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REVIEW

Developmental stress and birdsong: current evidence and future directions

Scott A. MacDougall-Shackleton · Karen A. Spencer

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Abstract The *developmental stress hypothesis* posits that the honesty of bird song is maintained by costs incurred during development, rather than at the time of adult song production. Song is learned, and the neural systems underlying song learning and production develop early in life at a time when nutritional and other stressors are prominent. Thus, adult song may reflect the early developmental conditions of a male and/or how well that male was able to cope with developmental stressors. Substantial evidence in support of the *developmental stress hypothesis* has accrued over the last decade, but much remains to be done. Here, we review the current evidence in support of the hypothesis and highlight future directions. With few exceptions, there is now solid evidence that a variety of developmental stressors impair development of song and the brain. We note that birdsong is potentially an example of a larger class of sexually-selected indicators of developmental conditions. Future issues include examining the effects of stress on females, resolving whether song indicates developmental stability or developmental environment, exploring the neuroendocrine mechanisms by which stress modifies song development, determining whether stressed birds are subject to phenotypic programming, and determining the effects of stressors on song in adult birds. The developmental stress hypothesis thus provides a rich framework for future integrative studies of birdsong and development.

Keywords Birdsong · HVC · Developmentally correlated traits · Glucocorticoids

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S. A. MacDougall-Shackleton (✉)
Department of Psychology, Advanced Facility for Avian Research, University of Western Ontario,
1151 Richmond Street, London, ON N6A 5C2, Canada
e-mail: smacdou2@uwo.ca

K. A. Spencer
School of Psychology, St Mary's College,
University of St. Andrews,
St. Andrews KY16 9JP, Scotland, UK

Birdsong as an indicator

There is a general consensus that the evolution of birdsong among many species is due, at least in part, to sexual selection (Searcy and Andersson 1986; Searcy 1992; MacDougall-Shackleton 1997; Catchpole and Slater 2008). One challenge, however, is explaining the tremendous variation in song among species. In some species, such as the Zebra Finch (*Taeniopygia guttata*), individual males sing a unique stereotyped song that differs between males. In other species, such as the White-crowned Sparrow (*Zonotrichia leucophrys*), individual males sing a single song similar to most other males in their area, with distinct dialect regions (Marler and Tamura 1964). In about 75% of songbird species, males sing repertoires of multiple song types, ranging from a few song types to thousands (MacDougall-Shackleton 1997). If song is under strong sexual selection, how can this variation be maintained within and between populations?

Nowicki and Searcy (2005a) have summarized three main kinds of song features that may be subject to inter- and intra-sexual selection: song output (e.g., singing rate, song length), song complexity (e.g., song or syllable repertoire size), and geographic origin (e.g., local dialect). If these song features have evolved as indicator signals, an important question is how the honesty of the signal can be

maintained. One widespread way that sexually selected signals can evolve to be, more or less, honest indicators of signaler quality is if they impose conditional handicaps (Zahavi 1975; Grafen 1990; Andersson 1994; Searcy and Nowicki 2005). In the case of song output, it seems a safe assumption that singing for 2 h per day would be more costly than singing 1 h per day due to increased energy expended, time spent, and increased conspicuousness to potential predators. In the case of responding differentially to songs of greater or lesser complexity, or to songs from different geographic regions, the costs that could maintain signal honesty are less clear.

The developmental stress hypothesis

Nowicki et al. (1998) proposed an innovative hypothesis to explain how features such as song dialects and song complexity could be maintained as honest signals. Their *nutritional stress hypothesis* posited that the costs associated with these song features are incurred early in life. Both song complexity and song dialects are a product of song learning, typically early in life. Catchpole (1996) pointed out that the costs of birdsong may involve the costs of having the brain regions that produce it. The brain regions critical for song learning develop early in life at a time when young birds typically face limited nutritional resources and other stressors (e.g., Sullivan 1989). These stressors could impair brain development, as well as song learning and development, and have a long-term effect on adult song. Thus, adult song has the potential to honestly reflect a singer's developmental conditions and quality. Because environmental stressors other than limited nutrition have the potential to impair brain development and song learning, the hypothesis has been more recently renamed the *developmental stress hypothesis* (Nowicki et al. 2002; Buchanan et al. 2003).

Support for the above hypothesis has rapidly accrued over the last decade. A variety of stressors experienced early in life—including food restriction, sibling competition, and disease—have been shown to affect both the development of song-control brain regions and adult song in a variety of songbird species (Table 1). Both experimental data and observed correlations indicate that the developmental stress hypothesis is a plausible process by which learned features of song could evolve as honest signals, but many questions remain. In this review, we first provide a survey of the experimental and observational tests of the developmental stress hypothesis. We then discuss several outstanding issues with the hypothesis, including considering the effects of developmental stress on both males and females, distinguishing between good developmental conditions versus good genes versions of the hypothesis, and considering physiological mechanisms.

Evidence for the hypothesis

Substantial evidence has been gathered in support of the developmental stress hypothesis, including observational studies in the field and experimental studies in the laboratory. In the field, features of song have been correlated to other indicators of developmental quality. In experimental studies, a variety of stressors during development have been demonstrated to impair the development of song-control brain regions as well as song learning and adult song (reviewed in Spencer and MacDougall-Shackleton 2011).

Observational studies

Several studies have found correlations between song characteristics and male quality. For example, in great tits (*Parus major*) song repertoire size is related to adult survivorship, and production of more and larger young (McGregor et al. 1981). In an island population of Western Song Sparrows (*Melospiza melodia morphna*), song repertoire size has been observed to correlate with longevity, territory tenure, initial mating success, immune function, and number of offspring and grand-offspring produced and recruited into the population (Hiebert et al. 1989; Reid et al. 2004, 2005a, b). Similarly, Eastern Song Sparrow (*M. m. melodia*) males with larger repertoires tend to be in better physiological condition (Pfaff et al. 2007). In Great Reed Warblers (*Acrocephalus arundinaceus*), the extra-pair offspring of males with larger repertoires have higher post-fledging survival (Hasselquist et al. 1996).

There is also evidence that song features related to geographical location may be correlated to male quality. For example, males that sing local dialects suffer lower parasite loads in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*; MacDougall-Shackleton et al. 2002). Similarly, Eastern Song Sparrows that sing a greater number of local song elements had fewer parasites and were in better condition than males that sing fewer local song elements (Stewart and MacDougall-Shackleton 2008). Thus, in many species of songbirds, males with larger repertoires or geographically local songs appear to have higher quality in a variety of ways, consistent with the idea that song is an indicator signal.

It is clear that, in many species of birds, features of song such as song complexity or song dialect correlate to aspects of male quality predictive of fitness. However, if we are to relate these findings to the developmental stress hypothesis, we need to determine if these indicators of male quality

Table 1 Experimental studies of the effects of developmental stressors on song and the song control system

Species	Stressor	Age of treatment	Effects	References
Zebra Finch (*Taeniopygia guttata*)	Food restriction	Nestling/fledgling	Reduced song duration	Spencer et al. (2003)
			Reduced syllables/song	Buchanan et al. (2004)
			Lower peak frequency of song	Spencer et al. (2005a)
			Reduced HVC volume	
			Reduced song attractiveness	
	Food restriction	Nestling/fledgling	Reduced accuracy of song syntax learning	Brumm et al. (2009)
			No effect on song duration, amplitude, or repertoire size	
	Corticosterone treatment	Nestling/fledgling	Reduced song duration	Spencer et al. (2003)
			Reduced syllables/song	Buchanan et al. (2004)
			Lower peak frequency of song	Spencer et al. (2005a)
			Reduced HVC volume	
			Reduced song attractiveness	
	Food restriction	Nestling/fledgling	Slower syllable rate	Zann and Cash (2008)
			Reduced frequency of maximum power	
			Increased song duration	
			Some effects on copying accuracy	
	Brood size manipulation	Nestling/fledgling	Reduced song rate from larger broods	de Kogel and Prijs (1996)
	Brood size manipulation	Nestling/fledgling	Increased song rate from larger broods	Tschirren et al. (2009)
	Brood size manipulation	Nestling/fledgling	No effects on song parameters	Gil et al. (2006), Naguib et al. (2006, 2008)
	Brood size manipulation	Nestling/fledgling	Reduced syntactical copying	Holveck et al. (2008)
			No effects on syllable number	
Domestic Canary (*Serinus canaria*)	Parasitic infection	Fledgling	Reduced syllable number	Spencer et al. (2005b)
			Reduced HVC volume	
European Starling (*Sturnus vulgaris*)	Unpredictable food	Fledgling/ juvenile	Reduced time spent singing	Buchanan et al. (2003)
			Shorter song bout duration	
			Reduced repertoire size	Spencer et al. (2004)
Blue Tit (*Parus caeruleus*)	Brood size manipulation (in wild)	Nestling	Shorter strophe length in enlarged brood	Dreiss et al. (2006)
Swamp Sparrow (*Melospiza georgiana*)	Food restriction	Nestling/fledgling	Extended period of subsong/plastic song	Nowicki et al. (2002)
			Less accurately copied song	
			Reduced telencephalon size	
			Reduced absolute HVC size	
			Reduced RA size relative to telencephalon	
Song Sparrow (*Melospiza melodia*)	Food restriction	Nestling/fledgling	Reduced relative HVC size in juveniles	MacDonald et al. (2006)

and song are correlated due to the conditions experienced during development. Some data indicate that this is the case. In Great Reed Warblers, the quality of feather growth during early development correlated with male repertoire size in adulthood (Nowicki et al. 2000). This is consistent with the hypothesis that both feather growth and repertoire were affected by developmental conditions. In Blue Tits (*Parus caeruleus*), tarsus length is affected by developmental conditions. In at least some populations of Blue Tits, tarsus length correlated with repertoire size during the dawn chorus (Doutrelant et al. 2000). Once again these data provide evidence in favour of the hypothesis that early developmental conditions have persistent effects on song and other traits such as tarsus length. Soma et al. (2006) similarly observed effects of early conditions on adult song in Bengalese Finches (*Lonchura striata*). Males from larger broods were smaller in size, and both brood size and brood sex ratio were related to male song complexity. Song complexity was lower with increasing male-biased brood sex ratio, and this effect was greater in larger broods (Soma et al. 2006). The endocrine response to stress in adult vertebrates is influenced by developmental conditions, including in birds (Pravosudov and Kitaysky 2006; Spencer et al. 2009) and this stress response has been correlated to song complexity in Song Sparrows (MacDougall-Shackleton et al. 2009). Gorissen et al. (2005) have used a natural experiment to test how environmental stressors affect birdsong. Great Tits (*Parus major*) living at a site heavily polluted with lead had less complex songs than those from less polluted sites nearby, with 30% fewer song types in their repertoires. The above studies thus provide correlational evidence that early developmental conditions can influence a variety of phenotypic characters, including song.

Experimental studies

The developmental stress hypothesis proposes that stress during development imposes trade-offs that result in less investment in the neural regions controlling song learning and production, and thus impair song learning and adult song. Several experimental studies have tested this idea by manipulating developmental conditions and then measuring song and/or the song-control brain regions (Table 1). Experimental manipulations have included food restriction, food predictability, increased brood size, parasite infection, and direct treatment with glucocorticoid hormones.

Experimental studies measuring song and song learning

Song learning in songbirds has been extensively studied (Kroodsma 1978; Catchpole and Slater 2008). Experimental studies have demonstrated a variety of effects on adult song. One of the first experimental tests of the developmental stress hypothesis directly measured the song learning process. Food restriction during the nestling and fledgling stages in Swamp Sparrows (*Melospiza georgiana*) resulted in birds beginning to produce subsong earlier, and thus extended the duration of the sensorimotor phase of song learning (Nowicki et al. 2002). In addition, the food restricted sparrows' crystallized songs were less accurate copies of the tutor songs than birds those of birds fed ad libitum (Nowicki et al. 2002). Thus, in Swamp Sparrows, nutritional stress in development results in changes in the song learning process—potentially a shortened sensory phase and extended sensorimotor phase. The consequence of this alteration in song learning is less accurate vocal imitation.

Most other experimental tests of the developmental stress hypothesis have measured adult song, following some sort of stressor experienced during the nestling, fledgling and/or post-fledgling phases (Table 1). For example, in several studies nestling Zebra Finches exposed to either elevated glucocorticoid hormone levels (corticosterone), food restriction or enlarged brood sizes during early postnatal development showed significantly altered song in adulthood (de Kogel and Prijs 1996; Spencer et al. 2003; Holveck et al. 2008; Brumm et al. 2009; but see Gil et al. 2006; Tschirren et al. 2009). The particular effects on song and song learning (if any) have been variable (Table 1), likely due to varied manipulations used in different laboratories (see below). Mate choice studies have also shown that females preferred songs from control males over developmentally stressed ones (Spencer et al. 2005a). In another study, Zebra Finches reared under food restriction exhibited some degree of reduced copying accuracy and sang adult songs with lower frequencies, and tended to sing syllables at a slower rate than those from unrestricted developmental conditions (Zann and Cash 2008). Open-ended song learners also appear to be sensitive to detrimental developmental conditions. European Starlings (*Sturnus vulgaris*) exhibit reduced song bout lengths and repertoires when exposed to unpredictable food availability during the post-fledging period (Buchanan et al. 2003; Spencer et al. 2004).

Experimental studies measuring the song control brain regions

In songbirds, a specialized network of brain regions referred to as the song-control system mediate song learning and song production (Nottebohm 2005). This song-control system is a relatively late-developing neural system, with much development occurring during the period of song learning (reviewed in Nowicki et al. 1998, 2002). It is thus plausible that stressors experienced early in

development could impair the development of this system, and thus impair song learning. Food restriction during nestling and early fledgling stages resulted in reduced volume of the song-control nucleus HVC at 3 weeks of age in Song Sparrows (MacDonald et al. 2006). At this age, Song Sparrows are just beginning the sensory phase of song learning (Marler and Peters 1987) and, based on studies of the congeneric Swamp Sparrow, HVC is rapidly growing (Nordeen et al. 1989). It has yet to be determined if early food restriction leads to long-term changes adult HVC size and song in song sparrows. However, in several other songbird species, exactly that has been found.

In many songbirds, stress during development has been shown to result in smaller song control regions in adults (Table 1). In Swamp Sparrows, food restriction during the nestling and fledgling stage resulted in smaller HVC and RA (robust nucleus of the arcopallium) size in adults (Nowicki et al. 2002). In addition, food-restricted birds had a smaller overall brain size. Only RA remained significantly smaller in food-restricted birds when the effects of overall telencephalon size were controlled. In contrast, other studies have found that HVC is specifically impacted by developmental stress. In Zebra Finches, food restriction or corticosterone treatment specifically affected adult HVC size, but neither overall brain size nor the size of some other song-control regions (Buchanan et al. 2004). In juvenile Song Sparrows, food restriction also specifically affected HVC size, even when controlling for effects on overall telencephalon size (MacDonald et al. 2006). In Domestic Canaries (*Serinus canaria*), infection with avian malaria (*Plasmodium* spp.) during development resulted in smaller adult HVC size; RA size and brain mass were unaffected (Spencer et al. 2005b). Although further work is clearly warranted, it appears that HVC is particularly susceptible to developmental stressors. Given that HVC is critical for both song learning and production, and is at the top of the hierarchical organization of motor control during singing, it is notable that it is this brain region that appears most sensitive to early environmental conditions.

Weighing the evidence

Not all experimental manipulations have supported the developmental stress hypothesis. For example, Gil et al. (2006) manipulated brood size in Zebra Finches as a test of the developmental stress hypothesis. Although the manipulations did have effects on physiological condition, there were no effects on brain mass, the size of song control regions, or on song learning, adult song features or attractiveness to females (Naguib et al. 2006, 2008). There are several potential reasons for these null results. First, manipulations of brood size are an indirect developmental stressor, and the level of stress experienced by a chick in an enlarged nest will be affected by a variety of housing conditions. Interestingly, brood size effects have impaired song learning in other studies of Zebra Finches and Bengalese Finches (Soma et al. 2006; Holveck et al. 2008). Moreover, exactly opposite effects on singing rate have been observed following brood size manipulations (de Kogel and Prijs 1996; Tschirren et al. 2009). Thus, it appears that brood size manipulations in particular have produced a range of results, some of which support the developmental stress hypothesis, and some that do not. As noted above, the extent to which a stressor will have an impact on neural development and song learning will depend both on the magnitude of the stressor and on the timing of it relative to the schedule of song learning. Although brood size manipulations have high external validity, mimicking processes that would occur in free-living birds, these manipulations have lower internal validity than food restriction or hormone treatment because the amount of the stressors applied is less controlled. How parents respond to brood size manipulations likely depend on other aspects of husbandry that may vary from laboratory to laboratory, and it is thus difficult to make controlled comparisons across studies, or indeed to determine the extent to which an enlarged brood creates a developmental stressor.

In a study of non-domesticated Zebra Finches, Zann and Cash (2008) found some reduced song imitation in some food-restricted birds but not others, differing from earlier work (Spencer et al. 2003). Once again, the impact of a developmental stressor may affect song learning differentially depending on the relative timing of the stress. This is important to note in comparing studies across species. Future work would be required to determine if and how these two strains differ in the timing of phases of song learning, or the timing of development of the stress response itself.

It is important to note that not all seemingly adverse early experiences may act as developmental stressors and disrupt song development. For example, Starlings exposed to a cocktail of endocrine disruptors mimicking those found in a sewage lagoon had impaired immune function, but larger HVC, longer song bouts, and a larger repertoire size (Markman et al. 2008). In this case, the estrogenic contaminants were unlikely to act as a stressor per se, but clearly had impact on the development of the brain and immune system.

On the whole, most published studies that have tested whether a developmental stressor can affect song and/or the development of the song control system have found results supporting the developmental stress hypothesis, particularly when the developmental stressors are controlled directly by the researchers (food restriction,

hormone treatment) rather than indirectly via brood size manipulation (Table 1). The variation among studies is likely a result of differences in the timing of song learning and the application of different stressor types that can affect more than one physiological system. An important future direction will be to apply stressors at different time points in the same species in order to determine how the timing of stress affects adult song. That said, it is clear from the experimental data that developmental stressors *can* impair neural development and song learning. In addition, correlations between song and indicators of developmental stress (reviewed above) suggest that this process *does* occur in the wild, at least in some species of songbirds.

Outstanding issues

There is a growing body of evidence in support of the developmental stress hypothesis and its importance in our understanding of the general principles of evolutionary processes. That said, there are a number of issues that remain unanswered and, in some cases, unasked. Below, we review several of these issues and indicate directions for future research.

Effects on females

Nowicki et al. (1998) noted that their hypothesis had the potential to apply to females as well as to males, but few data have been collected in this regard. Presumably females experience the same environmental stressors as males during development. Indeed in some cases they may experience more stress if they are less able to compete for limited resources than their brothers (Zanette et al. 2005; Rowland et al. 2007). In species where females sing, the developmental stress hypothesis provides a mechanism by which song can be an indicator signal for females as well as males. Less clear is what effect stressors during development have on female song perception and preferences? In at least some species, song preferences have clearly been shown to be learned via experience (Clayton 1990; Hernandez et al. 2009). Thus, early stressors could have an impact on female preferences as well as female song.

The neural systems underlying song perception and song preferences are less well understood than those underlying learning and production. A few studies suggest that lesions to song control brain regions disrupt normal song perception in some species (Brenowitz 1991; Del Negro et al. 1998; Burt et al. 2000) but not others (MacDougall-Shackleton et al. 1998). A large number of studies have indicated that the caudomedial mesopallium (CMM) and caudomedial nidopallium (NCM) are specialized for auditory processing and memorization of song (Bolhuis and Gahr 2006). Because CMM and NCM do not have distinct cytoarchitecture like the song control regions it is more difficult to quantify their size. As yet, no studies have examined changes in CMM or NCM structure or functioning as a result of developmental stress. One study of Song Sparrows found that HVC growth was impaired following food restriction in females (MacDonald et al. 2006). Although the timing of development of CMM and NCM relative to the song control regions is unknown, it is plausible that developmental stressors could impact both systems.

Few studies have examined the effects of stress during development on females' behavioral responses to song. Riebel et al. (2009) found that development in an enlarged brood did not affect song preferences of female Zebra Finches for their tutor's song. However, when choosing among unfamiliar songs, females from small broods had stronger preferences than other females. Holveck and Riebel (2010) found that females from enlarged broods preferred the songs of males from large broods over those of males from small broods. This intriguing result suggests that rather than impairing a female's ability to discriminate among songs, early stress may shift a female's preferences to males who have experience similar stressful conditions (see "Making the Best of a Bad Situation?" below). In another study of Zebra Finches, females were raised under control or nutritionally restricted conditions. Food restriction impaired growth, and led females to be less active during mate choice trials (Woodgate et al. 2010). However, there was no effect on which males were preferred. In addition, there was no effect on preferences for more complex songs as compared to less complex songs (Woodgate et al. 2011). There is thus no current evidence that early developmental stress alters female perception of songs, and only limited evidence that song preferences are affected. Clearly more research in this area is required.

Good genes, or good upbringing?

Individual differences in a trait such as birdsong could arise due to differences in environmental conditions experienced during development, or due to differences in individual ability to cope with those conditions, or an interaction of both. That adult song likely reflects both genotypic variation as well as developmental experience was articulated in the initial proposal of the developmental stress hypothesis (Nowicki et al. 1998, 2002). In the experimental studies reviewed above (Table 1), individuals are typically randomly assigned to treatment groups. Thus, between-group differences reflect differences in experience. It remains unclear what proportion of individual variation in song in

the wild results from developmental experience versus individual differences in developmental stability. There are different experimental approaches that could be used to address this issue, such as a behavioral genetics approach to partition variation into genetic and environmental components or testing whether offspring of known individuals are better or less able to cope with standardized developmental stressors. To date, however, no such studies have been published.

One may ask if it matters whether adult song reflects good genes or good developmental conditions. In one sense, as long as acoustic traits reflect either good genes, or direct benefits that result from a benign development, then song could act as an indicator signal. There are several reasons, however, that it might be important to distinguish these processes. First, the extent to which song reflects genes versus experience would influence extra-pair mating strategies. To the extent that song features reflect only a benign early ontogeny, those features should be discounted by females selecting extra-pair mates compared to within-pair mates (since extra-pair mates typically provide no direct benefits). In Great Reed Warblers, females select as extra-pair mates males who have song repertoires larger than their own mate, and the resultant offspring are more likely to survive (Hasselquist et al. 1996). In this species, then, it would appear that song repertoires should reflect individual variation in the ability to cope with developmental stressors to a greater extent than variation in rearing conditions. This has yet to be experimentally determined.

A second reason that it is important to distinguish between good genes versus good upbringing versions of the developmental stress hypothesis is that the predictive value of the signal in relation to the spatial and temporal stability of the environment differs for the two hypotheses. In environments with a high degree of variation in quality from territory to territory, or from year to year, the developmental stress hypothesis would predict greater individual variation in song. In stable environments, song variation should be lower, but what variation there is should more accurately predict genetic variation and indirect benefits to a female. In variable environments, song variation should less accurately predict genetic variation, and song preferences should switch to features that are more predictive of direct benefits. This idea has yet to be tested.

Another reason that it is important to distinguish between good genes and good upbringing versions of the developmental stress hypothesis is that this allows an evaluation of the relative importance of direct and indirect benefits in mate choice. Many studies, including those reviewed above, assess only direct or indirect benefits. It is likely that many, if not most, mate choice decisions are influenced by both. If we are to understand the relative importance of direct and indirect benefits in mate choice, and hence the process that underlies the evolution of complex sexual signals, then we need to take an integrative approach and evaluate both genetic and direct benefits. The developmental stress hypothesis provides a framework to do this.

Mechanisms: stress response or differential investment

One major outstanding issue for the developmental stress hypothesis is that of mechanism. The physiological and cellular processes by which food restriction or other stressors impair development of HVC are currently unknown, and there are many possibilities. More broadly, however, it is unknown if the reduced HVC size is a result of differential resource allocation or is a consequence of an adrenal stress response.

Stress response or differential resource allocation?

One view of the developmental stress hypothesis is that there are adaptive priorities set during development (Nowicki and Searcy 2005a, b). In the face of limited resources, priorities should be set that allow growth and survival over investment in ornamental traits. Thus, resources should be allocated to brain regions critical for survival before being invested in regions for song learning. Such adaptive priorities in neural development could explain the observed effects of developmental stress on HVC size and subsequent song learning.

An alternative model, however, is that the reduction in HVC size following a stressor is a pleiotropic effect of the stress response. (Here, we refer to pleiotropic effects of hormones as analogous to pleiotropic effects of genes.) The stress response is a conserved neuroendocrine reaction to stressors that move animals into an emergency life history stage (Wingfield 2005; Wingfield et al. 1998). Within minutes of experiencing real or perceived stress, the hypothalamo–pituitary–adrenal (HPA) axis is upregulated, resulting in secretion of glucocorticoids such as cortisol or corticosterone from the adrenal cortex. Glucocorticoids result in mobilizing energy from storage to circulation and inhibition of processes such as growth and reproduction in the longer term. The stress response is an adaptive response, allowing organisms to cope with immediate threats. Prolonged elevated glucocorticoids, however, have many deleterious effects, mainly due to an increase in allostatic load, including fatigue, neuronal cell atrophy, and immunosupression (de Kloet 2000; Sapolsky 2000a; Wingfield 2005).

When stressors such as food restriction lead to impaired HVC development, is this a result of adaptive differential

investment of energy and resources, or a pleiotropic effect of the stress response? Some experimental data support a role for glucocorticoids. First, activation of the HPA axis is the final common pathway in the stress response to a wide range of physical and psychological stressors. Thus, the variety of stressors shown to affect HVC size and song learning could all potentially be mediated by glucocorticoids. Second, in Zebra Finches, direct treatment with corticosterone produced effects on HVC size and song that directly paralleled the effects of food restriction (Spencer et al. 2003, 2005b; Buchanan et al. 2004). It is plausible that stressors such as food restriction affect glucocorticoid levels in nestling and fledgling songbirds (Pravosudov and Kitaysky 2006). The stress response appears to develop prior to song learning and the development of the song-control system, and several studies have shown that nestling birds can respond to external stressors (Blas et al. 2005; Sockman and Schwabl 2001; Kitaysky et al. 1999; Sims and Holberton 2000; Williams et al. 2008; Wada et al. 2007). Thus, it appears likely that many of the experimental stressors tested, such as food restriction, have their effects mediated through glucocorticoids.

If the experimental stressors that impair HVC development and song learning can be demonstrated to have their effects via the HPA axis, does this eliminate the adaptive priority hypothesis? Not necessarily. One of the important functions of hormones such as the glucocorticoids is to mediate transitions between physiological states, for example between a growth or maintenance state and an emergency state (Wingfield et al. 1998). Elevated corticosterone could thus act as the mechanism that implements adaptive priorities in development, shifting resources from long-term investment in neural development to short-term survival. This is a refinement of the idea that adaptive priorities in brain development result from differential investment in different systems (Nowicki and Searcy 2005b). Here, corticosterone could mediate trade-offs between physiological states, between development of the song control system and somatic growth, and short-term survival. On the other hand, impaired HVC growth due to elevated glucocorticoids could be a non-adaptive developmental constraint. Much further data are required to determine whether adaptive priorities in brain development are dependent on, or independent of, glucocorticoids. Testing this idea requires a far better understanding of the physiological and cellular mechanisms that mediate the effects of development stress in songbirds.

Potential physiological and cellular mechanisms

To date, we know very little about the mechanisms that result in reduced HVC size as a result of food restriction or other stressors. The fact that a variety of stressors, and corticosterone itself, can affect HVC size implicates glucocorticoids as part of the process. However, current data cannot eliminate the possibility that differential resource allocation results in impaired HVC growth, even in the absence of HPA activation. For example, cell division requires energy, and it is possible that mitotic activity in general is reduced when energy is limited. It is possible that the timing of such down-regulated mitosis could lead to fewer cells in HVC if the energy limitations occurred at a time that HVC was developing but other systems had more or less fully developed. Such a mechanism is possible, but we find it unlikely. Food restrictions that reduce song learning and HVC size have multiple effects, often including reduced growth rate. These food restrictions may occur throughout an extended period of growth and development. Yet, HVC can be specifically reduced in size, with no differences in overall brain size, or in other song control regions (Buchanan et al. 2004; MacDonald et al. 2006; Spencer et al. 2005b). It thus seems unlikely that smaller HVC results from a general reduction in mitotic activity. The mechanism requires some way that HVC is affected more by a stressor than other brain regions. The glucocorticoid stress response is a likely candidate.

Growth and plasticity in the brain involves several processes including neurogenesis (birth and migration of new neurons to specific brain regions) and apoptosis (programmed cell death). Steroid hormones can affect these processes, and brain regions rich in steroid receptors can thus respond to endocrine signals differentially compared with other brain regions. In mammals and birds, the hippocampus contains glucocorticoid and mineralocorticoid receptors and has been shown to be particularly sensitive to prolonged stress, as it represents one of the main sites for glucocorticoid negative feedback mechanisms (Sapolsky 2000a, b). It is possible that HVC is similarly sensitive to glucocorticoids. A prolonged stress response during development could thus result in decreased neurogenesis, increased apoptosis, or both in HVC. This mechanism is entirely plausible; however, there are few data to address it. Recent work suggests that the song-control system does express receptors for corticosterone (Suzuki et al. 2011). However, it remains unknown whether impaired HVC size due to developmental stressors results from fewer cells being recruited to HVC, increased apoptosis, or neither of theses mechanisms. Clearly, much further work is required to address these hypotheses. That said, based on a large literature on the effects of hippocampal development in mammals (McEwen 1999; Sapolsky 2000a, b), it seems likely to us that glucocorticoids play a central role in the developmental stress hypothesis.

Making the best of a bad situation?

The developmental stress hypothesis was proposed to explain how learned features of song could be honest indicators of male quality. According to the hypothesis, low quality males or males in a poor environment cannot afford the costs of developing the song-control regions of the brain, and prioritize growth and survival over the development of a sexual signal (song). In this view, males with poor songs are making the best of a bad situation. Their song quality is the best they can afford. Whether through adaptive resource allocation and/or pleiotropic effects of corticosterone, HVC size and song are sacrificed for survival. Presumably, it is better to be alive with low quality song, than to not be alive at all.

An alternative view of the development effects of corticosterone is that there may be an adaptive value to stress-induced phenotypes (Monaghan 2008). Love and Williams (2008) found that female Starlings in poor condition might benefit by depositing corticosterone in the yolks of their eggs, thus matching offspring demand with the mother's ability to provide. This raises the possibility that birds experiencing stress during development are not reducing HVC to make the best of a bad situation, but are adaptively altering their phenotype to be suitable in a stressful environment. Birds developing in stressful conditions may develop on a "live fast, die young" trajectory, with smaller body size and/or higher metabolic rates (Metcalfe and Monaghan 2001), and reduced song learning could be part of this phenotype. There are few data to address this. As reviewed above, Holveck and Riebel (2010) found that female Zebra Finches from large broods preferred song from males also from large broods. Perhaps in stressful environments females should select males who are well suited to stressful conditions.

Although the idea that songs could indicate males as being well suited to a stressful environment is intriguing, it does not have much support. First it is unclear that conditions early in life would be predictive of conditions for years to come in a songbird. The adaptive matching observed by Love and Williams (2008) was on a much shorter time scale. Second, apart from the study by Holveck and Riebel (2010), female preferences for songs of males in poorer condition have not been observed. That said, detecting condition- and context-dependent mate choice such as this in the wild would be difficult and may have been unobserved. Distinguishing between the hypotheses that males with a stressful development are making the best of the situation or are adaptively programming their phenotype requires further study.

Seasonal stress and open-ended song learning

Nowicki et al. (1998) noted that not all birds are closed-ended learners who would thus have a life-long signal of early developmental conditions. Although only conclusively demonstrated for Starlings (Chaiken et al. 1994), several species such as Canaries and other cardueline finches appear to be able to add new songs to their repertoire each year and are referred to as open-ended learners (e.g., Nottebohm et al. 1986). We still know very little about the song learning strategies of many species, however, as experimental work has focused on a few models (Spencer et al. 2007). How would the developmental stress hypothesis apply to open-ended learning species? One possibility is that song may provide a signal of more recent environmental stressors in such species (Nowicki et al. 1998). That is, song may indicate conditions or a male's ability to cope with them during the most recent period of song learning (such as the fall). Alternatively, it is possible that, even in open-ended song learners, conditions during the first months of life have a lasting impact on song. Males may be able to modify their songs through learning in adulthood, but those with poor developmental conditions may be on a lower trajectory than those with good developmental conditions. Thus, the residual song repertoire for a given male's age may indicate early development rather than absolute repertoire size. There are no data available to address this hypothesis.

In terms of somatic growth, it appears that many organisms can accelerate growth to make up for slower earlier development. This form of *catch-up* growth can have long-term costs, such as higher basal metabolic rate (Criscuolo et al. 2008). This principle may also apply to song learning in open-ended song learners. That is, males with impaired learning in their first year may be able to catch up by accelerating song learning in adulthood. However, there may be potential costs to this accelerated song development in terms of song quality. Again, there are no data available to address the hypothesis that compensatory nuclei growth can have long-term deleterious effects on subsequent song and neural development.

A feature of the song-control system that appears widespread, if not ubiquitous, is seasonal plasticity (Tramontin and Brenowitz 2000). The song-control regions undergo tremendous seasonal changes in size, with the largest size observed in the breeding season. These changes in region size derive from changes in neurogenesis, apoptosis, cell size, and cell spacing. Even in closed-ended learners, HVC undergoes tremendous annual variation in neuron number with thousands of neurons dying and being replaced each year. In these closed-ended learners, the annual change in HVC is not associated with annual learning of new songs but rather with the ability to produce

songs well in a highly stereotyped way (Smith et al. 1995, 1997). Thus, just as stressors in adulthood could affect song quality in an open-ended learner, stressors could have the potential to affect seasonal plasticity of HVC and therefore song production. Consistent with this, prolonged exposure to corticosterone reduces HVC size in adult Song Sparrows (Newman et al. 2010). However, the effects of prolonged adult stress on song stereotypy remain unknown.

Open-ended song learners and seasonal plasticity of the song system and song open the possibility that the developmental stress hypothesis can be broadened. Song could signal not only conditions and neural development in early life but more recent conditions in adulthood. It is possible that different aspects of song, such as song repertoire or dialect versus song stereotypy, could signal a male's experience with stress in early development versus adulthood.

Developmentally correlated traits

Prolonged stress during development can affect a host of physiological and behavioral systems resulting in outcomes such as decreased growth, impaired immune function, sexual dysfunction, and propensity to mental disorders (Kent et al. 1997; Ward et al. 1994; Dubovicky et al. 1999; Weinstock 2008). Indeed, it is rare to find a system that is not affected by exposure to stress during development. Given that the effects of developmental stress are so widespread, it is probable that a stressor at any given stage during development will affect several aspects of the adult phenotype. This will give rise to correlations in adulthood among traits that may be functionally independent of each other. We refer to these as developmentally correlated traits (Spencer and MacDougall-Shackleton 2011). Two traits that are independent in the adult animal may be correlated due only to the fact that the same environmental stressors affected them both at the same time. For example, there may be no causal link between skeletal asymmetry and immune function, but if both had similar critical periods of development, then differential developmental conditions could give rise to correlated traits in the adult population. Thus, developmentally correlated traits would allow any sexually selected signals that are indicators of development to be predictive of other aspects of the phenotype.

There are few data to document the existence of traits that are developmentally correlated with birdsong. As noted above, one study found correlations between song complexity and HPA function in Song Sparrows (MacDougall-Shackleton et al. 2009). In addition, performance on a foraging task was found to be correlated to song in Zebra Finches (Boogert et al. 2008). Both HPA function and spatial cognition are known to be affected by developmental stress (e.g., Pravosudov et al. 2005; Pravosudov and Kitaysky 2006). It is thus plausible that birdsong may be developmentally correlated to a variety of previously unsuspected traits.

Conclusions

In this review, we have traced the evolution of the developmental stress hypothesis, and evaluated the evidence in its favor. We have also highlighted several important directions for future research. Further work is required to understand the effects of developmental stress on females, and the effects of seasonally varying stress on open- and closed-ended song learners. Whether stress acts to constrain the development of song, or acts to phenotypically engineer song to match a stressful environment, remains untested. Future studies need to distinguish between good genes and good upbringing versions of the developmental stress hypothesis. Finally, our understanding of the physiological mechanisms related to this hypothesis requires a tremendous amount of further work. Corticosterone is likely a clear player, but much remains to be done.

One of Niko Tinbergen's greatest legacies was pointing out a central role for the development for our understanding of behavior (Tinbergen 1963). The developmental stress hypothesis follows this by highlighting the importance of ontogeny, and provides the best hypothesis to date as to how song learning can result in an honest signal of quality.

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