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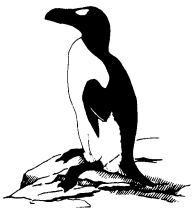

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PERSPECTIVES IN ORNITHOLOGY

SONG AND MATE CHOICE IN BIRDS: HOW THE DEVELOPMENT OF BEHAVIOR HELPS US UNDERSTAND FUNCTION

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Among his many contributions to the study of animal behavior, Nobel laureate Niko Tinbergen is perhaps best remembered for articulating the "four questions" of ethology, outlining four ways in which one could answer the broader question of "why" an animal behaves the way it does (Tinbergen 1951, 1963). Those four questions address (1) causation (i.e. what physiological mechanisms are responsible for the expression of the behavior?), (2) ontogeny (what factors affect the development of the behavior?), (3) function (how does the behavior enhance fitness?), and (4) evolution (what are the historical antecedents of the behavior?). Although researchers may focus their work on only one or a subset of those questions, Tinbergen maintained that all four must be addressed to answer completely the question of "why" an animal performs a behavior.

Tinbergen credited Julian Huxley (1942) with introducing the idea that causal, functional, and historical analyses represent distinct approaches to the study of behavior. Tinbergen's own contribution, he claimed, was to add ontogeny to Huxley's list (Tinbergen 1963). Thus, it is ironic that interest in development waned, to some degree, as the science of ethology that Tinbergen helped establish gave rise to the more contemporary disciplines of neuroethology, which focuses primarily on causal mechanisms, and behavioral ecology, which emphasizes functional and evolutionary analyses. Recently, however, new reasons for interest in development have emerged, as researchers have realized that developmental processes, interacting with neural and physiological mechanisms of causation, can have important consequences for the function and evolution of behavior. Nowhere is the interaction of development and causation with the function and evolution of behavior more apparent than in the study of bird song. Here, we explore the value of the interplay among Tinbergen's four questions for understanding a central question about bird song.

Development and Neurobiology of Bird Song

Bird song provides an exception to the generalization that behavioral development was relatively neglected in the period between Tinbergen's day and the present. Largely through the work of Peter Marler and his colleagues, bird song became the single most important model system for studying the development of behavior. Although most of that work was not directed specifically at functional questions, many of the findings turn out to have functional implications. The basic picture that

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emerged is that song in oscines is learned by young birds through listening to older birds sing. Males isolated at an early age to prevent learning through imitation subsequently produce songs that are abnormal in many features (Thorpe 1958, Marler 1970). Tutoring using tape-recorded songs (Marler 1970) or live tutors (Baptista and Petrinovich 1984) is sufficient to enable hand-reared males to develop normal songs. In the absence of any social cues, hand-reared males show a preference for learning conspecific over heterospecific songs (Thorpe 1958, Marler and Peters 1977). In some species, memorization of song models is concentrated within a limited "critical learning period," often roughly 20 to 60 days after hatching (Marler and Peters 1987, 1988), though social and other factors may modify the timing (Baptista and Petrinovich 1986, Petrinovich and Baptista 1987, Nelson 1998). Birds deafened after their critical learning period but before their own song has crystallized produce songs that are even more abnormal than those of isolate males (Konishi 1965), which implies that, to shape their songs to match the models they have learned, males must listen to their own production.

With the discovery that song is controlled by a relatively well-defined series of discrete brain nuclei (Nottebohm et al. 1976), song also became a major model system for the study of the neural control of behavior in vertebrates (Konishi et al. 1989). The "song system" of oscines is organized in two pathways (Mooney 1999). The motor pathway includes the nuclei HVC and RA. Lesion of either of those nuclei impairs an adult's ability to sing (Nottebohm et al. 1976), which indicates that they are important in storage and production of song. The anterior forebrain pathway includes Area X, DLM, and lMAN, with Area X receiving input from HVC and lMAN projecting to RA. Lesions of Area X or lMAN impair song learning in young birds, which suggests that the anterior forebrain pathway plays an important role in acquisition and development of song (Bottjer et al. 1984, Sohrabji et al. 1990). Development of the song system has been described in a few species of oscines and has been found to largely coincide with the memorization phase of song development (Bottjer et al. 1985, Nordeen and Nordeen 1988, Nordeen et al. 1989, Nowicki et al. 1998a). The size of some of the nuclei has been demonstrated to have functional implications. Volume of HVC, for example, has been shown to be positively associated with measures of song repertoire size, both in between-species comparisons (DeVoogd et al. 1993, Székely et al. 1996) and in comparisons between individuals within species (Nottebohm et al. 1981, Airey and DeVoogd 2000, Airey et al. 2000). Exceptions to that relationship have also been noted, however (Kirn et al. 1989, Brenowitz et al. 1991). The size of HVC and RA change seasonally; in Song Sparrows (*Melospiza melodia*), the change corresponds to seasonal changes in note stereotypy, such that notes are less stereotyped when HVC and RA volumes are low (Smith et al. 1997).

Functional Aspects of Song: Female Choice of Mate

In general, a male bird's song has two primary audiences (Searcy and Andersson 1986, Catchpole and Slater 1995). To conspecific males, song serves as a "keep out" signal, advertising the presence of a territorial male and repelling potential intruders from the space he is defending. Experimental evidence for that function comes from studies in which male birds are surgically muted and subsequently experience difficulty in maintaining their territories (Peek 1972, Smith 1979, McDonald 1989). Further evidence comes from studies in which males are removed entirely from their territories and replaced by loudspeakers that either do or do not broadcast song; territories remain free from intruders for a longer time with playback than without (Göransson et al. 1974, Krebs 1977, Yasukawa 1981, Falls 1988, Nowicki et al. 1998b).

Although those experiments demonstrate that song functions as a keep-out signal against other males, the designs they have used have not proved efficient for determining what features of song are important for that function (Searcy and Nowicki 2000). We know much more about the relationship between form and function with respect to the second major function of song, that of attracting and stimulating females. The best evidence that females are attracted to song has come from experimental studies with cavity-nesting species, in which unoccupied nest boxes were outfitted with loudspeakers. Boxes from which songs were played were inspected or occupied by females more quickly than boxes where the loudspeaker remained

silent (Eriksson and Wallin 1986, Mountjoy and Lemon 1991, Johnson and Searcy 1996). The effect of song on female reproductive behavior is demonstrated by laboratory studies showing that females increase nest building activity and courtship display when exposed to song (Hinde and Steel 1976, Kroodsma 1976, Searcy and Marler 1981) and by field studies showing that females lay their clutches earlier the more their mate sings (Wright and Cuthill 1992).

It is not hard to envision how selection would favor female response to conspecific male song if song only serves to identify the location of a potential mate: a female has to find at least one male of the correct species and mate with him to have any reproductive success at all. Much ethological work took that point of view and thus focused on the question of how species-distinctiveness is encoded in song (e.g. Emlen 1972, Becker 1982). But different males of the same species usually do not all sing the same way, and the strength of a female's response to song—or a female's song "preference"—depends on the way a particular male sings. In other words, female birds not only use song to find a conspecific male, they also use song to discriminate among males as they choose mates. The question of why females show preferences for specific attributes of male displays such as song has been a central problem in behavioral ecology (Andersson 1994).

Although there is almost immeasurable variety in the way different species of birds sing and how songs vary within a species, three categories of variation appear to have the most consistent effects on female response across different species (Searcy and Nowicki 2000, Nowicki et al. 2002a). Geographic differences represent the most ubiquitous kind of variation affecting female response. In some species, there is marked variation in song across very short distances, with distinct boundaries defining local "dialects" (Marler and Tamura 1962, McGregor 1980); in other species, geographic variation is more subtle and gradual, with differences becoming apparent only over a considerable distance (Searcy et al. 2002). In both cases, females generally prefer local songs to songs produced by males from distant populations (Searcy 1992a). A second kind of variation that commonly affects female response is song complexity, typically measured as the number of different song types or syllable types an individual male produces. In general, females are more attracted to and more likely to mate with males that have larger repertoires or sing more complex songs (Catchpole 1980; Searcy 1984; Catchpole et al. 1984, 1986; Hasselquist et al. 1996; Reid et al. 2004). The third dimension of song variation commonly affecting female response is the amount a male sings, or a male's "song output," with females preferring males that sing longer songs or longer song bouts, sing at a faster rate, and so forth (Gottlander 1987, Alatalo et al. 1990, Eens et al. 1991, Wasserman and Cigliano 1991, Kempenaers et al. 1997).

Why Should Female Birds Prefer Certain Song Traits to Others?

It is in addressing the question of why female songbirds show the song preferences they do that the interaction among the development, neurobiology, and function of song becomes important. Preference for a particular song characteristic will evolve if females receive some benefit from mating with a male whose songs exhibit that characteristic (Andersson 1994). Therefore, preferences for song traits may evolve if those traits are reliable indicators of some aspect of male quality that benefits the female. For a signal to serve as an indicator trait in the context of mate choice, variation in its expression must correspond reliably with some aspect of signaler quality, such as condition or viability. Because signalers can benefit in that context from exaggerating their quality, a signaling system can be maintained only if the reliability of the signal is somehow ensured (Searcy and Nowicki 2005).

One mechanism for ensuring the reliability of signals of quality is expressed by the handicap principle (Zahavi 1975, 1977), which states that signals are reliable because they are costly. Both the cost and the effectiveness of the signal are assumed to increase with signaling level. If the cost of a given signaling level is higher for signalers of low quality than for signalers of high quality, then the optimal signaling level is lower for the low-quality signaler than for the high-quality signaler (Grafen 1990a, Johnstone 1997). Under those assumptions, all signalers exhibit the level of signaling that is in their own best interests, and yet the signal is still reliable.

An indicator trait may correlate with some aspect of a male's phenotype that directly increases

the reproductive success of the female with which he mates, such as his ability to defend a territory, deter predators, provide parental care, and so forth. An indicator also may correlate with some aspect of a male's genetic quality, which will benefit females with which he mates by providing their offspring with "good genes" that affect their viability and future reproductive success. Theoretical models demonstrate that female preference for a trait can evolve if females obtain indirect benefits by mating with genotypically superior males (Andersson 1986, Pomiankowski 1987, Iwasa et al. 1991), and can also evolve if females obtain only direct benefits by mating with phenotypically superior males (Heywood 1989, Hoelzer 1989, Grafen 1990b).

The handicap mechanism provides an obvious explanation for female preferences based on song output: the relevant costs stem from the effects of singing on the singer's energy balance. Measurements of oxygen consumption during singing indicate that the energy costs of song are remarkably low (Oberweger and Goller 2001; Ward et al. 2003, 2004). Other studies have shown, however, that provisioning of males in the field has a strong positive effect on their singing rates (Searcy 1979, Davies and Lundberg 1984, Gottlander 1987). Thus, despite its low energy cost, singing must have a negative effect on energy balance, perhaps because time spent singing reduces time available for foraging. The negative effect of singing on energy balance provides a cost to song output that explains its reliability with regard to a male attribute that females might well be interested in—the present condition of the male.

Costs are not so easy to assign to the other categories of song traits preferred by females. Time and energy costs of singing a diverse repertoire of song or syllable types should be no greater than those of repeating single song or syllable types. Similarly, singing local variants of song cannot be consistently more expensive in time and energy than singing foreign variants. Alternative hypotheses exist, however, that explain female preferences on the basis of complexity and geography without invoking costs. One such hypothesis, which accounts only for preferences based on geographic origin, suggests that females benefit by mating with local males because those males carry alleles that are better adapted to the local environment (Nottebohm 1972, Baker and Cunningham 1985). That hypothesis also has difficulties as a general explanation, however. One difficulty is that males in at least some species learn their songs after dispersing, making the dialect a male sings a poor marker of his natal population (Baptista and Morton 1988). Another difficulty is that in species with continuous and gradual geographic differences in song, typical dispersal distances are such that it is unlikely a female would ever encounter a male producing a song outside of the range she would accept as a normal local dialect (Searcy et al. 2002). A third difficulty is that little evidence exists that mating with a conspecific male from outside the local population would actually be disadvantageous in birds or other animals (Pusey and Wolf 1996).

Two additional hypotheses that could explain the evolution of female preferences for a signal without requiring the signal to be costly are the Fisher mechanism and sensory bias. In the Fisher mechanism, a female preference becomes genetically correlated with the preferred trait, and both become exaggerated in a runaway process (Fisher 1930, Andersson 1994). Song attributes that vary geographically do not exhibit the exaggeration predicted by that hypothesis; but song complexity, in some cases, arguably does. Thus, the Fisher mechanism might explain female preferences for song complexity, though some theoreticians have argued that it should be a hypothesis of last resort (Grafen 1990a). The sensory bias hypothesis suggests that female preferences for male display traits are nonadaptive consequences of attributes of female perceptual or neurobiological mechanisms that are adaptive in other contexts (Ryan and Rand 1993, Ryan 1998). The sensory bias hypothesis is unlikely to explain preferences for geographic variants, given the reciprocal nature of such preferences. Although it has been suggested to explain female preferences for larger repertoires (Searcy 1992b, Collins 1999), the sensory bias hypothesis is not supported by historical evidence (Gray and Hagelin 1996).

We have proposed instead that female preferences based on complexity and geographic origin of song can be explained by the handicap principle, but with reliability enforced by developmental costs rather than production costs (Nowicki et al. 1998a, Nowicki and Searcy 2004). It is in this "developmental stress" hypothesis that the interplay of development, neurobiology, and function comes into focus.

The Developmental Stress Hypothesis

We have already seen that song learning, storage, and production are controlled in songbirds by a series of discrete brain structures and that those structures develop, in large part, during the first few months post-hatching. In Zebra Finches (*Taenopygia guttata*), for example, RA and HVC increase in size between 10 and 50 days after hatching (Bottjer et al. 1985, Konishi and Akutagawa 1985, Nordeen and Nordeen 1988), whereas the pathways connecting them develop between 15 and 35 days after hatching (Mooney and Rao 1994). Timing of development of those structures is similar or just slightly later in Common Canaries (*Serinus canaria*; Nottebohm et al. 1986, Alvarez-Buyalla et al. 1994) and Swamp Sparrows (*M. georgiana*; Nordeen et al. 1989). Nowicki et al. (1998a) pointed out that the period just after hatching, when the song system is developing and forming neural connections, is also a period in which young songbirds are particularly vulnerable to nutritional stress, first because of their dependence on their parents to provide food, and later because of their own inexperience as foragers. Because the young bird's general phenotype is developing rapidly during the same period, males are faced with a trade-off between investment in their song system and investment in other aspects of their phenotype. In such a situation, animals are expected to give priority to investment in traits that affect survival over investment in traits important in display (Andersson 1986). The song system may thus be among the first traits sacrificed if a young songbird experiences nutritional stress. Song, and especially learned features of song, therefore becomes a sensitive indicator of a male's history of nutritional stress and of the male's ability to withstand the effects of stress. Because song is thus an indicator of male quality, females are selected to prefer mating with males that have superior songs.

In the above formulation, we have emphasized the potential effect of nutritional stress on song development, following Nowicki et al. (1998a) in their original statement of what they termed the "nutritional stress hypothesis." Buchanan et al. (2003), however, have pointed out that other types of stresses can have similar effects on both song development and phenotypic development. Parasites, for example, can drain nutritional resources away from growth, and thus have effects that parallel those of direct nutritional deprivation. Exposure to cold temperatures may also have parallel effects. Such considerations have led to a consensus that the "nutritional stress hypothesis" should be broadened to a "developmental stress hypothesis" (Buchanan et al. 2003, Nowicki and Searcy 2004) to acknowledge the potential importance of sources of stress other than nutritional deprivation.

The developmental stress hypothesis leads to a number of testable predictions. One obvious prediction is that stress experienced soon after hatching will have lasting effects on development of the song system in the brain. Nowicki et al. (2002a) tested that prediction by manipulating nutrition in hand-reared Swamp Sparrows during the period when they would normally be dependent on their parents for food. A well-fed group was provided with unlimited amounts of hand-rearing diet while a nutritionally restricted group was limited to 70% of what the well-fed birds consumed. Brains were examined when the birds reached adulthood. The well-fed subjects had HVC volumes ~30% larger and RA volumes ~45% larger than the nutritionally restricted birds. Those differences can be explained, in part, by an effect of nutrition on overall telencephalon volume, which was 15% greater in the well-fed group. In addition, the ratio of RA volume to overall telencephalon volume was significantly greater in the well-fed group than in the nutritionally restricted birds, showing that RA, at least, was differentially affected by stress. Buchanan et al. (2004) have shown a similar effect of developmental stress on song-system nuclei in Zebra Finches; in that case, there appeared to be a differential effect of stress on HVC volume.

A second prediction is that developmental stress will affect song features, including features that are important to female preferences. In a correlational field study, Nowicki et al. (2000) showed that the rate of feather growth in nestling Great Reed Warblers (*Acrocephalus arundinaceus*) was positively associated with their syllable repertoire sizes as adults. Therefore, a large repertoire produced by an adult male indicates that he grew well when young. Evidence from both laboratory experiments (Catchpole et al. 1986) and field correlations (Hasselquist et al. 1996, Hasselquist 1998) indicate that female Great Reed Warblers prefer males that have large syllable repertoires.

This second prediction has also been tested experimentally in a series of studies. One such study is the manipulation of nutrition in hand-reared Swamp Sparrows described above (Nowicki et al. 2002a). In that experiment, well-fed males did not develop larger song repertoires than nutritionally restricted ones. Well-fed males did, however, learn their tutor songs significantly more accurately, as measured by spectrogram cross-correlations between model notes and learned copies. It is not known whether female Swamp Sparrows prefer well-learned songs, but there is evidence of such a preference in their congener, the Song Sparrow. Hand-reared male Song Sparrows were tutored with songs from a local population in Pennsylvania. Adult females from the same population subsequently showed a preference for those songs of the hand-reared males that were accurate copies of the tutor songs over songs that were poor copies (Nowicki et al. 2002b).

Buchanan et al. (2003) tested the effects of a rather different nutritional manipulation on song development in European Starlings (*Sturnus vulgaris*). Between the ages of roughly 40 and 120 days, control birds were given uninterrupted access to food while experimental birds were deprived of food each day for a randomly chosen 4-h period. The treatment had a counterintuitive effect on body mass, with the experimental birds maintaining higher average mass than the controls through most of the treatment period. Nevertheless, intermittent food deprivation had a negative effect on song development: deprived birds sang significantly shorter songs (Buchanan et al. 2003) and produced a significantly smaller repertoire of phrase types (Spencer et al. 2004). Song length and repertoire size are typically correlated with one another in European Starlings, and both are positively associated with female mating preferences (Eens et al. 1991, Mountjoy and Lemon 1996).

Spencer et al. (2003) manipulated nutrition in young Zebra Finches by limiting the amount of food available to parents to feed their young between the ages of 5 and 30 days post-hatching. A second treatment group was stressed, not by food deprivation but by daily doses of corticosterone. The latter treatment mimics a generalized stress, given that corticosterone is released in birds in response to various types of stresses. The two stress treatments had similar effects on song: males stressed by either food deprivation or corticosterone administration developed shorter songs with fewer syllables and lower peak frequencies than controls. Female Zebra Finches have been shown to prefer long songs over short ones in laboratory tests (Clayton and Pröve 1989)—again, developmental stresses change song in a direction less preferred by females.

A third prediction of the developmental stress hypothesis is that males subjected to stress during early development will possess inferior phenotypes as adults, with some of that inferiority in traits important to the fitness of their mates. Although this seems a logical expectation, few direct tests have been made. Searcy et al. (2004) manipulated nutrition in hand-reared Song Sparrows, using methods similar to those previously employed in Swamp Sparrows (Nowicki et al. 2002a). Nutritionally restricted Song Sparrows grew more slowly when young and were still significantly smaller in body size as adults. Studies of other species of birds have also found that restricting food provided to nestlings reduces their growth, with effects that may or may not persist into adulthood (Richner et al. 1989, Lacombe et al. 1994). Adult females prefer larger males as mates in some bird species but not in others (Schluter and Smith 1986, Weatherhead and Boag 1995). Early developmental stresses might be expected to affect more subtle aspects of the phenotype, such as immunocompetence and locomotor performance, but little is known about such effects in birds.

Although testing of the developmental stress hypothesis is still in its early days, the hypothesis has already received considerable support. It appears that early developmental stresses that might be expected to impair development of the overall phenotype also affect song development, and that the effects are in directions that make the song less preferred by conspecific females. There is also support for the idea that the effects of stress on song are mediated by effects on development of the song system in the brain. Much remains to be investigated; in particular, a large class of song variables has hardly been touched on, either with respect to the effects of developmental stress or with respect to functional considerations in general. That class of song variables can be termed "vocal performance."

Vocal Performance, Female Preferences, and Developmental Stress

When critics evaluate an opera singer, the criteria that we have so far applied to bird song are relatively unimportant. Repertoire size might be weighed a little, output less, and geographic origin not at all. Instead, the singer is likely to be assessed on traits such as vocal range (the range of frequencies produced), dynamics (the ability to increase and decrease sound intensity), intonation (the ability to achieve a desired pitch with precision), vibrato (production of a tremulous effect through slight and rapid changes in pitch), and so forth. All those criteria are concerned with how well the singer performs in aspects of singing that are physically difficult; we can categorize such criteria as measures of "vocal performance." It would seem logical that vocal performance might also be important in birds and, in particular, that female birds might judge prospective mates on performance features as well as on the traits we have already discussed. Attention has only recently been turned to that possibility, perhaps because of the difficulty of determining what sorts of feats are physically difficult for birds to perform when singing. Below, we discuss what is known thus far about female choice for vocal performance and then speculate about possible application of the developmental stress hypothesis to performance features.

The case that currently provides the best insight into what makes songs difficult for birds to perform involves a trade-off between frequency bandwidth and syllable repetition rate. To produce a high-frequency sound, a male songbird opens its beak wide, which effectively shortens the vocal tract and raises its resonance frequency. To produce a low-frequency sound, the male closes its bill, effectively lengthening the vocal tract and lowering its resonance frequency (Nowicki 1987; Westneat et al. 1993; Podos et al. 1995, 2004; Hoese et al. 2000). To produce a syllable encompassing a wide range of frequencies—that is, with a wide frequency bandwidth—the bird must open and close its bill over a wide angle. If syllables are produced at a low rate, enough time is available per syllable to allow a large angle of movement and thus a large bandwidth; as the syllable repetition rate increases, however, the time per syllable decreases, and so must the maximum angle of movement and the maximum bandwidth. Those considerations produce an upper limit to bandwidth that decreases as syllable repetition rate increases. Evidence for the reality of that upper limit comes from the distribution of frequency bandwidths and syllable rates between and within species of emberizids (Podos 1997, Ballentine et al. 2004); those distributions are triangular, such that no songs have both the highest bandwidths and the highest syllable rates.

The upper limit of bandwidth and rate defines a performance limit; males producing songs close to the limit may be said to have high vocal performance, and those producing songs far from the limit have low vocal performance (Podos 2001). Once we can measure vocal performance, we can test whether females prefer high performance to low. Ballentine et al. (2004) performed such a test with Swamp Sparrows, using the distribution of bandwidth and syllable rates in the species' songs to define its performance limit. They then tested female Swamp Sparrows for response to pairs of songs, one near the upper limit and one farther from it. Females showed a consistent preference for songs near the upper limit—that is, for the songs of higher vocal performance.

Common Canaries provide a related example of a female preference based on vocal performance. Vallet and Kreutzer (1995) found that female Common Canaries prefer a particular phrase type, labeled an "A" phrase, over other types of phrases found in male song. "A" phrases are characterized by the rapid repetition of syllables containing two, frequency-modulated notes. When presented with a range of "A" phrases, female Common Canaries are especially responsive to those with the highest repetition rates (Vallet et al. 1998). Those results suggest that female canaries attend to the same kind of performance limit operating in emberizids—that is, a limit on the speed at which syllables of high bandwidth can be repeated. To test that possibility, Draganoiu et al. (2002) presented females with syllables of different bandwidths, with either normal or artificially elevated repetition rates. Females responded most strongly to syllables that combined high bandwidth with elevated repetition rate. Again, the evidence supports a female preference for high vocal performance.

The existence of female preferences based on vocal performance leads to the familiar question

of how females might benefit from such preference. In the case of performance cues, the usual answer seems particularly appealing: that females benefit from preferring the display trait in question because it is a reliable indicator of male quality. That answer is appealing for performance measures because of the argument, made by Maynard Smith and Harper (2003), that the reliability of performance-based signals is inevitable and needs no special and onerous explanation like that provided by the handicap principle. Maynard Smith and Harper (1995, 2003) classify signals of that type as "index" signals, which they equate with Enquist's (1985) "performance-based" signals, and which they define as signals "whose intensity is causally related to the quality being signalled, and which cannot be faked." They give as examples of index signals the courtship dance of *Drosophila suboscura* and the display flights of fritillary butterflies (Maynard Smith and Harper 2003). The idea is that the performance of those signals is so intimately tied to the qualities that the receivers are interested in that exaggeration is not possible, and the signals are perforce reliable.

The index argument is not so straightforward with respect to song performance, however. Presumably, a female bird benefits from assessing aspects of male quality, such as parental ability or heritable viability. We know relatively little about the structures that affect a male's song performance, but presumably they might include the song nuclei in the brain, the nerves innervating the syrinx, the syringeal muscles, and so forth. The point is that the quality of the latter structures does not directly affect parental ability or male viability, and so the tie between male quality and song performance is not a direct one. A male could, in theory, invest in high song performance without investing in parental ability and viability, though that course may never be advantageous in practice. We therefore argue that the reliability of song performance as a cue to male quality is best explained by developmental costs, specifically by the trade-off between investment in the structures leading to superior song performance and in whatever aspects of the phenotype contribute to male parental ability, high viability, and the like. Put another way, we believe that the reliability of song performance as an indicator of male quality is better explained by the developmental stress hypothesis than by the index argument. Whether the index argument is ever the best explanation for signal reliability is a question we discuss in detail elsewhere (Searcy and Nowicki 2005).

Application of the developmental stress hypothesis to vocal performance is, at this point, speculative; we can adduce no evidence supporting the hypothesis with respect to performance features. The hypothesis can, however, be tested in the context of vocal performance just as it has been tested for other song features: by manipulating the environment of development and observing effects on aspects of vocal performance. A valuable adjunct of such experiments would be to study the anatomical and physiological properties that change along with performance features, so that we can begin to understand the physical and physiological basis of vocal performance.

Conclusion

Asking why female birds respond to song the way they do illustrates the enduring value of Tinbergen's "four questions," and at the same time generates a new appreciation for the central role of the second of those questions, that concerning ontogeny. Ontogeny is important to song function because of the role of developmental costs in enforcing signal reliability. The idea that developmental costs are important to maintaining reliability is not new, but such costs have usually been ascribed only to signals that depend on large and obviously expensive anatomical structures, such as antlers in deer or long tails in birds. Here, we have argued that developmental costs can also be important for understanding the function and evolution of complex behaviors such as bird song, even though no exaggerated external structures are involved.

The assumption that song has important developmental costs is supported by what we know about the neurological structures responsible for song learning and production and about the development of those structures. Especially important is that the timing of song-system development overlaps both with growth and maturation and with periods of extraordinary stress in a young bird's life. That overlap forces a developmental trade-off that can reveal a male's phenotypic and genetic quality. Evidence that developmental stress affects the

song system has so far been found on a gross anatomical level only, but there is every reason to believe that future studies will reveal cellular and molecular consequences of stress that have an equally pronounced effect on behavior.

Thus, in the case of bird song, progress on one of Tinbergen's four questions, that concerning function, is made possible by work on two others, those concerning development and causation. In turn, a new hypothesis regarding function—the developmental stress hypothesis—has led to new studies probing the development and causation of song, by studying the effects of early environmental stresses on neuroanatomy and on song learning. That his four questions turn out each to have implications for the others presumably would not have surprised Tinbergen.

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