Sexual signaling and speciation, a microevolutionary perspective

Christine R.B. Boake

Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Bldg., Knoxville, TN 37996-1610, USA (Phone: +1-865-974-1980; Fax: +1-865-974-3067; E-mail: cboake@utk.edu)

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Abstract

Despite the growing evidence that sexual selection can drive speciation, the evolution of sexual signals in natural populations is far from being well-understood. Sexual signals evolve in response to a variety of factors. Some of the most important selective factors are conspecifics, transmission efficiency in a particular environment, detection by predators, and phylogenetic constraints. These factors have been addressed quite successfully in studies of single types of signals in both vertebrates and invertebrates. However, it is less clear how multimodal signals evolve because the factors listed above will act on every component of the signaling system, and the relative weights of each type of signal must be taken into account. Species of Drosophila are excellent for such analyses because they are amenable to both phenotypic experimentation and genetic manipulation. This paper presents an approach that involves two analyses: studies of which signals are sexually selected within a species, and parallel studies of the signals that are involved in behavioral isolation between closely related species. If the same signal characteristics are involved in both processes, they would provide support for the hypothesis that sexual selection can drive speciation. This approach is illustrated with studies of Hawaiian Drosophila and a review of signals that could be sexually selected in Drosophila melanogaster.

Introduction

Recent models show that sexual selection can be a very powerful force in driving speciation (e.g., Lande, 1981; Wu, 1985; Lande & Kirkpatrick, 1988; Iwasa & Pomiankowski, 1995; Turner & Burrows, 1995; Payne & Krakauer, 1997; Gavrilets & Boake, 1998; Higashi et al., 1999; Kirkpatrick & Servedio, 1999). Despite the conclusions of the models, it is quite difficult to find cases that are consistent with sexual selection causing speciation. One approach, to study related species within a phylogenetic perspective, was reviewed recently by Panhuis et al. (2001). Here I will focus on a microevolutionary approach, which addresses ways to identify current examples of sexual selection being associated with the divergence of populations. I illustrate this approach with studies of insect behavior. First I discuss sexual selection and those aspects of signal theory that relate to mating behavior, then I consider examples.

A common definition of sexual selection is the differential variances in male and female mating success (Bateman, 1948; Wade & Arnold, 1980); males have a higher variance than females. The intermale variance in mating success is the source of selection on male traits. The usual processes of sexual selection are intrasexual competition and female mate choice, though any particular species is likely to have some combination of these factors in its behavioral mating system (Andersson, 1994).

Sexual selection is usually thought to lead to speciation as a result of females exerting mating preferences. Females are expected to be more discriminating than males because an inappropriate copulation could have costs to a female ranging from spending additional time to find an appropriate mate to failure of the clutch, whereas males might have lost time but
are unlikely to experience a major cost. Female mating preferences place strong selection on male signals when they increase the variance in male mating success. Conceivably, only one male in dozens or 100 could mate with the majority of females in a population. This intensity of selection is extremely rare for traits that are related to viability, which could explain the rapid speciation seen in some models (Turner & Burrows, 1995; Gavrilets & Boake, 1998).

Female discrimination is not perfect; sensory systems have bandwidths of sensitivity rather than sharp peaks. Sense organs and nervous systems are influenced by many genes as well as responding to considerable environmental input during development. This means that females will not agree perfectly in their choice of mates, and that at least some of the difference between females is likely to be under genetic control. There may be reasons in addition to sensory systems that underlie variation in female mating preferences. In the models of mate choice and speciation, mutations move female preferences beyond the range found in the initial population; these preferences select on male traits that are influenced by genes that are also mutating (Lande & Kirkpatrick, 1988; Turner & Burrows, 1995; Gavrilets & Boake, 1998). The models thus address elaboration of a trait along a specific axis, for example, increased plumage brightness, or increased size of an organ. In most of the models there is no directionality, so selection could just as easily lead to diminishing a signal. However related processes, such as selection for discriminability, could tend to move a population towards more elaborate signals (Lande & Kirkpatrick, 1988). Lande and Kirkpatrick (1988) pointed out that their model could also be applied to the elaboration of signals used in male–male competition; most models focus on female mating preferences.

A simple approach to evaluating the models would be to look for evidence of female mating preferences being involved in both sexual selection and species discrimination. If such an association is found, the models’ predictions that sexual selection can lead to speciation would be supported. A failure to find such an association would not falsify the models but would indicate that they are inappropriate for the species being studied. Tests of the models’ predictions would need to be conducted in populations that are in the process of diverging. Populations that have diverged substantially could have had time to evolve additional differences that obscure the process of divergence.

### Evolution in unimodal and multimodal signal systems

Several related hypotheses have influenced thought about the evolution of sexual signals in relation to speciation. Ryan’s concept of sensory exploitation suggests that females prefer signals that are not necessarily produced by males of their own species, but are produced by related species (Ryan, 1990). This could come about as a result of fairly simple neural mechanisms that are preserved within a clade (Enquist & Arak, 1993). Basolo (1990) extended the concept to develop the idea of a pre-existing bias, by showing that females in the swordtail fish group preferred males with swords even if their own species did not have swords.

Endler (1992) developed a related concept of sensory drive, which focuses attention on the environment in which a signal evolves. He pointed out several factors that could influence signal evolution, beyond phylogenetic effects; these factors probably play a major role in selecting for the capabilities of the sense organs used by a species. A major factor is the transmission properties of the environment, which may favor certain signal characteristics. So for example, low-frequency sounds are absorbed less by water than are high-frequency sounds, which can explain the use of low-frequency sounds for long-distance communication by whales (Tyack, 1998). Another environmental factor that Endler emphasized is selection exerted by the sensory capabilities of potential predators. He provided the example of guppies: in natural populations male color appears to be influenced by both female mating preferences and predator sensitivity. Endler argued that it is possible to predict the evolution of signals, given sufficient information about biophysics of the environment, the sensory capabilities of the signalers and their potential predators, and the behavior of all species involved.

Each of these concepts can help to explain the elaboration of a particular mode of signaling, whether it is the components of frog calls or the colors of male fishes. However, they may not get us far in dealing with the evolution of the multimodal signal systems that are found in many species. For example, bird signals often involve both plumage and song, and each of these signal modes may include several signals. The problem is to learn the role of each signal in the repertoire, including knowing the context in which it is produced, its physical range, and the kind of response it elicits. We might then be able to apply the