Host Shifts, the Evolution of Communication, and Speciation in the *Enchenopa binotata* Species Complex of Treehoppers

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Speciation in animals is promoted by the evolution of behavioral differences that reduce attraction, mating, and fertilization between individuals in diverging populations (Mayr 1963; West-Eberhard 1983; Eberhard 1985, 1994, 1996; Coyne and Orr 2004). Behavioral traits involved in communication between the sexes often provide the most immediate contributions to reproductive isolation (Blair 1955; Claridge 1990; Ryan and Rand 1993; Bridle and Ritchie 2001; Gerhardt and Huber 2002; Kirkpatrick and Ravigné 2002). Consequently, identifying the evolutionary forces that lead to changes in sexual communication is necessary to understand the evolution of behavioral isolation and its contribution to divergence and speciation.

The relationship between sexual communication and speciation depends on the extent of interactions between individuals from the diverging populations. When geography and/or ecology prevent such interactions during the speciation process, differences in mating signals and preferences may become important upon secondary contact, at which point the differences may be enhanced by selection against hybridization (Howard 1993; Kelly and Noor 1996; Coyne and Orr 1997; Jiggins and Mallet 2000; Servedio and Noor 2003). In contrast, when the geography and ecology of speciation do lead to interactions between individuals from the diverging populations (i.e., when speciation occurs in sympatry), behavioral causes of reproductive isolation are important from the outset (Kondrashov et al. 1998; Kondrashov and Kondrashov 1999; Kirkpatrick and Ravigné 2002).

Sympatric speciation is implicated in the diversification of host-specific, plant-feeding insects (Mallet 2001; Berlocher and Feder 2002; Bush and Butlin 2004). In these insects, which comprise a large fraction of animal diversity (Price 2002; Bush and Butlin 2004), speciation is often associated with changes in host-plant use. Host shifts have widespread consequences for life-history traits, and aspects of insect adaptation to their host plants can lead to assortative mating as a pleiotropic effect (Wood and Keese 1990; Craig et al. 1993; Wood 1993; Feder 1998; Berlocher and Feder 2002; see also Jiggins et al. 2005). Colonization of a new host environment may also have a profound influence on the evolution of communication.

In this chapter we examine the role of communication systems in the diversification of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae), a clade of 11 sap-feeding species distributed across eastern North America. Based on the career-long series of studies by T. K. Wood and colleagues, this group provides one of the most widely cited examples of sympatric speciation in plant-feeding insects (Tauber and Tauber 1989; Wood 1993; Berlocher and Feder 2002; Coyne and Orr 2004). The *E. binotata* complex is especially promising for studies of the relationship between host shifts and behavioral isolation (Landolt and Phillips 1997; Etges 2002), because of the rich understanding of its natural history, comparative biology, and communication behavior.

We first discuss the role of ecological factors in promoting assortative mating among populations of *E. binotata* on ancestral and novel species of host plant. We then examine the role of sexual communication in behavioral isolation among *E. binotata* species in the present. We explore sources of divergent sexual and natural selection that could alter the evolutionary trajectory of mating signals and preferences after a host shift. We also consider ways in which developmental influences on sexual communication may affect gene flow between populations on ancestral and novel hosts (before any evolutionary change in communication systems has occurred), and how developmental plasticity may generate changes in sexual selection regimes. We will argue that for plant-feeding insects, sexual communication systems provide an important link between host use, assortative mating, and divergent

selection and may be a key component of sympatric speciation through host shifts.

Ecological Isolation in the *E. binotata* Complex

Thomas K. Wood and colleagues developed the *E. binotata* complex as a model for evaluating the role of host shifts in promoting genetic divergence in sympatry (Wood and Guttman 1983; Wood 1993). (A complete list of Wood's publications is provided by Deitz and Bartlett [2004].) The central message of this research is that successful colonization of a novel host can lead to immediate assortative mating between populations on the original and novel hosts, facilitating a response to divergent selection imposed by differences between the host species.

The most immediate factor contributing to assortative mating after a host shift in *Enchenopa* is a change in life-history timing caused by differences in host-plant phenology (Wood and Guttman 1982; Wood and Keese 1990; Wood et al. 1990). Species in the *E. binotata* complex have one generation per year, with eggs deposited into host-plant tissue in late summer and fall, and developing in the spring (Wood 1993). Egg development is triggered by hydration from the flow of sap through plant stems, which happens on different schedules in different host species (Wood et al. 1990). As a consequence, egg hatch occurs at different times on different hosts. Depending on the rate of nymphal development on different hosts, the timing of adult eclosion and mating will also differ (Wood 1993). In an elegant experiment that isolated the effects of allochrony from other potential sources of reproductive isolation, Wood and Keese (1990) manipulated the phenology of *Celastrus scandens* plants containing egg masses of *E. binotata* from a single population to create a series of age classes. This experiment resulted in significant assortative mating by age, even though age classes were only five days apart (Wood and Keese 1990). Assortative mating apparently was a consequence of differences in the timing of female receptivity, as well as in male mortality schedules.

Assortative mating after a host shift is also promoted by host fidelity. In an experiment in which males and females of six species were placed in a common cage and allowed to choose mates and host plants, most matings occurred on the female's natal host (Wood 1980). A later study showed assortative mating by host among experimentally host-shifted populations, as a consequence of female and male host fidelity (Wood et al. 1999). Females also show high host fidelity in oviposition (Wood 1980).

Host shifts lead not only to assortative mating, but also to divergent natural selection. When females were forced to oviposit on nonnatal hosts, female fecundity and survivorship, as well as hatching rates and nymphal survivorship, were lower on nonnatal hosts (Wood and Guttman 1983). Experimental shifts to novel host-plant species also revealed the presence of the genetic variation necessary for successfully colonizing a new host (Tilmon et al. 1998). Thus, the

hypothesis that local adaptation to a novel host can occur in sympatry with the original host is supported by the combination of host fidelity during oviposition and mating, assortative mating among allochronically shifted age classes, and host-related ecological divergent selection.

In *Enchenopa* treehoppers, allochrony and host fidelity reduce, but do not eliminate, interactions among individuals on ancestral and novel hosts. The potential for interactions depends on the degree of allochrony among host-shifted populations, the extent of host fidelity, and the dispersal distance between plants (Wood 1980; Wood et al. 1999). There can be substantial overlap in mating periods between species on different hosts. In a study in which populations of six *E. binotata* species were established on natal host plants in a common environment, the average date of mating differed by only one to two days between species on certain hosts (Wood and Guttman 1982); as a consequence, the three- to four-week mating periods overlapped almost completely.

Overlap of mating periods leads to interactions between individuals from different hosts, at least in experimental populations in close proximity. In a study by Wood (1980), over 40% of courtships were between males and females of different species. Strikingly, however, only 6% of the matings were between heterospecifics. The common occurrence of mixed-species courtship, coupled with the rarity of mismating, suggested that behavioral isolation resulting from courtship interactions may be even stronger than ecological isolation. Dispersal between host plants by mate-searching males occurs not only in cage experiments, but also in the field. For example, in one sample of individuals collected during the breeding season on *Cercis canadensis* in Missouri, 88% of the males were *E. binotata* 'Cercis,' while 12% of the males were from another host-associated species in the complex (R.B.C., unpublished data). (*Note:* The species in this complex have not yet been formally named, and here we refer to them using the name of their host plants.)

We suggest that behavioral isolation arising from differences in sexual communication systems may act synergistically with allochrony and host fidelity to promote isolation and facilitate divergence among host-shifted populations. That is, while the isolation that arises as a consequence of differences in host phenology is clearly important in initiating divergence, the evolution of behavioral isolation may be important for completing the process of speciation (Rundle and Nosil 2005).

In the following sections, we examine the relationships between host shifts, sexual communication, and assortative mating in the *E. binotata* complex. We suggest that sexual communication can play several important roles. First, in the early stages of a host shift, a number of aspects of female choice and male signaling behavior may contribute to assortative mating even before any divergence in signals or preferences has occurred. Second, host shifts are likely to promote the diversification of sexual communication systems, contributing to the speciation process and/or facilitate

FIGURE 7.1. A. Signal of a male *Enchenopa binotata* 'Ptelea' (waveform *[above]* and spectrogram), showing the typical whine-and-pulses structure. B. Solitary mate-searching male of *E. binotata* 'Robinia.' C. Portion of a male-female duet in *E. binotata* 'Viburnum' (waveform and spectrogram). D. Aggregation of male and female *E. binotata* 'Viburnum'; grouped males often chorus for extended periods. Photo in part B by R. B. Cocroft, photo in part D by C. P. Lin, with permission.
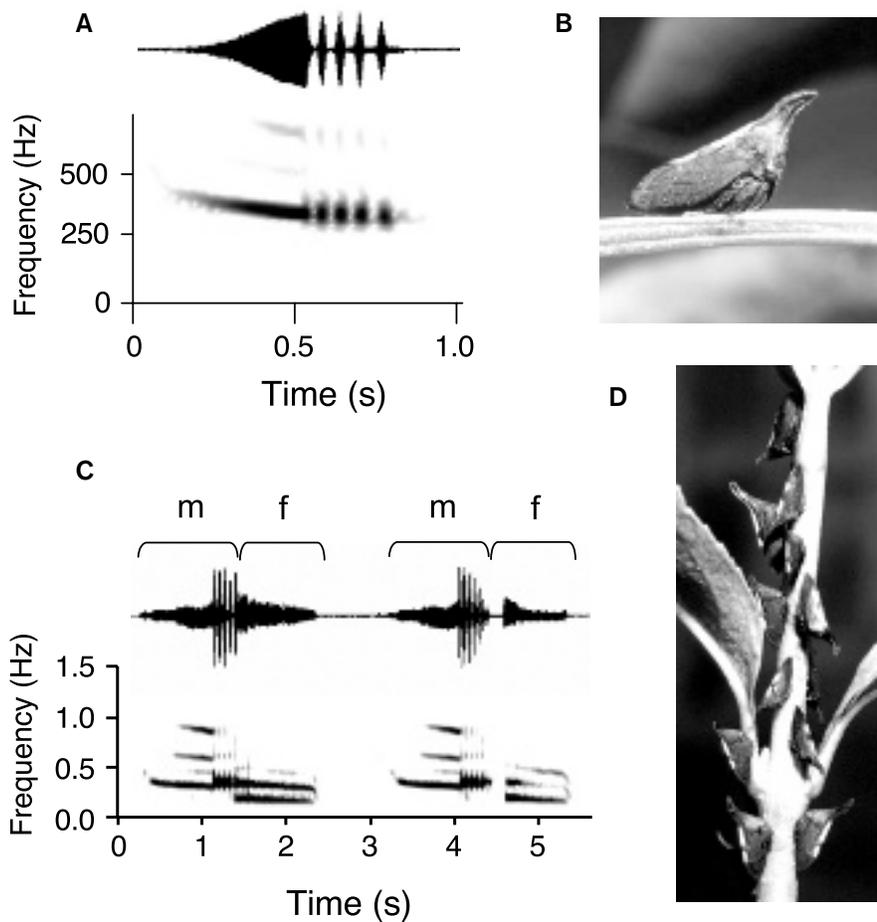
species coexistence. Third, female preferences for male signal traits provide not only a cause of assortative mating, but also a source of divergent selection. Finally, female choice for condition-dependent male signal traits may accelerate the process of adaptation to novel host plants.

Behavioral Sources of Assortative Mating

Evidence for Behavioral Isolation

What is the evidence that sexual communication systems contribute to behavioral isolation among species in *E. binotata* complex? We first describe the nature of the communication that takes place between males and females. We then review the evidence that signals contribute to reproductive isolation in *Enchenopa* and describe patterns of variation in signal traits in relation to host use and geography.

The first evidence that behavioral interactions during courtship contribute to mate recognition came from the studies described above (Wood 1980; Wood and Guttman 1982), which showed that although males frequently courted heterospecific females when species from different hosts were placed in close proximity, mismatings were rare. Insight into the mechanisms underlying female mate choice

was provided by Hunt (1994), whose study of *E. binotata* 'Cercis' revealed that males court females using substrate-borne vibrational signals that travel through the stems and petioles of their host plants.

For all species in the *E. binotata* complex, the male advertisement signal consists of a tone that drops in frequency (the "whine"), followed by a series of pulses (Fig. 7.1A). Males produce bouts of two or more signals in close succession. Signaling often occurs within a mate-searching strategy in which males move between a series of stems or plants, signaling on each one and waiting for a female response (Fig. 7.1B). When a female alternates her own response signals with those of the male (Fig. 7.1C), the male searches locally while continuing to duet. When the male finds the female, he climbs on her side; mating begins when the female allows the male to couple his genitalia, climb down from her side, and face away from her. At this point duetting ceases. As an alternative to active searching, males may remain in one location and chorus with other males, usually in the presence of one or more females (Fig. 7.1D). The lack of continued courtship during copulation, together with the striking similarity of male genitalia across the complex (Pratt and Wood 1993), suggests that premating sexual communication is the primary source of behavioral isolation in the *E. binotata* complex.
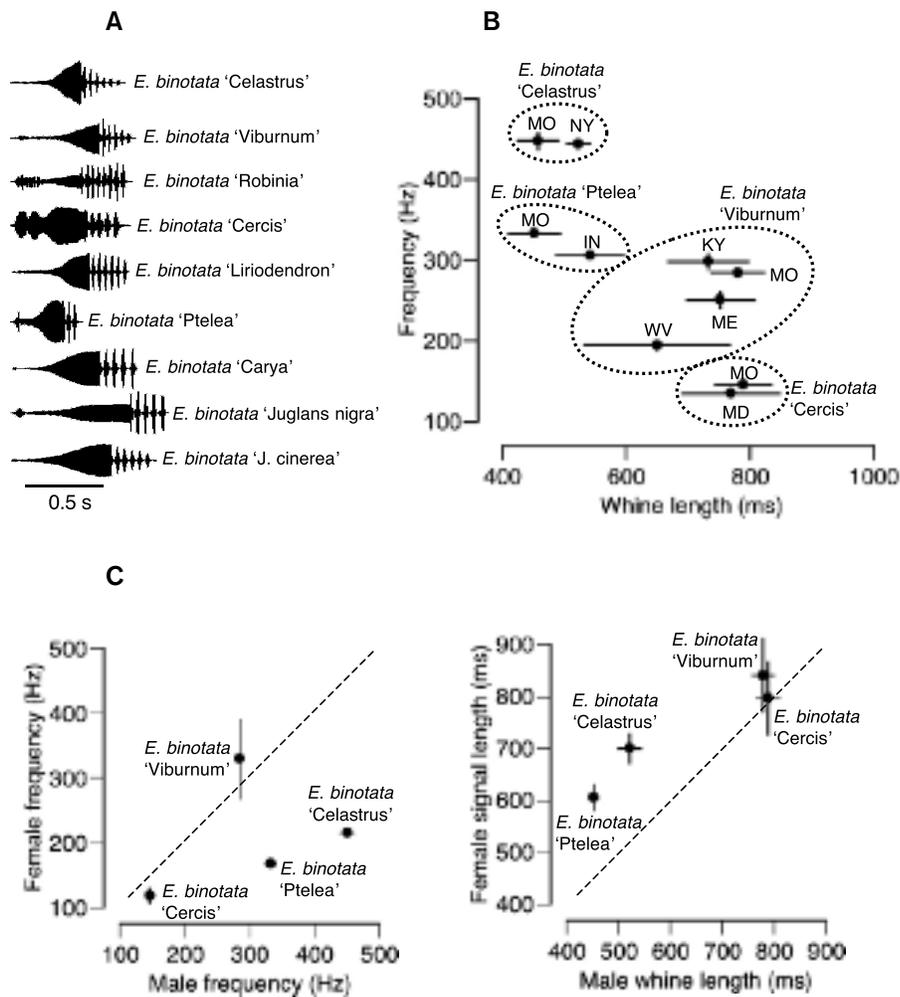
FIGURE 7.2. A. Waveforms of male signals for nine species in the *Enchenopa binotata* complex, showing similarity in signal structure. B. Variation in the frequency and whine length of male signals for four species in the *E. binotata* complex (U.S. state abbreviations indicate recording localities, which for each species span >600 km). C. Correspondence between the frequency and length of male and female signals for four species from Missouri. Dashed lines indicate a 1:1 relationship. Shown are mean signal values ±1 SE. Part C modified from Rodríguez and Cocroft (2006), with permission from Blackwell Publishing.

As a first step in evaluating the role of vibrational mating signals in behavioral isolation in the *E. binotata* complex, we presented receptive females of one species (*E. binotata* 'Viburnum') with playbacks of vibrational mating signals of males from their own population, as well as mating signals from sympatric populations of six other species. Females readily engaged in duets with male signals from their own population, but rarely with those from closely related species within the complex (Rodríguez et al. 2004). Female responses were also influenced by individual male identity within species, suggesting the presence of sexual selection. In a similar playback experiment, females of *E. binotata* 'Cercis' also responded to mating signals only of conspecific males (R.E.H., unpublished data). Females thus choose among potential mates on the basis of between-species and between-individual signal variation, and their decision to respond to a male will influence the likelihood of being found by him.

Although playback experiments with recorded natural signals revealed that signal differences can contribute to reproductive isolation among current-day species in the *E. binotata* complex, they provided only indirect evidence of the signal traits important for female choice. Furthermore, they provided no information on how female preferences differ among species, and whether female choice may exert divergent sexual selection on male signals. Our next steps, then, were to characterize variation in signal traits within and between species, and to characterize variation in female preferences for male signals among species.

Variation in Male and Female Signals

The evolutionary processes acting on communication systems in a group of closely related species result in a pattern of variation in signals and preferences among those species. Describing this variation can shed light on the processes that produced it; for example, marked differences in signals and preferences among closely related species, along with variation in the same traits among geographically separated populations within species, are "signatures" of the role of sexual selection in speciation (Panhuis et al. 2001). Describing geographic variation is less difficult for male signals than for female preferences and is the first step we have taken here.

Male advertisement signals are qualitatively similar among species in the *E. binotata* complex (Fig. 7.2A). However, signals differ quantitatively among species in multiple
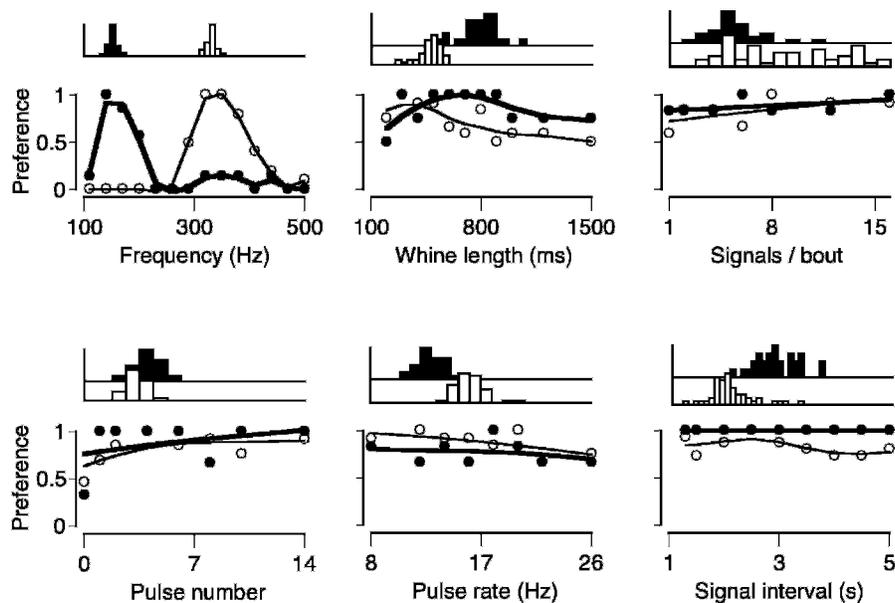
FIGURE 7.3 Variation in female preferences and the distribution of male signal traits in four species in the *Enchenopa binotata* complex. The curves and symbols indicate female preferences, and histograms indicate the distribution of male signal traits. Filled symbols and bars indicate *E. binotata* 'Cercis,' open symbols and bars indicate *E. binotata* 'Ptelea.' See Rodríguez et al. (2006) for a detailed analysis of preference-trait relationships.

characteristics, especially in frequency and length (Fig. 7.2B), but also in the number and rate of the pulses that follow the whine. In general, signal variation among species on different host plants is greater than geographic variation within species on a single host plant. As an example, here we show variation in signal frequency and length among populations of *E. binotata* 'Celastrus,' 'Cercis,' 'Ptelea,' and 'Viburnum' in eastern North America (Fig. 7.2B). Note that for three of the species, there are substantial differences in frequency between species, but little variation among geographically separated populations within a species. This pattern is typical of most other species in the complex (R.B.C., R.L.R., and R.E.H., unpublished), but there is one notable exception: for the species on *Viburnum,* geographic variation in mating signals is comparable to that between species (Fig. 7.2B). In general, there is a close association between speciation, host use, and signal divergence in the *E. binotata* complex. Given the consistent differences among signals of species on different hosts, the female preferences for the signals of conspecific males shown by Rodríguez et al. (2004) should lead to behavioral isolation among most species throughout their range.

In the duetting communication system of the *E. binotata* complex, species differences in female response signals may be as important as those in male signals. As with male advertisement signals, species differ in the frequency and length of female response signals (Fig. 7.2C) (Rodríguez and Cocroft 2006). Species also differ in the timing relationship between male and female signals during duetting interactions. Although we have not examined geographic variation in female signals, comparisons based on one population each from four species show that male and female signal traits covary (Fig. 7.2C). This pattern suggests that signal evolution in both sexes is correlated and/or influenced by shared or similar sources of selection. These sources of selec-

tion may be preferences for signal traits in both sexes, or selection on signal transmission exerted by the filtering properties of host plants (see "Sensory Drive and Signal Divergence," below). Alternatively, the signals of one sex may show a correlated response to selection on signals of the other.

Understanding signal evolution in the *E. binotata* complex will require characterizing these potential sources of selection on male and female signals. We begin by assessing the contribution of female preferences to male signal divergence, namely, the contribution of selection exerted by female choice.

Variation in Female Preferences

We have characterized female preferences for male signal traits in four *E. binotata* species (Rodríguez et al. 2006). For this study, we used female response signals as an assay of their preferences for computer-generated male signals. From the pattern of female responses we generated preference functions, which show the probability of response as a function of variation in the male trait. For some signal traits, female preference functions were closed (i.e., females preferred intermediate values), while for other traits preferences were open ended (females preferred higher or lower values). Between species, there were differences in the shape, preferred value, and strength (i.e., how strongly females discriminated against unattractive signals) of preferences for the same signal traits (Fig. 7.3).

Species differences in female preferences suggest that divergent sexual selection exerted by female choice may be responsible for differences in male signals across the *E. binotata* complex. We tested the predictions of this hypothesis by taking advantage of between-species variation in the shape and strength of female preferences for different signal

traits (Rodríguez et al. 2006). Briefly, for closed preferences the most preferred value should predict the mean of the male signal trait, with the match between preferred value and mean signal trait being greater for stronger preferences. By contrast, for open preferences the male trait values should be shifted toward the preferred extreme of the range. In addition, there should be a greater variability in signal traits for open than for closed preferences. We tested these predictions in four species in the *E. binotata* complex and found support for all of them (Rodríguez et al. 2006). These results point to female mate choice as an important agent of signal evolution in this complex.

Comparison of female preferences and the distribution of male signal traits can be used not only to infer past selection on male signals, but also to formulate hypotheses about the nature of current selection on male signals exerted by female choice. These hypotheses should ideally be tested within the framework of a comprehensive understanding of *E. binotata* mating systems and determinants of mating success, to which we now turn.

Mating Systems

Enchenopa mating systems can be described as a cursorial polygyny (Shuster and Wade 2003), in which reproductive females form aggregations, and males move between groups of females. In general, *E. binotata* females mate once (only about 5% mate a second time), while males may mate multiply (Wood 1993).

Measures of the relative variance in mating success between males and females reveal a high opportunity for sexual selection (L. E. Sullivan and R.B.C., unpublished). The large variance in male mating success is generated in part by the relatively asynchronous schedule of female receptivity: in an outdoor enclosure experiment in which life-history timing was close to that in the field, typically only a few females mated each day. Most courtship and mating occurred during a relatively narrow time window during the morning (activity ceased during the heat of the day), and males rarely mated more than once in a day. As a result, certain males had the opportunity to mate with multiple females, at the expense of other males. Preliminary results indicate that the number of signals a male produces—a potential reflection of condition—is important in mate choice under natural conditions.

The contribution of sexual communication to reproductive isolation and divergence may be increased by interactions with other behavioral sources of assortative mating, and with effects of host plants on signal variation. We next consider the consequences of mate choice in the context of shifts to novel host plants.

Communication in a New Host Environment

A new host plant represents a novel environment with potentially far-reaching effects on the function and evolution of communication and mating systems (Funk et al.

2002). The idea that changes in host-plant use can promote differences in mating signals is supported by species using chemical cues in mate choice (Landolt and Phillips 1997), where differences may arise either as a pleiotropic effect of host-plant adaptation (Funk 1998) or as a direct consequence of developing on a novel host (Etges 1998). Communication systems using substrate-borne signals might be expected to be especially sensitive to changes in host-plant use, given that host-plant tissues constitute the transmission channel. Here we examine how the communication system may play a role in assortative mating in the early stages of a host shift, and how traits involved in communication may evolve in response to differences in sexual and natural selection between hosts.

Substrate-Related Signal Variation

In considering the effect of a host shift on the evolution of vibrational communication systems, the first issue that arises is how an individual's signals may differ when produced on different plant species. Our finding is that when the same males are recorded on a host and a nonhost, the spectral and fine-temporal characteristics of their vibrational signals are unchanged. We have confirmed this result in two independent experiments with *Enchenopa*, using various host-plant and non-host-plant species (Sattman and Cocroft 2003; Rodríguez et al., in press), and in another experiment with *Umbonia* treehoppers (Cocroft et al. 2006). Thus, signal differences between species on different hosts are not replicated by simply moving individuals between those hosts. The constancy of *Enchenopa* mating signals across substrates is in part a consequence of the use of relatively pure tones (Sattman and Cocroft 2003).

Although the signals of male *E. binotata* retain their basic structure across plant substrates, males do reduce their signaling effort on nonhosts. In an experiment in which male *E. binotata* 'Ptelea' were recorded both on their own host and on a nonhost, the males produced fewer signals in a bout on the nonhost, and the signals they did produce were shorter (Sattman and Cocroft 2003). We view these changes in signaling behavior as host fidelity in mate searching, and they may influence the probability of mating between individuals on different hosts, because both changes will reduce a male's attractiveness (Fig. 7.3) (Rodríguez et al. 2006). Female preferences for male signal traits may thus interact with host fidelity to generate assortative mating in the early stages of a host shift, whether or not any divergence in sexual communication systems has occurred.

Origins of Diversity in Sexual Communication

Insect populations colonizing a novel host plant might acquire differences in signal or preference traits through developmental plasticity (Etges 2002; West-Eberhard 2003,

2005). We evaluated the role of plasticity in signal divergence in the *E. binotata* complex by rearing full-sib families of one species, *E. binotata* 'Ptelea,' on two different host-plant species: their native host and the host of another species in the complex *(Robinia pseudoacacia)*. The second host was chosen because it provides a relatively benign rearing environment, increasing the sample size of individuals reaching adulthood. Preliminary analysis of this experiment (Rodríguez et al., in press) indicates that overall host-plant effects have a small role in generating signal variation. However, there is substantial genetic variation in, as well as diversity in the reaction norms of, most signal traits. Indeed, full-sib families often differed so much in their signal reaction norms that their attractiveness ranking is expected to change across plant species, even if female preferences do not show similar plasticity. Such reaction norm diversity has the potential to alter selection regimes (Lynch and Walsh 1998; Rodríguez and Greenfield 2003; Greenfield and Rodríguez 2004), fostering divergent selection. Phenotypic plasticity in communication systems thus has the potential to promote divergence following a host shift.

In addition to potential changes in the regimes of sexual selection arising from developmental plasticity, host shifts may change selection on the communication system as a consequence of differences in the communication environment, a possibility we examine in the next section.

Sensory Drive and Signal Divergence

Because each host-plant species provides a unique environment for vibrational communication, use of different hosts has the potential to impose divergent natural selection on signals. The sensory drive hypothesis (Endler and Basolo 1998) predicts that when populations occupy environments that differ in their effects on signal transmission and perception, they will experience divergent natural selection on long-range communication systems (see Boughman 2001; Leal and Fleishman 2004; Maan et al. 2006).

Plant stems and leaves impose a frequency filter on vibrational signals (Michelsen et al. 1982; Cokl and Virant-Doberlet 2003; Cocroft and Rodríguez 2005). This phenomenon is easily observed by introducing a broadband noise signal with equal energy across a range of frequencies into a plant stem: the same signal recorded at various distances from the source will contain very unequal energy in different frequencies, with frequencies that transmit efficiently having a substantially higher amplitude. Host plants of closely related species can differ greatly in physical structure and have the potential to impose very different filters on the vibrational signals transmitted through them. Such differences among plant species would provide a source of divergent natural selection on signal frequency, with potentially important consequences for signal evolution and assortative mating.

The sensory drive hypothesis for vibrational signals predicts that if plant species differ predictably in their transmission characteristics, insects will use signals that transmit efficiently through tissues of their host. Support for the matching of insect songs to plant transmission characteristics comes from studies of vibrational communication in green stinkbugs, *Nezara viridula,* which use a variety of different host plants. Cokl et al. (2005) found that the low-frequency songs of *N. viridula* are transmitted efficiently in some of their commonly used hosts. Addressing the hypothesis that sensory drive leads to signal divergence, however, requires comparison among closely related species using different hosts. Henry and Wells (2004) tested for signal-environment matching in two green lacewing species *(Chrysoperla),* one inhabiting conifers and the other inhabiting a variety of meadow plants. The authors examined degradation during signal propagation using a hemlock and a grass species, but found no evidence of differential signal transmission.

Enchenopa treehoppers provide a powerful test of the sensory drive hypothesis for vibrational signals, because most species in the complex use only a single species of host plant, unlike the species studied by Henry and Wells (2004) and Cokl et al. (2005), which use a range of different hosts. Furthermore, the most important signal feature for assortative mating between *E. binotata* species on different hosts is frequency (Rodríguez et al. 2006), which could be under strong selection if plants differ in the efficiency with which they transmit signals of different frequencies.

We have measured the signal transmission properties of two of the host-plant species used by members of the *E. binotata* species complex (G. D. McNett and R.B.C., unpublished). For *E. binotata* 'Cercis,' the signal frequency used by males transmits with less attenuation than other frequencies in the range of the species complex. Male *E. binotata* 'Ptelea' also use a frequency that transmits well in their host plant, although substrate filtering in 'Ptelea' is weaker. Filtering properties of host-plant stems may thus impose divergent selection on the frequency of male vibrational signals. Because signal frequency is so important in mate choice, it may be a "magic trait" (Gavrilets 2004): one that greatly facilitates speciation because it is involved in both adaptation to the novel environment and assortative mating. Filtering properties of additional hosts are currently being investigated.

Environmental differences that can influence signal evolution are not limited to transmission characteristics. Predators can directly influence the evolution of mating systems and possibly facilitate speciation in cases where they exploit sexual signals (Bradbury and Vehrencamp 1998; Endler and Basolo 1998; Zuk and Kolluru 1998; Bailey 2006). Different host plants may harbor different predators or parasitoids, with a concomitant change in natural selection on communication systems. Environmental sources of noise that can interfere with signal reception are also an important influence on the evolution of communication systems (Endler

1992). The primary source of abiotic noise for vibrational signals is wind (Cocroft and Rodríguez 2005), and if the properties of wind-generated noise differ among plant species, this could favor signal differences in the insects inhabiting those plants.

Understanding how sexual selection will influence signal evolution and assortative mating after a host shift will require study of how colonization of a new host species might alter the mating system. We have not investigated this question in *E. binotata*, but in the next section we explore some of the potential relationships between host shifts and the evolution of mating systems.

Host Shifts, Mating Systems, and Signal Evolution

Colonization of a novel host plant can have far-reaching effects on the biology of herbivorous insects (e.g., Via 1990; Groman and Pellmyr 2000). These changes may include body size, shape, and color (Nosil et al. 2003; Messina 2004), as well as the spatial distribution of individuals. Host shifts may thus generate immediate alterations in mating systems, which may lead to divergent sexual selection among populations on different host plants in mating signals, mate-searching strategies, and mate preferences.

Differences in demographic factors between species on different hosts, such as density and the degree of spatial and temporal clumping of female receptivity, could favor different mate-searching strategies. For example, if population density is lower on the novel host than on the ancestral host, this may favor more active searching on the part of males and use of long-range signals, while if population density is higher this may favor other forms of competitive behavior. We can expect the greatest response to selection for the most commonly encountered context (Herre et al. 2001), and different forms of mate competition may favor different traits (e.g., Deinert et al. 1994). Accordingly, differences in density or patterns of female distribution on different hosts may lead to divergence in communication signals and other traits used in competition for mates.

In *E. binotata* treehoppers, population density varies greatly among species on different species of hosts, in part as a result of the aggregated egg-laying behavior of some species (Wood 1980). For example, in *E. binotata* 'Ptelea' it is common to encounter several hundred individuals on one 3- to 4-meter-tall host plant, while in *E. binotata* 'Liriodendron' it is typical to encounter only a few individuals on a large tree. Mate-searching males of these two species will encounter very different social contexts and as a result may experience divergent selection on their communication systems. An indication that mating signals have experienced different selection regimes related to these differences in adult density is that males of the low-density species (*E. binotata* 'Liriodendron') have higher-amplitude signals than males of the high-density species (*E. binotata* 'Ptelea') (R.E.H., unpublished data). The production of more intense signals by the rare species may be related to the need to communicate over longer distances.

The use of different host plants could also result in differences in the strength of sexual selection, if it leads to differences in the temporal and/or spatial distribution of receptive females (see Shuster and Wade 2003). Because female *E. binotata* mate only once, with mating occurring during a window of a few hours each day (L. E. Sullivan and R.B.C., unpublished), and because copulation lasts up to one to two hours, males usually do not have the opportunity to mate with more than one female in a day. If all females became receptive on the same day, few if any males would mate with more than one female, and there would be little opportunity for sexual selection. In contrast, if female receptivity is asynchronous, males would have the opportunity to mate multiply. Factors that influence the degree of female receptivity will thus determine the potential strength of sexual selection. We have observed that within a single population, individuals occupying host plants in different microclimates can mature at different times, from a few to several days. If a novel host occupied a greater range of microclimates than the ancestral host, the close association between plant phenology and insect life-history timing could result in greater developmental asynchrony among individuals within a breeding population. Furthermore, if mate-searching males are moving between hosts in different microclimates (as is likely in species in which the call-fly tactic is common), then a more asynchronous distribution of female receptivity among different plants might allow individual males to monopolize a greater number of females; in other words, the opportunity for sexual selection would be higher on the novel host.

The strength of sexual selection is influenced not only by the degree of synchrony in female receptivity, but also by the extent of spatial clustering among receptive females (Shuster and Wade 2003). Differences in structure and growth patterns among plant species will result in differences in resource distribution for insects that specialize on actively growing apical meristem tissue. Such differences in the distribution of resources are likely to be reflected in the distribution of adult females (Emlen and Oring 1977). If females occur singly at widely scattered locations, this would likely favor active searching by males and greater use of the call-fly strategy, whereas if females occur in groups, this could favor active location of a group followed by stationary strategies such as chorusing or mate guarding. Although density and the spatial and temporal distribution of female receptivity vary among *Enchenopa* species on different hosts (Wood and Guttman 1982, 1983), variation in the strength of selection and in mate-searching strategies among species has not been examined.

The impact of sexual selection may extend beyond the evolution of signals and preferences. We next explore the relationship between mate choice, male condition, and host shifts.

Sexual Selection and Local Adaptation

Recent models have shown that during colonization of a new environment, sexual selection by female choice can facilitate adaptation (Proulx 1999, 2001; Lorch et al. 2003). The link arises through condition-dependence of male signal traits: if male signals vary with male condition, and if individuals better adapted to the new environment are in better condition and produce more attractive signals, then female choice will favor locally adapted males. By condition we mean "the amount of resources available for fitness-enhancing traits" (Tomkins et al. 2004). The possibility of a mating advantage for locally adapted males does not depend entirely on the presence of female choice, but could also arise through male-male competition (Proulx 1999).

Male condition in a range of species is reflected in the overall rate or number of signals produced (Cotton et al. 2004). If this is true in *Enchenopa* treehoppers, then a male's condition may be reflected in the number of signals produced in a bout, a trait with significant repeatability over the course of a breeding season (Sattman and Cocroft 2003). Furthermore, this trait exhibits significant genotype by environment interaction, with the same genotypes producing different numbers of signals across environments (Rodríguez et al., in press). Condition may also be reflected in the total amount of signaling over a longer period of time, a trait that may be important in mate choice (see "Mating Systems," above). The importance of condition-based choice and its role in local adaptation to novel hosts is a fruitful area for further research. Furthermore, it is related to the question of whether signal or preference evolution is influenced by genetic correlations with life-history traits that may be under directional selection after colonization of a new host (Rice and Hostert 1993; Miyatake and Shimizu 1999).

The relationship of sexual selection to assortative mating depends not only on demographic factors within each host-associated population, but also on the extent of interactions among populations on different hosts. Accordingly, we need to consider how differences in the timing of mating between populations on different hosts may influence sexual selection and assortative mating, depending on the extent to which their mating windows overlap.

Allochrony, Age-Based Mate Choice, and Gene Flow

If host shifts result in allochronic life histories, individuals that develop on different hosts will fall into different age classes, with consequences for gene flow between populations on ancestral and novel hosts. Because *Enchenopa* females are highly philopatric, especially with regard to the location of mating (Wood 1993), we focus on the interactions between females on their natal host and dispersing males from a different host. The nature of potential interactions is inherently asymmetrical: for females in the earlier-developing population, immigrant males will be younger than males from their own population, while for females in the later-developing population, immigrant males will be older. Depending on the relative phenologies of the two host-plant species, average age differences will range from a few days to a few weeks (Wood and Guttman 1982). This time span may be significant for relatively short-lived organisms; for example, in a study with another treehopper *(Umbonia crassicornis),* older males had greater mating success than younger males, even though the age difference was only about 10 days (P. De Luca and R.B.C., unpublished).

The outcome of female encounters with males of different age classes will depend on whether or not there is age-based choice, and, if so, whether choice favors older or younger males. Although theoretical studies differ about the likelihood of female choice of younger or older males (Hansen and Price 1995; Kokko and Lindstrom 1996; Beck and Powell 2000; Proulx et al. 2002), for our purposes the question is an empirical one that bears on the likelihood of gene flow between populations on ancestral and novel host-plant species, especially during the early stages of a host shift when signal differences have not yet evolved.

Female preference for older males would have the effect of increasing the likelihood of gene flow when males disperse from the early population on one host to the later population on the other (i.e., it would lead to negative assortative mating). Such a preference might result in lower female fitness, if females frequently encounter immigrant males with genotypes not adapted to the female's host-plant species. In contrast, female preference for younger males would have the effect of decreasing gene flow resulting from male dispersal between hosts. For females in the earlier population, the pattern would be reversed. These factors would have consequences not only for selection on female mate preferences, but also for promoting or hindering local adaptation to the novel host plant.

It is unknown whether female *E. binotata* show age-based mate preferences. As a first step toward addressing this question, Sattman and Cocroft (2003) characterized age-related variation in male signals through repeated recordings of the same individuals over time. That study found no age-based differences in the signal characteristics measured, suggesting that female mate choice based on age-related signal traits is unlikely.

While the interactions among allochronically shifted individuals may result in assortative mating even in the early stages of a host shift, in later stages there may be selection favoring increased reproductive isolation between populations in the process of adaptation to different hosts, especially since fitness trade-offs between traits favored on different hosts are likely (Feder and Filchak 1999; Berlocher and Feder 2002).

Natural Selection for Mate Recognition

Once host specialization and divergence in communication systems have begun, the process of reinforcement may increase the degree of assortative mating. In reinforcement,

selection favoring avoidance of mismating with individuals adapted to different environments can result in an elaboration of signal differences or an increase in the strength of female preferences (Howard 1993; Kelly and Noor 1996; Higgie et al. 2000; Marshall et al. 2002; Höbel and Gerhardt 2003; Servedio and Noor 2003; Coyne and Orr 2004; Lukhtanov et al. 2005). Because mate-searching males are sometimes found on nonnatal hosts (see "Ecological Isolation in the *E. binotata* Complex," above), mate recognition may be an important source of selection on *E. binotata* communication systems.

Summary

In this chapter we have explored the relationships between host shifts, the evolution of mate communication systems, and speciation in a clade of host-specialist insects. Evolutionary change in signals and preferences is often invoked as a cause of speciation (Coyne and Orr 2004), and we suggest that it may play an especially important role in sympatric speciation initiated by host shifts in phytophagous insects. The allochrony and host fidelity that provide partial isolation among host-shifted populations can also have consequences for assortative mating through their effects on mate-searching tactics and mate choice. Furthermore, different host plants constitute different communication environments, with the potential to generate divergent natural and sexual selection on mating signals. All of these factors may also be important in the event of secondary contact between lineages on different hosts that have speciated in allopatry. These relationships between host shifts, signal evolution, and assortative mating are summarized in Fig. 7.4.

We have provided support for the importance of communication systems in speciation from our research with the *E. binotata* species complex of treehoppers. In this clade of host specialists, mating signals have differentiated in parallel with female preferences. There is also evidence that both signals and preferences may diverge in response to divergent natural selection arising from differences in the signal-transmitting properties of their host plants. There is little evidence that developmental plasticity itself leads to change in signals after a host shift in *E. binotata*. However, high levels of diversity in the reaction norms of signal traits suggest that female choice might favor different genotypes among host plants, potentially leading to divergent selection. Plasticity in mate-searching behavior of males (which produce fewer, shorter signals on nonhosts) may also contribute to assortative mating among populations on different hosts.

There are a number of productive directions for further research on the consequences of a host shift for the evolution of communication. Phytophagous insects such as *E. binotata* provide an opportunity for testing the role of female choice for condition-dependent signal traits in accelerating the process of local adaptation to a novel host. The possibility of age-related female preferences in generating
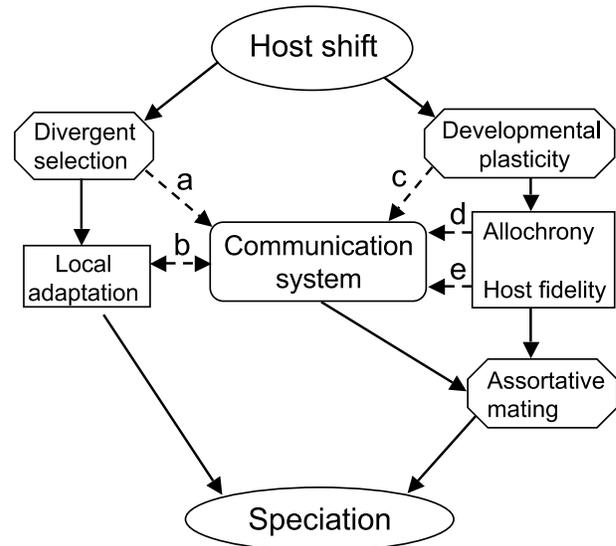
a Divergent natural and/or sexual selection on signal traits

b Female choice of condition-dependent signal traits; genetic correlations between life history and signal or preference traits

c Host effects and G x E interactions in signals and/or preferences

d Female choice of age-related signal traits

e Host fidelity in mate searching behavior

FIGURE 7.4. The relationships between host shifts, divergence in communication systems, and speciation.

positive (or negative) assortative mating should be investigated among allochronic but still overlapping populations.

In this review we have focused on deterministic effects rather than random influences such as genetic drift through founder events, which can also influence signal evolution (Tregenza et al. 2000). The presence of individual and genetic variation in all life-history and communication traits that we have examined offers the possibility for bottleneck effects on variation among host plants following a host shift, with the concomitant changes in selection regimes. The role of drift may be especially important when the adaptive landscape has ridges connecting trait combinations of equal fitness (Gavrilets 2003), facilitating divergence to alternative phenotypes.

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