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ULTIMATE MECHANISMS OF SONG LEARNING

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Brain development, song learning and mate choice in birds: a review and experimental test of the “nutritional stress hypothesis”

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Abstract The nutritional stress hypothesis explains how learned features of song, such as complexity and local dialect structure, can serve as indicators of male quality of interest to females in mate choice. The link between song and quality comes about because the brain structures underlying song learning largely develop during the first few months post-hatching. During this same period, songbirds are likely to be subject to nutritional and other stresses. Only individuals faring well in the face of stress are able to invest the resources in brain development necessary to optimize song learning. Learned features of song thus become reliable indicators of male quality, with reliability maintained by the developmental costs of song. We review the background and assumptions of the nutritional stress hypothesis, and present new experimental data demonstrating an effect of nestling nutrition on nestling growth, brain development, and song learning, providing support for a key prediction of the hypothesis.

Keywords Indicator mechanism · Neural development · Nutritional stress · Sexual selection · Song learning

Abbreviations *HVc* high vocal center nucleus (formerly nucleus hyperstriatum ventralis, pars caudalis) · *RA* robust nucleus of the archistriatum · *SCC* spectro-gram cross-correlation

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Introduction

The development of song in male oscine birds is supported by an extraordinary set of brain mechanisms specialized for the memorization of external song models and for the translation of these auditory memories into motor output. The endpoint is an equally remarkable acoustic display, which functions, in part, in attracting females and stimulating their courtship (Searcy and Andersson 1986; Catchpole and Slater 1995). In the context of mate choice, female birds show preferences based on a variety of song features (Searcy and Yasukawa 1996), some of which are the direct product of song development. Two of the commonest preferences are for complexity of song repertoires and for fidelity to the local dialect, features that reflect, respectively, the quantity and quality of learning in males. The existence of such preference raises the question of why females should care about male song learning. Stated another way: how do females benefit from choosing a male that has been, by some measure, successful in song development?

For a signaling system to be maintained by natural selection, both the signaler and receiver must benefit on average from the interaction. In the case of a mating signal such as birdsong, signalers (males) and receivers (females) have conflicting evolutionary interests. Males, on the one hand, are selected to produce signals that manipulate females to the male’s advantage, which is likely to mean that males will exaggerate their own quality when possible. Females, on the other hand, are selected to respond only to signals containing reliable information that is of value to them (Dawkins and Krebs 1978). Theory suggests that in such cases signaling systems will only be stable if the signals carry some cost that enforces their accuracy, or “honesty” (Zahavi 1975; Grafen 1990a). Only if song features are costly can they be reliable signals of something females want to know, such as male quality. This leads us to rephrase the question as follows: in what way could superior performance in song development be costly?

One potential answer to this question, the "nutritional stress hypothesis" (Nowicki et al. 1998), explicitly links the selective factors responsible for the evolution of song preferences in females to the brain mechanisms that underlie song development and production in males. Specifically, the hypothesis proposes 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 very likely to experience developmental stress resulting from undernutrition. Individuals may differ both in the magnitude of the stress they experience and in their developmental response to a given level of stress. Variation in brain development, the hypothesis argues, will translate into variation in song learning abilities among males. Better brains enable young songbirds to learn better or more, but are more costly to build (Catchpole 1996). Thus, the cost of song is a developmental one – by choosing males based on song features that reflect the outcome of song learning, females really are choosing males that fared better in the face of nutritional (and other) stresses experienced early in life. Such males are likely to be phenotypically or genotypically superior, or both. In either case, females gain reliable information about male quality based on song.

This paper is divided into four main sections. In the first, we briefly review current thinking about signal reliability and mate choice, to provide background on the evolutionary context from which our ideas emerge. Second, we review what is known about female preferences for male song, in order to establish which preferences can be accounted for by current theory and which cannot. Third, we review the nutritional stress hypothesis in detail, outlining previously published evidence in support of the argument. In the fourth section, we present new experimental data testing a key prediction of the hypothesis: that a limited period of nutritional stress experienced early in life will adversely affect brain development and song learning abilities.

Indicator mechanisms and the evolution of female preferences

An indicator is a trait that provides an index of individual condition or viability (Andersson 1994). Any trait that is a reliable indicator in one sex may be used by the opposite sex to identify superior mates, and in many cases the exaggeration of signals and ornaments associated with mating behavior is thought to be the result of sexual selection acting on such indicator traits (Andersson 1994). The interests of signaler and receiver in mate choice are rarely identical, however. Signalers may benefit from dishonesty (Dawkins and Krebs 1978), i.e., from producing a signal that indicates a higher quality than they actually possess. As a consequence, receivers should be selected to respond to a signal only if the reliability of that trait is somehow ensured (Grafen 1990a, 1990b). Theoretical modeling predicts in such situations that indicators will be reliable only if they are costly to produce (Zahavi 1975; Enquist 1985; Grafen 1990a; Johnstone and Grafen 1993). Signals used in mate choice are expected generally to be indicators of signaler quality whose reliability is maintained by production costs, which may include the time and energy expended during signaling, as well as costs associated with developing the display (Vehrencamp 2000).

Female choice for male traits that serve as indicators can evolve through either direct or indirect selection (Kirkpatrick and Ryan 1991). Direct selection means that females benefit from a preference by an increase in their own survival or fecundity, for example through obtaining a better territory or more parental care from the male. Indirect selection means that females benefit from their preference by an increase, not in their own fitness, but in the fitness of their offspring. Offspring fitness is enhanced, under indirect selection models, because the preferred males pass to their offspring superior genes for viability or attractiveness. Clearly, the expression of an indicator trait can be influenced by both environmental and genetic factors, and thus indicators can potentially signal either phenotypic or genotypic quality. Population genetics models suggest that female choice can evolve if females obtain only direct benefits by mating with phenotypically superior males (Grafen 1990b; Hoelzer 1989; Heywood 1989; Price et al. 1993), as well as if they obtain indirect benefits by mating with genotypically superior males (Andersson 1986; Pomiankowski 1987; Iwasa et al. 1991).

Work on plumage color provides an example of how the expression of indicator traits can be influenced by both environmental and genetic factors, and thus of how indicators can signal phenotypic quality, genotypic quality, or both to potential mates. Hill (1990, 1991) has shown that female house finches (*Carpodacus mexicanus*) prefer to mate with males having bright red plumage over duller males. Plumage brightness is strongly influenced by the amount and type of carotenoids present in the diet at the time of the post-winter molt, as well as by general nutritional status, making red feather color a reliable indicator of male nutritional status (Hill 1992, 2000). Brighter males provide better parental care, which is a direct benefit to the females that choose them as mates (Hill 1991). Brighter males also have a higher overwinter survival, suggesting that brightness is 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 (Hill 1991). Thus, females benefit directly and perhaps indirectly by preferring to mate with males having brighter red plumage, so selection is expected to favor the evolution of this female preference.

Features of birdsong that influence female choice

Empirical studies have identified a wide array of song features that affect female preferences in one species of songbird or another. Across all species, however, three broad categories of features have the most consistent effects: song output, song complexity, and local song structure (Searcy and Nowicki 2000).

Song output

In several species of songbirds, females prefer high song output in males, where output is measured in terms of the length of songs or the rate at which they are sung. In European starlings (*Sturnus vulgaris*), for example, males singing long song bouts pair earlier and obtain more mates in the field, and they are preferred by females in laboratory experiments (Eens et al. 1991). A correlation between male song rate and success in mate attraction has also been demonstrated for the pied flycatcher *Ficedula hypoleuca* (Gottlander 1987; Alatalo et al. 1990). Male blue tits (*Parus caeruleus*) singing long songs are more successful in obtaining extra-pair fertilizations and are less likely to lose paternity to other males (Kempenaers et al. 1997). In laboratory tests, female zebra finches (*Taenopygia guttata*) prefer to associate with males singing at higher rates (Collins et al. 1994) and female white-throated sparrows (*Zonotrichia albicollis*) perform more courtship display in response to longer songs (Wasserman and Cigliano 1991).

Song complexity

Female songbirds prefer more complex song repertoires in a number of species. Repertoire complexity is measured as either the number of song types or, in the case of species having more variable or continuous songs, as the number of syllable types the male is able to sing. Captive females perform more courtship displays in response to larger song type repertoires in song sparrows *Melospiza melodia* (Searcy and Marler 1981; Searcy 1984) and great tits *Parus major* (Baker et al. 1986) and in response to larger syllable repertoires in sedge warblers *Acrocephalus schoenobanus* (Catchpole et al. 1984) and great reed warblers *A. arundinaceus* (Catchpole et al. 1986). In the field, males with large repertoires attract mates earlier in sedge warblers (Buchanan and Catchpole 1997; Catchpole 1980), attract more mates in red-winged blackbirds *Agelaius phoeniceus* (Yasukawa et al. 1980) and great reed warblers (Hasselquist 1998), and obtain more extra-pair fertilizations in great reed warblers (Hasselquist et al. 1996).

Local song structure

Song in songbirds typically varies geographically. In some species, such as white-crowned sparrows *Zonotrichia leucophrys* (Marler and Tamura 1962) and corn buntings *Miliaria calandra* (McGregor 1980), extensive variation occurs over quite small distances with distinct boundaries between "dialect" regions. In other species, such as song sparrows (Searcy et al. 1997, 2002), variation is more gradual, with differences only apparent over broad geographic ranges. Irrespective of how songs vary geographically, females generally prefer songs sung by males from their own local population over songs recorded elsewhere, even when they are unfamiliar with the particular songs heard in both cases. This preferential response to local over foreign songs has been demonstrated in white-crowned sparrows (Baker and Cunningham 1985), song sparrows (Searcy et al. 1997, 2002), brown-headed cowbirds *Molothrus ater* (King et al. 1980), yellowhammers *Emberiza citrinella* (Baker et al. 1987), and red-winged blackbirds (Searcy 1990), among a number of other species (Searcy 1992).

Are song features reliable indicators?

Of these three categories of preferences, the preference for high song output seems easiest to explain evolutionarily. Singing incurs costs in both time and energy regardless of what is sung, so high song output can serve as a reliable indicator of a male's condition; males in better condition can afford to devote more time and energy to singing than can males in poorer condition. Male condition, in turn, may correlate with direct benefits a female obtains by nesting on a territory with superior resources or from having more parental care contributed by her mate. By choosing males in better condition, females also may obtain indirect benefits in the form of "good genes" for foraging ability or general viability.

The link between male quality and either song complexity or fidelity to a local dialect is much less clear. Empirical evidence indicates that such a link must exist, however, at least for song complexity. In a sample of male song sparrows from an island population, variation in repertoire size accounted for a staggering 50% of the variation in lifetime reproductive success, with repertoire size significantly correlated with both years of territory tenure and annual reproductive success (Hiebert et al. 1989). These relationships are not explained by repertoire size increasing with age; male song sparrows recorded in successive years show no change in the number of song types they produce (Searcy et al. 1985). Instead, the implication is that males with larger repertoires are of higher phenotypic quality at any given age. Strong correlations between repertoire size and fitness measures also have been found in great reed warblers (Hasselquist et al. 1996; Hasselquist 1998) and great tits (McGregor et al. 1981; Lambrechts and Dhondt 1986). Song repertoire size thus appears to be an indicator of male quality. The problem with this conclusion, however, is that singing multiple song or syllable types seems to entail no additional time or energy costs over producing single types so it is not clear how the reliability of this indicator is enforced. If anything, singing different song types may decrease exhaustion to the extent that different types use different patterns of neuromuscular activity (Lambrechts and Dhondt 1988).

The ability to produce songs with an acoustic structure appropriate for a given locality also seemingly requires little in the way of additional costs, making the production of local song an equally dubious candidate as a reliable indicator trait. A long-standing alternative hypothesis for the evolution of local song preferences is that females benefit by mating with locally born males by obtaining locally adapted genes to pass on to their offspring (Nottebohm 1969, 1972; Baker and Cunningham 1985). Local genetic adaptation, however, has never been demonstrated for birds on the small geographic scales at which song variation often occurs. Moreover, females in some species seem to prefer local song even when males learn the details of song after dispersal so that song does not reveal natal origin (Baker et al. 1981; Baptista and Morton 1988). In song sparrows, females discriminate against foreign songs over relatively short distances, but the distances that song sparrows disperse are even shorter, making it unlikely that females ever encounter foreign males whose songs are discriminably different from local ones (Searcy et al. 2002). The genetic adaptation hypothesis thus also seems doubtful as an explanation for the evolution of female preferences for local song, and we are again left with the question of how local song structure could signal some aspect of male quality that is of interest to females.

The nutritional stress hypothesis

According to the nutritional stress hypothesis, the reliability of song as an indicator of male quality is maintained by developmental costs associated with song learning and production. The acquisition and production of song are mediated by a well-described series of brain nuclei, collectively referred to as the ''song system'' (for review see Mooney 1999). Song system nuclei and the connections between them develop late relative to other parts of the nervous system (Alverez-Buylla et al. 1994; DeVoogd 1994). In the zebra finch, where the process has been best studied, much of this development occurs in the period 10–50 days post-hatching (e.g., Bottjer et al. 1985; Konishi and Akutagawa 1985; Nordeen and Nordeen 1988; Johnson and Bottjer 1992; Mooney and Rao 1994; see Nowicki et al. 1998 for review). For example, area X of the avian striatum (area X), a nucleus known to be important during song learning, increases in size between 20 and 55 days, while the high vocal center (HVc) and robust nucleus of the archistriatum (RA), areas important for both learning and production, increase in size between 10 and 50 days (Bottjer et al. 1985; Konishi and Akutagawa 1985; Nordeen and Nordeen 1988). Song memorization in zebra finches occurs at about the same time, from 25 to 65 days post-hatch (Slater et al. 1988). Functional connections between song system nuclei also continue to form during this period of post-hatch development. For example, the projection from HVc to RA, a pathway critical for both song learning and production, forms between 15 and 30 days of age in zebra finches, but the projecting neurons stop at the border of RA until 30 to 35 days when they rapidly invade the nucleus (Mooney and Rao 1994).

Zebra finches, the species most commonly used in studies of the song system, reach sexual maturity and complete song development within 90 days of hatching, much sooner than is typical for songbirds. Thus, although the timing of many post-hatch developmental events (such as appearance of feathers, body size increase, and time to fledging) are comparable to other species, some events in neural development may be compressed in zebra finches relative to other songbirds. The comparatively few studies done on other species, however, support the general conclusion that significant events in the development of the song system occur after hatching, during the period when young birds are likely to experience nutritional stress in the field. In canaries (*Serinus canaria*), RA doubles in size between days 30 and 60, while HVc grows at an even faster rate during this interval (Nottebohm et al. 1986). Nottebohm et al. (1986) observed continued HVc growth for up to 7 months, but later work by Alvarez-Buylla et al. (1992) suggests that HVc growth in canaries is complete by 4 months post-hatch. A single study by Nordeen et al. (1989) has examined song system development in swamp sparrows (*Melospiza georgiana*), a more typical songbird and the subject of our first nutritional stress manipulation experiment (see below). Nordeen et al. (1989) found the timing of song system development in swamp sparrows to be remarkably similar to that observed in zebra finches, with the majority of growth of HVc, RA and Area X completed by 61 days post-hatch.

These major events in the development of the song system coincide with a period early in life when birds are very likely to experience nutritional stress (Nowicki et al. 1998). Being altricial, young songbirds are completely dependent on their parents for food between hatching and fledging, and this dependence may continue for some time after leaving the nest. Growth is extremely rapid at this time, with nestlings reaching an average of 90% of their adult weight within 10 days (Ricklefs 1968), and energy requirements are correspondingly high (Ricklefs 1974). Both growth rates and survival rates are related to food abundance and level of provisioning by parents, and starvation is common (Ricklefs 1983; O'Connor 1984). The potential for nutritional stress may be even greater during the first few weeks of independence, after parents stop feeding their fledglings. Yellow-eyed juncos (*Junco phaeonotus*), for example, become independent at about 5 weeks post-hatching, at which time their foraging skills are still poor (Sullivan 1988). During the next 2 weeks the young juncos must forage more than 90% of daylight hours in order to maintain a positive energy balance; nonetheless about 40% of young die during this brief interval (Weathers and Sullivan 1989). Similar patterns of post-fledging mortality have been observed in many songbirds, with survival tied to the ability to obtain adequate nutrition during this period as well as to energy stores accumulated earlier when the young still received parental care (Lack 1966; Ringsby et al. 1998).

The effects of early nutritional stress on brain development are not well studied in birds, but significant deleterious effects have been described in mammals (Dobbing 1981; Smart 1986; Levitsky and Strupp 1995). Particularly relevant are studies of the mammalian hippocampus, which like the song system is closely tied to specific behavioral abilities, in this case involving spatial learning and memory (Jacobs 1995). In rats, poor nutrition early in life causes permanent reductions in cell size, cell number, and dendritic branching in the hippocampus (Levitsky and Strupp 1995; Castro and Rudy 1987). These anatomical effects are associated with physiological abnormalities and with reduced performance of adults on spatial memory tasks (Jordan et al. 1981; Goodlet et al. 1986). Development may be more buffered against nutritional deprivation in birds than in mammals (Schew and Ricklefs 1998), but the vertebrate brain in general is susceptible to the effects of stress (Dobbing 1981) and the avian brain in specific may be particularly vulnerable to undernutrition because of its relatively rapid development (Schew and Ricklefs 1998). The key question, which we have begun to address experimentally (see below), is whether a limited period of stress incurred early on will have effects that last through development and into adulthood. This question is especially relevant in the case of song learning, where growth (or regrowth) of the song system, and memorization and motor development of song, all may continue beyond the period when nutritional stress is most likely to be experienced. Lasting effects of early stress on neural development are known to occur in mammals (Dobbing 1981), and can be expected in general whenever there are critical periods in development.

Stressors other than undernutrition also may affect the development of the song system. Parasites attack young birds of most species, with a variety of detrimental effects (Loye and Zuk 1991; Clayton and Moore 1997). 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 (Sheldon and Verhulst 1996). Indeed, in a recent study of sedge warblers, Buchanan et al. (1999) 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. von Schantz et al. (1999) suggest that oxidative stress may be a critical common denominator linking the expression of sexual ornaments to an individual's condition. Oxidative stress is damage on a cellular level that results from the production of free radicals and reactive metabolites by activated immune and detoxification systems; such stress has been shown to have an adverse affect on neurogenesis in vertebrates (e.g., Saito et al. 1997). Thus, a variety of other stressors may act synergistically with undernutrition to degrade song system development and song learning.

If early nutritional stress does have a negative effect on the development of the song system, then both song learning and the songs subsequently produced by birds as adults would in turn be adversely affected. This conclusion seems likely given what is known of the relationship between structure and the function of song system nuclei, especially HVc and RA, which have been most studied in this regard (Brenowitz and Kroodsma 1996). The sizes of both these nuclei are known to correlate with adult song repertoire size across species (DeVoogd et al. 1993; Székely et al. 1996), between populations of a single species (Canady et al. 1984), and among individuals (Airey et al. 2000). Differences in the size of song nuclei between birds with different repertoire sizes reflect differences not only in number of neurons but also in the size of individual neurons (Brenowitz and Kroodsma 1996).

The structure of the song system also is likely to be important in determining the accuracy with which local song structure is copied during song development, though here the evidence is scantier. In canaries and song sparrows, RA and HVc vary in size seasonally, and the strongest behavioral correlate of this variation is song stereotypy: song tends to be stereotyped when brain nuclei are large and variable when nuclei are small (Nottebohm 1981; Nottebohm et al. 1986; Smith et al. 1997). In song sparrows these seasonal changes can be observed down to the level of the smallest subunits of song (notes), whose form is more stereotypic in the spring when HVc and RA are large, than in the fall when these nuclei are smaller (Smith et al. 1997). These results suggest that structural differences in song system nuclei may influence the ability of males to adhere to the kinds of small structural differences typical of geographic differences in song. If so, then female preferences for local song dialects may be explained in the same terms as preferences for larger repertoires, both features serving as honest signals of male quality.

Neither the size of song system nuclei nor the other structural measurements that have been made, such as synaptic density, necessarily reflect all the relevant neural underpinnings of song learning and production (Bolhuis and Macphail 2001; Gil and Gahr 2002). Nevertheless, these measurements can provide useful yardsticks of the quality of neural development. The important point is that variation in the development of the song system is likely to result in variation among individuals in their learning abilities.

A key prediction of the nutritional stress hypothesis is that variation in the growth or condition of individuals as nestlings or young fledglings should be reflected in their subsequent adult song production, in features that are used by females in mate choice. Doutrelant et al. (2000) provided a first field test of this prediction by examining the relationship between song repertoire size and adult tarsus length in blue tits. In this species, tarsus length has been shown to reflect the level of nutrition received early in life and also to correlate with juvenile survival (Merilä and Wiggins 1995). Thus, tarsus length can be used as a convenient proxy for the relative condition of individuals as nestlings or young fledglings. Doutrelant et al. (2000) found a positive correlation between repertoire size and tarsus length, consistent with idea that repertoire size reflects early nutrition.

Using data from a long-term study of great reed warblers (Bensch et al. 1998; Hasselquist 1998), Nowicki et al. (2000) offered a more direct field test of the prediction that variation in the condition of nestling males should be reflected in their adult song behavior. Syllable repertoire size is known to influence female mate choice in great reed warblers (Catchpole et al. 1986; Hasselquist 1998) and also to correlate with potential benefits females receive based on that choice (Hasselquist et al. 1996; Hasselquist 1998), suggesting this feature of song as a likely indicator of male quality in this species. Nowicki and his colleagues used two measures as estimates of nestling growth and developmental condition, body mass and the length of the innermost primary wing feather, and asked how well these measures predict the size of individual male's song repertoires as adults in their first year.

Each nestling could be measured only once because of the increased risk of predation associated with disturbing nests. Single point measurements of body mass are notoriously inaccurate measures of nestling growth, however, largely because weight gain in songbirds is non-linear (Ricklefs 1984). In spite of this limitation, Nowicki et al. (2000) found a positive relationship between nestling body mass and first-year repertoire size, with the regression closely approaching significance. Feather growth rate is more linear than weight gain, so single point measurements are a more accurate measure of growth and development than single point body mass measurements (Ricklefs 1984; Quinney et al. 1986). Feather growth also has been shown to reflect nutritional condition during nestling development in a number of species (Price 1985; Quinney et al. 1986). Nowicki and his colleagues found a statistically significant positive relationship between adult repertoire size and nestling feather length (Fig. 1). This relationship suggests that a female great reed warbler choosing a male with a large song repertoire obtains a mate that fared well in post-hatch development, as predicted by the nutritional stress hypothesis.

An experimental test of the nutritional stress hypothesis

Observing a correlation between nestling growth and adult song behavior in the field shows that a relationship between nestling condition and adult song can occur within the naturally occurring range of variation for both variables. To demonstrate a causal relationship between nutritional stress and song, however, an experiment is required, one that is more practical in the laboratory than in the field. As a first experimental test of the nutritional stress hypothesis, we compared brain development and song development in two groups of swamp sparrows hand-reared in the laboratory: a control group raised with unlimited food and an experimental group exposed to a period of nutritional stress at approximately the same time as such stress would be incurred in the field.

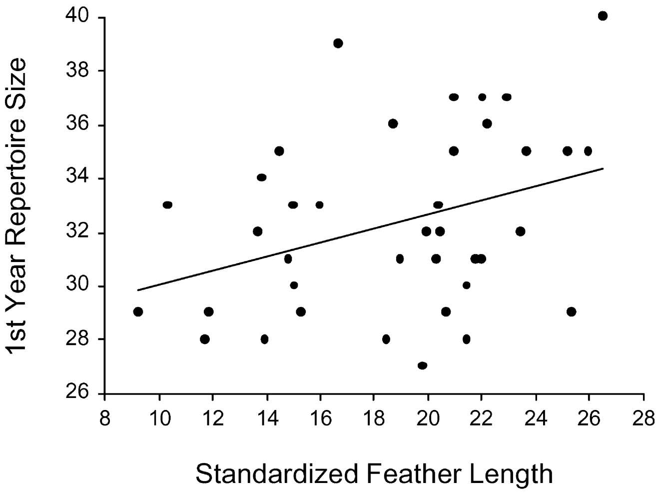

Fig. 1 Relationship between nestling primary feather growth and 1st-year repertoire size of male great reed warblers. Because individuals were not all measured at exactly the same time relative to hatching, feather length measurements were adjusted to account for the time offset from a standard measurement time, based on a regression of feather growth over time measured for all male chicks hatched in the population between 1987 and 1999. $n=38$, $r^2=0.127$, $P=0.028$. Reprinted from Nowicki et al. (2000)

Materials and methods

We collected nestling swamp sparrows at 3–7 days post-hatch, and assigned them either to the control group ($n=9$) or to the experimental group ($n=7$). All subjects were housed in a single, large sound isolation room and raised under identical conditions except for their feeding regimes. Siblings were kept together until 20 days, first in their nests and then in large cages. After 20 days, individuals were housed singly in cages. We tutored all birds with the same set of recorded swamp sparrow songs (16 song types from 10 males; see for example Fig. 2), beginning at about 20 days and continuing for 12 weeks, a period that brackets the memorization phase of learning in this species (Marler and Peters 1988). We chose training songs that were quite distinct from each other to ensure we could unambiguously identify which songs had served as models for learning.

From the time they were collected to when individuals were feeding completely independently (about 28 days of age), we hand-fed the birds a standard hand-rearing diet (see Marler and Peters 1988) by syringe, keeping track of the volume to the nearest 0.1 ml that each individual ate at each feeding. Birds in the control group were fed until sated. We then fed each bird in the experimental group 70% of the volume received on average by the controls for that feeding. Birds in both groups remained healthy throughout, although the difference in amount of food received had a pronounced effect on individual growth rates, as measured by daily

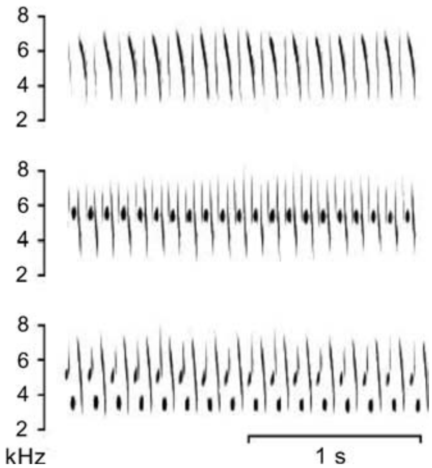

Fig. 2 Sonograms of a typical swamp sparrow male's song repertoire. Each song type is a trill of repeated "syllables," which are in turn are composed of a series of two or more distinctive note types

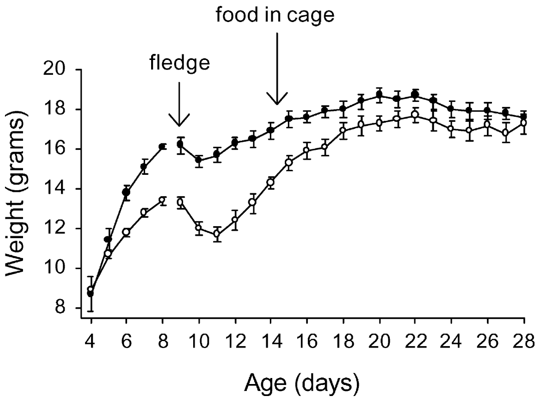

Fig. 3 Weight gain in control (*filled circles*) and experimental (*open circles*) swamp sparrows. The means ± SE shown for days 4–8 are based on nest averages because birds within nests were not yet individually marked during this period; means and standard errors from days 9–28 are based on individual measurements. The weight loss in both groups beginning at 9 days is typical for individuals after fledging (Ricklefs 1983)

weights (Fig. 3). Beginning at 14 days of age, birds were provided with a variety of foods (such as seed and mealworms) so that they could learn to feed themselves; from this point on, the disparity in weight between the two groups diminished and the mean weights of the two groups ceased to differ statistically by 21 days of age. We limited the stress that was experienced by the experimental group to a short period because this timing corresponds to when such stress is most likely to occur in the field. The nutritional stress hypothesis specifically predicts that even such a limited exposure will have lasting effects on brain development, song learning and adult song production.

All birds were recorded in individual sound isolation chambers. To document song development, we began recording a subset of the birds (four control, four experimental) on a weekly basis beginning at about 250 days of age. All birds were recorded intensively at about 1 year of age to document their crystallized song repertoires. One bird in the experimental group only sang sporadically. Because we did not record a sufficient number of songs from this individual, we did not include him in our behavioral analyses. Spectrograms of adult songs were compared to tutor models to determine which songs had been copied from which models. We used as a quantitative measure of copy accuracy the average pairwise spectrographic cross-correlation (SCC) value calculated for ten different renditions of each copy syllable against the training song syllable that had served as a model (Signal v 3.0 sound analysis software, Engineering Design, Belmont, MA; sample rate = 25 kpts/s, 128-pt FFT; see Clark et al. 1987 for more background on SCC).

At approximately 14 months of age, all birds were perfused and their brains removed using standard methods (e.g., Kirn et al. 1989; Burek et al. 1995). To determine the relative volume of brain nuclei, 40-μm brain sections were cut on a freezing microtome, mounted, and then stained with cresyl violet, again using standard techniques. The Nissl-defined borders of the nuclei HVc and RA were drawn from alternate sections with the aid of a camera lucida; the outline of the telencephalon was drawn from these same sections using a Bausch and Lomb slide projector set to 10× magnification. Areas were measured from these drawings using NIH Image or Scion Image software. We calculated volumes by multiplying the area of each section by 80 μm (e.g., 2 μm×40 μm, because only every second section was measured) and summing the results.

Results

The most striking difference in the adult song behavior of the two treatment groups is that the experimental birds produced significantly less accurate copies of the model songs from which they learned, as measured by SCC (Fig. 4). The two groups did not differ in song complexity, as measured by song repertoire size (experimental = 2.2 ± 0.8 versus control = 2.1 ± 0.3; mean ± SE). Swamp sparrows, however, have small song repertoires with little variation among males in a population (a range of two to four song types; see for example Fig. 2), so it is not surprising that we did not find an effect on repertoire size in this species. The groups did differ in the timing of song development, with the experimental group beginning to sing subsong earlier (270 ± 10 versus 293 ± 6 days old, Mann-Whitney $U = 12$, $P = 0.032$) and remaining in the subsong and

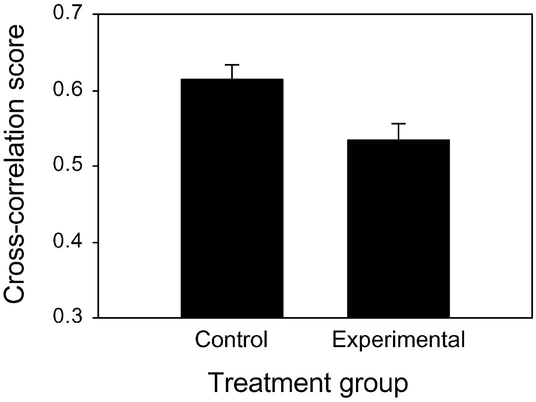

Fig. 4 Effect of early nutritional stress in young swamp sparrows on copy quality of learned song notes, as measured by spectrogram cross-correlation (SCC) of individuals' learned notes to the tutor models from which these notes were copied (Mann-Whitney $U = 47$, $P = 0.018$, $n = 9$ control, 6 experimental). One experimental bird was incompletely recorded and thus not used in the behavioral analysis, as explained in the text

early plastic stages longer (subsong: 22 ± 6 versus 9 ± 4 days, Mann-Whitney $U = 12$, $P = 0.030$; early plastic song: 29 ± 4 versus 18 ± 4 days, Mann-Whitney $U = 12$, $P = 0.030$). Both groups crystallized their songs at approximately the same age, however (339 ± 8 versus 347 ± 9 days).

We also found a significant effect of early nutritional stress on adult brain structure: the volumes of both HVc and RA were significantly smaller in nutritionally-stressed birds than in controls (Fig. 5A, B). These differences in the size of song system nuclei reflect an overall difference in the size of the telencephalon, which was significantly smaller for the stressed group (Fig. 5C). To determine whether song system nuclei were affected disproportionately by stress, beyond the overall effect on brain size we observed, we compared the ratios of nuclear volumes to telecephalon volume between the two groups. The HVc/telencephalon ratios did not differ between the two groups (experimental = $1.6\times10^{-3} \pm 0.1\times10^{-3}$ versus control = $1.8\times10^{-3} \pm 0.2\times10^{-3}$; mean ± SE), but the RA/telencephalon ratio was significantly smaller for the experimental group ($0.56\times10^{-3} \pm 0.04\times10^{-3}$ versus $0.70\times10^{-3} \pm 0.04\times10^{-3}$; Mann-Whitney $U = 47.0$, $P = 0.028$).

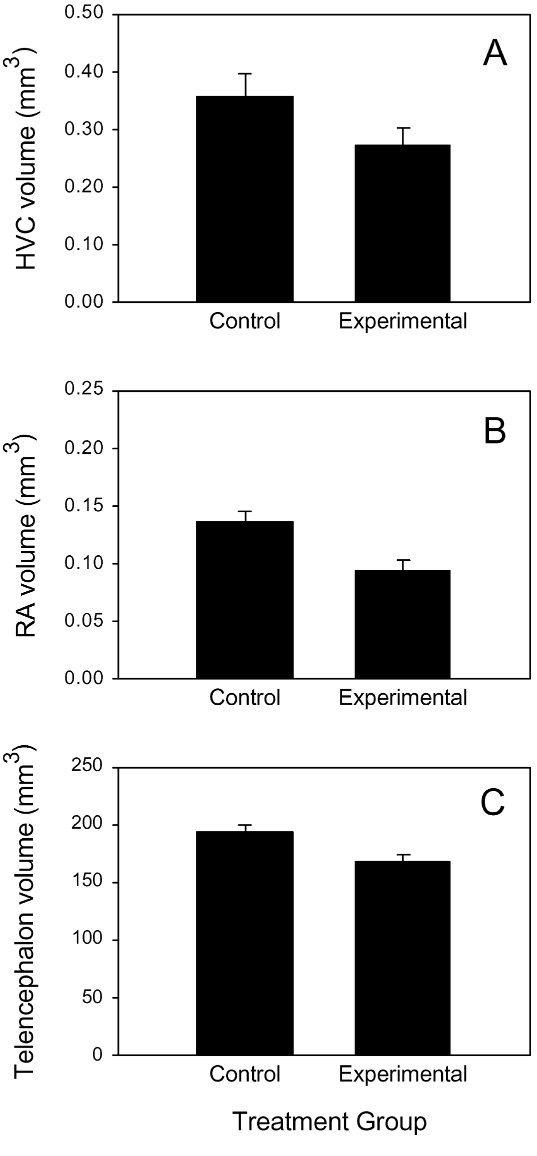

Fig. 5A–C Effects of early nutritional stress on volume of brain areas in adults. **A** High vocal center nucleus (HVc): Mann-Whitney $U = 47.0$, $P = 0.028$; **B** Robust nucleus of the archistriatum (RA): Mann-Whitney $U = 50.0$, $P = 0.011$; **C** Telencephalon: Mann-Whitney $U = 47.0$, $P = 0.028$. $n = 8$ control, 7 experimental birds in all cases. Volume data were averaged across left and right hemispheres for each individual in the analysis. One control bird was not included in the neuroanatomical analysis because it was poorly perfused

Discussion

Our results demonstrate that even a relatively brief period of undernutrition experienced early in life can affect the outcome of song learning (Fig. 4), directly supporting a key prediction of the nutritional stress hypothesis. More specifically, the effect we observed is consistent with the idea that not only repertoire size (i.e., the quantity of what is learned) but also the ability to copy precisely local song material (i.e., the quality of what is learned) can serve as an indicator of male developmental condition in some cases. We do not know yet how variation in the quality of song learning might influence mate choice in female swamp sparrows, but two lines of evidence suggest it would have a strong effect. First, swamp sparrows are particularly sensitive to the acoustic fine structure of the notes that comprise their songs, as adult males responding to perceptual tests (Nelson and Marler 1989), as young birds in learning experiments (Marler and Peters 1989), and most importantly as adult females responding in a copulation solicitation assay (Balaban 1988). Second, we recently have demonstrated that in song sparrows, closely related congeners of swamp sparrows, females respond preferentially to accurate copies of song, across a range of copy accuracy similar to that we observed in swamp sparrows (Nowicki et al. 2002).

Our results further show that developmental stress experienced early in life can have a lasting effect on brain structure (Fig. 5), thus providing critical evidence that the link between our nutritional manipulation and the effect on song learning we observed does indeed involve brain development. The effect of stress on brain development is not limited to the song system, as shown by a significant difference in the overall size of the telencephalon between experimental and control birds. However, it is not necessary that stress specifically affects development of the song system for song learning to serve as an indicator of male quality. As long as variation in brain development correlates with phenotypic or genetic factors that will benefit the female or her offspring, selection should favor a preference for song features that reflect such variation.

At least one region of the song system, nucleus RA, appears to be affected disproportionately by early stress. This finding is significant in light of data from both microstimulation and chronic recording studies that suggest RA may be responsible for specifying the acoustic fine-structure of individual note or syllable types, while HVc and other areas upstream in the song system are responsible for the temporal patterning of those elements (Vu et al. 1994; Yu and Margoliash 1996). Thus, the observed effects of stress on the quality of learned song notes (Fig. 4) occurred on the level of song organization thought to be controlled by RA, strengthening our interpretation that the effect of developmental stress on learning is causally related to variation in brain development. If it proves to be the case across different species that RA is generally more vulnerable to the effects of early stress, then this observation also suggests that a male's ability to learn and reproduce specific phonological features accurately may be an especially reliable indicator of early development, and thus of particular interest to females in the context of mate choice.

Conclusions

Data from both the laboratory and the field are beginning to provide empirical support for the nutritional stress hypothesis. The condition of young blue tits and great reed warblers in the field has been shown to correlate with the size of their adult song repertoires, a feature of song known to be subject to sexual selection by female choice (Doutrelant et al. 2000; Nowicki et al. 2000). In the laboratory, we have been able to demonstrate a causal effect of early nutritional stress on brain development and song learning in swamp sparrows. We did not observe an effect on repertoire size in this species. Instead we observed an effect on learning accuracy that may be related to an individual's ability to copy precisely features of a local dialect. We know that females of many species generally prefer males singing their local dialect; we suggest this preference reflects female choice for an accurate indicator of male quality, the same as preferences for larger song repertoires.

We are now repeating our early nutrition experiment using song sparrows, a species that has considerably greater variance among males in measures of repertoire size (Searcy 1984) and that also is sensitive to geographic variation in song structure (Searcy et al. 2002). We expect this work will enable us to look more carefully at how early developmental stress affects both these song features, and to ask how both these effects may influence female choice separately or together. It also is necessary to look in more detail at the brain, to determine if features of the song system other than nucleus size, such as cell size or density, synaptic density or neurophysiological properties, are sensitive to the effects of early stress. Finally, we are interested in knowing which aspects of male phenotype other than the song system are affected by developmental stress, including other aspects of brain function, as this information may lead to insight into specific mechanisms through which females benefit by their choice of males based on song.

Signal reliability is a general problem in the context of mate choice. Why should a male signal his quality honestly when he would benefit from exaggerating it? The broad outline of the mechanism by which reliability is maintained has been apparent for some time: indicators can be honest when they are costly, because the cost to high quality males will be relatively lower than for low quality males. But this general mechanism begs the question of what the costs are and how and when they affect the signal. The nutritional stress hypothesis helps to answer this question for one mating signal, bird song, for which the costs have been particularly enigmatic. To the extent that this hypothesis continues to receive empirical support, bird song may transform from an enigmatic example of a sexually selected trait to a particularly informative model system, given the wealth of detailed information available about the neural mechanisms responsible for the development and production of this trait.

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