SYMPOSIUM

Developmental Stress, Song-Learning, and Cognition

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Synopsis The evolution of enhanced cognitive ability has sometimes been attributed to sexual selection. An association between the mating success of males and their cognitive ability could arise either through male–male competition or through female choice. Specifically in the latter case, sexual selection would act more readily if males advertized their cognitive ability through display. Most traits involved in sexual display, however, seem unlikely to have any inherent relationship with cognition beyond that which arises through the effect of cognitive abilities on acquisition of resources and, in turn, the effect of resources on development of the display trait. In contrast, for displays whose development and expression require learning, a direct link with cognition is possible because of a shared dependence on brain function. The parallel effects of developmental stress on song-learning and cognition provide a compelling explanation for an association between attributes of the song and cognitive ability. We outline the hypothesis that sexually selected qualities of song serve as an indicator of cognitive abilities. We first present evidence that song-learning is itself a challenging cognitive task. We then give evidence that sexual selection favors well-learned song. Next, we review evidence that song and cognitive ability both are affected by developmental stresses. We consider recent experimental data testing the relationship between song and cognitive ability. Finally, we suggest that the accuracy with which songs are learned may be an optimal indicator of other cognitive abilities.

Introduction

The evolution of enhanced cognitive ability has sometimes been attributed to sexual selection, in particular, to choice of mates (Jacobs 1996; Shackleford et al. 2005; Boogert et al. 2011b). Males with higher cognitive ability might function better in competition for access to females or in competition for resources needed to attract females, and females might prefer males of higher cognitive ability as mates because they provide better resources, better genes, or both. In any of these cases, the action of sexual selection would be facilitated if males were able to advertise their cognitive ability. Most displays, however, seem unlikely to reflect cognition because of the absence of a link between expression of the display and the brain mechanisms underlying cognitive processes. Exceptions are most likely for those displays, such as bird song, whose development is influenced by learning. Early developmental stress is known to affect brain development in songbirds and, in turn, the development and expression of song as a mating signal (Nowicki et al. 2002b; Buchanan et al. 2003, 2004; Spencer et al. 2003; Schmidt et al. 2013). Differences in development of the brain, of course, would also be expected to affect cognitive capacity in general (Nowicki et al. 2000; Boogert et al. 2011a; Buchanan et al. 2013). The parallel effects of developmental stress on song-learning and other cognitive processes provide a powerful rationale for expecting an association between the attributes of song and cognitive ability, raising the possibility that song is used by female birds to assess the cognitive abilities of males.

We here explore the hypothesis that developmental stress forges an association between learned attributes of song and various cognitive abilities, an association that influences mate choice and can therefore drive the evolution of greater cognitive

ability. We begin by presenting evidence that song-learning is itself a challenging cognitive task. We then give evidence that sexual selection favors well-learned song. Next we review evidence that song-learning and other cognitive processes can be affected by the same developmental stressors. Finally, we present what is known so far about the relationship between song and cognitive ability.

Song-learning as a cognitive process

Following Shettleworth (1998) we define cognition as those "mechanisms by which animals acquire, process, store and act on information from the environment." Birds use sophisticated cognitive abilities in a number of tasks important to fitness. Caching birds, for example, use their prodigious spatial memory in storing and retrieving food (Shettleworth 2003). Similarly, hummingbirds have good memory for both spatial positions and time intervals and use these abilities to forage systematically on flowers, returning to previously visited flowers only when nectar has been renewed (Healy and Hurly 2003). Territorial songbirds learn to recognize their neighbors by song alone (Falls and Brooks 1975; Stoddard et al. 1991), retain this information in some instances from one year to the next (Godard 1991), and use memories of the past behavior of neighbors to modulate response to their songs (Akcay et al. 2009, 2010). In general, success in foraging, territorial defense, choice of mates and avoidance of predators, all involve cognitive abilities such as spatial memory, individual recognition, problem solving, and so forth. Song-learning, as a process involving perception, learning, memorization, and action, is also a cognitive ability, as we discuss below.

Vocal learning is the process whereby an individual modifies the form of its vocal signals as a result of experience with the vocalizations of others (Janik and Slater 2000). Vocal learning so defined has a limited distribution among vertebrates. A few mammals, most notably humans and cetaceans, are capable of vocal learning (Janik and Slater 1997). Among birds, three groups have been shown to be vocal learners: parrots (order Psittaciformes), hummingbirds (family Trochilidae, order Apodiformes), and especially songbirds (suborder Passeri, order Passeriformes) (Kroodsma and Baylis 1982; Beecher and Brenowitz 2005; Catchpole and Slater 2008). In temperate zone songbirds, it is generally the male that produces the species-typical songs used in territorial defense and attraction of mates (Catchpole and Slater 2008). In a few temperate-zone species and a much larger number of tropical species, females may

sing as much as, or more than, males and presumably learn their song in the same manner as males (Catchpole and Slater 2008). Whether they sing or not, if females use song to assess males they must presumably be capable of learning something about song, although female song-learning has been much less studied (Riebel et al. 2005; Anderson 2009; Lachlan and Nowicki 2012).

Perhaps the best demonstration of the importance of auditory learning comes from studies of birds raised in captivity, contrasting individuals that are exposed to recordings of their species-typical song with individuals raised without models. Male song sparrows (*Melospiza melodia*) and male swamp sparrows (*Melospiza georgiana*) that are isolated from adult song-models in their first year develop songs that are strikingly abnormal in many respects (Kroodsma 1977; Marler and Sherman 1985). Songs developed by birds isolated from adult song also have been shown to be less effective in communicating to conspecifics than are the songs of typical wild males (Searcy et al. 1985). In contrast, laboratory-raised males tutored with recorded song develop songs that closely match the tutors' songs (Marler and Peters 1977, 1987). Exposure to interactive social tutors may be even more effective in stimulating learning than is exposure to recorded song (Nordby et al. 2000; Beecher et al. 2007).

Certain attributes of song seem to be influenced relatively little by learning. In some species, for example, birds raised in isolation with no opportunity to learn from others still display the size of repertoire and structure of song that is characteristic of the species, for example, gray catbirds (*Dumetella carolinensis*) (Kroodsma et al. 1997) and European sedge warblers (*Acrocephalus schoenobaenus*) (Leitner et al. 2002). In other species, however, access to auditory experience results in an increase in the size of the repertoire, for example, marsh wrens (*Cistothorus palustris*) (Brenowitz et al. 1995), swamp sparrows (*M. georgiana*) and song sparrows (*M. melodia*) (Marler and Sherman 1985). Song sparrows provide evidence that another aspect of complexity, the amount of variation with which a song type is sung, is also not learned (Nowicki et al. 1999).

The most striking effect of exposure to species-typical song often is the acquisition of the detailed acoustic features associated with particular song-models (Catchpole and Slater 2008). Accuracy of learning can be measured in terms of how much of a bird's song or repertoire includes material copied from the models to which he was exposed, and in terms of how precisely that copied material is reproduced. The precision with which a copied song is

memorized and reproduced can in turn be measured on different hierarchical levels, including the accuracy of individual elements and the accuracy of their sequential arrangement within the song.

Song-learning occurs in two phases (Catchpole and Slater 2008). During an early "sensory" phase the young bird commits species-typical sounds to memory. This phase encompasses a sensitive period during which the probability of acquisition is at its peak (Marler and Peters 1987, 1988). In a few species males may learn from their fathers, but males of most species that have been studied do not, instead learning from territorial neighbors or more distant individuals (Catchpole and Slater 2008). In species with repertoires of different types of songs, young males often copy songs or parts of songs from multiple tutors (Beecher et al 1994; Nordby et al. 1999). During a later "sensorimotor" phase, the bird rehearses, listens to, and refines its song, more or less matching it to the memory of the songs heard during the sensory phase (Marler 1990; Mooney 1999). Song progresses from subsong through plastic song to crystallized song, at which point the song in most species has become highly stereotyped (Marler and Peters 1982c). The sensory and sensorimotor phases may overlap somewhat, as in zebra finches (*Taeniopygia guttata*), or may be separated by many months, as in song sparrows, swamp sparrows, and chaffinches (*Fringilla coelebs*) (Hultsch and Todt 2004; Catchpole and Slater 2008). A number of species have been identified as "open-ended learners", in that they continue to produce new songs later in life. The new songs may have been learned during the initial sensory phase, for example, nightingales (*Luscinia megarhynchos*) (Geberzahn et al. 2002; Geberzahn and Hultsch 2003) or acquired during an extension or reactivation of a sensitive period, for example, indigo buntings (*Passerina cyanea*) (Payne 1981), canaries (*Serinus canaria*) (Nottebohm et al. 1986, but see Belzner et al. 2009), and starlings (*Sturnus vulgaris*) (Eens et al. 1992; Chaiken et al. 1994). Auditory input is essential during both the sensory and the sensorimotor phases. Songs of young males prevented by deafening from hearing during either phase are even more abnormal than are songs of isolated birds (Nottebohm 1968; Marler and Sherman 1983) and are even less effective in communication (Searcy and Marler 1987).

Many songbirds show a preference during the sensory phase for learning conspecific over heterospecific models even in the absence of social cues as to which songs are which (Marler and Peters 1977; Catchpole and Slater 2008). Presumably, this selective learning is based on genetically encoded predispositions to learn

sounds with a species-typical acoustic structure (Dooling and Searcy 1980; Nelson and Marler 1993), although little is known about how such predispositions work. Selective learning also occurs during the sensorimotor phase. A number of species appear to memorize far more songs than will eventually be used by adults (Marler and Peters 1982a; Nelson 1992, 2000; Geberzahn et al. 2002); these species then selectively lose a subset of their repertoires during rehearsal. The attrition process during this phase may allow for additional rejection of non-imitated or heterospecific sounds, for example, by swamp sparrows (Marler and Peters 1982a). Social interactions, as in white-crowned sparrows and field sparrows, also can influence which song types are retained (Nelson 1992, 2000).

Song-learning in songbirds involves the memorization of the fine acoustic structure of song during the first few months of life, retention of these details in memory for many months, and then the use of these auditory memories to guide song production through to adulthood (Marler and Peters 1982b; Marler 1990; Tchernichovski et al. 2001; Beecher and Brenowitz 2005). Song-learning thus requires a bird to "acquire, process, store and act on information from the environment" as stipulated by Shettleworth's (1998) definition of cognition.

Sexual selection and song-learning

Male songbirds vary in how well they copy song-models, both in how well they reproduce the acoustic details of those models and in how much of a model they learn. Males may copy a model completely, note by note, or only partially. The sequence of notes within one model can be rearranged, and parts of songs used as models can be combined. Most songbird species include more than one type of song in their repertoire (Catchpole and Slater 2008) and males within a species vary in how many types of song they sing. Laboratory and field experiments have documented that all of these dimensions of variation in learning can be important in choice of mates.

Nowicki et al. (2002b) tutored laboratory-reared male song sparrows with songs from their natal population and then presented female song sparrows caught from that same population with songs developed by the laboratory-reared males. The songs chosen for playback differed: (1) in the amount of learned versus invented material included in the songs; and (2) the accuracy with which the material matched the model from which it was copied. Female song sparrows preferred songs that incorporated more learned than invented material, and also

preferred songs copied with a high level of accuracy to those that were copied less accurately. Likewise, in satin bowerbirds (*Ptilonorhynchus violaceus*), a species that includes imitations of other species' vocalizations in its display, the accuracy of vocal mimicry and the number of model species mimicked both are independently related to males' mating success (Coleman et al. 2007).

Song complexity, as measured by the size of the repertoire of songs or notes, also is influential in mate choice. Laboratory and field experiments demonstrate that females of many songbird species prefer to mate with males having larger repertoires (Searcy and Nowicki 2005; Catchpole and Slater 2008), although there are exceptions (Byers and Kroodsma 2009). In song sparrows, for example, females in the laboratory perform more courtship displays in response to larger repertoires of songs (Searcy 1984) and young females in the field, pairing for the first time, prefer to pair with males having larger repertoires (Reid et al. 2004). Similarly, in captive sedge warblers (*A. schoenobaenus*) females show a preferential response during courtship to males with larger repertoires of syllables (Catchpole et al. 1984) and in the field males having larger repertoires of syllables obtain mates earlier than do less versatile males (Buchanan and Catchpole 1997).

Why would females bias mate choice based on characteristics of song? One hypothesis is that song is an indicator trait, and several studies have demonstrated significant relationships between complexity of song and certain aspects of a male's quality. For example, male song sparrows with larger repertoires have better fitness; research on the Mandarte Island population of song sparrows shows that males with larger repertoires live longer, hold territories longer, and have more offspring and grand offspring that reach independence (Reid et al. 2004). Buchanan and Catchpole (1997) found that male sedge warblers with large repertoires had larger territories and gave more parental care to their offspring. Thus, the preference of females for larger repertoires gives them access to better resources or genes. Little is known about the relationship between the ability of males to learn songs and their fitness, raising the question of why females attend to this feature of song.

Developmental stress provides a mechanism tying song and cognition

The developmental-stress hypothesis provides a rationale for how song-learning may be related to quality of the male. Under this hypothesis, a link between quality of song and a male's quality is forged because the timing of the development of brain structures necessary for song-learning corresponds to the period during which young songbirds are most likely to undergo nutritional and other types of stress and during which many other aspects of the male's phenotype are developing (Nowicki et al. 1998; Buchanan 2011).

The memorization and subsequent production of song rely on specialized brain structures that form two interconnected pathways, collectively referred to as the "song system" (Fig. 1); for recent reviews see Kirn (2010) and Mooney (2009). One major pathway includes HVC, which projects to RA, which in turn projects to nXIIts and to respiratory motor neurons (see Fig. 1 for explanation of acronyms). This circuit often is referred to as the "motor" pathway because temporal activity along the pathway matches song production (Margoliash 1997) and because lesions to either HVC or RA disrupt the songs of adults (Nottebohm et al. 1976). A second major pathway, the anterior forebrain pathway, also starts with HVC from which a population of neurons (distinct from those projected to RA in the motor pathway) project to Area X, which in turn projects to DLM. DLM projects to LMAN, which in turn has bifurcating axons that terminate in Area X and RA (Vates and Nottebohm 1995). This circuit has been referred to as the "sensory" pathway because lesions along this pathway interfere with vocal development but do not disrupt the song of adults (Bottjer et al. 1984; Scharff and Nottebohm 1991). Both pathways exhibit sensory and motor properties, however, making the specific function of each area more complex (Kirn 2010).

Songbirds' brains are relatively small at the time of hatching and develop into relatively large brains by adulthood as compared with precocial birds, which have high levels of growth of the brain pre-hatching and lower levels post-hatching (Bennett and Harvey 1985). For example, in zebra finches, HVC, RA, and Area X increase in volume and connections are made between HVC and RA, DLM and LMAN, and LMAN and RA during the time individuals are dependent on parental care (Nowicki et al. 1998). Songbirds are altricial and depend on their parents for food at least during the period between hatching and fledging and in many cases for days or weeks after fledging (O'Connor 1984; Weathers and Sullivan 1989). Undernutrition could limit the resources available for development of the song system (Nowicki et al. 1998, 2002a), as could other stressors such as parasites and disease (Loye and Zuk 1991). Stress-response hormones, such as glucocorticoids, may shift resources from growth and maintenance to short-term survival or affect neural development directly (Wingfield et al.
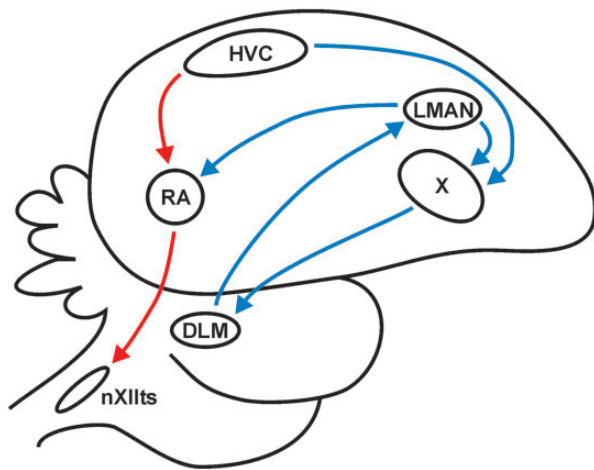
Fig. 1 Schematic of the avian song system. In this illustration of the main song-control nuclei and neuronal connections of the avian song system, the arrows in red indicate the motor pathway and the arrows in blue indicate the sensory or anterior forebrain pathway. HVC, used as a proper name; RA, robust nucleus of the arcopallium; nXIIts, the tracheosyringeal portion of the twelfth cranial nerve, which innervates the muscles of the trachea and syrinx; Area X, in the medial striatum area; DLM, dorsal lateral nucleus of the medial thalamus; LMAN, lateral magnocellular nucleus of the anterior nidopallium.

1998; MacDougall-Shackleton and Spencer 2012; Buchanan et al. 2013). All these stressors could compromise the development of the song system, and thus the accuracy with which songs are learned. Genetic factors may play a role in an individual's response to external stressors. To the extent that the effects of developmental stress on brain development are reflected in song-learning, song may be an honest indicator of a male's developmental history and therefore of other aspects of his quality.

Two field studies have found positive associations between the complexity of songs and measures of post-hatching growth, as predicted by the developmental-stress hypothesis. The repertoire size of great reed warblers (Acrocephalus arundinaceus) in their first year correlates to nestlings' growth as measured by the length of the innermost primary feather at post-hatch Day 9 (Nowicki et al. 2000). The tarsus length of blue tits (Parus caeruleus) correlates with repertoire size (Doutrelant et al. 2000). On the other hand, Bischoff et al. (2009) exposed nestlings of great tits (Parus major) to ectoparasites and then measured their vocal response to territorial challenge as adults. They found that the duration of the song of males exposed to parasites was reduced, but found no effect on the size of the repertoire.

More evidence comes from laboratory studies that have manipulated early developmental stress and

measured the effects on brain development and song-learning in a range of species (Table 1). In the first such study, Nowicki et al. (2002a) directly manipulated nutrition in hand-reared swamp sparrows by restricting experimental birds to 70% of the food consumed by controls. Some of the subsequent studies have restricted food in a similar way, but others have used alternative stressors (Table 1), including exposure to parasites, treatment with the stress hormone corticosterone, restriction of the parents' ability to feed their young, and manipulation of brood size, which is intended to alter the amount of parental care available per individual nestling. The type and severity of the applied stress can be expected to influence how much it affects song development, and we can expect an interaction between the form of the experimental treatment and aspects of the study species' life history, such as the timing of brain development and of the sensory phase for song-learning.

Nowicki et al. 2002a found that the volumes both of the RA and the HVC were reduced in swamp sparrows on restricted diets compared with controls. With respect to attributes of song, the accuracy with which young males copied tutors' songs was reduced in the food-restricted birds, whereas size of repertoire was unaffected. Subsequent studies have varied as to which brain nuclei and which attributes of song have been examined, with the latter to some extent dictated by the form of each study species' song. Some results have been positive, in the sense that stress resulted in a reduction in the size of some song system nucleus or in some measure of quality of song, while others have been negative, in the sense that stress had no effect on a particular outcome (Table 1). Some of the variation in outcomes can be ascribed to variation in methods; for example, manipulation of broods seems to be less effective than other stressors, such as corticosterone treatment or direct restriction of food, perhaps because parents can compensate to some extent for an increase in brood size by working harder. One generalization that emerges, however, is that the HVC seems to be particularly vulnerable to developmental stress (Buchanan et al. 2013), which is significant given that the HVC is an important constituent both of the motor and the sensory pathways. A second generalization is that in almost all species developmental stress affects at least one aspect of the male's song that is potentially assessable by females.

If early developmental stress affects areas of the brain that are important to song, it seems logical to expect brain areas important to other cognitive tasks also to be affected. An experiment with

Table 1 Experimental studies of the effects of developmental stress on the song-control system and on the attributes of song

Species	Stressor	Life-history stage of subject	Treatment's effect on song-control system	Attributes of song examined	Effect of treatment on attributes of song	Authority
Swamp sparrow (*Melospiza melodia*)	Restricted food	Nestling/fledgling	Reduced HVC volume Reduced RA volume Reduced telencephalon	Size of song repertoire Accuracy of copying notes Subsong/plastic song period	No effect Less accurate Extended	Nowicki et al. (2002a)
	Restricted food	Nestling/fledgling		Attractiveness of song	Reduced	Searcy et al. (2010)
European starling (*Sturnus vulgaris*)	Unpredictable food	Fledgling/juvenile		Time spent singing Number of song bouts Mean duration of song bout Size of song repertoire Latency to start singing	Reduced Reduced Shorter Reduced Longer	Buchanan et al. (2003) Spencer et al. (2004)
	Restricted food	Nestling/fledgling		Latency to start singing Duration of bout of song	Shorter Shorter	Farrell et al. (2012)
Zebra finch (*Taeniopygia guttata*)	Restricted food	Nestling/fledgling	Reduced HVC volume No effect on RA No effect on LMAN	Duration of motif Number of syllables/motif Number unique syllables/motif Peak frequency of motif Song rate Attractiveness of song	Reduced Reduced No effect Lower No effect Reduced	Spencer et al. (2003) Buchanan et al. (2004) Spencer et al. (2005a)
	Administration of corticosterone	Nestling/fledgling	Reduced HVC volume No effect on RA No effect on LMAN	Duration of motif Number of syllables/motif Number of unique syllables/motif Peak frequency of motif Song rate Attractiveness of song	Reduced Reduced No effect Lower No effect Reduced	Spencer et al. (2003) Buchanan et al. (2004) Spencer et al. (2005a)
	Restricted food	Nestling/fledgling		Number of different syllables Accuracy of learning Syllable rate Duration of phrase Frequency of maximum power	Reduced No effect Slower Increased Reduced	Zann and Cash (2008)
	Restricted food	Nestling/fledgling		Accuracy of the copy of the song's syntax Song's amplitude Phrase's duration Total number of syllables Number of syllable types Percent copied syllables Percent copied syllable types	Less accurate No effect No effect No effect No effect No effect No effect	Brumm et al. (2009)

(continued)

Table 1 Continued

Species	Stressor	Life-history stage of subject	Treatment's effect on song-control system	Attributes of song examined	Effect of treatment on attributes of song	Authority
	Manipulation of brood size	Nestling/fledgling	No effect on HVC No effect on RA No effect on LMAN	Percent tutor elements copied by tutee Percent tutee elements copied from tutor	No effect No effect	Gil et al. (2006)
				Song duration Element repertoire Song rate Song attractiveness	No effect No effect No effect No effect	Naguib et al. (2008)
	Manipulation of brood size	Nestling/fledgling		Syntax copying accuracy Number of imitated elements Song consistency	Less accurate No effect Reduced	Holveck et al. (2008)
	Manipulation of brood size	Nestling/fledgling		Song rate	Increased	Tschirren et al. (2009)
Domestic Canary (*Serinus canaria*)	Parasitic infection	Fledgling	Reduced HVC volume No effect on RA	Number of complex syllables "A" syllables	Reduced No effect	Spencer et al. (2005b)
	Manipulation of brood size	Nestling		Syllable repertoire size "A" syllables Song bout length	No effect No effect No effect	Müller et al. (2010)
	Post fledgling nutrition	fledgling		Syllable repertoire size "A" syllables Song bout length	No effect No effect No effect	Müller et al. (2010)
Song sparrow (*Melospiza melodia*)	Restricted food	Nestling/fledgling	Reduced HVC volume[a] No effect on RA[a] No effect on area X[a]			MacDonald et al. (2006)
	Restricted food	Nestling/fledgling	No effect on HVC Reduced RA volume No effect on Area X	Size of song repertoire Syllable repertoire size Song learning accuracy Song stereotypy	Reduced Reduced Less accurate No effect	Schmidt et al. (2013)
	Administration of corticosterone	Nestling/fledgling	No effect on HVC No effect on RA No effect on Area X	Size of song repertoire Syllable repertoire size Song learning accuracy Song stereotypy	Reduced Reduced No effect No effect	Schmidt et al. (2013)

(continued)

Table 1 Continued

Species	Stressor	Treatment's effect on song-control system	Life-history stage of subject	Attributes of song examined	Effect of treatment on attributes of song	Authority
Bengalese finch (*Lonchura domestica*)	Nestling growth (body size)			Duration of bout of song Number of notes per song bout Number of unique notes Linearity index	Reduced No effect Reduced[b] Reduced[b]	Soma et al. (2006)
Blue Tit (*Parus caeruleus*)	Manipulation of brood size		Nestling	Length of strophe bout	Reduced	Dreiss et al. (2006)

[a]Measured in juveniles; [b]When brood was more male-biased.

Western scrub jays (*Aphelocoma californica*) supports this inference. Scrub jays subjected to early nutritional stress developed smaller hippocampi and subsequently performed worse on spatial memory tasks than did controls (Pravosudov et al. 2005). Outside of songbirds, quality of early nutrition has been shown to affect measures of cognitive ability in humans (Griesel 1984; Lynn 2009) and rats (Fukuda et al. 2002; Valadares and Almeida 2005). If the same stresses impact both song-learning and other aspects of cognition, then it is logical to expect song to be an indicator of cognitive abilities.

Tests of song as an indicator of cognition

A number of laboratory experiments have been conducted to test for the predicted association between song and aspects of cognitive ability. In the first such study, Boogert et al. 2008 presented male zebra finches with a novel foraging task in which the birds had to learn to flip lids covering wells on a grid in order to retrieve seed. Male zebra finches have only one song in their repertoire but individuals differ in how many elements are included in the song. Males with more elements per song required fewer learning trials to solve this task. The duration of phases and the number of unique elements per phrase did not explain a significant proportion of the variance in learning.

Boogert et al. (2011a) presented male song sparrows with the same lid-flipping problem and found no correlation between ability to learn this task and the size of their repertoire of songs. The researchers also presented song sparrows with a color-association and color-reversal task; song sparrows had to learn that one of two colors was associated with a reward of food and the other not, then to reverse that association. There was no correlation between repertoire size and a male's ability to solve the color-association task. Surprisingly, males with larger repertoires performed worse than males with smaller repertoires on the color-reversal task, but the significance of this correlation did not withstand a Bonferroni correction. The one cognitive task that showed the predicted positive association with repertoire size involved "detour reaching", a test of inhibitory control. In this task, individuals are presented with a clear plastic cylinder containing food. Most individuals initially try to peck at the food directly through the plastic, and vary in how quickly they learn to inhibit this response in favor of detouring to one of the open ends of the cylinder. The ability to inhibit an instinctive or preprogrammed response that is unsuccessful is thought to reflect an ability to solve

problems (Vlamings et al. 2010). Boogert et al. (2011a) found that males with larger repertoires were significantly more successful in solving the detour reaching task, with a correlation that was sufficiently robust to withstand Bonferonni correction.

Sewall et al. (2013) tested the relationship between the size of the repertoire of songs and success in completing a spatial foraging task in male song sparrows. The birds were tested using a grid with 12 wells, six of which were covered with lids, and only one of which was baited with food. The task was to learn the position of the baited well, which was kept constant from trial to trial. Contrary to prediction, an inverse relationship was found between size of the repertoire and the speed with which this task was learned; in other words, birds with larger repertoires learned more slowly. Sewall et al. (2013) suggested that this inverse relationship between song and spatial learning may be due to a tradeoff between investment in the song system and investment in those areas of the brain that support spatial learning, especially the hippocampus (Pravosudov and Roth 2013). By this logic, inverse relationships between song and cognition may be particularly likely for cognitive abilities that are strongly tied to specific regions of the brain.

Farrell et al. (2012) examined the relationship between song and cognition in European starlings while simultaneously measuring the effects of developmental stress on both. Starlings were raised with either a control or restricted diet for about their first 3 months of life. Some months later the birds were tested on a task requiring acquisition of a novel foraging skill and a task requiring spatial memory. Birds subjected to the restricted diet performed better on the novel foraging task and worse on the spatial learning task than did controls. Restriction of food had a significant negative effect on the length of bouts of song, an attribute that is typically strongly correlated with size of the repertoire in this species. The only significant association between song and cognitive performance was a negative correlation between length of bouts of song and number of errors on the spatial learning task; males with longer bouts committed fewer errors. This study is particularly significant in showing how a link between song and cognitive abilities can be forged through the effects of developmental stress on both.

Conclusions

The developmental-stress hypothesis lays out a pathway that connects song-learning to other aspects of cognition and that ought to result in an association between learned aspects of song and cognitive abilities. The links in this pathway have gained support from a number of empirical studies. The learning and production of songs have been shown to depend on dedicated brain nuclei and connections among those nuclei that develop during a period in a young songbird's life when developmental stresses are particularly likely. Experimental studies have shown that a variety of environmental stressors affect the development of the song system as well as particular aspects of the adult's song. Experimental evidence also shows that other aspects of cognitive ability are influenced by the same kinds of developmental stresses. Thus, it seems logical to predict positive associations between song and cognition.

Nevertheless, results to date on the associations between aspects of adults' songs and cognitive abilities have been mixed. Some results to be sure have been as predicted; these include a positive association between the number of elements per song and success in learning a new foraging task in zebra finches (Boogert et al. 2008), an association between size of repertoire and success in learning the detour reaching task in song sparrows (Boogert et al. 2011a), and a positive association between the average length of a bout of song and success on a spatial learning task in starlings (Farrell et al. 2012). Other results, however, have been negative; for example, no association was found in zebra finches between success in learning the foraging task and in two other aspects of the adults' song (Boogert et al. 2008), and in song sparrows, size of song repertoire failed to correlate with success in several additional learning tasks (Boogert et al. 2011a). Furthermore, one result is opposite to the prediction: size of the repertoire of songs was negatively related to spatial learning ability in a second study of song sparrows (Sewall et al. 2013).

How can we reconcile these mixed results with the strong logic of the underlying hypothesis? One consideration is that the choice of traits of song measured in cognitive studies perhaps has not been optimal. Results have shown that a particular environmental stressor may affect one aspect of song but not another (Table 1); thus the mechanisms linking developmental stress to cognitive function may function better for some traits of the song than for others. Much emphasis has been placed on the size of the repertoire of songs in studies relating song to cognition, but it is not clear how strongly the size of the repertoire is influenced by learning. Certainly, other attributes of the song are more clearly dependent on learning, notably the accuracy with which songs are learned. No study to date has compared

cognitive ability to the accuracy of learning, that is, to how well a male copies the fine acoustic structure of a song. Such a study would almost certainly require using hand-reared birds tutored with song in the laboratory, so that the models could be specified with confidence.

Another consideration is that different aspects of cognitive performance may not be as strongly associated with each other in birds as they are in mammals. Positive association in performance on different cognitive tasks is well established for mice (Galsworthy et al. 2002, 2005; Matzel et al. 2003) and humans (Spearman 1904; Carroll 1993; Plomin 2001). In contrast, Boogert et al. (2011a) found a mix of weak positive and weak negative correlations between measures of success on four cognitive tasks in song sparrows. Similarly, Keagy et al. (2012) found a mix of non-significant positive and negative correlations between measures of success on five cognitive tasks in male satin bowerbirds. Isden et al. (2013) found mainly positive correlations between measures of success on six cognitive tasks in male spotted bowerbirds (*Chlamydera maculata*), but most of the correlations were weak and all were non-significant. The weaker the associations between different measures of cognitive ability in birds, the less likely it is that a given aspect of song will be simultaneously correlated with multiple measures. Thus, rather than signaling all aspects of cognitive ability, a particular trait may signal only a specific cognitive ability. Which traits of the song are tied to which cognitive abilities, and why particular links are formed, should be the subject of future study.

A variety of assays have been devised to measure cognition in songbirds, but it is not always obvious how the ability to solve these tasks translate into traits that affect fitness. If females are interested in the cognitive abilities of potential mates, they should only be interested in those traits that benefit them or their offspring. Thus, to understand whether song functions as an indicator of male cognition we also will need to map the ability to solve any of these tasks onto behavioral traits that actually matter to the animals, and much more work still needs to be done in this regard.

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