

Song Function and the Evolution of Female Preferences

Why Birds Sing, Why Brains Matter

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ABSTRACT: Analyzing the function of song and its evolution as a communication signal provides an essential backdrop for understanding the physiological and neural mechanisms responsible for song learning, perception, and production. The reverse also is true—understanding the mechanisms underlying song learning provides insight into how song has evolved as a communication signal. Song has two primary functions: to repel other males from a defended space and to attract females and stimulate their courtship. The developmental stress hypothesis we present here builds on studies of the development of the song system to suggest how learned features of song, including complexity and local dialect structure, can serve as indicators of male quality useful to females in mate choice. The link between song and male quality depends on the fact that brain structures underlying song learning largely develop during the first few months post-hatching and that during this same period, songbirds are likely to be subject to nutritional and other developmental stresses. Individuals faring well in the face of stress are able to invest more resources to brain development and are expected to be correspondingly better at song learning. Learned features of song thus become reliable indicators of male quality, with reliability maintained by the developmental costs of song. Data from both field and laboratory studies are now beginning to provide broad support for the developmental stress hypothesis, illustrating the utility of connecting mechanistic and evolutionary analyses of song learning.

KEYWORDS: female choice; sexual selection; song development; nutritional stress; indicator mechanism; reliable signaling

INTRODUCTION

Syrinx, according to Greek mythology, was a nymph who chanced to attract the unwanted attentions of Pan, the amorous god of fields, flocks, and fertility. Syrinx fled from Pan, but he pursued her relentlessly, eventually trapping the unfortunate nymph at the marshy edge of a stream. There, in a final effort to preserve her chastity, Syrinx was transformed into a reed, which Pan took and turned into a flute—the pan-

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pipe—that he played ever after in her memory. Some thousands of years after this myth originated, comparative anatomists thought it fitting to name the vocal apparatus of birds in honor of the nymph Syrinx, given the extraordinarily musical and flute-like sounds this organ can produce.

The choice of the name “syrinx” for the avian sound-producing organ is apt for another reason, having to do with Pan’s intentions rather than Syrinx’s fate, and specifically with the similarity between Pan’s motivation and that of a singing male bird. For all the beauty of bird song and the intricacies of its production, the function of song nonetheless boils down to sex. A male bird’s song attracts females and stimulates them to mate. Song also is directed at other males, but the point of the effort typically is to gain exclusive access to an area so that females will settle there for nesting. Either way, song has evolved in the context of singers being selected to increase their individual reproductive success.

Understanding the function of song is important even for the most reductionist analyses because function defines the context in which the mechanisms responsible for the development, production, and perception of song have evolved. We therefore begin this chapter by providing an overview of how song functions as a communication signal. The transfer of insight between ultimate and proximate levels of analysis is, however, a two-way street. A second aim of this essay is to suggest that the question of why female birds respond preferentially to certain features of male song (a persistent problem for behavioral ecologists) might be clarified by considering the brain mechanisms responsible for song learning and production, especially their development. Thus, the remainder of this chapter focuses on implications of these developmental mechanisms for female preferences based on song. Here, we outline an hypothesis that we think can explain how song functions as an indicator of male quality, based on developmental trade-offs affecting brain growth and learning abilities, and we review data from our own work and that of others that addresses predictions of this hypothesis.

THE FUNCTIONS OF BIRD SONG

Does Song Repel Males?

In most species, the peak of singing activity is associated with breeding.^{1,2} During this time, males often sing for hours on end without obviously interacting with other birds, and it is difficult to know whether females, other males, or both are the intended audience. However, if two males interact aggressively, as for example when a neighbor crosses an established territory boundary, they often increase their rate of singing or start singing if they were previously silent.³ If song is played from a loudspeaker within the boundaries of a male’s territory, the territory owner again often increases its singing rate, while approaching and searching for the apparent intruder. Further, when males interact, they often respond to each other using stylized patterns of singing behavior, such as overlapping each others’ songs,^{4,6} changing the rate at which they switch between song types,^{7,8} or matching songs with similar song types.^{9–11} This association between patterns of singing and territorial aggression suggests that song must act as a signal to other males in the context of territory defense.

More direct evidence that song functions in territorial defense comes from experimental approaches such as muting. Muting can be accomplished by either syringeal denervation¹² or puncture of the interclavicular air sac,¹³ and tests whether an inability to sing hampers defense. The most thorough study of this type was done by MacDonald,¹⁴ working with Scott's seaside sparrow (*Ammodramus maritimus*). Males muted by airsac puncture lost all or part of their territories, while the territories of control males increased in size. Both airsac puncture and syringeal denervation are potentially debilitating,¹⁵ but MacDonald¹⁴ found that her muted males showed activity levels just as high as those of the controls, indicating that it was the inability to sing rather than an overall decline in vigor that was responsible for the difficulties the muted males experienced in holding territory.

If loss of song diminishes a male's ability to defend its territory, can song alone be shown to maintain territory? To answer this question, researchers have removed males from their territories and replaced them with loudspeakers from which male song was broadcast at regular intervals. The results of these studies—done with thrush nightingales (*Luscinia luscinia*),¹⁶ great tits (*Parus major*),¹⁷ red-winged blackbirds,¹⁸ white-throated sparrows (*Zonotrichia albicollis*),¹⁹ and song sparrows (*Melospiza melodia*)²⁰—show that territories from which song is broadcast take longer to be reoccupied than territories that remain silent.

Does Song Attract and Stimulate Females?

Observations of singing behavior also suggest that song functions in communicating to females. Peaks in the frequency of male song typically occur during the period when a male is attempting to attract a female to his territory¹ or, slightly later, during the period when females are producing fertile eggs.² If a female is removed from a territory, the territorial male's song rate increases, only to decline again when his mate is returned.^{21,22}

These kinds of behavioral correlations are consistent with the view that song functions as a mate attraction signal, but again it is necessary to demonstrate directly that song influences female behavior. Eriksson and Wallin²³ provided the first such demonstration. They set up nest boxes in a mixed population of pied and collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*), outfitting each box with a stuffed male decoy but providing only half the boxes with loudspeakers playing male songs. Most females caught inspecting nest boxes were found at boxes with song, supporting the function of song as a mate attraction signal. Similar experiments with starlings (*Sturnus vulgaris*)²⁴ and house wrens (*Troglodytes aedon*)²⁵ have confirmed this result.

Beginning with the pioneering work of Lehrman on doves,^{26,27} the effect of song on female reproductive behavior has been demonstrated in a number of bird species. For example, Hinde and Steele²⁸ demonstrated that captive female canaries (*Serinus canaria*) increase their nest building activity when exposed to conspecific song, while Wright and Cuthill²⁹ showed that wild starling females laid their clutch earlier the more their mate sang. A striking short-term effect of song on female behavior is that it provokes in many passerines a distinctive and stereotypic precopulatory display, in which the female crouches and raise her tail in preparation for copulation, often while shivering her wings and making precopulatory calls. A patient observer will observe this response in the field, but the display also can be elicited in captive

females of many species by exposing them to recorded song.^{30,31} This fact both provides further evidence that song functions in female mate choice and led to the development of what is now a widely used laboratory method—the “solicitation assay”—for determining what features of song are preferred by females.

SONG AS AN INDICATOR MECHANISM IN MATE CHOICE

The term “indicator” refers to a signal that correlates reliably with the condition or viability of the signaler, with the correlation between signal expression and individual quality being maintained by some cost associated with the signal. If a signal is a reliable indicator, it may be used by an individual of the opposite sex to identify a high quality mate.³² The idea that an indicator trait must have some underlying cost is critical to understanding how indicators work in mate choice. Females, as the sex investing more in reproduction, are expected to be choosier than males about the quality of their mates. Males, as the sex more eager to mate, are expected to exaggerate their quality whenever it is possible to do so. Females therefore should respond to signals of male quality only if the reliability of the signal, that is the correlation between signal properties and male quality, is somehow ensured. Signal costs can ensure reliability if the costs fall differentially on low quality males, so that optimal signaling levels (where costs balance benefits) are lower for low quality than for high quality males. Signal costs that can maintain reliability may include the time and energy expended during signaling, but they also may include the costs associated with developing the trait or display.^{33–37}

Indicator traits may provide information related to both “indirect” and “direct” benefits a female might receive by mating with a particular male. If the expression of a trait is somehow linked to a male’s genetic quality, for example because he has “good genes” that allow him to avoid parasites and thus have more resources to produce a high-quality signal, then the female may obtain “indirect benefits” that affect her fitness through improved viability of her offspring.³⁸ A female also may benefit from mating with a phenotypically superior male because such males provide better territories, better parental care, or other “direct benefits” that improve the female’s own survival and fecundity.³⁸ Note that the expression of an indicator trait can be influenced by both environmental and genetic factors, and thus indicators can potentially signal both phenotypic and genotypic quality. Theoretical models demonstrate that female preferences can evolve either when females obtain only direct benefits by mating with phenotypically superior males^{38–42} or when they obtain indirect benefits by mating with genotypically superior males.^{43–45}

The emblematic example of an indicator trait is the elaborate train of the male peacock (*Pavo cristatus*). Females prefer to mate with males having larger tails, specifically those that have more “eyesspots” in the train. Producing and maintaining such large tails is costly, however, and not all males are able to produce equally large trains. Males with large trains have offspring with better growth and survival,⁴⁶ so females receive an indirect benefit from preferring these males. In another well-known example, male house finches (*Carpodacus mexicanus*) have red coloration on the feathers of their head and breast, but there is considerable variation among individual males in the extent to which this color is expressed and female house finches prefer males with bright plumage.^{47–49} Plumage brightness is strongly influenced by

the amount and type of carotenoids present in the diet at the time of the post-winter molt and thus can serve as a reliable indicator of male condition.⁵⁰ Brighter males provide better parental care, which is a direct benefit to the females that choose them as mates.⁴⁸ Brighter males also have a higher overwinter survival, suggesting that brightness may be an indicator of viability. Brightness of fathers is positively correlated with brightness of sons, consistent with the idea that females also obtain indirect benefits for their offspring by mating with brighter males.⁴⁸

The fact that a male bird's song may influence a female's choice of mates suggests that song may function, like the peacock's tail and the house finch's red coloration, as an indicator of male quality.^{32,51,52} This suggestion, however, raises a difficulty in that many of the features of song on which female birds base their preferences have no obvious costs.

SONG FEATURES THAT INFLUENCE FEMALE CHOICE

As a prelude to addressing how song can serve as an honest indicator of male quality, we next ask what features of song appear to be important in female choice. Not surprisingly, not all species exhibit preferences for the same song features, and certain female preferences may be idiosyncratic to particular species. However, three broad categories of features seem to have the most consistent effects: song output, song complexity, and local song structure. A fourth category, vocal performance, is only now beginning to emerge as a feature of song important to female mate choice. For each of these categories, we first point out key studies illustrating the preference and we then ask what, if any, cost might be associated with the song feature that could maintain its reliability as a signal of male quality.

Song Output

In many species, females prefer males that have a higher song output, that is, that simply sing more. In some species (e.g., European starlings) males that sing longer song bouts pair earlier, obtain more mates in the field, and are preferred by females in laboratory solicitation assays.⁵³ Male blue tits (*Parus caeruleus*) singing longer songs are more successful in obtaining extra-pair fertilizations and are less likely to lose paternity to other males.⁵⁴ Female white-throated sparrows also respond more to longer songs in the lab.⁵⁵ In other species, females have been shown to prefer males that sing at a faster rate. Female pied flycatchers pair more quickly in the field with males that have faster song rates^{56,57} and female zebra finches (*Taenopygia guttata*) respond more to higher song rates in laboratory tests.⁵⁸

It is easy to understand how song output can be a costly signal of male quality. Although the energetic costs of producing song appear to be low,^{59,60} singing costs something in time if not in energy, regardless of what is sung. Presumably, males in better condition can afford to devote more time and effort to singing than can males in poorer condition. Male condition, in turn, may correlate with direct benefits a female obtains, if males in good condition have superior territories or provide better parental care, or may correlate with indirect benefits to the extent that condition reflects "good genes" affecting offspring viability.

Song Complexity

One of the most commonly demonstrated song preferences is a preference for more complex song repertoires. Complexity can be measured either as the number of discrete song types a male can produce or, in the case of species having more continuous songs, as the number of syllable types in a male's repertoire. For example, male sedge warblers (*Acrocephalus schoenobaenus*) with larger syllable type repertoires have been shown in field studies to obtain mates at an earlier date,^{61,62} while male great reed warblers (*A. arundinaceus*) with larger syllable repertoires obtain more extra-pair fertilizations.⁶³ Great reed warblers males with larger syllable repertoires also attract more social mates,⁶⁴ as do male red-winged blackbirds (*Agelaius phoeniceus*) with larger song type repertoires.⁶⁵ In the laboratory, females have been shown to perform more courtship displays in response to larger song type repertoires in song sparrows^{31,66} and great tits,⁶⁷ and in response to larger syllable repertoires in sedge warblers⁶⁸ and great reed warblers.⁶⁹ Unlike song output, song complexity is hard to explain as a reliable indicator of quality because it is not apparent why complex songs would be more costly to produce than simple ones.

Local Song Structure

A third aspect of song that affects female preferences is whether songs are local or foreign in origin. In white-crowned sparrows (*Zonotrichia leucophrys*)⁷⁰ and corn buntings (*Miliaria calandra*),⁷¹ geographic variation in song is pronounced over very short distances with distinct boundaries occurring between "dialect" regions. In most species, however, variation is more gradual with differences only apparent over broad geographic ranges.⁷² In either case, females generally discriminate against songs recorded from foreign populations and prefer songs sung by males from their own local population.⁷³

The differences between songs from two geographic locales can be subtle⁷⁴ and it is unclear how producing songs typical of one locale can be more costly than producing songs typical of another. One oft-cited hypothesis for the evolution of local song preferences is that females benefit by mating with locally born males by obtaining genes that are particularly well adapted to local conditions.^{75,76} There is scant direct support for local genetic adaptation in birds, however. Further, females seem to prefer local song even in species in which males learn song after dispersal, in which case song is not indicative of a male's natal population.^{77,78} Equally problematic is the fact that, in species with gradual geographic variation, typical dispersal distances may make it unlikely that a female would ever hear a song outside the range that she accepts as equally attractive to local song.⁷² Thus, the genetic adaptation hypothesis does not appear to be a general explanation for the evolution of female preferences for local song.

Vocal Performance

Performance features are attributes of song that affect how difficult a song is to produce. Physical and physiological constraints must exist that limit the sounds that birds are able to produce, and performance features are song traits that exhibit how closely a male is able to push those limits. There is now growing evidence that how well a male produces these sounds, or whether he produces them at all, serves as a

measure of male quality.^{79,80} Examples of female preferences based on vocal performance include a preference in canaries for a particular class of complex syllables,⁸¹ a preference in dusky warblers (*Phylloscopus fuscatus*) for songs maintaining a consistently high amplitude across elements,⁸² and a preference in swamp sparrows (*Melospiza georgiana*) for songs having both a rapid trill rate and a wide frequency bandwidth.⁸³ In the last case, the biomechanical basis of the performance limitation is particularly well understood. When producing a high frequency sound, songbirds must open their beaks widely, shortening the vocal tract and raising its resonance frequency. Conversely, to produce a low frequency sound the beak must be relatively closed, lengthening the tract and lowering its resonance frequency.^{84,85} Because trilled swamp sparrow songs are composed of rapid frequency-modulated notes, there is a performance trade-off between how fast a bird can repeat syllables in a trill (trill rate) and how broad a range of frequencies each repeated syllable encompasses (frequency bandwidth).⁸⁶ In simple terms, the trade-off is a consequence of the fact that it is difficult for birds to open and close their beaks both widely and rapidly. Balentine and colleagues⁸³ demonstrated that female swamp sparrows respond preferentially to songs that lie near the upper limit of the bandwidth–trill rate tradeoff relative to songs that lie farther from that limit, consistent with the hypothesis that females use vocal performance to assess males in this species.

To the extent that vocal performance is like any other “performance” measure, for example the performance of a lizard running on a treadmill, then song may correlate with other aspects of male phenotype that directly affect female reproductive success, or aspects of male genotype that reflect heritable factors affecting performance. This idea, however, begs the question of how song performance is linked to other aspects of phenotype or genotype.

THE “DEVELOPMENTAL STRESS HYPOTHESIS”

Theory holds that signals can be reliable indicators of quality if they are costly,³⁵ yet many of the features of song on which female birds base their preferences appear to be cheap to produce. To resolve this apparent paradox, Nowicki and colleagues⁸⁷ proposed what they originally named the “nutritional stress hypothesis.” This hypothesis postulates that learned features of song can serve as reliable indicators of male quality because the brain structures underlying song learning and production develop during a period early in life when young birds are likely to be susceptible to developmental stress, largely due to undernutrition. Individuals may differ both in the magnitude of the stress they experience and in their developmental response to a given level of stress. In either case, individuals faring well in the face of this potential stress will be better able to invest resources necessary for development in general and for brain development in particular. Variation in brain development, in turn, will translate into variation in song learning abilities among males. By choosing males based on song features that reflect the outcome of song learning, females obtain mates that have fared better in the face of developmental stresses experienced early in life. The reliability of song as an indicator of male quality, then, is maintained by the cost of developing the neural substrate for song learning.

Buchanan and colleagues⁸⁸ have argued that stressors other than undernutrition also may affect brain development and thus have suggested renaming this hypothesis

the “developmental stress hypothesis.” For example, parasites attack young birds of most species, with a variety of detrimental effects.^{89,90} In some respects, the effects are parallel to those of undernutrition, in that parasites can potentially drain away resources from the host and cause the host to mount energetically costly defenses.⁹¹ Indeed, in a recent study of sedge warblers, Buchanan and colleagues⁹² found a negative relationship between parasite load and aspects of song, including repertoire size, consistent with the hypothesis that parasite-induced stress lowers condition in males, which in turn affects their singing behavior. Similarly, unpredictable food supplies may also have stressful effects on development.⁸⁸ Social interactions may impose developmental costs through the activation of hormonal stress pathways. Thus, a number of stressors experienced early in life may act synergistically to adversely affect song system development and song learning. In any case, the amount of stress experienced by an individual and that individual’s response to the stress it experiences should be reflected in brain development and song learning. In this way, the expression of song features may correlate with male quality, with the reliability of the signal maintained by the fact that brains are costly to build.

Song learning may be a particularly good indicator of the effects of post-hatch developmental stress because the song system develops later than other parts of the nervous system (FIG. 1).^{87,93,94} The general pattern, based largely on work with ze-

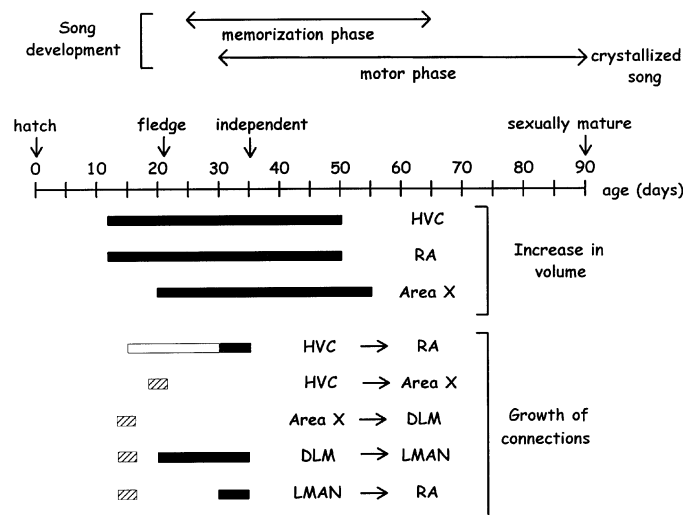


FIGURE 1. Time line of zebra finch life history events, song learning, and development of the song system. The memorization phase spans approximately 25 to 65 days of age, and the motor phase begins at about 30 days of age and continues until crystallized song production.^{131,132} Zebra finches fledge at about 20 days of age¹³¹ and are not fully independent from parental care until approximately 35 days of age.⁵² *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 other references in text. (From Nowicki and colleagues,⁸⁷ reproduced with permission.)

bra finches, is that the song system undergoes considerable growth, from approximately 10 to 50 days post-hatching.⁹⁵⁻⁹⁹ 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.^{95,97} 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.^{95,96} Most neurons in the canary HVC also are added after hatching.^{100,101} In this species, the increase in size of HVC and RA begins later than in zebra finches, around 30 days of age; RA doubles in size by 60 days with correspondingly large increases in the size of HVC, although HVC continues to grow incrementally for another several months.¹⁰² The progression is similar in swamp sparrows¹⁰³ with the majority of growth of HVC, RA, and Area X completed by 61 days post-hatch.

Even more critical from a functional point of view, synaptic connections between song system nuclei also continue to develop in the first several weeks after hatching (FIG. 1). In the zebra finch, for example, HVC neurons project to RA between 15 and 30 days of age and then hold at the border⁹⁹ until they rapidly innervate RA between 30 and 35 days of age.⁹⁶ Although HVC connections to Area X in the canary are almost all completed in the embryo stage, some connections also are established after hatching.¹⁰⁰ Area X connections to DLM in the zebra finch appear to be established in the first 15 days post-hatch.⁹⁸ DLM axons appear to innervate LMAN by 15 days of age as well in the zebra finch, but there is "exuberant" growth from DLM to LMAN between 20 and 35 days of age.⁹⁸ Finally, in the zebra finch, some LMAN projections may reach RA as early as day 15, but they are readily detected after day 30.⁹⁹

At the same time these critical events in song system development are occurring, young songbirds are particularly susceptible to developmental stress. A typical songbird nestling reaches 90% of its adult weight within the first 10 days of life.¹⁰⁴ Growth rates depend on the amount of food delivered by parents, and starvation is common.^{105,106} Even after fledging, young songbirds depend on their parents to deliver food for several days or even weeks as their own foraging skills improve.¹⁰⁷ In general, the growth and survival of young songbirds is clearly tied to the level of nutrition provided by parents during the nestling and fledgling stages.^{108,109}

The deleterious effects of early nutritional and other developmental stressors on brain development are well-established in mammals.¹¹⁰⁻¹¹² Development may be more buffered against resource deprivation in birds than in mammals, but the rapid development of structures in the avian brain may be particularly vulnerable to undernutrition.¹¹³ To the extent that developmental stress does affect brain development in young songbirds, variation in the development of brain structures responsible for song learning and production will lead to variation in song learning abilities among males. Females mating with males that have learned better will be choosing mates that fared better in the face of stresses experienced early in life and who thus have otherwise superior phenotypes, and to the extent that response to stress involves heritable factors, superior genotypes as well. Both how much and how well song is learned may be equally useful cues for females to use when assessing males. Indeed, the common preference of females for local versus foreign songs may reflect the perception that they are less well learned.^{72,114} The "developmental stress hypothesis" thus accounts for the widespread preferences both for more complex songs and for more local-sounding songs, with signal reliability being maintained by developmental costs in each case.

TESTING PREDICTIONS

The developmental stress hypothesis makes a number of straightforward predictions that we can use to test the validity of this idea. First, developmental stress experienced in the nestling and fledgling stages of a bird's life should have a lasting effect on brain structures involved in song memory and production. Second, early stress should affect features of the songs of adult males that females attend to in mate choice. Third, developmental stress should affect other aspects of male phenotype that are important to a female when choosing a mate. This last is necessary if song traits are to be honest indicators of aspects of male phenotype of interest to females. Below, we address each of these predictions in turn.

Prediction 1: Stress Affects Brain Development

Nowicki and colleagues¹¹⁵ hand-raised two groups of swamp sparrow nestlings, a control group fed *ad libitum* and an experimental group fed only 70% of the volume of food given the controls. The groups were otherwise raised under identical conditions. The nutritional restriction was maintained for 14–18 days, but the major difference in amount of food available to the two groups only lasted 7–10 days because birds began to feed themselves after they fledged. At 14 months, during what would be their first breeding season, birds were perfused and their brains measured. The nutritional manipulation had a clear effect on the song system, with the controls having significantly greater volumes for both HVC and RA than the stressed group (FIG. 2). Of course, these differences could be accounted for by an overall size difference in the brains of the two groups and indeed the telencephalon as a whole also was significantly larger for the control group. However, the ratio of RA:telencephalon also was significantly greater in the controls than the experimentals, demonstrating that this nucleus was disproportionately affected by stress during development.

Thus, in swamp sparrows, a brief exposure to nutritional stress occurring within the first couple of weeks after hatching has a measurable and lasting effect on the brain and on the song system. Developmental programs may be able to compensate for limitations by redirecting resources from less critical phenotypic component in order to buffer more essential components such as the brain, by delaying the rate of maturation, or through compensatory growth later on in life.¹¹³ The result of Nowicki and colleagues¹¹⁵ shows that such strategies do not completely compensate for the effects of early stress on brain development.

Prediction 2: Stress Affects Features of Song Important to Females

Two studies have tested this prediction with correlative field data. Doutrelant and colleagues¹¹⁶ found a positive correlation between repertoire size and tarsus length in adult blue tits, with the latter measure known to reflect early nutrition. In a more direct test, Nowicki and colleagues¹¹⁷ found that nestling feather growth, also known to be influenced by nutritional stress, was positively correlated with syllable repertoire size of adults in great reed warblers (FIG. 3). Female great reed warblers are known to prefer males with large repertoires,^{64,69} so this result supports the idea that developmental stress affects song parameters important to females.

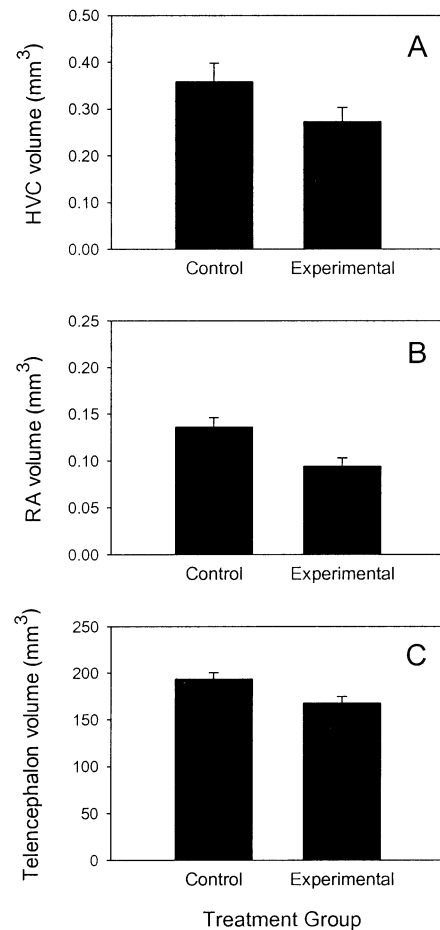


FIGURE 2. Effects of early nutritional stress on volume of brain areas in adult male swamp sparrows. (A) Nucleus HVC ($P=0.028$); (B) nucleus RA ($P=0.011$); (C) telencephalon ($P=0.028$). $N=8$ control, 7 experimental birds in all cases. Volume data were averaged across left and right hemispheres for each individual in the analysis. (From Nowicki and colleagues,¹¹⁵ reproduced with permission.)

Several recent experimental tests also test this prediction. In the experiment with swamp sparrows described above, Nowicki and colleagues¹¹⁵ measured the effects of early nutritional stress on several aspects of adult song. Song repertoire sizes did not differ between the stressed experimental males and the well-fed controls. Experimentals and controls did differ, however, in the accuracy with which they copied the songs they heard when young, as measured by calculating spectrogram cross correlations between learned notes and tutor notes. No test has yet been made of whether female swamp sparrows prefer accurately copied songs, but Nowicki and colleagues¹¹⁴ tested this prediction in a close relative, the song sparrow. Male song sparrows were taken as nestlings and hand-reared, either with or without nutritional restriction, and tutored during their sensitive phase with songs recorded in their natal locality. The songs produced by these males as adults were assessed for accuracy of learning, based on the proportion of notes that were copied from the tutor songs and the mean spectrogram cross correlations between the learned notes and the tutor

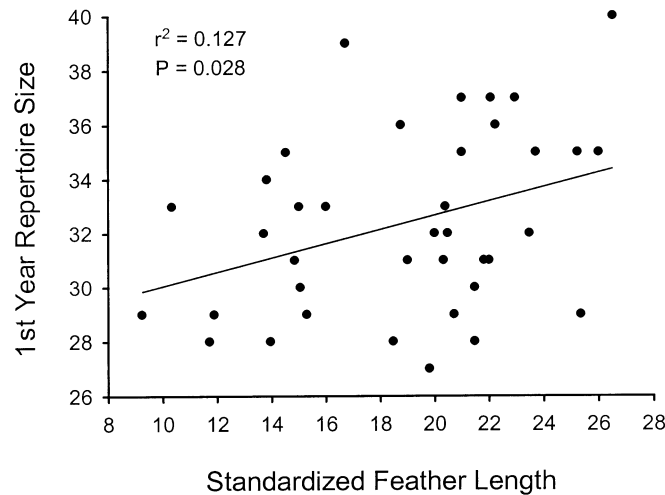
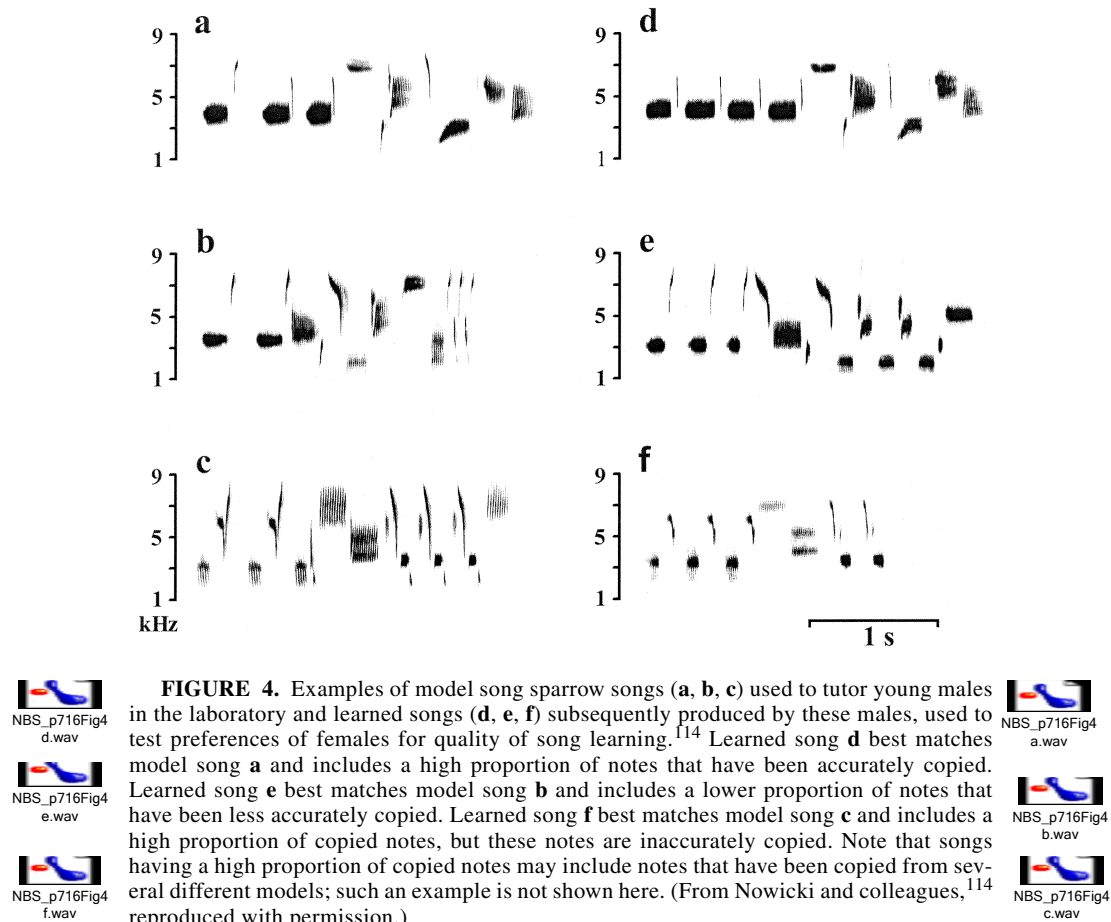


FIGURE 3. The relationship between standardized nestling primary feather length and subsequent first-year repertoire size of individual male great reed warblers, demonstrating a relationship between measures of growth and development and subsequent repertoire complexity in a field population. $N=38$, $r^2=0.127$, $P=0.028$. (From Nowicki and colleagues,¹¹⁷ reproduced with permission.)

notes. Females from the same locality were then tested for response to sets of these songs that differed in learning accuracy (FIG. 4). In one test, females responded with significantly more courtship displays to well-learned songs, when the well-learned songs differed from the poorly learned songs in both the proportion of copied notes and copy accuracy. In a second test, the proportion of copied notes was held constant, and females still showed a preference for well-learned songs that differed only in copy accuracy from the poorly learned songs. These results, then, provide evidence for a female preference in song sparrows based on a song trait known to be influenced by early nutritional stress in the congeneric swamp sparrow.

Buchanan and colleagues⁸⁸ stressed fledgling starlings for 80 days starting at 35–50 days post-hatching—a time when some song control nuclei, notably RA, are expected to increase in size—by removing food unpredictably from the experimental group for four hours each day. When song traits were measured at the start of the next breeding season, previously stressed birds had lower song output by a number of measures, including time spent singing, number of song bouts, and mean song bout duration. The last measure is particularly interesting, as bout duration is correlated with syllable repertoire size in starlings, and female starlings prefer males with longer song bouts and higher repertoire sizes.^{53,118}

Spencer and colleagues¹¹⁹ stressed zebra finches between 5 and 30 days, by two methods. In one, the parents were given restricted access to food; in the other, the young birds were directly fed corticosterone, a hormone that mediates stress in birds. Both treatments affected the subsequent adult songs of the stressed birds with respect to song duration, number of syllables per song, and maximum frequency. Clay-



ton and Pröve¹²⁰ had previously shown that female zebra finches discriminate in courtship based on two of these song parameters, song duration and number of syllables per song. The zebra finch results are thus in accord with the other studies showing that females attend to song features affected by early stress.

Prediction 3: Stress Affects Male Phenotypic Quality

We have tested this prediction in song sparrows,¹²¹ using nutritional treatments slightly more severe but parallel to those shown to affect song learning in swamp sparrows.¹¹⁵ The controls had significantly higher growth rates and at the end of treatment (at 18 days) were approximately 7% larger in tarsus length, 10% larger in primary length, and 40% larger in mass. As adults, the controls remained significantly larger in body size, as measured by a principal component measure combining

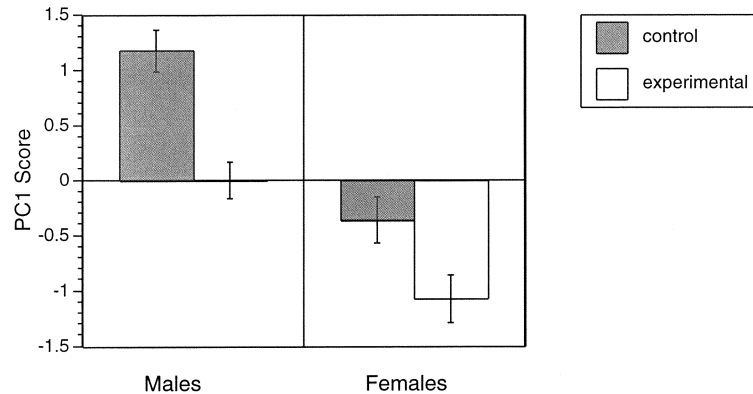


FIGURE 5. Adult body size of song sparrows as measured by the PC1 scores combining six post-mortem skeletal measurements, illustrating the lasting phenotypic effect of limited exposure to nutritional stress experienced when young. The scores are shown as the means of the brood/sex means (\pm SE). Both treatment and sex effects are significant. (From Searcy and colleagues,¹²¹ reproduced with permission.)

post-mortem measurements of six skeletal characters (FIG. 5). Individual bone lengths in the controls were about 2–3% larger than in the stressed birds. Early nutrition has also been shown to affect adult size in zebra finches¹²² and ring-necked pheasants (*Phasianus colchicus*).¹²³

Body size is known to affect fitness in birds. Large individuals, for example, often have a survival advantage during adverse weather,^{124–126} and in some species female birds prefer large over small males as mates.^{54,127} Since early nutrition affects both song and adult size, female might use song to assess size in potential mates. It seems more likely, however, that females would assess size visually, and use song to assess more subtle aspects of phenotypic quality. Birds whose growth rates are nutritionally restricted for some period are often able to catch up later, at least in part, using compensatory strategies such as delayed maturation and accelerated growth.¹¹³ The nutritionally restricted birds in our song sparrow study, for example, reduced their size disadvantage relative to the controls after the end of the diet manipulation by means of a slight delay in maturation and a large reduction in the magnitude of post-fledging weight recession. Compensatory strategies such as these, however, entail a variety of costs in terms of the quality of development.¹²⁸ Experimental evidence exists showing that compensation for depressed growth does produce costs, including adult obesity in rats (*Rattus norvegicus*),¹²⁹ depressed locomotory performance in Coho salmon (*Oncorhynchus kisutch*),¹³⁰ and shorter lifespan in zebra finches.¹²²

Another negative phenotypic consequence of early nutritional stress is poor development of the immune system. Again, such a cost might be incurred either as a direct effect of a nutritional deficit or as an effect of attempts to catch up in growth after the period of poor nutrition has ended. Buchanan and colleagues⁸⁸ found that nutritional stress in young starlings depressed humoral immune response relative to controls during the period of stress, but they did not assess whether immune response

continued to be depressed later in life. Our experiment with nutrition in song sparrows produced evidence that early stress has a negative effect on humoral immune response that persists into adulthood (Hasselquist, Nowicki, Duckworth and Searcy, unpublished data).

CONCLUSIONS

Studies of the function of song by behavioral ecologists and of the mechanisms of song development and production by neurobiologists should inform and guide each other. A review of the evidence from behavioral ecology demonstrates that the primary functions of bird song are in male-male competition for territory and in the attraction of females for mating. These general functions, and their variations across species, should help us interpret why the mechanisms of song development and production work the way they do. At the same time, whatever is learned about mechanisms can be used to illuminate and deepen hypotheses on the evolution of song as a communication signal. The developmental stress hypothesis illustrates the way in which knowledge of mechanisms informs a functional hypothesis.

The developmental stress hypothesis is primarily an idea about the hidden costs of the song traits used by females to choose mates. Theoretical analyses of the evolution of animal communication have shown that mating signals should be costly if they are to be reliable. Studies of behavior have determined what aspects of song are important to females in mate choice. With the exception of song output, preferred song traits have little or nothing in the way of immediate production costs, suggesting that the important costs must be developmental. Knowledge of the brain structures that support song in songbirds and of the timing of the development of these structures, suggests when and how stresses might operate to influence song development. The evidence available to date confirms key predictions of the developmental stress hypothesis: there are effects of early stress on the development of the song control system in the brain, and on at least some of the song traits on which female birds base their mating preferences, and these same preferences affect other aspects of the phenotype that might in turn affect the direct and indirect benefits females receive from mating with particular males. The developmental stress hypothesis thus has been successful, both in receiving empirical support from new data, and, perhaps more importantly, in suggesting new avenues for investigation.

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