develop their normal repertoires (although this has not been tested), but it is still surprising that they can develop their large repertoires of species-typical songs without ever hearing external conspecific song models.

Degree of canalization

In white-crowned sparrows and several other species, birds copy tutor material only if it fits tightly constrained species-specific parameters and, in these cases, song learning would be classified as environmentally canalized (*sensu* Waddington). Other species are less selective as to what material they will copy for their songs. For example, in a common-environment experiment on two closely related species, Marler and Peters [20] found that when presented with the same tape-recorded regime of song sparrow and swamp sparrow songs, song sparrows will copy heterospecific as well as conspecific elements, but swamp sparrows will not. Other species are capable of copying most things that they hear, the best-known examples being brown thrashers, northern mockingbirds *Mimus polyglottus*, marsh warblers *Acrocephalus palustris*, Indian hill mynahs *Gracula religiosa* and superb lyrebirds *Menura novaehollandiae*. Mimicry might be more common than is generally appreciated (e.g. [23]).

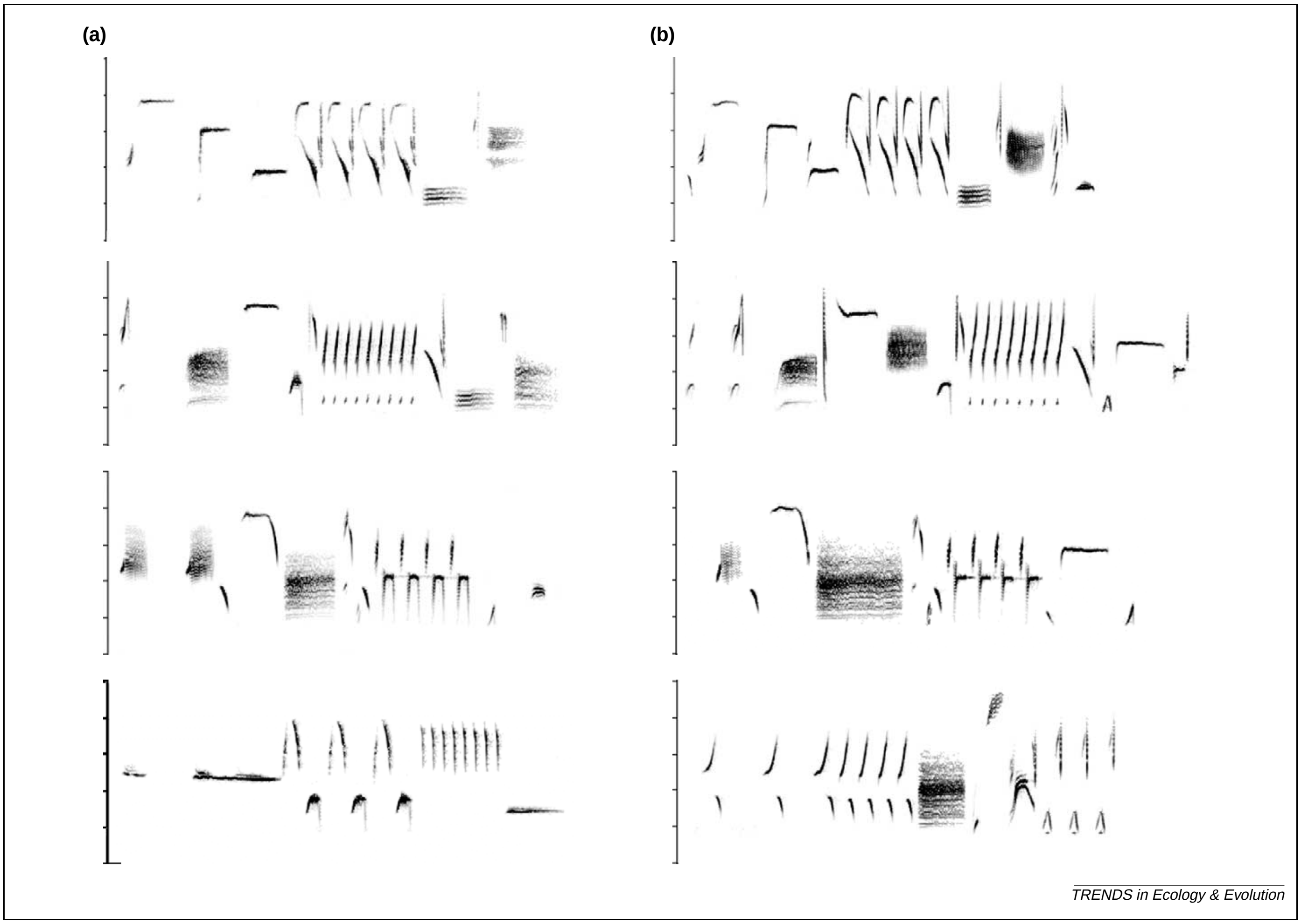

Figure 1. Partial song repertoires of two neighboring song sparrows. Birds A **(a)** and B **(b)** shared three songs in their nine-song repertoires (33% sharing). The shared songs of two birds are shown in the top three rows, whereas 2 of their remaining unshared types are shown in the bottom row. Frequency (vertical) scale: 0–10 kHz, markers at 2-kHz intervals. Songs are 2–3 secs long.

As a final caveat, we could have added responsiveness to social factors as another dimension in song learning. Social factors are an important but often neglected variable in song learning, and their role in song learning is discussed in Box 2.

Functional hypotheses of song learning

How do we explain the diversity of song-learning programs? One cannot discuss the function of a song-learning program without some hypothesis about what it is supposed to accomplish. Most functional hypotheses of song, however, have focused on the adult song repertoire, and have not directly addressed the song-learning strategy by which the bird reaches that final repertoire. Song hypotheses fall into two general classes, those that view song repertoire size as the target of selection and those that view song sharing as the target. According to the Repertoire hypothesis, the song-learning program is designed to give the bird a large song repertoire, whereas according to the Sharing hypothesis, it is designed to give the bird songs that it shares with its neighbors or group members. Although these two goals are not incompatible, song sharing does not require a large repertoire and, in some cases, might favor smaller repertoires.

There is considerable empirical support for the hypothesis that repertoire size is under strong directional sexual selection in some songbirds [1–3,24]. The evidence comes from several large-repertoire species (reviewed in [25] but see [26]) and, in these cases, the evidence suggests that repertoire size is driven by female choice. The applicability of the Repertoire hypothesis is limited, however, by the fact that most songbird species have just one or a few songs. About 30% of species have single-song repertoires, and at least another 50% have very small repertoires (fewer than five or so song types). Small repertoires can perhaps be explained as being the result of the high costs of large repertoires, but evidence that song repertoires are costly is limited [24]. Perhaps the best candidate for such a cost is the demand for more brain space that is made by larger repertoires [27]. A related hypothesis is that a complex network of brain nuclei devoted to song learning might entail special developmental and energetic costs [28]. This hypothesis is supported by recent evidence that brain centers involved in song learning are selectively affected by developmental stress [29]. However, it is not obvious that large-repertoire species should be more affected by this cost than should small-repertoire species. The prevalence of small-repertoire species suggests that we should consider alternative hypotheses that posit selection pressures on some aspect of song other than repertoire size.

Sharing hypotheses focus on the advantages of song sharing [13,30–33]. One account of how song sharing might facilitate communicative interactions between neighboring songbirds is detailed in Box 3. Song sharing is common in songbirds and is found in a variety of social contexts, not only in territorial neighbors (the most commonly studied context), but also in lekking species and communal breeders [13,31,34]. If the goal of the song-learning program is the acquisition of a repertoire of songs shared with certain key individuals, it is generally true that this goal can be met with a relatively small repertoire. Thus, the Sharing hypothesis could explain the prevalence of small repertoire species, while specifying a counter-force that might hold down repertoire size in species with intermediate-sized repertoires.

Does sharing songs increase the reproductive success of a bird? In indigo buntings, first-year birds that shared their single song with an older neighbor were more successful in acquiring a territory, mating and fledging young than were birds that did not [13]. Several recent studies of song sparrows in western USA populations (average repertoire size eight or nine songs) have compared the contributions of repertoire size versus song sharing to reproductive success. One study found that first-year song sparrows that shared more of their songs with their neighborhood group held their territories for more years than did birds that shared fewer; by contrast, repertoire size did not predict lifetime territory tenure [35]. Another study of a different western population found a similar correlation between survival and song sharing [36]. In a third study of western song sparrows, it was found that repertoire size predicted mating success but not territory acquisition in a bird's first year [37]; song sharing was not measured in this study. These three studies taken together suggest that, in western song sparrows, female choice might select for large song repertoires and male–male competition might select for song sharing.

Box 2. Social factors: the wildcard in song learning

Most song-learning experiments have used recorded song to tutor young birds. The 'tape tutor' design enables precise experimental control of the key features of song exposure, such as timing and dosage, and it simplifies the analysis because the experimenter knows exactly what the bird heard and when it heard it. The method, however, has one limitation: the omission of possibly the key variable in song learning, what we loosely label 'social factors'. The particular songs that a bird learns could depend as much or more on which bird is singing and how it sings, as it does on the amount and the timing of song exposure. In song-learning experiments with white-crowned sparrows, Baptista and Petrinovich [58] showed that the rules of song learning derived from Marler's classic experiments with this species were stretched or broken when the song tutors were live birds. For example, whereas tape-tutored white crowns reject heterospecific song and any song presented beyond 50 days, live-tutored white crowns can learn conspecific or heterospecific song presented after day 50 (but see [59]).

In another example, Nordby *et al.* [60] found that song sparrows tutored by live tutors learned more from late tutors (introduced after day 150) than they did from early tutors (removed on day 90). This outcome contrasts with an earlier tape tutor study by Marler and Peters [61] which found early tutors to be more effective than late tutors, with most of the songs the bird ultimately sang having been heard before day 90. Although other differences between the two studies are confounded with the live versus tape tutor difference, the contrast between the two sets of results illustrates the potential problem for interpreting song-learning experiments: Social factors have the potential to modify the effects of all the other variables (e.g. extend the sensitive period, make late tutors more effective than early tutors, reduce canalization, change a bird from an improviser to a copier, etc. [59,62,63]). A new approach to reconciling the conflicting results that have been obtained with live tutors and tape tutors is the 'virtual tutor': the computer presentation of digitized song streams to an isolated young bird in a fashion designed to simulate typical tutor–tutor and tutor–tutee song interactions [63].

Box 3. The role of song sharing in counter-singing interactions

Song sharing in the neighbor context is best understood in the context of the Dear Enemy hypothesis [30]. According to this hypothesis, long-term neighbors are preferred to newcomers because newcomers are inherently expansionist, whereas old neighbors generally respect territory boundaries once they have been mutually established. Neither preferring nor cooperating with familiar neighbors requires shared songs, but shared songs are a reliable signal (a 'badge') of familiarity or locality because they must be learned in the local neighborhood. Consistent with this hypothesis, a recent study [64] found that neighboring song sparrows sharing fewer songs were more aggressive with one another than were neighbors sharing more songs.

A corollary of the Dear Enemy hypothesis for territorial songbirds is that established neighbors should use their songs in place of time- and energy-costly physical interactions to minimize unnecessary territorial conflicts. Playback studies of song sparrows and banded wrens have supported this prediction [65–69]. The model in Figure I summarizes the results of these experiments, showing how birds use their mix of shared and unshared song types to form a graded signaling system for mediating territorial interactions. Even when neighbors do not share any song types (with respect to the investigators' criterion), they might still be able to song match using songs in their repertoires that they perceive as being most similar [68,70].

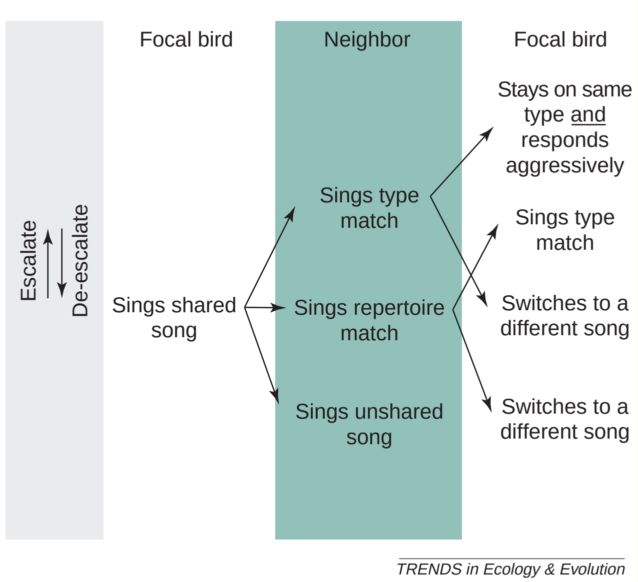

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Figure I. How song sparrows use their shared songs in countersinging. A song sparrow typically engages a neighboring bird by singing one of the song types that they share. The neighbor then either (i) returns a directed but low-threat signal by repertoire matching; that is, by replying with a shared type other than the one that the neighbor just sang; or (ii) escalates the interaction by song (type) matching; that is, by replying with the same song type as the neighbor just sang; or (iii) de-escalates by replying with an unshared type. The figure represents an interaction between a focal bird and his neighbor. Escalation is indicated by behaviors higher in the figure, and de-escalation by behaviors lower in the figure. Here, the interaction begins when the focal bird sings a shared song type toward the neighbor. The neighbor can then either type match (an escalation), repertoire match (a directed but neutral signal) or sing an unshared song (a de-escalation). If the focal bird is type matched, it might respond to the escalation by continuing to sing the same type and responding aggressively (a further escalation) or de-escalate by switching to another song type and not responding strongly.

That selection for song sharing and selection for large song repertoires are at least partially contrary is a simple logical consequence of the fact that a song-learning strategy cannot optimize both goals. Song learning designed to maximize the number of songs copied from a set of birds, the 'tutors', (such as, for example, the present neighbors) cannot also maximize the percentage of songs shared with this or a similar set of birds (e.g. the future neighbors). The bird that learns just those songs shared by its tutor-neighbors will necessarily have both a smaller repertoire and a higher sharing index than will the bird that learns all of their individual songs. It is also the case that such a learning preference for tutor-shared songs (e.g. the songs in the top rows versus those in the bottom row of Figure 1) will increase the chance that the song learner will still share songs with tutor-neighbors even if some of those neighbors die or move away. Precisely this pattern of song learning was found in a recent study of western song sparrows [38].

The Sharing hypothesis also provides a novel perspective on the difference between closed-ended and open-ended learners. If the 'goal' of a bird is to develop songs that are similar to those of its neighbors, then an open-ended learner could add and drop songs each year so as to increase song sharing with its new neighbors. Such a pattern has been observed in several species examined so far [15,34,39–42]. A similar result has been found for birds that change their song in the beginning of their first or second breeding season [13,43,44]. Moreover, the optimal repertoire size should be smaller for open-ended learners than for comparable closed-ended learners, because open-ended learners have the opportunity to replace non-matching songs with matching songs. Contrariwise, a closed-ended learner does not have the ability to change its repertoire to increase sharing, but if it has more songs to begin with, it has a better chance of finding a suitable match. In support of this prediction is the fact that most of the open-ended learners that replace songs to increase sharing have smaller repertoires than do comparable closed-ended learners [13,15,40,45,46].

If the most general prediction of the Sharing hypothesis is that the song-learning program should equip a bird with songs that it shares with its neighbors, then what is the best song-learning strategy in populations where neighbors change within, as well as between, breeding seasons? Kroodsma [12] has argued that, for birds without long-term neighbors, there is no advantage to shared songs, and so the development of generalized species-typical songs will be favored. The sedge wren *Cistothorus platensis* provides a test of this prediction. Northern populations of sedge wrens are migratory and semi-nomadic during the breeding season, and so an individual has a constantly changing set of neighbors. When tutored with taped song, North American sedge wrens do not imitate these songs but rather improvise or invent songs, all of them normal species songs [47]. By contrast, the closely related but sedentary marsh wrens faithfully copy tutor songs in comparable experiments, and in the field they share songs with their neighbors. Furthermore, tropical populations of sedge wrens, which unlike the semi-nomadic northern populations are sedentary, show the common pattern of song sharing with neighbors that is generally taken to imply song learning from neighbors [48].

Strong predictions are difficult, however, because it seems likely that different species or lineages might well have adopted different song-learning solutions to similar adaptive problems. Thus, we suggest that the best approach to understanding these different learning strategies will be to view them in a phylogenetic context.

Phylogenetic approaches to the evolution of song

Several recent studies have plotted song features on molecular-based evolutionary reconstructions, with the goal of correlating these traits with ecological and evolutionary variables that might be expected to affect song [49–51]. Price and Lanyon [50] looked for a correlation between the intensity of sexual selection (measured as sexual dimorphism) and song complexity in the oropendolas and caciques. They detected effects of sexual selection and found that different aspects of song were affected in different lineages. In an earlier study, Irwin [52] found that variation in song repertoire size was not explained by directional sexual selection in New World blackbirds (Icterinae), and a similar explanation is possible in this case. In a study of emberizine sparrows (Emberizinae), Irwin [53] found the most parsimonious hypothesis to be that the common ancestor of these species was a repertoire species, indicating that there had been selection for smaller repertoires in several of these species (including the one-song white-crowned sparrow). If this conclusion is correct, we should examine species in this group for clues as to what factors select for simplicity and uniformity of song; that is, a partial reversion to the suboscine pattern. In another recent phylogenetic study, Handley and Nelson [49] examined 65 populations in the family Fringillidae. They found that song sharing or song dialects evolved rapidly in response to local conditions, being responsive to whether the species was migratory or sedentary and to breeding latitude (higher song sharing for sedentary species and low breeding latitudes). Local song sharing was randomly distributed on the phylogeny. Repertoire size and song sharing were uncorrelated, consistent with the hypothesis that they are responsive to different selective forces.

These new phylogenetic studies have been aptly summarized by Price and Lanyon: ‘Song appears to provide multiple potential targets for selection … and as a consequence, different evolutionary patterns have emerged in different lineages’ [50]. We suggest that a profitable line of future research will be to plot characteristics of song learning on songbird phylogenies. A phylogenetic analysis might reveal, as these recent analyses suggest, that song-learning programs have evolved along different trajectories in different lineages. For example, perhaps female choice has favored large song repertoires in one lineage, lifetime song learning in another, and mimicry in a third lineage. At this point, the only real impediment to the proposed project is the lack of data on song learning as compared to the much larger database on song traits such as repertoire size.

Conclusions

Song learning evolved early during the oscine lineage and led to enhanced complexity and diversity of song. This song complexity and/or diversity has been lost or reduced in some oscines and conversely, song learning has been curtailed in some of the oscine species with the most complex, diverse song repertoires (e.g. the sedge warblers and catbirds who develop species-typical song even when isolated from song models). The diversity of song-learning strategies in oscine species varies on at least five dimensions: (i) closed-ended versus open-ended learning; (ii) repertoire size; (iii) imitation versus improvisation versus invention; (iv) external versus internal song models; and (v) selective song learning versus mimicry. How does one make sense of this diversity? We have argued that pure functional hypotheses are a start, particularly if we broaden our reach beyond the standard hypothesis of strong directional selection on repertoire size. But to account for much, these hypotheses will need to be placed in a phylogenetic context. The most difficult problem for functional hypotheses is presented by different oscine lineages responding to similar selection pressures with different modifications of the song-learning program. For example, perhaps the song-learning programs of sedge warblers and marsh wrens have been driven by sexual selection to the same goal of developing a large song repertoire. But if so, then the differences in the song-learning programs of these two species – one requiring external song models and the other not – might best be explained not in terms of different selection pressures but in terms of different ancestries. We believe that many questions about the evolution of song learning will yield to an integrated approach in which comparative data on song-learning strategies are analyzed in a full phylogenetic context.

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References

1 Searcy, W.A. and Andersson, M. (1986) Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst.* 17, 507–533
2 Kroodsma, D.E. and Miller, E.H. eds (1996) *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press
3 Catchpole, C.K. and Slater, P.J.B. (1995) *Bird Song: Biological Themes and Variations*, Cambridge University Press
4 Zeigler, H.P. and Marler, P. eds (2004) *Behavioral Neurobiology of Birdsong*, Annals of the New York Academy of Sciences
5 Baker, M.C. (2001) Bird song research: the past 100 years. *Bird Behav.* 14, 3–50
6 Slater, P.J.B. (2003) Fifty years of bird song research: a case study in animal behaviour. *Anim. Behav.* 65, 633–639
7 Doupe, A.J. and Kuhl, P.K. (1999) Birdsong and human speech: common themes and mechanisms. *Annu. Rev. Neurosci.* 22, 567–631
8 Brainard, M.S. and Doupe, A.J. (2002) What songbirds teach us about learning. *Nature* 417, 351–358
9 Goldstein, M.H. *et al.* (2003) Social interaction shapes babbling: testing parallels between birdsong and speech. *Proc. Natl. Acad. Sci. U. S. A.* 100, 8030–8035
10 Nottebohm, F. (1972) The origins of vocal learning. *Am. Nat.* 106, 116–140
11 Marler, P. (1970) A comparative approach to vocal learning: song development in white-crowned sparrows. *J. Comp. Physiol. Psychol. Monogr.* 71, 1–25
12 Kroodsma, D.E. (1996) Ecology of passerine song development. In *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E. and Miller, E.H., eds), pp. 3–19, Cornell University Press
13 Payne, R.B. and Payne, L.L. (1997) Field observations, experimental design, and the time and place of learning bird songs. In *Social Influences on Vocal Development* (Snowdon, C.T. and Hausberger, M., eds), pp. 57–84, Cambridge University Press
14 Lachlan, R. and Slater, P. (2003) Song learning by chaffinches: how accurate, and from where? *Anim. Behav.* 65, 957–969

15 McGregor, P.K. and Krebs, J.R. (1989) Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour* 108, 139–159

16 Espmark, Y.O. and Lampe, H.M. (1993) Variations in the song of the pied flycatcher within and between breeding seasons. *Bioacoustics* 5, 33–65

17 Gil, D. *et al*. (2001) Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. *Anim. Behav.* 62, 689–694

18 Nordby, J.C. *et al*. (2002) Adult song sparrows do not alter their song repertoires. *Ethology* 108, 39–50

19 Kroodsma, D.E. and Canady, R.A. (1985) Differences in repertoire size, singing behavior, and associated neuroanatomy among marsh wren populations have a genetic basis. *Auk* 102, 439–446

20 Marler, P. and Peters, S. (1988) The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*. *Ethology* 77, 125–149

21 Leitner, S. *et al*. (2002) Song and the song control pathway in the brain can develop independently of exposure to song in the sedge warbler. *Proc R. Soc. Lond. Ser. B* 269, 2519–2524

22 Kroodsma, D.E. *et al*. (1997) Song development by grey catbirds. *Anim. Behav.* 54, 457–464

23 Murray, R.L. *et al*. (2004) Bachman's sparrows mimic the vocalizations of the common yellowthroat and the indigo bunting. *J. Field. Ornithol.* 75, 51–52

24 Gil, D. and Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* 17, 133–141

25 Searcy, W.A. and Yasukawa, K. (1996) Song and female choice. In *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E.M. and Edward, H., eds), pp. 454–473, Cornell University Press

26 Forstmeier, W. and Leisler, B. (2004) Repertoire size, sexual selection, and offspring viability in the great reed warbler: changing patterns in space and time. *Behav. Ecol.* 15, 555–563

27 Garamszegi, L.E., M. (2004) Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behaviour in songbirds. *Brain Res. Rev.* 44, 187–193

28 Nowicki, S. *et al*. (1998) Song learning, early nutrition and sexual selection in songbirds. *Am. Zool.* 38, 179–190

29 Buchanan, K.L. *et al*. (2004) Developmental stress selectively affects the song control nucleus HVC in the zebra finch. *Proc. R. Soc. Lond. Ser. B* 271, 2381–2386

30 Beecher, M.D. *et al*. (1997) What is the function of song learning in songbirds?. In *Perspectives in Ethology, Vol. 12: Communication* (Owings, D.H. *et al*., eds), pp. 77–97, Plenum Press

31 Brown, E.D. and Farabaugh, S.M. (1997) What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. In *Social Influences on Vocal Development* (Snowdon, C.T. and Hausberger, M., eds), pp. 98–127, Cambridge University Press

32 Vehrencamp, S.L. (2000) Handicap, index, and conventional signal elements of bird song. In *Animal Signals: Signalling and Signal Design in Animal Communication* (Espmark, Y. *et al*., eds), pp. 277–300, Tapir Academic Press

33 Lachlan, R.F. *et al*. (2004) The evolution of conformity-enforcing behaviour in cultural communication systems. *Anim. Behav.* 68, 561–570

34 Trainer, J.M. (1989) Cultural evolution in song dialects of yellow-rumped caciques in Panama. *Ethology* 80, 190–204

35 Beecher, M.D. *et al*. (2000) Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Anim. Behav.* 59, 29–37

36 Wilson, P.L. *et al*. (2000) Survival and song-type sharing in a sedentary subspecies of the song sparrow. *Condor* 102, 355–363

37 Reid, J.M. *et al*. (2004) Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Anim. Behav.* 68, 1055–1063

38 Nordby, J.C. *et al*. (1999) Ecological correlates of song learning in song sparrows. *Behav. Ecol.* 10, 287–297

39 Sorjonen, J. (1986) Song structure and singing strategies in the genus *Luscinia* in different habitats and geographical areas. *Behav.* 98, 274–285

40 Lemon, R.E. *et al*. (1994) Dual strategies of song development in American redstarts, *Setophaga ruticilla*. *Anim. Behav.* 47, 317–329

41 Martens, J. and Kessler, P. (2000) Territorial song and song neighbourhoods in the scarlet rosefinch *Carpodacus erythrinus*. *J. Avian Biol.* 31, 399–411

42 Rasmussen, R. and Dabelsteen, T. (2002) Song repertoires and repertoire sharing in a local group of blackbirds. *Bioacoustics* 13, 63–76

43 O'Loghlen, A.L. and Rothstein, S.I. (2002) Ecological effects on song learning: delayed development is widespread in wild populations of brown-headed cowbirds. *Anim. Behav.* 63, 475–486

44 Briskie, J.V. (1999) Song variation and the structure of local song dialects in the polygynandrous Smith's longspur. *Can. J. Zool.* 77, 1587–1594

45 Griessmann, B. and Naguib, M. (2002) Song sharing in neighboring and non-neighboring thrush nightingales (*Luscina luscina*) and its implications for communication. *Ethology* 108, 377–387

46 Kipper, S. *et al*. (2004) Long-term persistence of song performance rules in nightingales (*Luscinia megarhynchos*): a longitudinal field study on repertoire size and composition. *Behav.* 141, 371–390

47 Kroodsma, D.E. *et al*. (1999) The ecology of song improvisation as illustrated by North American sedge wrens. *Auk* 116, 373–386

48 Kroodsma, D.E. *et al*. (1999) Sedentary life style of Neotropical sedge wrens promotes song imitation. *Anim. Behav.* 57, 855–863

49 Handley, H.G. and Nelson, D.A. Ecological and phylogenetic effects on song sharing in songbirds. *Ethology* (in press)

50 Price, J.J. and Lanyon, S.M. (2004) Patterns of song evolution and sexual selection in the oropendolas and caciques. *Behav. Ecol.* 15, 485–497

51 Irwin, D.E. (2000) Song variation in an avian ring species. *Evol.* 54, 998–1010

52 Irwin, R.E. (1990) Directional sexual selection cannot explain variation in song repertoire size in the New World blackbirds (Icterinae). *Ethology* 85, 212–224

53 Irwin, R.E. (1988) The evolutionary significance of behavioral development: the ontogeny and phylogeny of bird song. *Anim. Behav.* 36, 814–824

54 Brenowitz, E.A. and Beecher, M.D. Song learning in birds: diversity and plasticity, opportunities and challenges. *Trends Neurosci.* (in press)

55 Brenowitz, E.A. (1997) Comparative approaches to the avian song system. *J. Neurobiol.* 133, 517–531

56 Brenowitz, E.A. and Kroodsma, D.E. (1996) The neuroethology of birdsong. In *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D.E. and Miller, E.H., eds), pp. 269–281, Cornell University Press

57 Ball, G.F. (2004) Seasonal plasticity in the song control system: multiple brain sites of steroid hormone action and the importance of variation in song behavior. *Ann. NY Acad. Sci.* 1016, 586–610

58 Baptista, L.F. and Petrinovich, L. (1984) Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Anim. Behav.* 32, 172–181

59 Nelson, D.A. (1997) Social interaction and sensitive phases for song learning: a critical review. In *Social Influences on Vocal Development* (Snowdon, C.T. and Hausberger, M., eds), pp. 7–22, Cambridge University Press

60 Nordby, J.C. *et al*. (2001) Late song learning in song sparrows. *Anim. Behav.* 61, 835–846

61 Marler, P. and Peters, S. (1987) A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*, a case of age-limited learning. *Ethology* 76, 89–100

62 Baptista, L.F. and Gaunt, S.L.L. (1997) Social interaction and vocal development in birds. In *Social Influences on Vocal Development* (Snowdon, C.T. and Hausberger, M., eds), pp. 23–40, Cambridge University Press

63 Beecher, M.D. and Burt, J.M. (2004) The role of social interaction in bird song learning. *Curr. Direct. Psychol. Sci.* 13, 224–228

64 Wilson, P.L. and Vehrencamp, S.L. (2001) A test of the deceptive mimicry hypothesis in song-sharing song sparrows. *Anim. Behav.* 62, 1197–1205

65 Beecher, M.D. *et al*. (1996) Repertoire matching between neighbouring song sparrows. *Anim. Behav.* 51, 917–923

66 Beecher, M.D. *et al*. (2000) Song type matching between neighbouring song sparrows. *Anim. Behav.* 59, 21–27

67 Burt, J.M. *et al*. (2001) Song type matching as threat: a test using interactive playback. *Anim. Behav.* 62, 1163–1170

68 Burt, J.M. *et al*. (2002) Alternative forms of song matching in song sparrows. *Anim. Behav.* 63, 1143–1151

69 Molles, L.E. and Vehrencamp, S.L. (2001) Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. *Proc. R. Soc. Ser. B* 268, 2013–2019

70 Anderson, R.C. *et al*. Partial matching in an eastern population of song sparrows, *Melospiza melodia*. *Anim. Behav.* (in press)