

Song Learning, Early Nutrition and Sexual Selection in Songbirds¹

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SYNOPSIS. The developmental processes through which songbirds acquire their species-typical songs have been well-studied from a proximate perspective, but less attention has been given to the ultimate question of why birds learn to sing. We present a new hypothesis for the adaptive significance of song learning in songbirds, suggesting that this specialized form of vocal development provides an indicator mechanism by which females can accurately assess the quality of potential mates. This hypothesis expands on the established idea that song can provide an indicator of male quality, but it explicitly links the variation in song expression that females use to choose mates to the developmental processes through which song is acquired. How well a male sings—reflected in repertoire size or in other learned features of a male's singing behavior—provides an honest indicator of quality because the timing of song learning and, more importantly, the timing of the development of brain structures mediating learning corresponds to a period in development during which young songbirds are most likely to undergo nutritional stress. This correspondence means that song learning can provide a sensitive indicator of early developmental history in general, which in turn reflects various aspects of the phenotypic and genotypic quality of a potential mate.

INTRODUCTION

When formulating hypotheses about the evolution of a trait, we often ask how selection acts on the phenotypic endpoint of development, be it a behavior or other kind of trait. Recently, however, several authors have emphasized the need to consider also how selection acts on mechanisms underlying the development of traits (*e.g.*, Alberch, 1982; Nijhout, 1991; West-Eberhard, 1992). Because evolutionary changes in an organism's phenotype are necessarily linked to changes in the ontogenetic processes that produce it, we may gain greater insight into how evolution has shaped a trait by considering how that trait develops. This paper considers the connection between development and evolution for a particularly well-studied behavioral phenotype, bird song. Song has long been the subject of extensive research, much of which has taken an ultimate perspective, asking why birds sing the way they do in terms of the selective forces that have shaped the expres-

sion of this behavior (Catchpole and Slater, 1995; Kroodsma and Miller, 1996). The development of bird song also has been well-studied, but more from a proximate perspective, with an emphasis on how vocal behavior in songbirds is learned (Marler, 1970; Slater, 1989). By comparison, relatively little has been written about the evolutionary significance of song learning.

Here we present a new hypothesis for the adaptive significance of song learning, suggesting that song learning provides a mechanism by which song can be used by females to assess the quality of potential mates. We argue that learned features of song can provide an accurate indicator of male quality because they reflect variation in the development of brain areas mediating the learning process, which in turn reflects variation in the response of individuals to nutritional stresses faced early in life.

OVERVIEW OF SONG LEARNING

All songbirds (suborder Passeri, order Passeriformes; also called "oscine" birds) appear to learn their species-typical songs by copying models heard early in life (Kroodsma and Baylis, 1982; Marler, 1990). Other birds, including "suboscine"

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passerines, do not learn to sing by imitation (Kroodsma and Konishi, 1991; Kroodsma, 1996). Two exceptions to this generalization are parrots (Psittaciformes) and hummingbirds (Apodiformes); members of both groups use imitation in the development of their species-typical vocalizations (Fara-baugh and Dooling, 1996; Baptista and Schuchmann, 1990).

Song learning in songbirds is a two-step process during which a young bird must first hear and memorize acceptable song models and then reproduce those songs through a gradual process during which it matches its own vocal output to memorized models (Marler, 1970; Slater, 1989; Konishi, 1994). The first part of this process, called the "memorization phase," normally occurs during a narrow sensitive period, usually beginning within a week or so after hatching. During the second part, the "motor phase," birds sing amorphous and variable sounds (subsong and plastic song) that gradually develop into stereotyped (crystalized) copies of models they memorized earlier. These two phases are separated in time for some species, but overlap in others (Catchpole and Slater, 1995).

Two key features characterize the song learning process. The first is a dependence on imitation. Young songbirds deprived of models early in life generally produce abnormal songs that bear only little resemblance to species-typical song patterns (*e.g.*, Marler and Sherman, 1985). If young birds are exposed to model songs during the memorization phase, however, they subsequently reproduce accurate copies of the models they hear (*e.g.*, Marler and Peters, 1988*b*). This dependence on imitation can be extreme in some species, although there are exceptions such as the brood-parasitic brown-headed cowbird, *Molothrus ater* (West and King, 1996).

A second key feature of song learning is that the process is confined to a relatively limited period of life. In many species, so-called "age-limited" learners, the time window for learning occurs briefly in the young bird's first year of life (Marler, 1990). The timing of the memorization and motor phases of song learning, and the factors that influence this timing vary among species

(Slater, 1989; Kroodsma, 1996) but, in general, the song learning process occurs early in the life of an individual. Other species, referred to as "open-ended" learners, are thought to be capable of learning new songs later in life. We focus our remarks on age-limited learners, but return to the issue of open-ended learning at the end of the paper.

The acquisition and production of song is mediated by a discrete series of brain nuclei—the "song system"—which form two interconnected pathways (see Doupe [1993] Konishi [1994] Brenowitz and Kroodsma [1996] for illustrations). The main descending or motor pathway (HVC → RA → nXIIIts) is necessary for song production, as demonstrated by the fact that lesions in HVC or RA disrupt adult song (Nottebohm *et al.*, 1976). A second pathway, the anterior forebrain pathway (HVC → Area X → DLM → IMAN → RA) is necessary for song learning to occur, but not for production of adult song (Bottjer *et al.*, 1984, Scharff and Nottebohm, 1991).

Vocal learning appears to have originated just once in the Passeriformes, in the common ancestor of the oscines. Evidence for this assumption comes from the observation that all oscines studied to date learn to sing (Kroodsma and Baylis, 1982), while suboscines show no evidence of song learning (Kroodsma, 1996). It is likely that vocal learning evolved independently in both the parrots and hummingbirds (Ball, 1994; Striedter, 1994). Because much less is known about vocal development in these groups as compared to songbirds, we do not consider them in detail here. Given that vocal learning evolved only once in oscines, it is difficult to speculate on its evolutionary origin. A number of ideas have been advanced, however, to account for the evolutionary maintenance and elaboration of vocal learning in this group once dependence on auditory feedback and imitation was established.

One long held view is that vocal learning is necessary for the cultural transmission of complex motor patterns associated with song production (Andrew, 1962; Slater, 1989). This argument suggests that it is difficult to encode such complex motor information genetically, so precise transmission

of song patterns must rely on imitation. A second group of hypotheses state that vocal learning enables songs to be better adapted to local conditions. For example, song matching may promote the development of local dialects, facilitating population recognition and thus permitting fine-tuned genetic adaptation to local environments (Marler and Tamura, 1964; Nottebohm, 1972; Baker and Cunningham, 1985; but see Baptista and Morton, 1982; Chilton *et al.*, 1990). Songs also may be adapted to social conditions, for example by allowing song matching in a local neighborhood (*e.g.*, Payne, 1982). Hansen (1979) proposed that song learning enables adaptation to local acoustic environments, especially important for species occurring across a wide range of habitats with different environmental conditions (Hunter and Krebs, 1979).

Another general hypothesis for the adaptive significance of song learning is that it permits increased complexity in song, which in turn enhances the signal's functional effectiveness (Nottebohm, 1972). Although "complexity" is hard to define, one commonly used metric is repertoire size. Large repertoires have been shown in several species to be more effective both in repelling territorial intrusions by other males (Searcy and Andersson, 1986) and in attracting females and stimulating courtship behavior (Searcy and Yasukawa, 1996). The use of large repertoires by some oscines as compared to suboscine species (Krebs and Kroodsma, 1980) is consistent with the view that song learning permits males to acquire a greater number of song types. Once established, a trend toward increasing vocal complexity enabled by learning could be further enhanced by sexual selection in a number of ways, including Fisherian runaway selection or selection for song as an indicator of male quality (Andersson, 1994).

SONG LEARNING AS A MECHANISM FOR INDICATING MALE QUALITY

Our hypothesis expands on the idea that song provides an indicator of male quality, but explicitly links the variation in song expression that females may use to choose

mates to the developmental processes through which song is acquired. In so doing, it provides a mechanism by which song might serve as an honest indicator. The idea that female songbirds may choose mates based on song is well-established (Searcy and Andersson, 1986; Catchpole and Slater, 1995; Catchpole, 1996); it is less clear what benefits females derive from this choice, whether direct benefits such as resources or parental care, or indirect benefits in the form of "good genes" (Andersson, 1994). In either case, a critical question remains largely unanswered: How can a male's songs provide an honest indicator of his quality?

A first step in demonstrating that a sexually selected trait serves as an honest indicator is to marshal evidence that the trait in question accurately reflects male quality, with more elaborate or exaggerated phenotypes marking superior males. Perhaps the best known example of this relationship come from studies of the effects of parasite loads and disease on the expression of secondary sex characteristics (Hamilton and Zuk, 1982). Animals with superior resistance to parasites or disease remain healthier in the face of a given parasite load, and healthier animals can devote a larger proportion of their metabolic resources to ornament growth and development (reviewed in Møller, 1994; Andersson, 1994). Females choosing mates based on ornament condition therefore are choosing males with superior phenotypes and genotypes.

The relationship between a male's quality and the expression of his song is less apparent (Searcy and Andersson, 1986). Experiments in which male condition was manipulated, through food supplements, have shown that singing rate may honestly reflect a male's current physiological condition (*e.g.*, Alatalo *et al.*, 1990, reviewed in Catchpole and Slater, 1995). Other studies have demonstrated a relationship between song repertoire size, female choice, and various measures of reproductive success (reviewed in Searcy and Andersson, 1986; Searcy and Yasukawa, 1996). A recent paper by Hasselquist *et al.* (1996) provides the best evidence to date that repertoire size may correlate with overall genetic quality.

By analyzing patterns of paternity and fledgling survival in the great reed warbler (*Acrocephalus arundinaceus*), Hasselquist and his colleagues demonstrated that a male's repertoire size is the best predictor of the relative post-fledging survival of his genetic offspring, suggesting that females choosing males with larger repertoires obtain indirect benefits in terms of more fit genotypes associated with the increased likelihood that offspring will survive to breed. We are still left, however, with an unanswered question: What is the connection between song and male quality?

We propose that song may provide an honest indicator of male quality because the timing of song learning, and more importantly the timing of the development of the brain structures that mediate song learning, corresponds to a period in development during which a young bird is most likely to undergo nutritional stress. Differences in the response to nutritional stress incurred by individuals will be reflected in a constellation of developmental differences, including the development of the song system. Variation in the development of the song system will translate into variation in the song learning abilities of males. This correspondence means females choosing males on the basis of song features which reflect the outcome of learning—including, but not necessarily limited to, repertoire size—in fact are choosing males that fared better during post-natal development in the face of potentially limiting nutritional resources. Differences in developmental history in turn may reflect the phenotypic or genotypic quality of the male.

LIFE HISTORY, DEVELOPMENT AND NUTRITION IN SONGBIRDS

Young songbirds are particularly susceptible to nutritional stress as nestlings and young fledglings. Songbirds are altricial and completely dependent on parental care during the postnatal period between hatching and fledging, which can range from as little as 8 days in some species up to 42 days in others (Ricklefs, 1983; O'Connor, 1984). Post-hatching development in altricial birds is characterized by remarkably rapid growth, especially in oscines, with

nestlings typically reaching 90% of their final weight in less than 10 days (calculated from Table 2 in Ricklefs 1968). Parental care and good nutrition are critical; low survivorship in nestlings can be attributed in part to insufficient food, and partial or complete brood loss in altricial species frequently results from starvation (O'Connor, 1984). Most oscines continue to grow after they fledge (O'Connor, 1984) and continue to rely on their parents for food for 2 to 4 weeks before acquiring foraging proficiency (O'Connor, 1984; Weathers and Sullivan, 1989; Kopachena and Falls, 1992). The several days following complete independence from the parents also is likely to be a time of high nutritional stress.

Growth rates vary considerably among individuals within a population (*e.g.*, Ricklefs and Peters, 1979). Individual variation in growth and development can be related to genetic factors (Garnett, 1981), as well as to external factors such as brood size, locality, season and weather, all of which may influence food availability (Ricklefs and Peters, 1981). Another important influence on growth rates may be the age and experience of parents and individual variability in the quality of parental care (Ricklefs and Peters, 1981; Ricklefs, 1983).

Undernutrition in birds may result in delayed development. For example, Emlen *et al.* (1991) report retarded development and a prolonged nestling stage in the white-fronted bee-eater when food availability was restricted. A more commonly reported response to undernutrition is lower final nestling weight, without any change in the rate of development (Ricklefs, 1968, 1983; O'Connor, 1984; Boag, 1987). Richner *et al.* (1989) found that carrion crows (*Corvus corone*) raised during the nestling period with limited food had significantly depressed growth rates and lower final weights and smaller size as compared to control nestlings fed *ad libitum*. Boag (1987) found that size differences in zebra finches resulting from manipulating the food intake of nestlings remained consistent throughout adulthood.

WHAT ASPECTS OF MALE QUALITY MIGHT BE INDICATED?

Individual differences in response to nutritional stress could provide an honest in-

indicator of at least three things important to females when choosing mates. The first of these is the male's overall phenotypic condition, as suggested by the effects of undernutrition on weight and size outlined above. There is evidence that the intensity or size of secondary sex characters correlated with male reproductive success may be reduced as a result of postnatal food deficiency. For example, male zebra finches raised in large broods with less food available per chick develop less intense beak color than do males raised in small broods (de Kogel and Prijs, 1996). Similarly, young male collared flycatchers (*Ficedula albicollis*) raised in large broods develop smaller white forehead patches than males raised in small broods (Gustafsson *et al.*, 1995).

Differences in the phenotypic responses of young birds to nutritional stress most likely reflect genotypic differences as well. As suggested by Williams (1966, p. 184), individuals with generally more fit genotypes are expected to have more robust phenotypes in the face of difficulties associated with disease or undernutrition. Therefore, male phenotypic characters that vary in response to disease- or nutrition-related stress can potentially provide females with accurate information about the genotypic quality of their potential mate (Andersson, 1994).

Finally, it is conceivable that consequences of the quality of early nutrition might provide females with information about heritable aspects of male parental care. This suggestion is speculative given the lack of evidence from vertebrates for heritability of the propensity for parental care. However, to the extent that male parental care plays an important role in the early nutrition of offspring, offspring that receive more care from their male parents may be expected both to develop better phenotypes (and learn better) and also to carry genes for good parenting.

NUTRITIONAL EFFECTS ON BRAIN DEVELOPMENT, LEARNING AND MEMORY

The vertebrate brain is particularly vulnerable to the effects of undernutrition during its early growth and development (Dobbing, 1981). We know of no studies of the

long-term effects of undernutrition on the growth and development of the avian brain, but nutritional deficits early in life have been shown in a number of mammalian species to result in permanent effects on the size and structure of various brain areas and also to cause learning deficits later in life (reviewed in Smart, 1986; Levitsky and Strupp, 1995). Studies of the mammalian hippocampus are particularly informative because its role in spatial learning and memory is well-documented (Schacter and Tulving, 1994). Poor nutrition early in life results in a number of permanent anatomical and physiological abnormalities in the rat hippocampus, including reductions in cell number, cell size and dendritic branching, and altered patterns of neuronal firing and long-term potentiation (reviews in Castro and Rudy, 1987; Levitsky and Strupp, 1995). Early nutritional deficits also have obvious effects on adult performance in spatial memory tasks (*e.g.*, Jordan *et al.*, 1981; Goodlett *et al.*, 1986; but see Hall, 1983). For example, Castro and Rudy (1987) found that undernourished pups (with restricted access to lactating females) performed significantly less well in a distal-cue spatial navigation task when young as compared to a control group. By 30 days of age, performance in the undernourished group had improved significantly, but was still impaired compared to controls.

TIMING OF DEVELOPMENT OF THE SONG SYSTEM

The timing of development of avian brain areas mediating song acquisition and production coincides with the period of greatest potential for nutrition-related stress (Fig. 1). The vast majority of work on neuroanatomical development in songbirds has been done on the canary and especially the zebra finch. The song system develops late relative to the rest of the brain (Alvarez-Buylla *et al.*, 1994; DeVoogd, 1994). In zebra finches, the development of the anterior forebrain pathway coincides with the initial phases of the memorization phase, and the descending motor pathway develops with the onset of the motor phase of learning (Doupe, 1993; Brenowitz and Kroodsma, 1996). Developmental processes during

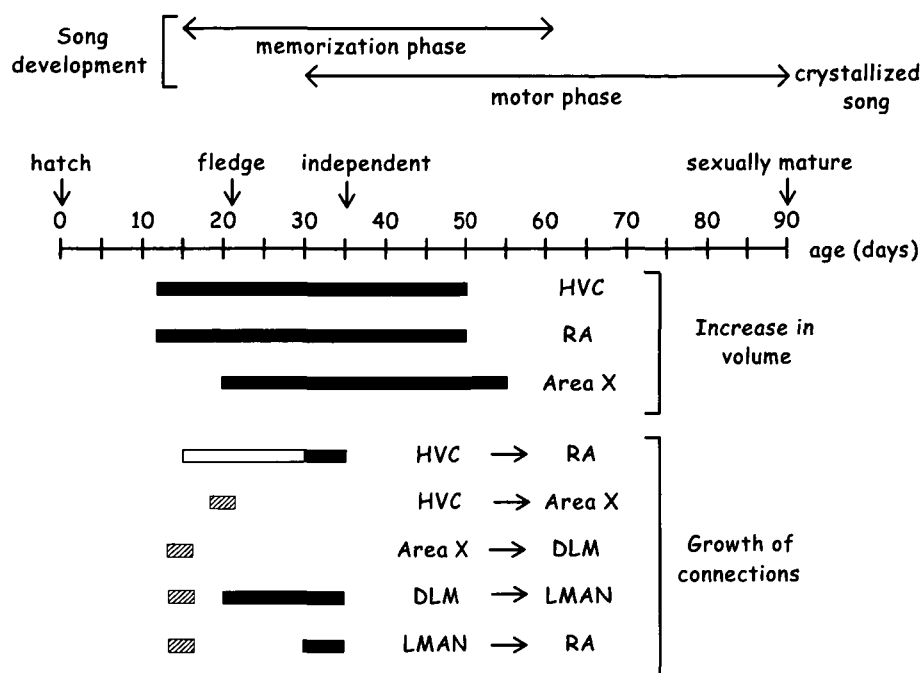


FIG. 1. Time line of zebra finch life history events, song learning and development of the song control system. The memorization phase spans approximately 25 to 65 days of age, and the motor phase begins at about 30 days of age and continues until crystallized song production (Immelmann, 1969; Slater *et al.*, 1988). Zebra finches fledge at about 20 days of age (Immelmann, 1969) and are not fully independent from parental care until approximately 35 days of age (Catchpole and Slater, 1995). Black bars indicate reported periods of volume increase for brain nuclei and growth of connections between nuclei. Shaded bars indicate earliest time for which functional connections between nuclei have been reported. The open bar shows that HVC neurons project to RA between 15 and 30 days of age, but do not make functional connections until day 30. See references in text.

these periods include neurogenesis, the growth of existing neurons, and the formation of functional connections between nuclei.

In the zebra finch, neurogenesis leads to a significant increase in the number of neurons in HVC between 10 and 50 days, and in Area X between 20 and 50 days (Bottjer *et al.*, 1985; Nordeen and Nordeen, 1988). Most neurons in the canary HVC also are added after hatching (Alvarez-Buylla *et al.*, 1988; Alvarez-Buylla *et al.*, 1992). RA volume in the zebra finch increases between 10 and 50 days of age due to an increase in neuron size, greater spacing between neurons and an increase in synaptic density (Bottjer *et al.*, 1985; Konishi and Akutagawa, 1985).

Zebra finch HVC neurons project to RA between 15 and 30 days of age (Fig. 1) and then hold at the border (Mooney and Rao,

1994) until an abrupt innervation of RA is accomplished between 30 and 35 days of age (Konishi and Akutagawa, 1985). Many of the connections in the anterior forebrain pathway probably become functional by 15 days post-hatch (Brenowitz and Kroodsma, 1996; Nordeen and Nordeen, 1990; Doupe, 1993) and HVC projects to Area X by day 20 (Mooney and Rao, 1994). Although HVC connections to Area X in the canary are almost all completed in the embryo stage, some connections also are established after hatching (Alvarez-Buylla *et al.*, 1988). Area X connections to DLM in the zebra finch are probably established by 15 days (Johnson and Bottjer, 1992). DLM axons arrive in zebra finch lMAN at 15 days of age, and between 20 and 35 days of age there is "exuberant" growth from DLM to lMAN (Johnson and Bottjer, 1992). Finally, in the zebra finch, lMAN projects to RA

as early as day 15, and is readily detected after day 30 (Mooney and Rao, 1994).

We conclude that the song system is developing, and critical early events of song learning are occurring, just at the time when the young bird is most susceptible to the effects of nutritional stress. More work needs to be done on species for which the memorization and motor phases are separated in time, but we expect that the potential for nutritional stress is likely to overlap with the timing of the development of the anterior forebrain pathway and the memorization phase of learning in most if not all songbirds.

FURTHER EVIDENCE IN SUPPORT OF THE HYPOTHESIS

The general effects of nutrition on brain development, and the timing of song learning and song system development, are consistent with the hypothesis that song learning could provide females with an honest indicator of a potential mate's phenotypic and genotypic quality. In this section we address three additional points necessary to support the hypothesis. The first is to ask whether males exhibit variation in their learning abilities. If all males in a population learn more or less equally well, then it is impossible to make the functional link between learning and female choice for song features that vary among males. The second point is to ask whether variation in the development of the song system in the brain leads to variation in singing behavior. Is there evidence that variation in the size of brain nuclei, for example, is reflected in the quality of a male's singing? The final question to ask is whether variation in early nutrition can be shown to have a direct effect on an individual male's ability to learn songs.

Intraspecific variation in song learning

Intraspecific differences in song features (e.g., repertoire size, song length, song "quality") are evident in the wild, but it is difficult to determine the origin of this variation. In the laboratory, however, it is possible to trace variation in male song to differences in how much and how well individual birds learn under controlled condi-

tions. Although we know of no study that explicitly analyzes individual variation in learning success, it is possible to extract examples from the literature. Some studies report that one or more birds failed to learn even though other individuals experiencing the same acoustic conditions learned well (e.g., Nelson *et al.*, 1995; Marler and Peters, 1988b). In an experiment in which 12 swamp sparrows each heard exactly the same array of model song types, 4 males learned only one model, 7 males learned 2 models and one male learned 3 models (Marler and Peters, 1988a). Hultsch (1991) reports that the learning success of 4 nightingales (*Luscinia megarhynchos*) exposed to conspecific song ranged from 70–90% (measured as the percentage of presented song types that were acquired). In three separate song learning experiments in which song sparrows were exposed to tape recordings of conspecific songs, Peters and Nowicki (unpublished data) found individual variability in learning performance (measured as percentage of note copies produced in crystallized repertoire) to range from 24–90% (n = 6), 16–74% (n = 7) and 21–93% (n = 8).

These data demonstrate that there can be significant variation in the learning abilities of individual males. The factors responsible for this variation are less clear. Although acoustic experience is controlled in such experiments, there is enormous potential for variation in other factors experienced by the birds. The nutritional histories of birds especially are likely to differ because birds brought in at early ages experience a different feeding regime than those brought in later.

Brain space and repertoire size

If differences in early nutrition affect the development of a young bird's brain, can the resulting neuroanatomical differences influence the quality of song produced? Some data suggest that differences in the size of song system nuclei correlate with at least one measure of song production, the number of song types in a male's repertoire. Nottebohm (1981) originally found that HVC and RA sizes both correlate with repertoire size in canaries. Eastern and western

populations of marsh wrens (*Cistothorus palustris*) differ in the size of their song repertoires and these differences also correlate with the size of HVC and RA (Canady *et al.*, 1984, Kroodsma and Canady, 1985, Brenowitz *et al.*, 1994). Interspecific comparisons also reveal a consistent relationship between the volume of song system nuclei and repertoire size (Brenowitz and Arnold, 1986). In a recent comparative study, Székely *et al.* (1996) used Felsenstein's (1985) independent contrast method to demonstrate a significant positive relationship between HVC volume and repertoire size among 8 closely-related species of warblers in the family Sylviidae.

Although the majority of this work involves inter-population or interspecific comparisons, these data strongly suggest that available "brain space" puts an upper limit on how much or how well an individual bird can sing (Nottebohm, 1981; Catchpole, 1996; Jacobs, 1996); that is, "learning more songs is associated with having more and bigger neurons" (Brenowitz and Kroodsma, 1996, p. 299). Brenowitz and Kroodsma (1996) point out, however, that such correlations could be observed either if early exposure to larger song repertoires during song learning determined the growth and eventual size of song system nuclei or, conversely, if the size of the song system determined the number of songs learned. To distinguish between these possibilities, Brenowitz *et al.* (1995) raised two groups of eastern marsh wrens under identical conditions, exposing one group to a large number of model song types while exposing the other group to a small number of song types, many fewer than are normally sung by individual males of this species. As expected, the birds exposed to more songs during their memorization phase developed larger repertoires. The groups did not differ in the size of HVC or RA, however, which suggests that brain space determines repertoire size, not vice versa.

Direct effects of nutrition on song learning

The most direct test of our hypothesis would be to demonstrate that variation in response to early nutritional experience

leads to variation in how well individual birds learn to sing. To our knowledge, there are as yet no data that address this question, although a laboratory experiment would be simple to design: Two groups of nestlings could be raised under different nutritional regimes, but otherwise exposed to identical conditions including the same regime of model songs. Unlike typical laboratory learning experiments, it would be essential to capture birds as early as possible and at the same age to minimize between-nest variation in nutritional experience, and important to keep track of individual feeding and growth patterns to help account for sources of within-nest variation. We currently have such an experiment in progress using swamp sparrows as subjects. A field test would be logistically more difficult to carry out, but also conceptually simple to design. For example, one could monitor feeding rates and growth rates for a cohort of nestlings in the field, and then correlate these rates with measures of song quality obtained later.

CONCLUSIONS AND FUTURE DIRECTIONS

We have proposed that song learning provides a mechanism by which a male bird's songs may serve as an honest indicator of his quality. We suggest that, because of this relationship, sexual selection exerted by female choice may have played an important role in the evolution of song learning in general, providing at least part of the answer to the question of why birds learn to sing. There are many potential implications and complications of this idea that we do not have the space to develop here. For example, we have considered the hypothesis solely in terms of effects on male song production, but have not yet addressed the equally important issue of how early nutrition affects female perception of song. We close with an overview of two other issues that are particularly relevant.

"Open-ended" learners

Some songbird species are thought to be open-ended learners, meaning that they are able to acquire and develop new songs each spring. Surprisingly little is known about this phenomenon. The canary often is cited

as an example of an open-ended learner because males add new syllables to their repertoires each spring (Nottebohm *et al.*, 1986). As Catchpole and Slater (1995) point out, however, it is not clear whether changes in the adult repertoire involve the development of newly-learned material or simply the production of material that had been learned during an early sensitive phase, because the complete acoustic experience of individuals is not known. To our knowledge, only a single study on starlings (*Sturnus vulgaris*) has demonstrated unequivocally that new song material is memorized in subsequent years of life (Chaiken *et al.*, 1994).

If a species is capable of open-ended learning, however, then its song learning abilities may be contingent not only on the nutritional state of the young bird in its first year of life, but also on nutrition or other factors that exert an influence across the lifetime of the individual. One implication is that song learning in open-ended learners may allow song to serve as a more immediate indicator of a male's condition, and not just an indicator of his condition as a nestling or young fledgling. For example, song learning may provide information on how well a male fared the previous winter, similar to other seasonal condition-dependent secondary sex traits (reviewed in Andersson, 1994).

Repertoire vs. non-repertoire species

Much evidence supports the idea that sexual selection has been responsible for the elaboration of male singing behavior, especially in the evolution of large song repertoires (reviewed in Searcy and Andersson, 1986; Catchpole and Slater, 1995). A key prediction of this idea is that species subject to more intense sexual selection should have more elaborate song repertoires than species experiencing less intense selective pressure. Several studies have examined this relationship, with mixed results. In a comparison of North American wrens, Kroodsmas (1977) found a significant relationship between degree of polygyny (a commonly used correlate of the intensity of sexual selection) and repertoire size. Catchpole (1980) and Catchpole and McGregor

(1985) found the opposite trend in *Acrocephalus* warblers and *Emberiza* buntings, although they argued that song should be under more intense inter-sexual selection in monogamous species in these groups. By contrast, Irwin (1990), did not find a consistent relationship between mating system and repertoire size in a comparative study of icterine blackbirds; nor did Shutler and Weatherhead (1990) observe a pattern in their study of wood warblers (see also Read and Weary, 1992).

Why should the relationship between sexual selection and repertoire size be apparent in some groups but apparently absent in others? Our hypothesis offers a possible explanation for this seeming inconsistency; If sexual selection acts on the learning process itself (see Jacobs, 1996), not simply on the behavioral endpoint of this process, then any measure of how well a male learned to sing that can be assessed by the female will serve as well to provide an accurate indicator of male quality. That is, it is not necessarily how much a male learns that matters, but more generally how well he learns. In some groups, how well a male learned to sing may be evidenced by the quantity of song material that male was capable of learning. In other species, however, how well males learn to sing may be manifest in other ways, such as how precisely a male can copy a particular pattern—perhaps of just a single song type. In these cases, females could assess a male's quality by how well his song conforms to a particular species-specific or population-specific pattern. By focusing attention on the song learning process itself, as opposed to the behavioral endpoint of this process, we may better understand the ways in which female choice has driven the evolution of song in general.

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