

Commentaries on Invited Review

Stressing out about singing

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Listening to the melodic songs of winter wrens, the perfect timing of interspersed notes of duetting slate-colored boubous, or marveling at the repertoire of song sparrows, one cannot help but notice the amazing complexity birds display in songs. Truly, bird songs are an excellent example of the power of sexual selection to elaborate traits. But why does such complexity and variation exist given the strong selection imposed by females for specific song traits? This question is not limited to bird song and is applicable to every sexually selected trait throughout the animal kingdom. Rowe and Houle (1996) provide conceptual insight in their seminal paper on condition dependence, describing how high condition (i.e., quality) males can develop and maintain costly traits better than poor condition males. The questions that still remain are why there is variation in the ability to develop such traits and what is contributing to this variation?

In their review, Spencer and MacDougall-Shackleton invoke the developmental stress hypothesis as a potential mechanism for the maintenance of variation in song complexity and repertoire size. They amass a body of literature demonstrating that stress arising from reduced food availability during specific juvenile periods has detrimental effects on song development by specifically affecting the regions of the brain associated with song learning. Individuals that can better develop complex songs or larger repertoires while in this period of stress would signal their ability to avoid or handle stress and therefore their higher quality. In such a manner, stress maintains the honesty of sexually selected traits and provides females with reliable cues of male quality.

Although Spencer and MacDougall-Shackleton piece together evidence across several fields and studies to support the developmental stress hypothesis, they admit the shortcomings of the field, outlining the highly correlational nature of the majority of the data and the necessity to apply a rigid methodology that allows comparison between studies. The field is unfortunately suffering from another limitation—a poor understanding of the relative contribution of genes toward the strong environmental effect seen on brain development (Buchanan et al. 2003). If females are judging quality on the ability of the developmental system to function under stress, there must be some heritable component. Furthermore, the likelihood of a juvenile experiencing food stress will depend on parental provisioning—a factor that individuals are likely to vary in. Researchers with large data sets could potentially use an animal model (Kruuk 2004) to provide insight into the relative contribution of parental provisioning, genes, the environment, and their interaction; but given the difficulty in collecting such data, this information will likely remain elusive for some time.

This review also hints at a novel view of examining male quality—females choose males based on their song, which signals the ability of the male's developmental system to handle stress. As a result, females are also choosing the quality of a male's developmental system rather than simply specific traits, and therefore,

the traits that we measure are meaningless without placing them within the context of their development. Just as researchers have recently recognized that what occurs in overwintering grounds has an effect on fitness during the breeding season (Marra et al. 1998), researchers must take into consideration the juvenile environment on adult fitness. Although such data are more difficult to gather as they require monitoring of an individual over its lifetime, this will result in a better understanding of what we deem male quality and help explain the variation we see in traits (Wilson and Nussey 2009).

Regardless, Spencer and MacDougall-Shackleton have created the scaffold that allows future researchers to build an understanding of the complex interactions that lead to the development of bird song. Although the review sets out to provide a better understanding of the effect of the juvenile environment on song development in birds, the insights provided here can be extrapolated toward other sexually selected traits in other systems helping researchers to gain a better understanding of the evolution and expression of sexually selected traits in general.

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