

# The Oxford Handbook of Comparative Evolutionary Psychology

Todd K. Shackelford and Jennifer Vonk

Print publication date: Sep 2012  
Print ISBN-13: 9780199738182  
Published to Oxford Handbooks Online: Sep-12  
Subject: Psychology, Personality and Social Psychology  
DOI: 10.1093/oxfordhb/9780199738182.001.0001

## Female Preference Functions Provide a Window into Cognition, the Evolution of Communication, and Speciation in Plant-Feeding Insects

Reginald B. Cocroft, Laura E. Sullivan-Beckers

DOI: 10.1093/oxfordhb/9780199738182.013.0018

### Abstract and Keywords

When female mate choice is based on male signals, female responses can be characterized in the form of preference functions that relate signal variation to attractiveness. Within a population, male displays will vary in multiple dimensions; preference functions reveal which of these dimensions are important for female mating decisions, suggest how sensory information is processed, and allow us to make predictions about the relationship between male signal variation and fitness. Here we discuss how characterizing female preference functions helps us understand the process of diversification in plant-feeding insects, an important component of terrestrial biodiversity. In the clade of insects we are studying, speciation is initiated by a shift from one host plant species to another. Host shifts lead to changes in the timing and location of mating, but the evolutionary changes that occur in mating signals and preferences are just as important for reducing gene flow among populations on different hosts. We focus on a subset of male signal traits for which female preference functions differ in strength and shape, and explore the effect of female preferences on male fitness within a population and on reproductive isolation among species. Integration of studies in the laboratory and field reveal how preference functions provide insights into the cognitive processes underlying mate choice, as well as the evolutionary forces that shape signal evolution.

sexual selection, phytophagous insects, Enchenopa, vibrational communication

## Introduction

In species in which females choose mates on the basis of their mating displays, filtering of information by the sensory system and further processing of that information by the nervous system cause females to respond to some signals more than others. The cognitive mechanisms underlying the response to signals are strongly shaped by evolutionary forces, given the importance of mate choice for female fitness. Female responses to signals are, in turn, important causes of evolutionary change, forging the link between signal properties and the reproductive fitness of the signaler. Although the information obtained from signals is only one component of mate choice, female preferences based on male signals are central to the field of sexual selection both because of their theoretical importance and because of their accessibility to measurement. As a consequence, preference functions—curves that relate mating responses to variation in male signal traits—provide both a window into the cognitive processes involved in sexual selection and a description of an evolutionarily important phenotype. In this chapter we discuss how studying the cause-and-effect relationships between female preferences and evolutionary change helps us understand the process of speciation in a diverse group of organisms.

We first provide the ecological background for understanding diversification in the species we are studying, which are a clade of plant-feeding insects. We describe their mating systems and mode of communication, and argue that sexual selection is the key to understanding the evolution of reproductive isolation among incipient species in this group. We discuss how female preference for male signals can be quantified in the laboratory, and we provide examples that illustrate evolutionarily important ways in which preference functions can differ among species and among different components of the same signal. We then assess the external validity of female preferences characterized under laboratory conditions, drawing from measurements of phenotypic selection on male signals under realistic conditions, and from comparative evidence of signal-preference evolution. Both lines of evidence support the hypothesis that divergence in female preferences among species leads to the evolution of reproductive isolation. Finally, we explore some of the factors that may lead to evolutionary change in female preferences between species adapted to different environments. We suggest that these herbivorous insects provide an excellent window into the evolution of cognition and behavior, because their natural history allows us to replicate important aspects of their world in the laboratory, and

to make unobtrusive observations under field conditions; that is, we can integrate studies with high internal and external validity.

## Host Shifts and Speciation in Herbivorous Insects

Terrestrial food webs involving plants, herbivorous insects, and their predators constitute up to 75 percent of terrestrial biodiversity (Price, 2002). Herbivorous insects alone are so diverse that it has been estimated that 4 in 10 terrestrial animal species are small, plant-feeding insects (Bush & Butlin, 2004). A key to the evolutionary history of herbivorous insects lies in their specialization on a subset of the available host plant species. In many cases, closely related species feed on different hosts, suggesting an important relationship between host shifts and speciation (Berlocher & Feder, 2002). This relationship has been confirmed by experimental studies showing that host shifts can lead not only to divergent natural selection, but also to life history changes that reduce interbreeding between populations on the ancestral and novel hosts (Bolnick & Fitzpatrick, 2007; Funk et al. 2002). Thus, herbivorous insects have played a major role in the study of ecological speciation – that is, divergence in which adaptation to different resources leads to reproductive isolation (Bush & Butlin, 2004).

Whereas the role of ecology in the diversification of herbivorous insects has been well studied, the role of sexual selection has not. This is perhaps surprising, given a general recognition that the evolution of behavioral barriers to interbreeding is a key component of speciation in animals (Coyne & Orr, 2004), and that sexual selection is a powerful diversifying force that can lead to behavioral isolation (West-Eberhard, 1983). For plant-feeding insects, the perspective has recently begun to change (e.g., Etges, 2002, Etges et al., 2007; Etges, Cardoso de Oliveira, Ritchie, & Noor, 2009), but for most taxa the focus has been on ecological barriers to interbreeding (e.g., Feder 1998; but see Claridge 1985, 1990). As a result, there are few cases in which the traits involved in mate choice have been identified, allowing an exploration of the links between host use and the development and evolution of mating signals and preferences (though see Landolt & Phillips, 1997). We suggest that understanding how host shifts can influence sexual communication is a key to understanding host-associated speciation. Host shifts can influence the development and evolution of mate communication systems in many ways. For example, when juveniles develop in a novel host environment, they may differ from those developing on the ancestral host in the cues or signals used in mate choice (Etges et al. 2009; Rodriguez, Sullivan, Snyder & Coccoft, 2008). The new environment may favor the

evolution of differences in signal form (McNett & Coccoft, 2008). Furthermore, populations on the new host may differ in body size, density, or resource-driven dispersion patterns, all of which can affect sexual selection (reviewed in Coccoft, Rodriguez, & Hunt, 2008). There is growing evidence that these and other factors can lead to changes in the nature of sexual selection in host-shifted populations, even in the first generation that develops on a new host.

Comparative evidence suggests that studying ecology alone is insufficient for understanding speciation in many groups of plant-feeding insects. The importance of mate choice is highlighted by a review of the biology of “host races,” which are genetically differentiated populations that are adapted to feeding on different hosts, but between which there is still substantial gene flow (Dres & Mallet, 2003). Whether host races represent speciation in progress or an equilibrium condition is unclear (Bolnick & Fitzpatrick, 2007), but the key difference that separates them from full species is a lack of behavioral reproductive isolation (Dres & Mallet, 2003). If the ecological differences that separate host races in nature—that is, differences in the timing and location of mating—are removed, most will readily interbreed. In contrast, host-associated species will usually not interbreed under these conditions, because of differences in the traits involved in mate choice. This pattern suggests that host-associated speciation requires both ecological and behavioral forms of reproductive isolation. However, it is also possible that divergence in mate choice could have evolved only after speciation occurred from other causes, such as ecological or geographic isolation. What is now needed, then, is a mechanistic understanding of how host shifts can cause changes in sexual selection, and whether ecological and sexual selection act in concert to cause speciation.

### The *Enchenopa Binotata* Species Complex of Treehoppers

Our research with a clade of herbivorous insects explores the causal links between host shifts and the evolution of communication (Coccoft et al., 2008, 2010). Our study species are treehoppers (Hemiptera: Membracidae), which are small plant-feeding insects related to cicadas. Treehoppers are found on a range of woody and herbaceous plants, where they feed on phloem sap (Wood, 1993a). Their diversity is highest in the tropics, especially the New World, but their distribution extends well into the temperate zone, and at a given locality in eastern North America there may be over 60 species. Many treehoppers, especially in the temperate zone, are specialized on hosts from a particular plant species, genus or family (Wood, 1993a).

The *Enchenopa binotata* species complex is a clade of 11 species of small treehoppers (Figure 18.1; most are less than 5 mm in length) that occur in North America, from southern Canada to Mexico (Lin & Wood, 2002). This group was once thought to be a single species that used a variety of woody host plants, but it was subsequently revealed to be a set of closely related specialists (Wood, 1993b). Each species uses either a single species of host, or a few closely related congeneric hosts; as the species in the *E. binotata* complex have not yet been formally described, we refer to them using the name of their host plant. As a result of a career-long series of studies by T. K. Wood, this group is one of the two most frequently cited examples of host-associated speciation (Coyne & Orr, 2004).

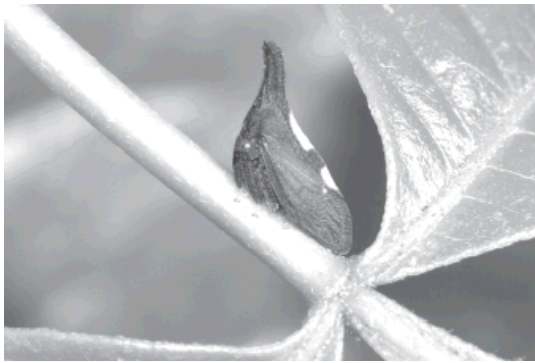


Figure 18.1 Female *Enchenopa binotata* “Ptelea” (total length about 5 mm) on the petiole of a host plant (*Ptelea trifoliata*).

The original speciation hypothesis for *Enchenopa* treehoppers is based on the consequences of a change in host use, and the resulting ecological factors that reduce interbreeding between populations on different host plants (Wood, 1993b). For *Enchenopa* treehoppers, the causes of host shifts are still unknown, but may involve changes in the local abundance or suitability of hosts (Agosta, Janz, & Brooks, 2010; Singer, Wee, Hawkins, & Butcher, 2008). In any case, the host plants used by different members of the *E. binotata* complex represent very different selective environments. Although our current understanding of *Enchenopa* phylogeny does not allow us to identify the historical sequence of host shifts, reciprocal transplants show that, between many of the possible host pairs, offspring survivorship is much reduced on the wrong host (Wood & Guttman, 1983). When a host shift occurs, there may thus be strong divergent natural selection between populations on ancestral and novel hosts. Although the traits involved in adaptation to particular host plants have not been identified, *Enchenopa* treehoppers have colonized a diverse collection of distantly related plant

species, which likely differ in many traits including chemical defenses and the architecture of the vascular system on which the insects feed (Wood & Guttman, 1982).

The shift to a novel host will not only favor some genotypes over others; it may also—through genotype-by-environment interactions or direct host effects—influence the traits expressed by a given genotype. This developmental plasticity is the key to understanding the ecological barriers to interbreeding between *Enchenopa* populations on different hosts (Tilmon, Wood, & Pesek, 1998). These insects have a single generation per year, with eggs laid under the bark of the host in the fall and hatching in the spring (Wood & Guttman, 1982). Because the eggs are in contact with the plant's vascular system, seasonal differences in hydration of the stem enable the insects to reliably track their host's phenology. Egg development is triggered by movement of water into the stems (Wood & Keese, 1990), and this leads to hatching at about the time of leaf flush, a period of rich nutrition for plant parasites such as *Enchenopa* (Coley & Barone, 1996). This difference in the timing of egg hatch between populations on different hosts also leads to differences in the timing of mating (Wood, Olmstead, & Guttman, 1990). Adults are relatively sedentary, and females prefer to mate on their host plant (Wood, Tilmon, Shantz, Harris, & Pesek, 1999). Changes in the timing of development, coupled with high host fidelity, thus provide an ecological barrier to interbreeding.

### Behavioral isolation in *ENCHENOPA*

Given divergent natural selection, and host-related sources of ecological isolation, what is the role for sexual selection in speciation in this system? Although *E. binotata* treehoppers on different hosts mate at different times and locations, these barriers to interbreeding are incomplete. Differences in the timing of egg hatch on different hosts at the same site range from 1 to 10 days (Wood & Guttman, 1982), whereas mating periods can last 6–10 weeks (Sullivan-Beckers & Coccoft, 2010). Thus, there is considerable overlap among the breeding seasons of sympatric species using different hosts. Furthermore, host fidelity is not absolute, and mate-searching males sometimes occur on the “wrong” host during the breeding season (Coccoft et al., 2008). As a result, it is unlikely that ecological differences alone provide sufficient reproductive isolation to allow a response to divergent selection on different hosts. Although ecological isolation is probably essential for initiating divergence between populations on different hosts, behavioral isolation is likely necessary for completing the process of speciation.

Evidence that behavioral differences among *Enchenopa* populations on different hosts provided stronger isolation than ecological differences comes from a study of host-associated species maintained in close proximity (Wood, 1980). When multiple species were kept in the same outdoor enclosures during the breeding season, courtship was frequently observed between males and females of different *Enchenopa* species. However, these between-species courtships almost never resulted in mating. The behavioral basis for female mate choice was revealed some years later by Hunt (1994), who described complex vibrational courtship signaling in one species in the *E. binotata* complex.

## Vibrational Communication

The study of communication in *Enchenopa* treehoppers leads us into a world to which our unaided senses provide little access. The use of substrate-borne vibrations is an ancient and widespread form of communication in arthropods, and it occurs in many vertebrates as well (Cocroft & Rodriguez, 2005; Hill, 2008). When the vibrational signals of plant-dwelling insects are transduced and played back as airborne sound, many are more reminiscent of the songs of birds, frogs, primates, and whales than of the familiar songs of katydids and crickets. The differences between the vibrational songs of plant-dwelling insects and the familiar airborne songs of backyard insects arises in part from the very different relationship between size and frequency in the two modalities. Although the physics of airborne sound limit the use of low frequencies to large animals, the constraints are very different for substrate-borne signals (Cocroft & DeLuca, 2006). As a result, a 1-cm treehopper can transmit signals with the same low frequencies as a bullfrog that is 10,000 times more massive (Cocroft & Rodriguez, 2005). Furthermore, although the signals of most acoustic insects are relatively constant in frequency, those of many substrate-signaling insects contain dramatic changes in frequency, reinforcing the auditory impression that one is listening to a bird or primate.

For *Enchenopa* and many other plant-dwelling arthropods, the medium through which signals are transmitted is the host plant itself. A substrate, such as a plant stem, can be set into vibration by almost any movement of an organism in contact with it. Some vibrationally communicating species generate percussive signals by striking the substrate with some part of their body; many produce vibrations through direct muscle contractions, such as “tremulation” of the abdomen or vibration of the flight muscles. Still others use a frequency-multiplier system such as a file-and-scraper, or a tymbal—that is, a rigid cuticular structure whose deformation causes

one or more broad-band clicks for each muscle contraction (Cokl & Virant-Doberlet, 2003). Many species use two different mechanisms simultaneously or in succession, such that there is a relatively pure-tone component (with or without associated harmonics) accompanied by higher-frequency broadband clicks (Cocroft & McNett, 2006).

Insects and other arthropods detect plant-borne signals using vibration-sensing organs in their legs. Although little work has been done with treehoppers, vibration sensing in related Hemiptera occurs through several types of receptors. The most important is the subgenual organ, a highly sensitive vibration-transducing structure located within the tibia. A second important structure, the femoral chordotonal organ, spans the femur-tibia joint (Virant-Doberlet & Cokl, 2004).

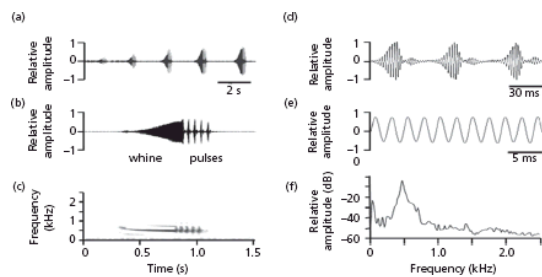


Figure 18.2. Representative substrate-borne male advertisement signal of a male *Enchenopa*. This example is from *Enchenopa binotata* “Celastrus” in Missouri, United States. (a) Waveform, showing one bout of five signals. (b) Waveform showing whine and pulse components of fourth signal from bout shown in (a). (c) A spectrogram of the same signal. (d) Waveform showing three pulses. (e) Waveform of a signal near the end of the whine, showing its tonal, sinusoidal nature. (f) Amplitude spectrum of the entire signal, showing single prominent frequency peak with other components 20 dB or more below.

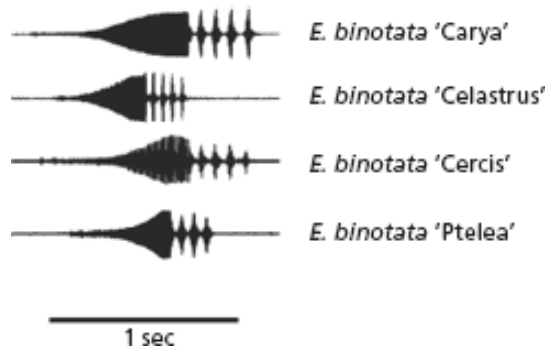




Figure 18.3. Male advertisement signals of four species in the *E. binotata* species complex, with waveforms illustrating the shared whine + pulses signal structure.

In *Enchenopa*, male signals consist of a relatively pure-tone downward-frequency sweep, followed by a series of pulses at the final frequency (Figure 18.2). This basic whine + pulses structure is conserved throughout the species complex (Figure 18.3), and even occurs in several related genera (Cocroft, unpub. data). This similarity in signal structure among species facilitates comparisons, avoiding the need for difficult decisions about homology between signal features in different species. There is also a series of relatively low-amplitude broad-band clicks at the beginning of the signal of most species, and although we now have indirect evidence that these play a role in communication (Holan, Wikle, Sullivan- Beckers, & Cocroft, 2010), we have not studied their function and will not discuss them further here.

Signal differences between *E. binotata* species on different hosts reflect genetic rather than environmental differences. Male signals do not change in structure when the male signals on a different host; although males may produce fewer, shorter signals, their frequency and other temporal characteristics remain the same (Cocroft, Shugart, Conrad, & Tibbs, 2006; Rodriguez et al. 2008; Sattman & Cocroft, 2003). Furthermore, average signal traits do not differ between siblings raised on hosts versus non-hosts (Rodriguez et al., 2008). Although we do not yet have similar data for female preferences, our working hypothesis is that differences between species in the preferred value of signal traits reflect genetic rather than environmental differences, as is true for male signals.

Vibrational signals in *Enchenopa* are produced in the context of a density-dependent mate-searching pattern. At low densities, males fly from one host plant to another, producing a few bouts of advertisement signals on each. If a receptive female is present on the plant, she produces a vibrational reply; this causes the male to search the plant, stopping periodically to signal and elicit another vibrational reply to update his information about female location. Once the female is located, the male will remain near her, producing signals for sometimes several hours before mating. At higher densities, when multiple males occur in close proximity on a host, males may signal in alternating choruses that can continue for hours. Chorusing males are largely stationary, but occasionally move to another location on the same plant where they may join another chorus (pers. obs.).

Signaling, courtship and mating occur over a breeding season that can last 6–10 weeks (Wood & Guttman, 1982). We have studied the mating system of one species in detail, and describe it here to illustrate the nature of sexual selection on males. In *Enchenopa binotata* “Ptelea,” females have a relatively asynchronous mating schedule such that, in a population of 100+ females, on most days during the breeding season only one to three females mate (Sullivan-Beckers, 2008). By the time most females mate, then, they will have been exposed to many male signals in the preceding days and weeks. When females become receptive, they begin producing vibrational replies to male signals (Figure 18.4). Females will respond to signals of more than one male on the plant, drawing those males into close proximity. When females have multiple males to choose from, they take significantly longer to select a mate, up to a day and a half, during which time the males produce thousands of signals (Sullivan-Beckers & Cocroft, unpublished data.). Male advertisement signals can be detected using sensitive vibration transducers after traveling up to two or more meters through the plant (personal observation), and can likely be detected by females at even greater distances. However, nearest-neighbor distances are less than 20 cm (McNett & Cocroft, 2008), and most communicative interactions likely take place when the insects are less than 1 m apart on the plant. Female signals are typically lower in amplitude than male signals (Rodríguez & Cocroft, 2006), and, as a consequence, it will be the males' ability to detect female signals that limits the range over which duetting can take place.

## Female Preference Functions

### Characterizing Female preferences

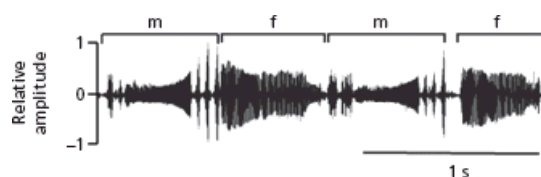


Figure 18.4. Duet between a male and female *E. binotata* ‘Ptelea’ from Missouri, USA (waveform; m=male, f=female).

The duetting mate-localization system of *Enchenopa* and many other plant-dwelling insects makes them among the easiest of organisms for which to characterize female preferences. The response signals of females provide a localization beacon for mate-searching males, so the female can reject a

male by failing to respond to his signals, thereby withholding cues of her presence and location. Female selectivity can thus be characterized by playback of male signals, with the presence or absence of a female reply providing an assay of preference (Rodríguez, Sullivan, & Coccoft, 2004). In contrast, for the many species in which females approach a signaling male, movement is the usual assay of preference, and females are typically tested in a two-choice experimental design (Wagner, 1998). When characterizing female preference functions requires a series of two-choice contrasts, the need for multiple tests makes it more difficult to construct curves that describe the preferences of individual females across the range of trait values desired. Furthermore, because choice decisions are not always transitive (Ryan, Akre, & Kirkpatrick, 2009), constructing a preference curve from the results of multiple contrasts can be problematic. In contrast, for duetting insects, female preferences can be tested with a large number of stimuli over a period of a few minutes; the approach is analogous to giving an individual a questionnaire (thanks to R. Rodríguez for the analogy) containing all the trait values of interest. Each set of stimuli can be presented to an individual female multiple times, with the order varied, to assess the repeatability of female responses and any possible dependence of response probability on the order of presentation.

The concept of a preference function that describes the relationship between attractiveness and signal variation is closely related to that of a fitness function that describes the relationship between reproductive success and variation in a phenotypic trait. Fitness functions can have complex shapes that are not adequately captured by linear or quadratic coefficients from a regression of fitness on phenotypic variation (Blows et al., 2003; Brodie, Moore, & Janzen, 1995; Brooks et al. 2005; Ritchie 1996, 2007), and cubic splines (a form of nonparametric regression) provide a much less restrictive way to characterize the shape of the curve (Schluter, 1988). We likewise use cubic splines to estimate the shape of female preference functions (Rodríguez, Ramaswamy, & Coccoft, 2006). Although the shape of the curve representing female responses to male signals may be complex, there are two general categories of curves: “closed” preference functions, for which responses are strongest for an intermediate value, with decreased responsiveness at higher or lower values; and “open” preference functions, for which higher values are more attractive than low or intermediate values. In addition to the shape of the curve, we can estimate its strength, comparable to the intensity of selection (Schluter, 1988). Just as the strength of selection describes the degree to which trait variation influences fitness,

the strength of a preference function indicates the extent to which variation in a given trait influences attractiveness.

The use of similar approaches to characterizing preference functions and fitness curves allows us to more easily explore the causal relationships between the two (see later). Closed preference functions have the potential to exert stabilizing selection on male traits, if the peak preference coincides with the average trait value in the population. Alternatively, they can impose directional selection, if the peak preference is for a value above or below the average trait value. Open preference functions can exert directional selection for higher (or lower) trait values (Sullivan-Beckers & Cocroft, 2010).

### Female Preference Functions in *Enchenopa*

We have characterized female preference functions for *Enchenopa* in the lab using vibrational playback of both natural and computer-generated signals, which evoke similar levels of response. For testing, a receptive female is placed on a host plant stem and played a series of signals using a vibrational playback device (see Cocroft & Rodriguez, 2005), with the amplitude and frequency characteristics of the vibrations calibrated at the location of the female. “Receptive” females are defined as those that will produce vibrational responses to at least some male signals. Female response signals can be recorded with a vibration transducer such as an accelerometer attached to the stem a few centimeters from the female. These responses can, in turn, be used to generate preference functions for individual females or for a population of females using, for example, the proportion of times that stimuli with a given trait value elicited a response. Female response signals are themselves variable, especially in duration, and this variation likely has consequences for the efficiency of male localization and could provide a more fine-grained indication of female preference. In any case, there is a strong positive correlation between the likelihood that a female will produce a response to a given signal variant and the duration of the female response signal; so for our purposes, the presence/absence scoring of female responses provides the most clearly interpretable measure of preference.

The use of duetting responses as an assay of female mate choice has revealed that *Enchenopa* females are very selective indeed. This selectivity causes females to respond almost exclusively to the signals of conspecific males, while remaining silent during playback of vibrational signals of heterospecific males (Rodriguez, Sullivan, & Cocroft, 2004). That is, differences in signals and preference among *Enchenopa* species do indeed

result in behavioral isolation (Cocroft et al., 2008, 2010; Rodriguez et al., 2004, 2006). We first describe how female responses are influenced by variation in male signals in one species in the *E. binotata* complex, both at an individual and a population level. We will then show how measuring selection on signals under natural conditions enables us to make the link between lab-based preference tests and selection in natural populations. Next, we will show how variation among species in female preferences has influenced the evolution of male signals. Finally, we will discuss how these results re-focus the research on the causes of divergence in female preferences.

The species in the *E. binotata* complex that occurs on the host *Ptelea trifoliata* (Rutaceae) is the one for which we have the most data on, not only female preferences, but also on male and female behavior during mate choice, and on selection on male signals under natural conditions. To characterize female preferences, we used vibrational playback to elicit female duetting responses. Using computer-generated signals we varied one signal trait at a time, while holding all other traits constant at the population mean (Rodriguez & Cocroft, 2006).

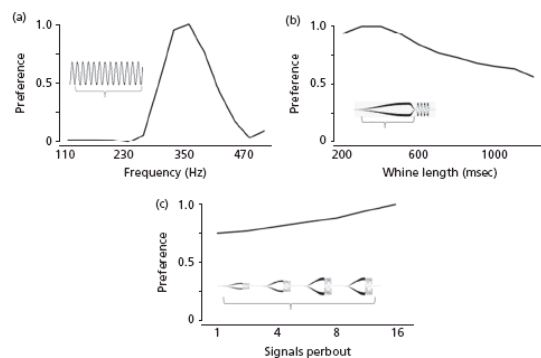


Figure 18.5. Preference function estimates for a population of *E. binotata* “Ptelea” females, illustrating differences in preference function shape and strength. (a) Strong, closed preference for male signal frequency. (b) Weak, closed preference for male whine duration. (c) Weak, open preference for the number of signals per bout. The curves are cubic splines based on signaling responses of 15 females to synthesized male signals (see Rodriguez et al. 2006 for details).

Preference functions of female *E. binotata* “Ptelea” vary in both shape and strength, depending on the signal trait. Here, we illustrate three preference functions that range from strong to weak and from closed to open. For male signal frequency, females had a strong, closed preference (Figure 18.5a): closed, because females responded most strongly to an intermediate value

of signal frequency; and strong, because above and below the intermediate value, signals were almost completely unattractive. Thus, male signal frequency has the potential to be an important phenotype for the evolution of signal differences leading to speciation, because females are unlikely to mate with males from populations or species whose signal frequency does not match their preferred value. Female preferences for the duration of the whine component were also closed, but much weaker (Figure 18.5b): although females preferred an intermediate value of whine duration, females often responded to signals with greater or lesser duration. Differences among populations or species in the duration of the whine may thus also cause females to prefer males from their own population, but are likely to have a smaller effect than differences in signal frequency. In contrast, females had a weak, open preference for the number of signals per bout (Figure 18.5c): females responded more often to bouts containing more signals, but they still usually responded, even when they received only one signal. This signal trait, then, is unlikely to have much effect on reproductive isolation, even if it differs among populations or species.

All tests with a given female were done on one day, so we do not have a good long-term measure of repeatability, as we do with male signals (Sattman & Cocroft, 2003). However, within a testing session (several minutes) during which females were repeatedly presented with the same set of signal variants, there were significant differences among the preference curves of individual females (Rodriguez et al., 2006). Figure 18.6 illustrates some of these individual differences for signal frequency: some females have narrow closed functions similar to the average curve for the population, whereas others have broad functions, indicating that that female was essentially nonselective over the range of values tested. Relatively few studies provide both individual and population preference functions, but this pattern of a relatively strong closed population curve and widely varying individual curves is also seen in a planthopper (Butlin, 1993) and may be widespread.

If individual differences in female preference functions are consistent over the relevant few days between when a female *E. binotata* becomes receptive and when she decides to mate, then they will have the following important consequences. First, there is significant broad-sense heritability in male signal traits (Rodriguez et al., 2008), so if the observed differences in preference functions reflect genetic variation among females, the conditions are present for evolutionary change in signals and preferences through a Fisherian process (Prum, 2010). Second, because female preferences are a

source of strong selection on male signals (Sullivan-Beckers & Cocroft, 2010), variation in preferences should translate into variation in selection and thus to maintenance of genetic variation in male signals. Third, less selective females may be at an advantage in some circumstances, such as when there are few males available from which to choose (Kaneshiro, 1989).

### Female preference functions as a source of selection on male signals

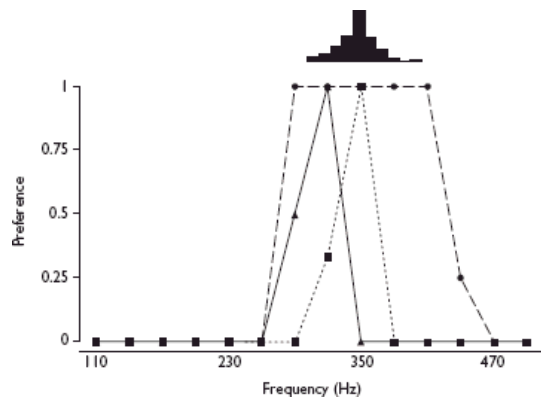


Figure 18.6. Preference functions of three female *E. binotata* “Ptelea,” showing individual differences in female preference for male signal frequency. The distribution of male signal frequencies in the population is shown in the histogram above. All three preferences functions are closed. Two are narrow, with one female (dotted line) preferring an average frequency and one (solid line) preferring a below-average frequency. The third female (dashed line) has a broad frequency preference, reflected in responses to signals across the entire range of frequencies present in the population. Preference data are drawn from the study described in Rodriguez et al. (2006), and male signal data are drawn from the study described in Sullivan Beckers and Cocroft (2010).

For females, mate selection will depend, not only on mating preferences, but also on how those preferences are expressed in nature in the form of mate choice. The degree of female choosiness will be influenced by factors such as how widely females sample males before making a choice, environmental factors such as background noise that may interfere with females' ability to discriminate signals, the presence of predators that may make females less choosy, and male-male competition that may circumvent female preferences (Hunt Breuker, Sadowski, & Moore, 2009; Jennions & Petrie, 1997; Wagner, 1998). As a consequence, although it is common to characterize female preferences in the laboratory and then assume that these translate directly

into selection on male signals, this assumption is not well justified. Instead, it is important to measure selection on male signals under natural conditions where multiple sources of selection are present. The resulting fitness curves can then be compared to curves characterizing those sources of selection, to allow inferences of which source(s) produced the observed relationship between signal variation and fitness (Sullivan-Beckers & Cocroft, 2010).

We have measured sexual selection on male mating signals over two breeding seasons for *E. binotata* "Ptelea." We established populations on potted host plants in outdoor enclosures, with sex ratio and densities typical of natural populations and under conditions (i.e., forest edge) typical of those encountered in nearby field sites from which the experimental individuals were collected as immatures (Sullivan-Beckers & Cocroft, 2010). To characterize male signal phenotypes, we recorded male vibrational advertisement signals at the beginning of the season; note that signal variation in this species is repeatable (i.e., there are consistent individual differences over a period of weeks; Sattman & Cocroft, 2003). We then measured male mating success throughout the breeding season. Importantly, because females mate only once in this species, the number of copulations a male obtains is a reliable index of lifetime reproductive success.

Male fitness, measured as the lifetime number of matings, was strongly correlated with signal variation (Sullivan-Beckers & Cocroft, 2010). Each of the three traits we focus on here (frequency, whine duration, number of signals per bout) was under selection. There was considerable year-to-year variation in the relationship between signals and mating success, and for each of these traits, the relationship was significant in only one of the two years (Sullivan-Beckers & Cocroft, 2010). Spatial and temporal variation in selection on mating traits is common (e.g., Bertin & Fairbairn, 2005; Lehtonen, Wong, & Lindstrom, 2010), and likely reflects the sensitivity of sexual selection to variation in various biotic and abiotic factors. One of the two breeding seasons observed in this study occurred during a prolonged drought, which may have had important effects on both plants and insects.

At this point, then, we have two patterns: laboratory characterization of female preferences for male signal traits; and male mating success based on signal traits under realistic outdoor conditions. How can we determine whether the observed patterns of mating success were caused, at least in part, by female mate choice? Our approach was to compare the observed relationships between signal traits and fitness with those predicted by female



choice, along with two other potential sources of selection. In addition to female choice, we examined the relationship between signal variation and success in male-male competition, using mating trials with two males and one female, during which males engage in “contest” behavior that seems to influence male mating success). We also characterized the signal-transmitting properties of the host plant tissue through which communication takes place; substrate properties likely influence the evolution of signal frequency more than gross-temporal signal features (McNett & Cocroft, 2008).

Both of the additional potential sources of selection we evaluated can be quantitatively characterized. For example, host plant tissues act as filters for the vibrational signals they transmit, and if these plant properties are important in signal/preference evolution, then signals that transmit more efficiently (i.e., with less excess attenuation) through the substrate will be favored (McNett & Cocroft, 2008). Attenuation curves can thus be used, analogous to female preference functions, to predict which males should be more successful, based on the frequency of their vibrational mating signals. If the observed relationship between signals and fitness was influenced by substrate properties, then males with frequencies that transmit more efficiently will have higher mating success.

Female preference functions were the only significant predictor of the relationship between male signal variation and mating success (see Sullivan-Beckers & Cocroft [2010] for details of the statistical method used). For example, in the second year of the study, males with intermediate frequencies had higher fitness than those with higher or lower frequencies; this pattern was quantitatively predicted by the relationship between signal frequency and female preference (Figure 18.7), but not by that between signal frequency and male-male competition or signal transmission. In the second year of the study, males with intermediate whine durations had higher fitness, although the fitness curve did not match that predicted by female preferences. In the first year of the study, males that produced more signals per bout had higher fitness, as predicted by female preferences (Figure 18.7) but not by male-male competition. In other words, we have successfully bridged the gap between laboratory and field: female preferences measured in the laboratory predicted patterns of male mating success for at least some important male signal traits under realistic conditions. Our conclusion is that female preferences are an important agent of selection on male signal traits in contemporary populations.

## Comparative Evidence of Signal/Preference Coevolution

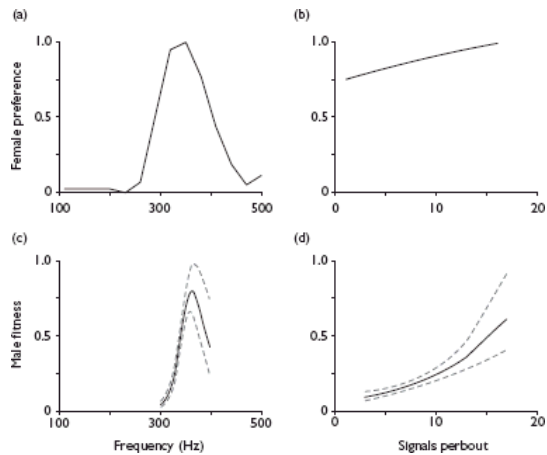


Figure 18.7. Female preferences measured in the laboratory predicted the lifetime mating success of males under realistic conditions. The curves in the left-hand column show how male signal frequency influenced attractiveness (a) and mating success (c); those in the right-hand column show how the number of signals per bout influenced attractiveness (b) and mating success (d). The dotted curves in (b) and (d) indicate  $\pm 1$  standard error.

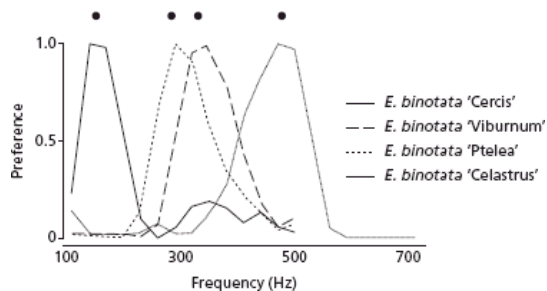


Figure 18.8.

We can learn about the evolutionary importance of female preference functions not only from studying selection in contemporary populations, but also from comparing preferences and signal traits among species. An observed correlation between preferences and traits does not in itself resolve the issue of whether change in female preferences is causing change in male signals or vice versa. However, we can make some additional comparisons that may allow us to infer the direction of causation.

We have compared female preference functions with male traits in four species in the *E. binotata* complex (Rodriguez et al., 2006). The four species

occur sympatrically on different hosts at a single locality. For a given trait, the shape of female preference functions is similar among species; for example, females in all four species examined have strong closed preferences based on male signal frequency (Figure 18.8). However, the peak values are shifted, such that females in one species prefer higher-pitched signals whereas females in another species prefer lower-pitched signals. For whine duration, females in all four species likewise have relatively weak closed preferences. There is less overall divergence, with some overlap between species in the preferred whine duration. For signal number, in contrast, females in all four species have weak open preferences, responding more to signal bouts containing more signals.

The relationship between male traits and female preferences depends on preference shape and strength. For frequency—strong closed preference functions—male signals precisely match the preferred value. For whine duration—weak closed preferences—male whine durations are shorter in the two species in which females prefer shorter signals, and longer in the two species in which females prefer longer signals. For the number of signals per bout, there is no difference among species in either female preferences or male traits.

We can make additional predictions that help us establish the arrow of evolutionary causation. If divergence in female preferences is causing divergence in male signal traits, then, for stronger preferences, we expect a closer match between trait and preference and a smaller coefficient of variation in male traits. For the signal/preference comparisons in these four species, both predictions are met. Coupled with evidence of the importance of female preferences in causing selection on male signal traits in a contemporary population of one species in the complex, these results strongly support the hypothesis that, within the *E. binotata* complex, divergence in female preferences is responsible for divergence in male signal traits. Because behavioral isolation arising from differences in mating signals and preferences is the most important source of reproductive isolation in *Enchenopa* treehoppers (Rodriguez et al., 2004), changes in the nature of sexual selection among species on different hosts likely contributed to speciation in this clade. Thus, female preference functions represent a phenotype that is central both to microevolutionary processes occurring within populations, and to macroevolutionary patterns of diversification.

Although we now have a clearer picture of the evolutionary importance of female preference functions, the neural underpinnings of female responses

to male signals remain a black box. In the case of male signal frequency, however, we can make some predictions based on behavioral data. In insects, there are two common mechanisms by which individuals distinguish between signals with small differences in spectral content. One is based on a resonance mechanism, such that frequency differences are translated into amplitude differences (Hoy, Popper, & Fay, 1998; Saberi & Hafter, 1995); the other is based on frequency discrimination per se (Fonseca, Münch, & Hennig, 2000; Gerhardt & Huber, 2002). Female responses to playback of male signals differing in both frequency and amplitude suggest that female preferences for signal frequency in *E. binotata* treehoppers are based on frequency discrimination. When signal amplitude is held constant while frequency is varied, female responses decrease above and below an optimum frequency. If this pattern of responses were based on a transformation of frequency differences into perceived amplitude differences, then female responses should increase when we raise the amplitude of nonpreferred frequencies. However, females fail to respond to nonpreferred frequencies, even when their amplitude is much higher than that of preferred frequencies (unpublished data). Furthermore, female responses to preferred frequencies are actually highest for signals of very low amplitude (McNett, Luan, & Cocroft, 2010).

Two other lines of evidence suggest that different *Enchenopa* species likely detect signals over the same range of frequencies, even if they respond to them differently. First, although differences in body size can lead to differences in the carrier frequency of acoustic signals through their effects on signal producing and receiving structures (Gillooly & Ophir, 2010), body size is similar across the *E. binotata* complex, and it is, indeed, identical between two species with contrasting frequency preferences (McNett & Cocroft, 2008). Second, *Enchenopa* treehoppers also produce signals during the juvenile stage, and these are broadband, harmonically structured grunts that are almost identical across species (unpublished data); this similarity among signals of juveniles is consistent with similarity in perceptual abilities at least during the juvenile stage. The evolutionary changes in female preferences for signal frequency would seem, then, to be due to changes in a process such as selective attention rather than to changes in peripheral sensory structures.

## Causes of Divergence of Female Preferences

It would be tempting to stop here, with our conclusion that sexual selection is an important cause of speciation in this clade of insects. However, although

female preferences are imposing sexual selection on male signal traits, we still need an explanation for why female preference functions differ among species. Without identifying causes of change in the female preferences that are important for behavioral isolation, we are left with an incomplete explanation of species divergence.

We can now pose the question that will be the focus of the final section of the chapter, namely, What causes evolutionary change in the preferred value of closed female preferences? Note that this is not the usual perspective on sexual selection as a diversifying force, which draws on the “creative” role of sexual selection in trait evolution by virtue of female preferences for exaggerated traits (Andersson, 1994). In fact, such preferences are, in terms of diversification, rather unimportant. Most open-ended preferences are a force for convergence among species, rather than divergence; as in the *Enchenopa* treehoppers discussed here, when given a choice between male signals differing in some measure of overall energy (more signals, more intense signals) females of most species tested similarly preferred the greater quantity (Ryan & Keddy-Hector, 1992). Instead, it is closed female preferences that are important for the evolution of behavioral isolation, because, when the preferred values differ between populations or species, this leads to decreased mutual attractiveness (Mendelson & Shaw, 2005). One focus of our research program, then, has been to identify factors that can cause divergence in closed female preferences in *Enchenopa*. The most evolutionarily important female preference is for male signal frequency. Frequency is an important target of sexual selection (Sullivan-Beckers & Cocroft, 2010); it is important for efficient signal transmission (McNett & Cocroft, 2008); it is the most important trait for mate recognition (Rodriguez et al., 2004, 2006); and it differs between species more than any other signal trait (Cocroft et al., 2010).

Here, we briefly consider both adaptive and nonadaptive causes of change in female preferences. Adaptive explanations for changes in female preferences include selection against mating mistakes; changes in the relationship between traits or trait values and the benefits of mate choice; selection arising from differences in the signaling environment on different hosts; differences in predation between populations on novel and ancestral hosts; or changes in the evolutionary dynamics of trait-preference co-evolution (reviewed in Cocroft et al., 2008). Nonadaptive causes of change in female preferences include genetic drift (Tregenza, Pritchard, & Butlin, 2000), which may be important when a new host is colonized; gene flow; and genotype × environment interactions that cause changes in the mean phenotype, or

in correlations among phenotypic traits, when individuals develop in a novel environment (Greenfield & Rodriguez, 2004).

In *Enchenopa* we have so far evaluated two potential causes of change in sexual selection: change in the developmental environment (Rodriguez et al., 2008), and sensory drive (McNett & Cocroft 2008; McNett & Cocroft, unpub. data). We will first discuss how changes in the signaling environment— both in terms of which signals will transmit most efficiently and which signals will most effectively avoid masking by noise— might influence selection on female frequency preferences.

For insects and other organisms that communicate using plant-borne vibrations, they must first impart vibrations into a region of the plant; these vibrations then travel some distance along the plant stems before being detected by receivers. Thus, there are two aspects of signal transmission that may be affected by the physical structure of the host plant: the initial loading of the signal into the plant, and the subsequent transmission of the signal along plant stems or leaves. The question of whether there is frequency-dependent impedance matching between signal and substrate remains completely unstudied. The question of whether organisms use signals whose frequency characteristics are adapted to travel efficiently through their host plant or other substrate has been addressed in several species (reviewed in McNett & Cocroft, 2008). However, few studies have investigated host specialists rather than generalists (we would expect more precise signal-substrate matches for organisms using a narrower range of transmission environments), few have used adequate sample sizes for incorporating plant-to-plant variation, and, indeed, few have determined exactly which parts of the plant are used by the organisms to transmit their signals. Our study of signal-substrate matching in *Enchenopa* meets all of these criteria; the limitation is that so far we have examined the match in only two of the 11 species, and the pattern in these two species differs, precluding general statements about the importance of signal-substrate matching.

We investigated the signal-transmitting properties of two hosts of species in the *E. binotata* complex: *Cercis canadensis* (Fabaceae) and *Ptelea trifoliata* (Rutaceae). Both are woody plants, and in both cases the insects primarily use the distal portions of branches (#3 mm diameter) for communication. However, the species on *Cercis* uses woody stems much more frequently than leaf petioles, whereas the reverse is true for the species on *Ptelea* (McNett & Cocroft, 2008). For both species, we characterized the vibration-

transmitting properties of one stem from each of 20 plants, where the stem selected was in use by communicating insects during the breeding season. For the species on *Cercis*, there is a close match between the frequency that transmits with least attenuation through the substrate, and the frequency of male signals. For the species on *Ptelea*, there is less of a match, but the frequency used by males of this species transmits better on *Ptelea* than does the frequency used by males of the species on *Cercis*. These results suggest that, in at least some cases, substrate transmission properties have influenced the evolution of signal frequency. Although this study provides evidence that, in at least one case, substrate transmission properties have influenced the evolution of signal frequency, only when we have examined this question in a larger sample of species will we be able to generalize about the role of substrate properties in signal evolution.

Another potential cause of divergence in female preference may be host plant-specific noise in the communication channel. Wind is the major source of abiotic noise for organisms that communicate via plant-borne vibrations (Cocroft & Rodriguez, 2005; McNett et al., 2010; Tishechkin, 2007). In addition to the low-frequency motion of plant stems and leaves displaced by moving air, higher-frequency vibrations are generated through impact of one plant part on another, or through friction between plant parts moving relative to one another. The result is a characteristic spectrum dominated by low-frequency energy, but with a long tail extending into the kilohertz range.

Adaptations for communication in the presence of noise may involve using signal frequencies different from those present in the noise or communicating at times or locations where the amplitude of noise is low (Greenfield, 1994). A salient feature of wind-generated noise is its temporal variability, with predictable differences in average wind velocity at different times of day, and short-term fluctuations in velocity on a scale of seconds (Cocroft & Rodriguez, 2005). For insects communicating via plant-borne vibrations, individuals in at least some species use gap detection to communicate during brief dips in wind velocity (McNett et al., 2010; Tishechkin, 2007). In *E. binotata* "*Ptelea*," females were less likely to respond to male signals produced in the presence of wind-induced vibrations, especially if the male signals were low in amplitude. Furthermore, most communication in the field took place at times of day when average wind velocity was lowest (McNett et al., 2010). However, because wind is a ubiquitous feature of natural environments, and options for temporal avoidance of noise will sometimes be limited, we can also expect

vibrationally communicating organisms to evolve signal frequencies that minimize overlap with frequencies prominent in wind-induced vibrations.

The frequency spectrum of wind on plants is similar to that of rushing water, which has favored the repeated evolution of high frequency airborne acoustic signals in torrent-breeding frogs (Arch, Grafe, & Narins, 2008). Given that wind spectra can vary among structurally different plant species (Barth, 1988), organisms that communicate via plant-borne vibrations provide exceptional comparative possibilities for evaluating the role of abiotic noise in the evolution of signal diversity. No such data are yet available, but we have taken a first step in evaluating this possibility for *Enchenopa* treehoppers by characterizing wind-generated noise spectra for multiple hostplants (McNett & Cocroft, unpublished data). The question is whether the amplitude spectra of wind-induced noise differ among host plants, in which they would favor signal divergence across hosts, or whether they are similar among hosts, in which case they would provide a consistent source of selection that may favor similar signals on different hosts.

We have measured the properties of wind-induced vibrations for hosts of 4 of the 11 species in the *E. binotata* complex (McNett & Cocroft, unpublished data). The *Enchenopa* hosts for which we have data have very similar amplitude spectra: most energy in low frequencies (<math>\#30\text{ Hz}</math>), with a gradual roll-off in amplitude at higher frequencies (see Cocroft & Rodriguez, 2005). The hosts were structurally similar woody plants, so it is not surprising that the wind spectra were so similar. In any case, it would seem that, for this set of *Enchenopa* hosts, the properties of wind-generated noise provide a common source of selection against the use of very low frequencies and constitute a conservative force in signal / preference evolution, rather than a diversifying one.

## Future Directions

Our thesis in this chapter is that the evolution of mating preferences is an important component of speciation in plant-feeding insects, which constitute a large fraction of terrestrial biodiversity. By combining results of experimental studies in the laboratory with those from observational studies outdoors, we have shown that female preferences can exert selection on male signals in contemporary populations. From the pattern of signal-preference correlation across species, we can infer that divergence in female preferences causes evolutionary change in male signals, leading to reproductive isolation. The claim that changes in sexual selection are important for speciation in this group of plant-feeding insects does not



negate the importance of host shifts in initiating divergence. It is unclear whether sexual selection alone can cause speciation in the absence of geographic or ecological differences; in contrast, the combination of divergent ecological and sexual selection is an especially potent cause of speciation (Kirkpatrick & Ravigné, 2002). Consequently, in recognition of the close links between ecology and sexual selection (Shuster & Wade, 2003), we recommend an approach to studying speciation in phytophagous insects that acknowledges their synergistic effects in the evolution of reproductive isolation.

The study of female preference functions gives us important insights into the evolutionary forces acting on mate communication signals, but a more difficult problem is to identify the evolutionary forces that cause divergence in female preferences. Although we have characterized some of the factors that may cause evolutionary change in female mating preferences after colonization of a novel host plant, it would be difficult to measure selection on female preference functions under natural conditions. Genetic approaches could at least reveal whether changes in preferences were due to natural selection or drift, and whether correlated changes in preferences and signals are due to pleiotropy or linkage (Wiley & Shaw, 2010). Neurobiological and psychophysical approaches would be useful for determining the nature of the traits involved in evolutionary change in female preferences. For example, in the case of female preferences for male signal frequency in *Enchenopa*, are differences among populations and species due to changes in sensory structures in the periphery, or to changes in more central processes that result in differences in selective attention? Finally, although we have atomized both signals and preferences into a series of separate traits, at some level the signal is perceived as a unitary, multivariate phenotype. Although our study of selection on male signals did not reveal interactions between traits in their effect on mating success, and a statistical approach that used entire signals as predictors of mating success (Holan et al., 2010) matched the results of our univariate study (Sullivan-Beckers & Coccoft, 2010), characterization of multivariate preferences is needed to evaluate the potential for nonlinear effects of trait combinations on signal attractiveness (Gerhardt & Brooks, 2009). For all of these questions, plant-feeding insects provide a promising model system, allowing us to integrate laboratory and field, behavioral mechanisms and evolution, to understand the origins and maintenance of diversity in an important component of terrestrial ecosystems.

## References

Agosta, S. J., Janz, N., & Brooks, D. R. (2010). How specialists can be generalists: Resolving the “parasite paradox” and implications for emerging infectious diseases. *Zoologia*, *27*, 151–162.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Arch, V. S., Grafe, T. U., & Narins, P. M. (2008). Ultrasonic signalling by a Bornean frog. *Biology Letters*, *4*, 19–22.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Barth, F. G. (1988). Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae) II. On the vibratory environment of a wandering spider. *Oecologia*, *77*, 194–201.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Berlocher, S. H., & Feder, J. L. (2002). Sympatric speciation in phytophagous insects: Moving beyond controversy? *Annual Review of Entomology*, *47*, 773–815.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Bertin, A., & Fairbairn, D. J. (2005). One tool, many uses: Precopulatory sexual selection on genital morphology in *Aquarius remigis*. *Journal of Evolutionary Biology*, *18*, 949–961.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Bolnick, D. I., & Fitzpatrick, B. (2007). Sympatric speciation: Theory and empirical data. *Annual Review of Ecology Evolution and Systematics*, 38, 459–487.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Brodie, E. D., Moore, A. J., & Janzen, F. J. (1995). Visualizing and quantifying natural selection. *Trends in Ecology and Evolution*, 10, 313–318.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Brooks, R., Hunt, J., Blows, M. W., Smith, M. J., Bussière, L. F., & Jennions, M. D. (2005). Experimental evidence for multivariate stabilizing sexual selection. *Evolution*, 59, 871–880.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Bush, G. L., & Butlin, R. K. (2004). Sympatric speciation in insects. In U. Dieckmann, M. Doebeli, J. A. J. Metz, & D. Tautz. (Eds.), *Adaptive speciation* (pp. 229–248). Cambridge, England: Cambridge University Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Butlin, R. K. (1993). The variability of mating signals and preferences in the brown planthopper, *Nilaparvata lugens*. *Journal of Insect Behavior*, 6, 125–140.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Claridge, M. F. (1985). Acoustic behavior of leafhoppers and planthoppers: Species problems and speciation. In L. R. Nault & J. G. Rodríguez (Eds.), *The*

*leafhoppers and planthoppers* (pp. 103–125). Brisbane, Australia: John Wiley & Sons.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Claridge, M. F. (1990). Acoustic recognition signals: Barriers to hybridization in Homoptera Auchenorrhyncha. *Canadian Journal of Zoology*, *68*, 1741–1746.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., & DeLuca, P. A. (2006). Size-frequency relationships in insect vibrational signals. In M. F. Claridge, & S. Drosopoulos (Eds.), *Insect sounds and communication: Physiology, ecology and evolution* (pp. 99–110). Boca Raton, FL: Taylor & Francis.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., & McNett, G. D. (2006). Vibrational communication in treehoppers (Hemiptera: Membracidae). In M. F. Claridge & S. Drosopoulos (Eds.), *Insect sounds and communication: physiology, ecology and evolution* (pp. 305–317). Boca Raton, FL: Taylor & Francis.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *BioScience*, *55*, 323–334.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., Rodríguez, R. L., & Hunt, R. E. (2008). Host shifts, the evolution of communication and speciation in the *Enchenopa binotata* species complex

of treehoppers. In K. J. Tilmon (Ed.), *Speciation, specialization and radiation: The evolutionary biology of insect and plant interactions* (pp. 88–100). Berkeley, CA: University of California Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., Rodriguez, R. L., & Hunt, R. E. (2010). Host shifts and signal divergence: Mating signals covary with host use in a complex of specialized plant-feeding insects. *Biological Journal of the Linnean Society*, 99, 60–72.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cocroft, R. B., Shugart, H, Konrad, K., & Tibbs, K. (2006). Variation in plant substrates and its consequences for insect vibrational communication. *Ethology*, 112, 779–789.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Cokl, A., & Virant-Doberlet, M. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annual Review of Entomology*, 48, 29–50.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 27, 305–33.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Coyne, J. A., & Orr, H. A. 2004. *Speciation*. Sunderland, MA: Sinauer.

Find This Resource

-

- [Worldcat](#)
- [Google Preview](#)

Dres, M., & Mallet, J. (2003). Host races in plant-feeding insects and their importance in sympatric speciation. *Philosophical Transactions of the Royal Society of London B*, 357, 471–492.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Etges, W. J. (2002). Divergence in mate choice systems: Does evolution play by rules? *Genetica*, 116, 151–166.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Etges, W. J., Cardoso de Oliveira, C., Gragg, E., Ortíz-Barrientos, D., Noor, M. A. F., & Ritchie, M. G. (2007). Genetics of incipient speciation in *Drosophila mojavensis*. I. Male courtship song, mating success, and genotype × environment interactions. *Evolution*, 61, 1106–1119.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Etges, W. J., Cardoso de Oliveira, C., Ritchie, M. G., & Noor, M. A. F. (2009). Genetics of incipient speciation in *Drosophila mojavensis*: II. Host plants and mating status influence cuticular hydrocarbon QTL expression and G × E interactions. *Evolution*, 63, 1712–1730.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Feder, J. L. (1998). The apple maggot fly, *Rhagoletis pomonella*: Flies in the face of conventional wisdom about speciation. In D. J. Howard & S. H. Berlocher (Eds.), *Endless forms: Species and speciation* (pp. 130–14). New York: Oxford University Press.

Find This Resource

-

- [Worldcat](#)
- [Google Preview](#)

Fonseca, P. J., Münch, D., & Hennig, R. M. (2000). How cicadas interpret acoustic signals. *Nature*, *405*, 297–298.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Funk, D. J., Filchak, K. E., & Feder, J. L. (2002). Herbivorous insects: Model systems for comparative study of speciation ecology. *Genetica*, *116*, 261–267.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Gerhardt, H. C., & Brooks, R. C. (2009). Experimental analysis of multivariate female choice in gray treefrogs (*Hyla versicolor*): Evidence for directional and stabilizing selection. *Evolution*, *63*, 2504–2512.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Gerhardt, H. C., & Huber, F. (2002). *Acoustic communication in insects and anurans*. Chicago: University of Chicago Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Gillooly, J. F., & Ophir, A. G. (2010). The energetic basis of acoustic communication. *Proceedings of the Royal Society B*, *277*, 1325–133.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Greenfield, M. D. (1994) Synchronous and alternating choruses in insects and anurans: Common mechanisms and diverse functions. *American Zoologist*, 34, 605–615.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Greenfield, M. D., & Rodríguez, R. L. (2004). Genotype–environment interaction and the reliability of mating signals. *Animal Behaviour*, 68, 1461–1468

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Hill, P. S. M. (2008). *Vibrational communication in animals*. Cambridge, MA: Harvard University Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Holan, S. H., Wikle, C. K., Sullivan Beckers, L. E., & Cocroft, R. B. (2010). Modeling complex phenotypes: Generalized linear models using spectrogram predictors of animal communication signals. *Biometrics*, 66, 914–924.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Hoy, R. R., Popper, A. N., & Fay, R. R. (1998). *Comparative hearing: Insects*. New York: Springer.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Hunt, R. E. (1994). Vibrational signals associated with mating behavior in the treehopper, *Enchenopa binotata* Say (Hemiptera: Homoptera: Membracidae). *Journal of the New York Entomological Society*, 102, 266–270.

Find This Resource



- 
- [Worldcat](#)
- [Google Preview](#)

Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male-male competition, female mate choice and their interaction: Determining total sexual selection. *Journal of Evolutionary Biology*, 22, 13–26.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, 72, 283–327.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Kaneshiro, K. Y. (1989). The dynamics of sexual selection and founder effects in species formation. In L. V. Giddings, K. Y. Kaneshiro, & W. W. Anderson (Eds.), *Genetics, speciation and the founder principle* (pp. 279–296). Oxford, England: Oxford University Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Landolt, P. J., & Phillips, T. W. (1997). Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology*, 42, 371–391.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Lehtonen, T. K., Wong, B. B. M, & Lindstrom, K. (2010). Fluctuating mate preferences in a marine fish. *Biology Letters*, 6, 21–23.

Find This Resource

- 
- [Worldcat](#)

- [Google Preview](#)

Lin, C. P., & Wood, T. K. (2002). Molecular phylogeny of the North American *Enchenopa binotata* (Homoptera: Membracidae) species complex. *Annals of the Entomological Society of America*, 95, 162–171.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Kirkpatrick, M., & Ravnigné, V. (2002). Speciation by natural and sexual selection: Models and experiments. *American Naturalist*, 159, S23–S35.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in *Enchenopa binotata* treehoppers. *Behavioral Ecology*, 19, 650–656.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

McNett, G. D., Luan, L., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology (online first)*.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Mendelson, T. C., & Shaw, K. L. (2005). Sexual behavior: Rapid speciation in an arthropod. *Nature*, 433, 375–337.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Price, P. W. (2002). Resource-driven terrestrial interaction webs. *Ecological Research*, 17, 241–247.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Prum, R. O. (2010). The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. *Evolution*, *64*, 3085–3100.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Ritchie, M. G. (1996). The shape of female mating preferences. *Proceedings of the National Academy of Sciences, USA*, *93*, 14628–14631.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Ritchie, M. G. (2007). Sexual selection and speciation. *Annual Review of Ecology, Evolution and Systematics*, *38*, 79–102.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Rodríguez, R. L., & Cocroft, R. B. (2006). Divergence in female duetting signals in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membradicae). *Ethology*, *112*, 1231–1238.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Rodríguez, R. L., Ramaswamy, K., & Cocroft, R. B. (2006). Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. *Proceedings of the Royal Society B*, *273*, 2585–2593.

Find This Resource

- 
- [Worldcat](#)

- [Google Preview](#)

Rodríguez, R. L., Sullivan, L. E., & Cocroft, R. B. (2004). Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Evolution*, 58, 571–578.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Rodríguez, R. L., Sullivan, L. M., Snyder, R. L., & Cocroft, R. B. (2008). Host shifts and the beginning of signal divergence. *Evolution*, 62, 12–20.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Ryan, M. J., Akre, K. L., & Kirkpatrick, M. (2009). Cognitive mate choice. In R. Dukas & J. M. Ratcliffe (Eds.), *Cognitive Ecology II*. Chicago: University of Chicago Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Ryan, M. J., & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, 139, S4–S35.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Saberi, K., & Hafter, E. R. (1995). A common neural code for frequency- and amplitude-modulated sounds. *Nature*, 374, 537–539.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Sattman, D. A., & Cocroft, R. B. (2003). Phenotypic plasticity and repeatability in the mating signals of *Enchenopa* treehoppers, with implications for reduced gene flow among host-shifted populations. *Ethology*, 109, 981–994.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Schluter, D. (1988). Estimating the form of natural selection on a quantitative trait. *Evolution*, 42, 849–861.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Shuster, S. M. & Wade, M. J. (2003). *Mating Systems and Strategies*. Princeton, NJ: Princeton University Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Singer, M. C., Wee, B., Hawkins, S., & Butcher, M. (2008). Rapid natural and anthropogenic diet evolution: Three examples from checkerspot butterflies. In K. J. Tilmon (Ed.), *Specialization, speciation and radiation: The evolutionary biology of herbivorous insects* (pp. 311–324). Berkeley, CA: University of California Press.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Sullivan-Beckers, L. E. (2008). The ecology of mate choice: Identifying the agents of sexual selection on mating signals in *Enchenopa* treehoppers. (Unpublished doctoral dissertation). University of Missouri, Columbia.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Sullivan Beckers, L. E., & Cocroft, R. B. (2010). The importance of female choice, male-male competition and signal transmission as causes of selection on male mating signals. *Evolution*, 64, 3158–3171.

Find This Resource

-

- [Worldcat](#)
- [Google Preview](#)

Tilmon, K. J., Wood, T. K., & Pesek, J. D. (1998). Genetic variation in performance traits and the potential for host shifts in *Enchenopa* treehoppers (Homoptera: Membracidae). *Annals of the Entomological Society of America*, 91, 397–403

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Tishechkin, D. Y. (2007). Background noises in vibratory communication channels of Homoptera (Cicadinea and Psyllinea). *Russian Entomological Journal*, 16, 39–46.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Tregenza, T., Pritchard, V. L., & Butlin, R. K. (2000). Patterns of trait divergence between populations of the meadow grasshopper, *Chorthippus parallelus*. *Evolution*, 54, 574–585.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Virant-Doberlet, M., & Cokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33, 121–134.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wagner, W. E., Jr. (1998). Measuring female mating preferences. *Animal Behaviour*, 55, 1029–1042.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 58, 155–183.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wiley, C., & Shaw, K. L. (2010). Multiple genetic linkages between female preference and male signal in rapidly speciating Hawaiian crickets. *Evolution*, 64, 2238–2245.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K. (1980). Divergence in the *Enchenopa binotata* Say complex (Homoptera: Membracidae) effected by host plant adaptation. *Evolution*, 34, 147–160.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K. (1993a). Diversity in the New World Membracidae. *Annual Review of Entomology*, 38, 409–433.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K. (1993b). Speciation of the *Enchenopa binotata* complex (Insecta: Homoptera: Membracidae). In D. R. Lees & D. Edwards (Eds.), *Evolutionary patterns and processes* (pp. 299–317). New York: Academic Press

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K., & Guttman, S. I. (1982). Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera: Membracidae). *Evolution*, 36, 233–242.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K., & Guttman, S. I. (1983). *Enchenopa binotata* complex: Sympatric speciation? *Science*, 220, 310–312.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K., & Keese, M. C. (1990). Host-plant-induced assortative mating in *Enchenopa* treehoppers. *Evolution*, 44, 619–628.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K., Olmstead, K. L., & Guttman, S. I. (1990). Insect phenology mediated by host-plant water relations. *Evolution*, 44, 629–636.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

Wood, T. K., Tilmon, K. J., Shantz, A. B., Harris, C. K., & Pesek, J. (1999). The role of host-plant fidelity in initiating insect race formation. *Evolutionary Ecology Research*, 1, 317–332.

Find This Resource

- 
- [Worldcat](#)
- [Google Preview](#)

