

Female Song Sparrows Prefer Males That Learn Well

BY KEN YASUKAWA

When Darwin published his groundbreaking book on the origin of species in 1859, he included a few pages on “sexual selection,” a topic he would later consider at length. Darwin was proposing an alternative mechanism to natural selection, because he believed that certain characteristics of animals could not be explained by superior ability to survive and reproduce. In 1871 Darwin published *The Descent of Man, and Selection in Relation to Sex*, most of which focused on this alternative mechanism of evolution. He envisioned two forms of sexual selection, one involving competition with members of the same sex (usually males) for access to members of the other sex, and one in which members of the other sex (usually females) found certain characteristics attractive. Today we call these two forms intrasexual and intersexual selection, respectively. In discussing intersexual selection, Darwin proposed that the “ornaments [of males]—their contrivances for producing vocal or instrumental music—and their glands for emitting odors” as “serving only to allure or excite the female.” He then argued that such female mating preferences are the result of sexual and not “ordinary” selection, because “unornamented, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, but for the presence of better endowed males.”

Despite his efforts to document and defend the notion that characteristics could evolve by sexual selection, Darwin’s contemporaries roundly rejected this alternative mechanism. Julian Huxley (1938) noted, “None of Darwin’s theories has been so heavily attacked as that of sexual selection.”

In the 100 years following the publication of *The Descent of Man, and Selection in Relation to Sex*, sexual selection gained widespread, though not universal, acceptance among evolutionary biologists as a result of a considerable body of research (Campbell 1972), although intersexual selection continued to be debated. Today, both forms of sexual selection are well-established mechanisms of evolution (e.g., Andersson 1994, Birkhead and Møller 1998), and they continue to attract attention from biologists.

One notable example of the continued interest in sexual selection, and especially in intersexual selection, is a recent study of the mate preferences expressed by female song sparrows, *Melospiza melodia* (Nowicki et al. 2002). The study demonstrates for the first time that the quality of song learning by males affects female mate preferences. It may thus provide a functional explanation for song learning in general.

Song is very important in the life of song sparrows, as their common name implies, and in the research careers of the biologists who study them. Studies of North American sparrows, and of song sparrows in particular, have provided much of our knowledge of song development, neural control, endocrine mediation, organization, and function. Stephen Nowicki, William A. Searcy, and Susan Peters were interested in the connection between two important and well-studied phenomena in birds: the development of song by learning in early life and the role of song in mate choice by females. Classic studies of song development have shown that males who are deprived of the opportunity to learn to sing normally are unable to attract mates, and

previous research had shown that two components of singing behavior, amount of singing (“verbosity”) and the size of the singer’s repertoire (“virtuosity”), affect female choice. Nowicki and colleagues were interested in looking for more fine-grained influences of song on female choice of mate. Specifically, they wanted to know whether female song sparrows pay attention to the quality of the male’s song learning (“veracity”). In other words, if a female had a choice between a male who sang good copies of the songs he heard as a youngster and another male who sang poor copies of the same song, whom would she prefer?

Nowicki and colleagues performed three experiments, each comparing two song categories and all using a well-established bioassay of female mate preference—female copulation solicitation. The so-called solicitation display assay involved capturing female song sparrows from a wild population, bringing them to the laboratory, implanting them with silastic tubing stuffed with 17- β estradiol (an avian estrogen), and then exposing them to various kinds of stimuli. Female preferences are revealed when primed (implanted) females respond to effective stimuli by adopting a characteristic “solicitation” posture, which free-living females adopt in preparation for copulation.

In their first experiment, Nowicki and colleagues gave females a “choice” between tape-recorded songs of laboratory-raised males who sang accurate copies of the model songs they heard when young and recordings of other lab-raised males who sang less accurate copies. Learning accuracy was measured as the proportion of accurately copied (“learned”) versus not copied

("invented") notes in the songs. In the second experiment, females were also given a choice between well-learned and poorly learned songs played from a tape recorder, but this time learning was defined as the degree to which copied notes matched those in the model songs (as determined by spectrographic cross-correlation analysis). In this experiment, the proportion of copied notes in the well-learned and poorly learned songs was the same. The two experiments showed that better-learned songs—by either measure of learning accuracy—evoked more solicitation displays from the females.

A third experiment was run to validate the presumed high quality of well-learned songs. Nowicki and colleagues played to their wild-caught females tapes of the wild males who provided the models used to train the lab-raised male song sparrows and the high-quality copies recorded from those lab-raised males. In this case, the females did not differ in their solicitation responses to best-learned songs of lab-raised males and the model songs of their wild-caught male tutors.


What these clever experiments demonstrate is that differences in the learning abilities of males are a functionally important aspect of a sexually selected, learned trait—bird song. This result raises some interesting questions. Why should a female pay attention to a learned trait? Does the quality of learning indicate something about the quality of the male? If learning quality accurately indicates male quality, what aspect of male quality (genetic, conditional, parental) is so indicated, and what produces the accuracy of the indicator? Nowicki and colleagues propose that song-learning ability reflects the amount of nutritional stress during development, perhaps because early nutritional stress affects brain development. In addition, the response of the developing brain to nutritional stress may depend on the genetic constitution of the developing bird.

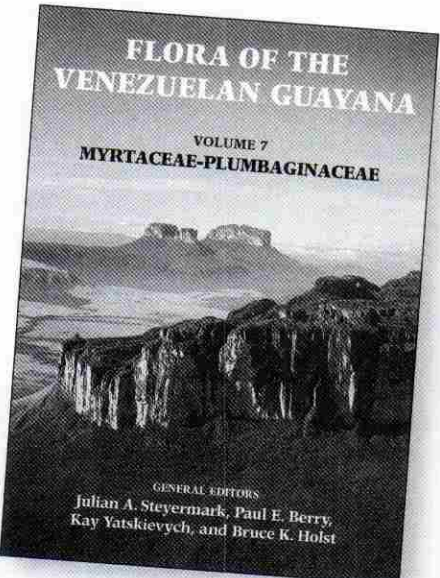
The study has also attracted the attention of the press. For example, Bill Wineke, who wrote "In Tune with the War of the Sexes" for the 14 September 2002 *Wisconsin State Journal*, worries, tongue-in-cheek, whether women pay attention to the singing abilities of men. In any case, whatever the mechanism that leads females to attend to a learned trait, Nowicki and colleagues' study is an important contribution. That the apparent explanation for song learning relies on sexual selection by mate choice would make Darwin smile.

References cited

- Andersson M. 1994. *Sexual Selection*. Princeton (NJ): Princeton University Press.
- Birkhead TR, Møller AP. 1998. *Sperm Competition and Sexual Selection*. San Diego: Academic Press.
- Campbell B. 1972. *Sexual Selection and the Descent of Man, 1871–1971*. Chicago: Aldine.
- Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- . 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- Huxley J. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *American Naturalist* 72: 416–433.
- Nowicki S, Searcy WA, Peters S. 2002. Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society of London, B* 269: 1949–1954.

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