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Are better singers smarter?

Stephen Nowicki[a] and William A. Searcy[b]
[a]Department of Biology, Duke University, Durham, NC 27708, USA and [b]Department of Biology, University of Miami, Coral Gables, FL 33124, USA

A simple restatement of the developmental stress hypothesis is that certain attributes of bird song are honest indicators of signaler quality because of their developmental costs. Spencer and

MacDougall-Shackleton argue that this hypothesis can be grouped with other hypotheses linking animal signals to developmental stability using fluctuating asymmetry in visual ornaments as their principal example. We agree with this grouping but point out one important distinction: Whereas visual symmetry depends inherently on anatomical structures, bird song is a purely behavioral trait. Developmental costs are always expected for anatomical structures, but it is only the confluence of a particular suite of attributes of bird song that produces developmental costs with the properties necessary to enforce signal reliability. First, many features of bird song are learned during an early critical learning period and are thereafter set for life. Second, song learning and production depend on the development of a set of specialized brain structures, and third, the growth of these structures is concurrent with a period of accelerated growth in the young bird as a whole. Together, these developmental characteristics make a tie between song quality and phenotypic quality particularly likely; whether parallel characteristics are found in the development of other display behaviors remains to be determined.

mong the many aspects of phenotypic quality that might be indicated by song quality, cognitive ability is perhaps the most intriguing possibility (Nowicki et al. 2000, Boogert et al. 2008, Searcy and Nowicki 2009). An association between song and cognition seems reasonable because song learning and memory are themselves cognitive tasks, and abilities on various cognitive tasks tend to be positively associated, at least in humans (Plonim 2001). Furthermore, Boogert et al. (2008) have provided experimental evidence of such an association in zebra finches (*Taeniopygia guttata*). These authors tested cognition in male zebra finches using a foraging task that required prying plastic lids off wooden wells to obtain food rewards. The number of trials required to solve this problem was negatively correlated with a measure of song complexity, the total number of elements per song. Put more simply, smarter birds had more complex songs.

The developmental stress hypothesis provides one mechanism leading to a tie between song and cognition. As reviewed by Spencer and MacDougall-Shackleton, early nutritional restriction has been shown to cause detriments in various aspects of song. Similar nutritional stresses have also been shown to have negative effects on learning and memory in rats (Fukuda et al. 2002) and humans (Lynn 2009) and most pertinently on spatial memory in western scrub-jays (*Aphelecoma californica*) (Pravosudov et al. 2005).

Other mechanisms, however, could also tie song to cognition. In song sparrows (*Melospiza melodia*), Reid et al. (2005) found a strong negative association between levels of inbreeding and song repertoire size, and in humans, inbreeding is negatively associated with performance on intelligence tests (Jensen 1983). Obviously, the inbreeding argument would be stronger if inbreeding could be shown to be associated with performance on cognitive tasks in birds, such as song sparrows as well as in humans, and we are interested in investigating this possibility. Note that a link between song and cognition due to inbreeding effects might be subsumed under the developmental stress hypothesis if inbreeding affects developmental stability in the face of stress.

A reliable link between song and cognition would influence the evolution of female choice if cognitive abilities affect either a male's parenting abilities or its viability. In the former case, a female choosing a male with superior song gains the direct benefit of having a superior father as a social mate; in the latter, she may gain the indirect benefits of "good genes." Cognitive abilities, especially ones measured on foraging and spatial location tasks, might well affect a male's food-finding capability and through foraging success both parental ability and viability.

FUNDING

National Science Foundation (IBN-0315377 to S.N. and IBN-0315566 to W.A.S.).

Key words: bird song, developmental stress, indicator trait.

Address correspondence to S. Nowicki. E-mail: snowicki@duke.edu.

Received 7 February 2010; revised 7 February 2010; accepted 3 May 2010.

doi: 10.1093/beheco/arq081

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