Chapter 2
Evolution of Acoustic Communication in Insects

Michael D. Greenfield

Abstract Tympanal organs for hearing in the far field have evolved on multiple occasions among insects and are currently found in seven orders. Many, if not most, cases of insect hearing probably originated as a means for detecting and avoiding predators. In particular, sensitivity to ultrasound appears to have coevolved with echolocation signaling by insectivorous bats. However, on an overall scale, hearing is relatively rare among insects in comparison with other modalities of perception, including detection of substrate vibration. Sound signaling in insects, which typically occurs in the context of mating communication, is rarer still and is known in only five orders. Phylogenetic analyses suggest that acoustic communication in the Lepidoptera and in the suborder Caelifera (grasshoppers) of the Orthoptera originated via a "sensory bias" mechanism. Hearing was ancestral and sound signaling by males subsequently arose on multiple, independent occasions. On the other hand, acoustic communication in the Cicadidae and in the suborder Ensifera (crickets, katydids) of the Orthoptera may have originated via coevolution between female perception and male signaling. The diversity of songs among acoustic insects may reflect genetic drift and reproductive character displacement. There is little evidence, however, that insect songs are adapted to specific physical environments. In one clade of acoustic insects, the diversification of song is associated with an unusually high rate of population differentiation and speciation, which may be facilitated by a genomic co-localization of loci influencing female response/preference and male signaling. The extent to which co-localization is a general factor in speciation remains to be explored.

Keywords Coevolution • Convergence • Courtship • Ecological speciation • Fisherian mechanism • Genetic drift • Phylogenetic inference • Pleiotropy • Reinforcement • Reproductive character displacement • Sensory bias • Sexual advertisement • Sexual dimorphism • Size constraints • Ultrasound

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2.1 Introduction

Evolution of acoustic communication is one of the more intriguing topics in insect hearing, but it is also one of the more intractable. The several books devoted to this topic since the 1980s attest to a general interest (e.g., Ewing 1989; Bailey 1991; Gerhardt and Huber 2002; Drosopoulos and Claridge 2006; Hedwig 2014). Some of this attraction might be explained by curious similarities between vertebrate hearing and its counterpart among insects (e.g., Boekhoff-Falk 2005; Montealegre-Z et al. 2012). The intractable nature of the topic stems from certain attributes that are common to communication in all animals. Communication entails signal production as well as the perception of those signals, and understanding the evolution of communication demands attention to these two functions as distinct entities as well as to their inseparability (Greenfield 2014a). Like other aspects of behavior, communication seldom leaves direct fossil evidence, and one must often resort to rather indirect, phylogenetic inferences to speculate on its origin. Moreover, the insect fossil record is notoriously incomplete, and where it does exist for acoustic species, the representations of the signaling and perceptual organs are generally lopsided in favor of the former (cf. Senter 2008). Nonetheless, current paleontological (e.g., Gu et al. 2012) and phylogenetic (Regier et al. 2013; Misof et al. 2014) information allows the formulation of new overviews of the evolution of acoustic communication in insects, which are presented in this chapter.

The basic propositions for the evolution of acoustic communication are that its two components, sound production and hearing, either arose jointly or that one component preceded the other. In the context of sexual communication, which is the major focus here, these two possibilities are the Fisherian mechanism (Lande 1981; Kirkpatrick 1982), wherein mating signals and preferences coevolved at and following their origin, and the so-called "sensory bias" mechanism in which the perceptual function was ancestral (Endler and Basolo 1998; see Arnqvist 2006 for a more extensive treatment of these possibilities). In this chapter a considerable amount of evidence consistent with one component, usually perception, preceding the other is presented. The various factors that may have been selected for the origin of hearing or sound production are considered, followed by discussions of how and why sound production or hearing then appeared at some later time and how and why one or both components changed over the course of their evolutionary history.

2.2 What Is Acoustic Communication?

This seemingly straightforward question is actually fraught with diverse interpretations. Although it might appear that acoustic communication could be defined simply as the transmission, via sound waves, of intraspecific messages that are, on average, mutually beneficial to the signaler and receiver (cf. Hauser 1996; Bradbury and Vehrencamp 2011), problems arise in distinguishing sound and vibration. This distinction is critical because the perception of substrate vibration and the transmission of vibration signals are rather widespread among insects and other arthropods, but hearing and acoustic signaling are quite rare (Greenfield 2002). Thus, an understanding of how acoustic communication evolved in insects demands a clear distinction between sound and vibration that is relevant to biology.

One major difference observed among sound and vibration phenomena concerns the pattern of wave dispersion in the environment. Sound waves in air or water spread more or less omnidirectionally in all three dimensions, although some local attenuation and amplification of amplitude may result from vegetation and other barriers (Römer 1993), impedance differences within the air or water arising from thermal layering (Van Staaden and Römer 1997), or the morphology and posture of the animal that is signaling (Forrest 1982). Vibrations in the substrate, on the other hand, are typically confined to the same medium in which the signaler initially generated them, for example, surface of the ground (or water), vegetation, silk webbing, or social insect nest material. Consequently, for communication to occur, the receiver(s) as well as the signaler should remain on that specific medium, implying that vibration signals usually spread in one or two dimensions only. Moreover, the transmission of a vibration signal may be strongly attenuated when the quality of the medium is altered (Elias and Mason 2014). For example, vibration signals that are transmitted effectively on wet sand may be severely weakened on dry sand (Aicher and Tautz 1990), or the carrier frequency and amplitude of signals that an herbivorous insect transmits in stems and leaves of its host plant may be greatly modified in another plant species (McNett and Cocroft 2008). The upshot of this assessment is that sound signals in air or water have the potential to reach many more local receivers than do vibration signals. Relevant to the evolution of acoustic communication, patterns of wave dispersion may have hindered certain mechanisms of speciation from functioning among insects that send and receive sound signals (see Sect. 2.6.1). Recognizing this distinguishing feature, the current chapter focuses on the evolution of sound signals propagating in the fluid medium within which the communicating individuals are immersed and of the organs that perceive these signals. Vibration communication is discussed in detail by Yack, Chapter 5.

In addition to signal dispersion, acoustic communication is also distinguished by the use of specialized perceptual organs. In the far field, most insects use tympanal organs, chordotonal organs that are fitted with an exterior membrane, the tympanum, and an air cavity behind the membrane to detect the pressure waves of sound broadcast in air or water (Hoy and Robert 1996). Notable exceptions include pneumorid grasshoppers (Van Staaden and Römer 1998) and possibly some cockroaches (Shaw 1994), which perceive sound with internal chordotonal organs that lack external anatomical features, as well as one group of sphingid moths in which overlapping scales form a "functional tympanum" (Göpfert et al. 2002). Body size may be a constraining factor in the evolution of tympanal organs, as the membrane would have to exceed a minimum diameter or be under extreme tension to respond effectively to sound delivered at all but the very highest carrier frequencies (cf. Fletcher

1992). For example, a 0.5-mm-diameter tympanum may respond maximally to 100-kHz sound delivered above a threshold amplitude of 60 dB sound pressure level (SPL; 0 dB = 20 μPa) (Rodriguez et al. 2005). Thus, the smallest insects generally do not possess tympanal organs and lack the ability to hear far-field sound (e.g., Roces and Tautz 2001). The transmission of sound into the far field, normally considered as beginning approximately one wavelength from the source, may be similarly constrained, as the diameter of the sound radiating structure may have to exceed a minimum fraction of the wavelength of the structure's vibration frequency (cf. Fletcher 1992). For example, a 0.4-mm-diameter tymbal may resonate at 100 kHz (wavelength = 3.4 mm) and generate a sound amplitude of ≈95 dB at 1 cm (Spangler et al. 1984). Such size constraints may influence the perception and propagation of substrate vibration much less, a factor that could explain, in part, why vibration communication is relatively ubiquitous among insects, even among small to minute species, less than 10 mm in length (Cocroft and Rodriguez 2005). In the near field, however, insects generally detect the particle-velocity aspect of sound with relatively unspecialized filiform hairs or other structures on the body (Tautz and Markl 1978) and appendages (Göpfert and Robert 2000), and these organs may not be strongly limited by size (e.g., Göpfert and Robert 2001). The propagation of sound into the near field, typically low in carrier frequency and generated by simple movement of unmodified wings, may also be relatively free of size constraints. Accordingly, some very small insects, for example, *Drosophila* spp. (Bennet-Clark 1971; Hoy et al. 1988), have well-developed acoustic communication in the near field. Overall, however, near-field sound signaling is not a common form of communication among insects, and other factors, possibly low inefficiency for transmitting information, may have limited its evolution. But biologists may have also overlooked some cases of near-field sound communication, as few studies have been equipped to detect it, particularly in the field.

Respecting this chapter's restriction of sound signals to those transmitted in air or water, there are several situations where the potential for acoustic communication needs clarification. Many insect species generate airborne sound as a by-product of substrate vibration signals, and in some cases biologists can monitor this signaling activity by registering the resulting sounds (Greenfield 2002). But unless the receiving individuals are equipped with hearing organs sensitive to those sounds, any communication would be along the vibration channel only. A more complex situation arises when an individual produces a substrate vibration signal that generates a concomitant airborne sound that may then cause certain distant substrates to vibrate. If a potential receiver resting on one of these distant substrates detects and responds to the vibration, then this situation would constitute acoustic communication. The air has served as the channel for transmitting the signal, and the substrate beneath the signaler and receiver functioned only to transfer the vibration between the insect and the air. Nonetheless, this particular form of acoustic communication would be somewhat restricted, being limited by the requirement that both signaler and receiver remain on a specific substrate. Potential cases may occur in spiders, and it is presented mostly as an exercise for evaluating the nature of signals and communication.

2.3 Acoustic Communication: Who Are the Actors and What Are Their Actions For?

From a phylogenetic perspective, hearing and acoustic communication are poorly represented in the animal kingdom; see Gagliano (2013) for discussion of the possibility of acoustic communication in plants. Ears that are sensitive to sound waves in air or water are known only in vertebrates and some arthropods and cephalopods. In arthropods, they are largely restricted to several orders of insects. Recent findings show that some spiders (Gordon and Uetz 2012) and crustaceans (Hughes et al. 2014) are sensitive to airborne and waterborne sound, respectively, but it is not clear whether these taxa exhibit acoustic communication as defined in Sect. 2.2. Similarly, sensitivity to waterborne sound is reported in cephalopods (Mooney et al. 2010), but there is no indication of acoustic communication in these species.

Unlike vertebrates, in which inner ear structures are found in all classes and appear to have descended from a single evolutionary origin during the Devonian Period (approx. 400 MYA before present) or earlier (Popper et al. 1992), insect ears that perceive the pressure waves of far-field sound are known in only 8 of the 32 recognized orders (Table 2.1) but have evolved independently at least 24 times, and perhaps as many as 29 (cf. Yager 1999). The uncertainty reflects the various phylogenies that have been proposed in several groups, particularly Lepidoptera and Orthoptera, and the unresolved status of these phylogenies at present. Current information shows that pressure-sensitive ears are present in the following insect orders: Orthoptera (grasshoppers, crickets, katydids), Mantodea (mantises), Hemiptera (true bugs, plant lice, cicadas), Neuroptera (net-winged insects), Diptera (true flies), Lepidoptera (moths and butterflies), Coleoptera (beetles), and possibly Blattodea (cockroaches) (Table 2.1). However, pressure-sensitive ears are not found throughout any of these orders, and in some they are known in only a few isolated groups. For example, in the Coleoptera, hearing is reported only in certain tiger and scarab beetles (Cicindellidae, Scarabaeidae; Spangler 1988; Forrest et al. 1997). When acoustic communication is considered, the distribution of confirmed cases is restricted further: Orthoptera, Hemiptera, Lepidoptera, and possibly Blattodea for pressure waves in the far field; Diptera and Hymenoptera for near-field sound (Table 2.1). Moreover, it is only in two groups of Orthoptera and one group of Hemiptera that communication by sound is widespread and a dominant form of signaling. Acoustic communication in the other orders is rare and/or a complementary behavior that functions alongside other signaling modalities. Thus, a concentration on the evolution of acoustic communication in insects is sustained by an interest in how a behavior best known in birds, mammals, and anurans originated in very different groups of organisms and attained similar levels of development despite operating under some severe handicaps, namely small size (e.g., Sueur et al. 2011). In addition, some acoustic insects have served as focal species for the study of sexual selection (Zuk et al. 2014) and speciation (Mendelson and Shaw 2005).

In all but one case, acoustic communication in insects functions in the context of mating: sexual advertisement, courtship, or intrasexual competition, the latter

Table 2.1 Distribution of hearing of airborne or waterborne sound, and production of airborne or waterborne sound, among the 32 extant orders of insects recognized by Misof et al. (2014)

Insect orders	Hearing	Sound production
Protura (coneheads)		
Collembola (springtails)		
Diplura (two-pronged bristletails)		
Archaeognatha (jumping bristletails)		
Zygentoma (silverfish)		
Odonata (dragonflies and damselflies)		
Ephemeroptera (mayflies)		
Zoraptera (ground lice)		
Dermaptera (earwigs)		
Plecoptera (stoneflies)		
Orthoptera (grasshoppers, crickets, katydids)	Tympana in several major families; internal abdominal organs in Pneumoridae	Stridulation and wing mechanisms in several major families; various sound frequencies
Mantophasmatodea (gladiators)		
Grylloblattodea (ice crawlers)		
Embioptera (web spinners)		
Phasmatodea (stick and leaf insects)		
Mantodea (mantises)	Tympana in many groups; ultrasound sensitivity	
Blattodea (cockroaches)	Internal tibial organs in one family; possible detection of far-field sound	Expulsion of tracheal air in one family; audible sound
Isoptera (termites)		
Thysanoptera (thrips)		
Hemiptera (true bugs, plant lice, cicadas)	Tympana in two families	Tymbals in two families; audible sound
Psocodea (barklice, true lice)		
Hymenoptera (sawflies, wasps, bees, ants)	Antennal organs for near-field hearing in honeybees	Wingbeat mechanism; low-frequency sound in the near field
Raphidioptera (snakeflies)		
Megaloptera (alderflies, dobsonflies)		
Neuroptera (net-winged insects)	Tympana in one family; ultrasound sensitivity	
Strepsiptera (twisted-wing parasites)		
Coleoptera (beetles)	Tympana in several genera in two families; ultrasound sensitivity	
Trichoptera (caddisflies)		
Lepidoptera (moths and butterflies)	Tympana in three major superfamilies and several additional families; ultrasound sensitivity in most groups	Tymbals, stridulation, and wing mechanisms in isolated genera and species in various groups; ultrasound frequencies typical

(continued)

Table 2.1 (continued)

Insect orders	Hearing	Sound production
Siphonaptera (fleas)		
Mecoptera (scorpionflies)		
Diptera (true flies)	Tympana confirmed in two families, with possible tympanal hearing in a third (Tuck et al. 2009); antennal organs for near-field hearing in several families	Wingbeat mechanisms in several families; low-frequency sound in the near field

Hearing refers to the perception of far-field sound except in those cases where the perception of near-field sound is associated with detecting conspecific signals. Sound production refers to acoustic signals that function in the context of intraspecific communication

including conventional display, territorial defense, and a prelude or accompaniment to aggression (see Balakrishnan, Chapter 3). Most signals are broadcast by males, but in some cases females respond to male advertisement or courtship signals with their own song and a duet ensues (Bailey 2003). These female replies are usually less intense and transmitted over a shorter distance than the male song, and they may be produced by structures that are not homologous with the male sound-producing device (Nickle and Carlysle 1975). Mosquitoes may represent an exception, as it is the female that initially broadcasts the advertisement song and is an equal partner with the male in their dialogue (Cator et al. 2009). Unlike sound production, hearing typically functions in both sexes in acoustic insects, although some level of sexual dimorphism may be present (e.g., Robert et al. 1994). Social insects use many vibration signals in various behavioral contexts, but there is only one confirmed case in which a social signal includes airborne sound that is detected and evaluated by receivers: the forager recruitment dances in *Apis* spp. honeybees (Hunt and Richard 2013). But dance language sounds function only across very short distances (Michelsen et al. 1986; Towne and Kirchner 1989) and are accompanied by substrate vibration (Nieh and Tautz 2000) and tactile signals (Rohrseitz and Tautz 1999), as well as by odor. Consequently, the sound signals of honeybees are not treated further in this chapter. Readers desiring further information on these signals and their evolution may consult Dreller and Kirchner (1993) and Kirchner (1997).

2.4 How Did Acoustic Communication Originate in Various Insect Groups?

Because hearing is more widespread than acoustic communication in insects, one may begin by considering the origin of ears and acoustic perception. One focuses on tympanal ears because these are the organs, with the exception of the abdominal chordotonal structures in pneumorid grasshoppers, that can perceive sound broadcast over relatively long distances and thereby function in all aspects of communication. It is noted that the air cavity behind the tympanal membrane is generally derived from part of the tracheal system (Hoy and Robert 1996), and among arthropods it is insects that fly or that are descended from flying ancestors that have particularly well-developed tracheal systems. Thus, it may not be a coincidence that arthropod tympanal organs are restricted to adult pterygote insects. These are the forms that already had membranous structures that could be "borrowed" for organs sensitive to the pressure waves of far-field sound should the right selection pressure occur. But what may that selection pressure have been?

2.4.1 Ultrasound Sensitivity: Insect–Bat Coevolution

Tympanate insects include Mantodea, Orthoptera (Ensifera and Caelifera), Hemiptera (Corixidae and Cicadidae), Neuroptera (Chrysopidae; lacewings), Diptera (Sarcophagidae, Tachinidae), Coleoptera (Cicindellidae, Scarabaeidae), and Lepidoptera (8 superfamilies). It is noteworthy that in 4 of these orders (Mantodea, Neuroptera, Coleoptera, Lepidoptera), comprising no fewer than 14 independent origins, tympanal hearing is specifically sensitive to ultrasound frequencies (Hoy 1992). Independence of evolution of hearing in the several groups having ultrasound sensitivity is inferred from their ears being nonhomologous organs and the principle of parsimony. The latter assumes that a recent origin of the hearing trait in the common ancestor of a group of extant species is more likely than a more ancient origin in a broader group, followed by subsequent loss of the trait in all but one lineage. Moreover, fossil evidence, molecular analyses, and historical biogeography indicate that most cases of ultrasound hearing have evolved rather recently, primarily since the beginning of the Paleogene Period (Cenozoic Era; 65 MYA before present). This inferred date for the origins of ultrasound hearing in Neuroptera, Coleoptera, and most Lepidoptera suggests a coevolutionary response to predation by insectivorous bats, whose ultrasound echolocation signals arose at that time. Among the groups with specialized ultrasound hearing, tympanal organs appear to have evolved prior to the Cenozoic Era only in the Mantodea (Yager and Svenson 2008) and in one family of the Lepidoptera [Tineidae; clothes moths (Davis 1998); note that ultrasound sensitivity is not confirmed in this group]. In the Mantodea, it is unclear whether ultrasound sensitivity arose at the origin of hearing, possibly as an adaptation for detecting inadvertent sounds made by various predators, or later as a modification of general hearing alongside the appearance of echolocation signals in bats. In summary, nocturnal flight became too dangerous in the Paleogene Period for most insects unless they were equipped to detect, and then evade, the new hunting technique employed by aerial predators. Converting part of the tracheal system for a vital perceptual function was therefore adaptive in that changing biological community (cf. Yager 1999).

The strongest evidence supporting the coevolution of insect hearing and bat predation is found in the Lepidoptera. All but one of the 10–12 independent origins of hearing in the Lepidoptera (cf. Fig. 2.1) appear to have occurred following the

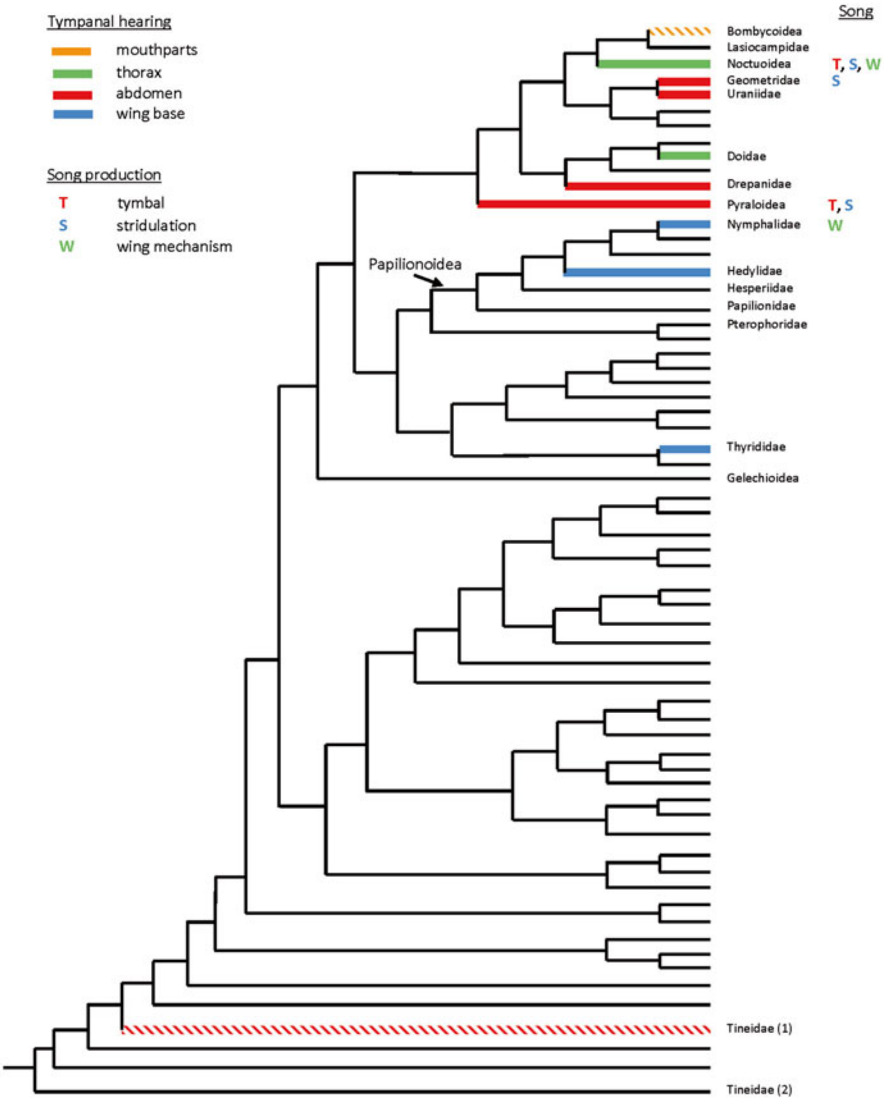

Fig. 2.1 Phylogeny of the "advanced" moths and butterflies (Lepidoptera, section Ditrisia) following maximum likelihood analyses in Regier et al. (2013), showing distribution of hearing and acoustic signaling among the superfamilies and families. In groups indicated by colored bars with diagonal shading, hearing is found only in a small percentage of genera; two independent origins of hearing are reported for the Bombycoidea (silk moths, emperor moths, and sphinx moths; Göpfert et al. 2002). In each of the four groups where acoustic signaling is indicated, song is reported in only a small percentage of species and generally involves multiple independent origins (Greenfield 2014b); there is only one confirmed report of acoustic communication in the Geometridae (geometer moths; Nakano et al. 2009)

beginning of the Paleogene Period (cf. Yack and Fullard 2000). In three of these groups with acoustic perception—Pyraloidea, Geometroidea, and Noctuoidea—ultrasound-sensitive hearing is widespread throughout a very large superfamily. Cases of hearing absence or reduction in pyraloid, geometroid, and noctuoid moths generally involve species found in regions lacking insectivorous bats (Fullard 1994) or that fly at times of the day or year when bats are not active (Fullard et al. 1997). Butterflies (Papilionoidea), which are secondarily diurnal, do not possess ultrasound hearing, but their sister group, the night-flying Hedyloidea (American butterfly moths), do (Yack and Fullard 2000). Certain thoracic structures in butterflies may be vestiges of ancestral hearing organs, and in some butterfly species these structures are adapted to hear audible sound, possibly from birds or other daytime predators (Lucas et al. 2014). Thus, a pattern of secondary loss or shift in frequency sensitivity in hearing emerges in lepidopterans that have escaped the selection pressure imposed by predatory bats. A similar process may have occurred in the Mantodea wherein most species with auditory function exhibit some level of sexual dimorphism in hearing: Female mantises, which have shorter wings, fly less, and are therefore exposed to less bat predation, generally have reduced tympanal organs (Yager 1999).

2.4.2 Sensitivity to Audible and Broadband Sound Frequencies

Hearing in the remaining groups of tympanate insects appears to be much less related to avoiding bat predation, although detection of other predators may have been a critical factor. The tympanate Caelifera (Orthoptera) and Hemiptera are largely diurnal, and their hearing is primarily sensitive to audible sound, far below the frequencies of bat echolocation signals. The tympanate Diptera are mostly nocturnal, but their hearing is also most sensitive in the audible frequency range and serves mostly as a means by which females localize their acoustic insect hosts (Lakes-Harlan and Heller 1992). In Ensifera (Orthoptera), hearing is sensitive to a broad range of frequencies, including ultrasound. Their hearing may have been the earliest to evolve among insects (prior to 250 MYA; Otte 1992), considerably before the appearance of echolocation signals in bats. However, many ensiferans are very sensitive to ultrasound sound frequencies and some exhibit specialized detection and evasion of bat echolocation signals (Faure and Hoy 2000; Schulze and Schul 2001). Paleontological evidence suggests that ultrasound sensitivity was present in katydids as early as the Paleogene Period (Rust et al. 1999).

2.4.3 Sound Signaling

The distribution of acoustic communication signals in insects differs somewhat from the distribution of hearing. Sound signaling is not only found in fewer insect orders (four as opposed to eight), but within some groups of tympanate insects,

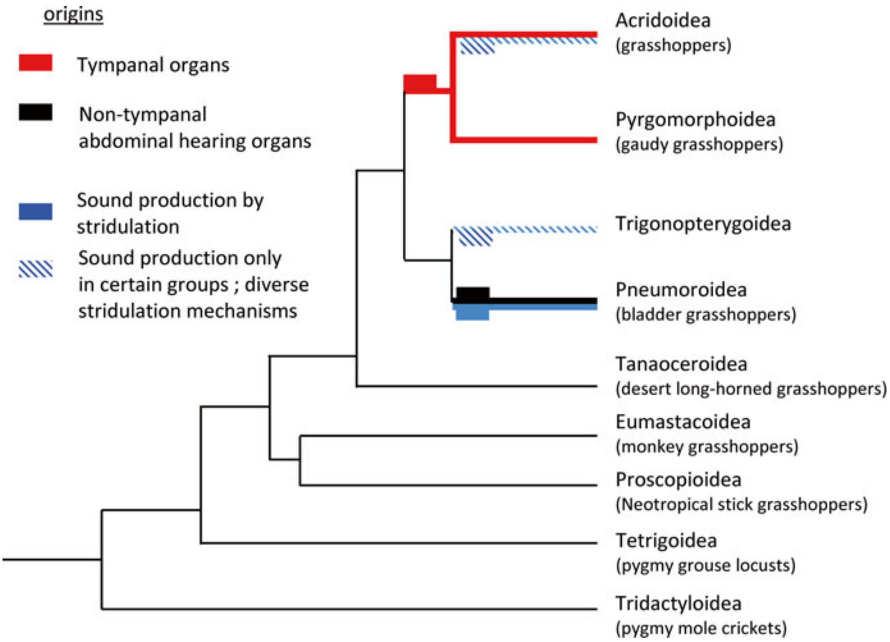

Fig. 2.2 Total evidence phylogeny of the Orthoptera, suborder Califera (short-horned grasshoppers) following maximum likelihood analysis in Song et al. (2015), showing distribution of hearing and acoustic signaling among the superfamilies (cf. Flook et al. 2000). In superfamilies indicated by colored bars with diagonal shading, acoustic signaling is found only in a portion of the group and most likely represents multiple independent origins

sound signaling occurs in only a small percentage of species. Moreover, sound signaling has evolved independently on a great many occasions in several of these groups (Greenfield 2014b).

The Lepidoptera serve as the better example of the above pattern (Fig. 2.1). Tympanal organs occur in nine superfamilies, among which they are distributed on the metathorax (two), abdomen (four), wing bases (two), and mouthparts (one). Based on current phylogenies and nonhomology of the structures, these organs represent between 10 and 12 independent origins (cf. Kristensen 2012; Regier et al. 2013). Sound signaling is known primarily in the Pyraloidea, Papilionoidea, and Noctuoidea, and within each of these three superfamilies, it is distributed in multiple, unrelated genera and species but is absent in most. These various cases of sound signaling involve nonhomologous stridulatory or percussive structures and generally represent many independent evolutionary origins.

The suborder Caelifera of the Orthoptera serves as the second example of the pattern of widespread hearing and a restricted incidence of sound signaling (Fig. 2.2). Tympanal hearing occurs only in the clade including Acridoidea (grasshoppers) and Pyrgomorphoidea (gaudy grasshoppers), although nontympanal hearing is also found in the related Pneumoroidea (bladder grasshoppers). An original

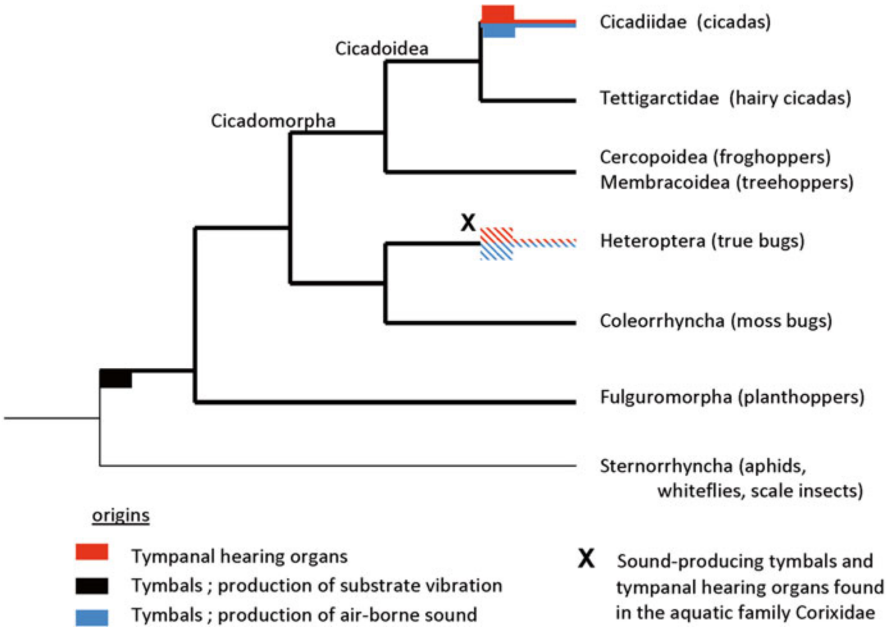

Fig. 2.3 Phylogeny of the Hemiptera (true bugs, plant lice, and cicadas) following Hoch et al. (2006) showing distribution of hearing, vibration signaling, and acoustic signaling among the major subdivisions. In subdivisions indicated by colored bars with diagonal shading, hearing as well as acoustic signaling are found only in a small portion of the group

function of hearing in the Caelifera may have been detecting the inadvertent sounds made by terrestrial predators, for example, such as mammals, reptiles, and other arthropods (Riede 1987; Flook et al. 2000). Sound signaling among Caelifera is more limited, occurring primarily in the Acridoidea, but not in all groups, and the Pneumoroidea (Flook et al. 2000). Stridulatory movements are also present in several additional families (Strauss and Lakes-Harlan 2014) where it may function in substrate or tactile vibration and/or as a visual signal. Thus, sound signaling either evolved basally in a major part of the Caelifera and was subsequently lost in many groups or, as in the Lepidoptera, evolved independently on multiple occasions. The fact that stridulation in Caelifera involves different movements and modified structures in the various groups that sing favors the latter interpretation (cf. Flook et al. 2000; Strauss and Lakes-Harlan 2014).

Acoustic communication in both the Hemiptera and the Ensifera (Orthoptera) differs from the preceding examples in that a fairly close match exists between the incidence of hearing and sound signaling. In the Hemiptera, tympanal hearing is via abdominal organs and is found only in the Corixidae (water boatmen) and the Cicadidae (cicadas; Fig. 2.3). In the latter, it is basal and occurs throughout the family, but it is not found in the sister group, the Tettigarctidae (Australian hairy cicadas; Moulds 2005; Strauss and Lakes-Harlan 2014). Most Hemiptera are sensitive to substrate vibration, though, which they detect via subgenual organs. Signaling

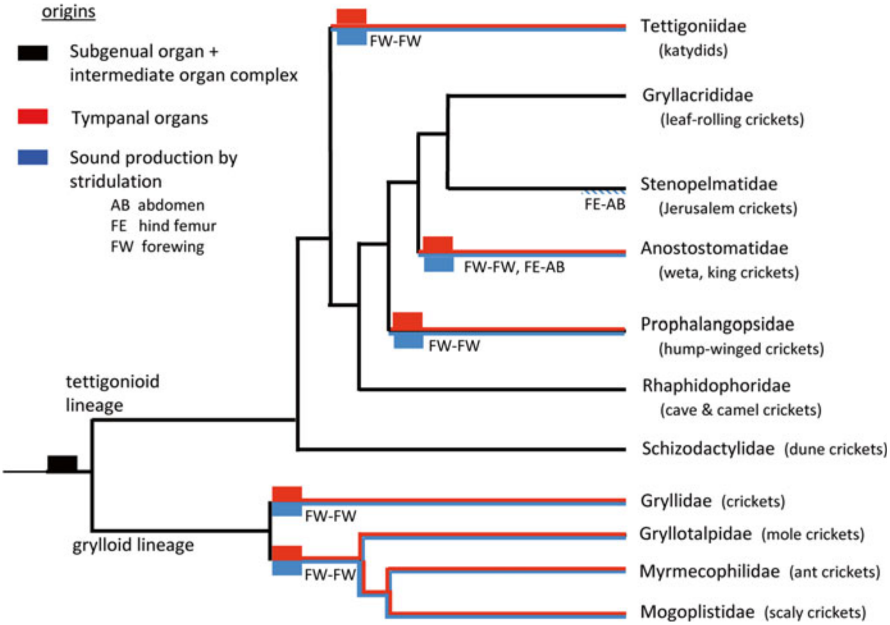

Fig. 2.4 Total evidence phylogeny of the Orthoptera, suborder Ensifera (crickets and katydids) following maximum likelihood analysis in Song et al. (2015), showing distribution of hearing and acoustic signaling among the several families (cf. Desutter-Grandcolas 2003). In groups indicated by colored bars with diagonal shading, acoustic signaling is found only in a portion of the group (and does not function in the context of intraspecific communication). The topology of families in the tettigonioid lineage is not definitive, and the number of independent origins of tympanal hearing remains uncertain. The topology of families in the grylloid lineage is more stable, but the number of independent origins of tympanal hearing in this clade is also uncertain, with one to four origins being possible based on current understanding

via specialized tymbal organs that are adapted for broadcasting waterborne or airborne sound is also found only in the Corixidae and Cicadidae. Again, in the Cicadidae, these organs are found throughout the family but are absent in the Tettigarctidae (Strauss and Lakes-Harlan 2014). Homologous tymbal organs that generate substrate vibration are much more broadly distributed in the Hemiptera, however, and the sound-producing tymbals in Cicadidae have probably evolved from these less specialized structures, which may be a basal character in all Hemiptera minus the Sternorrhyncha clade (Strauss and Lakes-Harlan 2014).

Similarly in the Ensifera, tympanal hearing occurs in several groups in both the tettigonioid and grylloid "lineages," and sound signaling is found throughout all tympanate groups in both lineages (Fig. 2.4). Tympanal organs are all located in the foretibiae, but they have probably evolved independently several times. The ancestral structure appears to be the subgenual organ/intermediate organ complex to which the tympanum and other features (e.g., crista acustica) were added in hearing species (Strauss and Lakes-Harlan 2014). Sound signaling is by means of tegminal-tegminal (forewing-forewing) stridulation in the grylloid lineage, but both tegminal-tegminal and femoroabdominal stridulation are found in the tettigonioid lineage (Strauss and Lakes-Harlan 2014). Additional, nontympanate groups in the tettigonioid lineage exhibit femoroabdominal stridulation, either to effect substrate vibration in the context of communication or as a means of startling predators. Sound signaling has been lost secondarily in some species, notably where levels of attack by phonotactic parasites are unacceptably high (e.g., Tinghitella et al. 2009). The higher level phylogeny of the Ensifera is not fully resolved (Legendre et al. 2010; cf. Song et al. 2015), and it is currently not possible to indicate relationships between some of the acoustic and nonacoustic groups with any certainty.

Acoustic communication in the Blattodea reverses the pattern described in the Lepidoptera and Caelifera. Sound production is more widespread than hearing, which is accomplished via internal chordotonal (subgenual) organs in certain species (Shaw 1994), and it has been argued that the initial and general function of sound was in startling predators. In the Diptera, sound production has been studied intensively in the Drosophilidae (fruit flies; Bennet-Clark 1971; Bennet-Clark et al. 1980), the Tephritidae (true fruit flies; Sivinski et al. 1984), and the Culicidae (mosquitoes; Cator et al. 2009; Jackson et al. 2009). These dipteran songs are relatively low in frequency (mostly <1,200 Hz) and, given that hearing in the receivers is not tympanate, effect communication primarily in the near field. There is relatively little information on sound production and hearing in related groups, which prevents evolutionary inferences at this time.

2.4.4 Origins of Acoustic Communication: Sensory Bias, Coevolution, and Motor Bias

An overall evolutionary trend that emerges from the survey presented in this section is that prior evolution of hearing in a defensive context followed by later appearance of sound signaling in some of the auditory species was likely throughout the Lepidoptera and in the Caelifera. This inferred phylogenetic sequence of events suggests the role of sensory bias in the origin of acoustic communication in these groups. As a possible scenario of the process, in an ancestral species in which males were engaging in stereotypical movement of appendages during courtship to disperse pheronomes or to create a vibration or visual display, a novel behavioral or structural modification that added sound to the display would have found an audience: hearing females. Based on the matched distributions of hearing and sound signaling in both the Hemiptera and the Ensifera, a sensory bias process appears much less likely in these two groups. There is no definitive phylogeny for the Ensifera, and the possibility that hearing and sound signaling originated at the same time via a coevolutionary process cannot be eliminated in the lineages leading to the Gryllidae and to the Tettigoniidae (cf. Desutter-Grandcolas 2003).

Acoustic communication is not a major feature of the Blattodea (cf. Nelson and Fraser 1980), but it illustrates what may be an unusual case of "motor bias." Various species were producing defensive sounds that may have involved activity and movement that males also displayed during courtship. Thus, a novel modification to the vibration-detecting subgenual organs that afforded hearing of airborne sound would have allowed improved evaluation of local males. Here, sensory modification in both males and females would be expected, as both sexes would benefit from precise evaluation of male display.

2.5 What Evolutionary Changes in Acoustic Communication Followed Its Origin?

Communication involves much more than simply detecting a stimulus and making one that can be detected. Communication implies the transfer of reliable information that reduces uncertainty about a signaler's identity, capability, and motivation. Thus, some modification of a stimulus is expected following its origin, whether via sensory bias or a coevolutionary process. Similarly, some modification in perception that would improve a receiver's evaluation is equally likely (cf. Alem et al. 2013). In acoustic communication in insects, these features would generally include identification of the signaler as a suitably compatible mate (e.g., conspecific of the opposite sex), as a potential rival (e.g., a conspecific male, for a male receiver), as a sexually mature adult, and as having a certain "quality" over and beyond merely being suitably compatible or rival. And in the case of long-range advertisement, the source of the signal would have to be localized.

Tracing the evolution of expected modifications in signals and perception would be done best with a group that currently includes a range of communication formats at different stages of development. This specification would remove the Orthoptera—both Caelifera and Ensifera—and the Cicadidae from consideration, as acoustic communication in these groups is fully fledged in most species that do sing and includes all of the elements listed previously in this section. Moreover, in the Ensifera and Cicadidae, sound signaling appears to have originated independently on very few occasions, probably only once in the Cicadidae. On the other hand, the Lepidoptera offer more possibilities for evolutionary inference because sound signaling has originated multiple times, and it exists in diverse formats ranging from simple courtship conducted at very close range to long-range advertisement.

In the nocturnal Lepidoptera, sound signaling is invariably associated at some level with bats and their ultrasound echolocation signals (Greenfield 2014b). Many species of noctuoid moths emit ultrasound signals that either jam bat echolocation systems or warn bats about the insect's chemical noxiousness (Conner 2014). In several species, these very same ultrasound signals serve as a close-range male courtship song (Simmons and Conner 1996). In other noctuoid and pyraloid moths that do not emit sound signals when interacting with bats, the males emit a very quiet call during courtship (Nakano et al. 2008, 2009) that acoustically mimics a generic bat echolocation signal (Nakano et al. 2010). These quiet calls, as well as the bat echolocation signals that they imitate, elicit an arrestment of movement in the female. In an encounter with a bat gleaning insects off surfaces by listening to their telltale noise, this arrestment response would afford a female moth some protection by silencing the sounds she inadvertently makes while moving on the substrate. But when a courting male moth is emitting the ultrasound signal, the result is that the female may remain in a receptive posture or location for a longer duration. Thus, in some cases male moths seem to have co-opted defensive signals for use in courtship, and in others they have evolved a novel courtship call that elicits a female response, increasing the likelihood that mating will take place. This latter format may be described as a male signal that "exploits" an ancestral female response exhibited in a nonsexual context, and it is consistent with male signal evolution via the sensory bias mechanism.

In both formats of acoustic courtship in moths, the male call functions only during the very final part of pair formation, most of which had been effected via a female-emitted advertisement pheromone that attracted the male. Such chemical communication is basal in Lepidoptera (Löfstedt and Kozlov 1997), and it is found in most groups except some diurnal ones, such as in the Papilionoidea (butterflies). But in several species of pyraloid and noctuoid moths, the male calls function over a much longer distance (Greenfield 2014b). Here, the male sound signals may function as an advertisement that replaces the female sex pheromone, which had been secondarily lost over evolutionary time. Such acoustic communication poses several questions. At a mechanistic level, given that the female hears both bat echolocation signaling and the male call and responds with negative phonotaxis to the former and with positive phonotaxis to the latter, how does she distinguish them? One could argue that discrimination may not be strongly selected for in moth species where the only acoustic signal is a close-range male courtship song that happens to imitate bats but where females orient over long distances to male advertisement calls, any failure to recognize males correctly could be fatal. However, this expected discrimination is problematic when one notes that moth ears, the simplest known in the animal kingdom, have only one to four peripheral neurons each (cf. Surlykke et al. 2003) and that carrier frequency, being comparable in both moth calls and bat echolocation signaling, could not be used effectively. At an evolutionary level, the major question arising is the transition from an acoustic component of courtship that plausibly appeared via a sensory bias process to a long-range male advertisement song and the concomitant loss of the female sex pheromone. What can be inferred about the evolutionary route(s) along which the various changes occurred?

Solutions to the above conundrum, as well as further questions, are forthcoming from or suggested by analyses of one acoustic moth species that has been studied intensively, *Achroia grisella* (Pyralidae: Galleriinae; lesser wax moth). Male *A. grisella* broadcast an advertisement song comprising a train of ultrasonic pulses delivered at 80–120 $\cdot$ s^{-1} (Spangler et al. 1984; Jang and Greenfield 1996). The song is produced while males remain stationary on the substrate and fan their wings, an activity that causes a pair of tymbals at the wing bases to resonate during each upstroke and downstroke of the wings. Each tymbal resonation yields a brief (≈100 μs) pulse of high-frequency (70–110 kHz) sound. Female *A. grisella* respond to the male song by running toward the sound source, but they arrest their movement in response to a slower (<25–55 $\cdot$ s^{-1}) pulse rate (Greig and Greenfield 2004), which is representative of most bat echolocation signaling during the search phase of hunting (Neuweiler 2000). Thus, the moths distinguish male song and bat echolocation signaling as expected, they do so in spite of having only three peripheral neurons per ear, and the discrimination is effected via temporal rather than spectral characters of the signals.

Nonetheless, direct evidence is limited on the evolution of the male calling song in *A. grisella* and other moths exhibiting similar pair formation. Assuming an origin via a sensory bias process, an evolutionary model must account for a radical shift in female response to an ultrasound signal from arrestment of movement, or even negative phonotaxis, to the attraction described previously in this section (see Arnqvist 2006 on the occurrence of sexual conflict in signal evolution via sensory bias). In addition, some level of signal discrimination by females and signal modification by males has probably evolved. At present, it is unknown whether the original male song was already distinguished from bat echolocation signaling by a faster pulse rate or whether the rapid rate characteristic of male song evolved later and offered females the possibility of reliable discrimination of predators and mates. Similarly, it is unknown whether females originally identified bats via their relatively slow pulse rate or whether discrimination of bat echolocation signaling and male song based on pulse rate developed once male song had evolved. In addition, male *A. grisella* emit a sex pheromone during wing fanning that currently has a weak effect on the general movement of females but not their specific orientation toward a given male. A pertinent question is whether this odor played a more critical role early during the evolution of male song by affording females a reliable opportunity to discriminate males and predators. The ability of female, and male, *A. grisella* to localize the source of male song poses yet another evolutionary question, as the defensive hearing found throughout the Pyraloidea and other moths may entail little directionality. Some resolution of these possibilities and problems could be achieved by comparative studies of acoustic species that are conducted within a phylogenetic framework.

2.6 How Do Songs Diversify?

The evolution of sound signaling and perception does not cease once acoustic communication develops as a viable means for transmitting various types of information at all stages of the mating process. Section 2.5 speculated on the evolutionary trajectory along which a simple courtship sound was eventually modified to a long-range advertisement song that indicates certain aspects of male "quality" (cf. Jia and Greenfield 1997; Jang and Greenfield 1998; Reinhold et al. 1998). But in addition to the inferred elaboration of song, lateral shifts in acoustic parameters are also expected. These latter modifications may reflect adaptation to changes in the physical and biotic environment, sexual selection favoring exaggeration of male signals, and, of course, chance, otherwise termed genetic drift (Wilkins et al. 2013). An important category of modifications are those that entail divergence between populations, which can lead to speciation. This final section reviews the circumstances under which interpopulation divergence in song may occur, which song parameters are likely to diverge, and when the end result may be speciation.

2.6.1 On the Role of Ecological Speciation

A major question in the formation of species concerns the extent to which ecological factors and chance are responsible for the initial stages of population divergence. The first possibility would occur when a single, panmictic population becomes divided in two, each part subject to a different environment that selects for a specific phenotype. When mating signals and preferences are associated with those specific phenotypes and population divergence proceeds to complete separation, "ecological speciation" is said to have taken place (Nosil 2012). Such signals and preferences are termed "magic traits" (Servedio et al. 2011) because of their dual function and consequent potential for permitting speciation. Insects associated with a particular host plant appear to be especially prone to exhibiting magic traits and undergoing ecological speciation. For example, in the Californian stick insect *Timema cristiniae* (Phasmatodea: Timematidae), two color morphs are known, one typically found on *Adenostema* shrubs and the other typically on *Ceanothus* shrubs (Nosil et al. 2002). Each form is more cryptic on its typical host shrub, and laboratory trials show that each form also prefers insects of that same form as mating partners. These mate preferences appear to be maintained indirectly by natural selection against hybrids, which are intermediate color morphs and therefore cryptic on neither host shrub.

Has ecological speciation played a role in the diversification of song among acoustic insects? A review of potential cases of this process in vibration signaling in insects provides some supporting evidence for this idea. Ultimately, these cases help illustrate why ecological speciation is much less likely to be a factor in acoustic insects. In *Enchenopa binotata* treehoppers (Hemiptera: Membracidae), several different forms are found on specific host plants that differ in the elastic properties of their branches and stems. Consequently, the vibration frequencies at which bending waves are transmitted with the least attenuation along stems differ among the plants. Male *E. binotata* transmit vibration signals along the stems of their host plants, and the peak vibration frequency observed in the signals of a population found on a given host plant corresponds with the vibration frequency that is transmitted best in the stems of that host plant (McNett and Cocroft 2008). As in *T. cristiniae* stick insects, the various *E. binotata* populations are potentially en route to speciation, with the initial stages of divergence appearing to have been facilitated by mating signals that are adapted to the specific environment of a given population (Rebar and Rodriguez 2015). However, in *E. binotata* it is unknown whether the receivers in each population are maximally tuned to these best vibration frequencies, a factor that would accelerate divergence of these incipient species (cf. Nosil 2012).

Similar correspondence has been noted between physical properties of the substrate and spectral characteristics of vibration signals in other insects and arachnids, with the general suggestion made that signalers exploit resonance to maximize transmission of their messages (e.g., Cokl et al. 2005; Polajnar et al. 2012). But processes other than ecological speciation may be responsible for diversification of vibration signals. In a survey of *Nesodyne* planthoppers in Hawaii (Hemiptera: Delphacidae), a group that has expanded via adaptive radiation, comparative analyses suggested that diversification of vibration signals arose via no fewer than three processes, ecological speciation (otherwise termed “sensory drive”), reproductive character displacement, and chance (Goodman et al. 2015). And in lacewings in the genus *Chrysoperla*, similar analyses (Henry and Wells 2004) did not reveal any correspondence between characteristics of vibration signals and mechanical properties of host plant stems and branches.

For acoustic insects, inquiry on signal diversification has yielded a markedly different picture than for vibration signaling. To date, there is no unequivocal evidence that features of the physical environment influence acoustic characters of insect song. Among birds and other vertebrates, such influences have sometimes been investigated under the rubric of the “acoustic adaptation hypothesis,” which proposes that a species’ sounds have been shaped by selection such that their transmission is maximized in the typical habitat (Morton 1975). Whereas some evidence in support of the acoustic adaptation hypothesis has been found for vertebrate species, particularly birds (Ryan and Brenowitz 1985; Wiley 1991), none has been revealed in comparable studies of acoustic insects (e.g., Jain and Balakrishnan 2012). Perhaps this difference reflects the shorter distances over which communication generally occurs in insects, which would impose less selection pressure favoring acoustic characters that engender maximum transmission in a habitat with a particular amount and type of clutter or other forms of interference. Some general features of insect song do appear to be adaptations for signaling in cluttered habitats, but there is little indication that they are specific characteristics of those species that frequent these environments. For example, broadband sound generally suffers less reverberation than pure-tone frequencies when transmitted through dense vegetation, a quality that would tend to preserve temporal patterns of amplitude modulation such as chirps and pulse rhythms (Römer and Lewald 1992). But broadband sound is characteristic of most cicadas, acridids, and tettigoniids, and it may simply emerge from the mechanisms of sound production in these groups. Similarly, most gryllids produce song with a rather narrow frequency band regardless of the physical habitat in which they signal (see Schmidt et al. 2013 on the adaptation of gryllid frequency bands to the biological habitat, the acoustic environment formed by other singing insects). Nonetheless, the recent analysis of a fossilized Mesozoic haglid, an extinct orthopteran group that is proposed as basal to all extant tettigonioids, indicates that these insects produced a resonant, pure-tone song via bilaterally symmetrical wings (Gu et al. 2012), a finding that may be instructive. It is inferred that such songs would have been transmitted effectively in the relatively open forests of that earlier era (cf. Römer 1993) and that asymmetrical wings and nonresonant production of songs composed of broadband frequencies—features that characterize extant tettigonioids—evolved later, possibly as the acoustic landscape changed. In an independent but parallel fashion, the ancestral condition in grylloids may have also been bilaterally symmetrical wings and pure-tone song. But asymmetric wings and broadband songs have evolved in one extant clade of eneopterine crickets (Robillard and Desutter-Grandcolas 2004). Possible selection pressures favoring such morphological and song novelty are unknown.

Among insects, the difference between acoustic adaptation and vibration adaptation, which does occur, is probably due to the strong dependence of vibration communication on the habitat. In general, the quality of a vibration signal is affected markedly by a change in substrate, whereas sound signals are affected much less by changes in the fluid medium and the general habitat, especially over short distances. Consequently, ecological speciation may be less likely to have been an important factor in the diversification of songs of acoustic insects.

2.6.2 On the Roles of Chance and Reproductive Character Displacement

If habitat is a relatively weak factor in the diversification of insect song, what accounts for the great variation in sound signals among acoustic insects? At a crude level, body size and morphology of the sound radiator may influence the carrier frequency of song, with higher frequencies generally found in smaller species (Bennet-Clark 1998). But species of a given size range often broadcast markedly different songs, and these differences usually involve temporal rather than spectral features. The best cases for analysis of song diversity in the time domain would be the several species-rich genera of nocturnal singers for which thorough phylogenetic analysis is available. Nocturnal singers are proposed because song is likely to be the major element of pair formation, as visual signaling is probably less critical. In North America two genera of Ensifera satisfy these criteria, *Gryllus* (field crickets; Gryllidae) and *Neoconocephalus* (coneheaded katydids; Tettigoniidae). Both genera exhibit a variety of intense male advertisement songs that include continuous “trills,” “whines,” and “rattles”; continuous songs that are interrupted with regular pauses; and discontinuous “chirps” that are repeated with a regular rhythm. The fundamental acoustic unit of these songs is the “pulse,” the sound emitted during one cycle of wing movement. Thus, songs are fashioned from a continuous train of pulses, a train that is regularly interrupted by a gap representing a certain number of missing pulses, or groups of pulses (chirps) that have their own group rhythm. Pulses may also be fused into “double pulses” by more complex cycles of wing movement (Walker et al. 1973; Walker 1975). When the different temporal patterns of song exhibited in a taxon are placed in an independent phylogeny, there are few evolutionary patterns that emerge (see Snyder et al. 2009 for *Neoconocephalus*). Analysis of *Gryllus* suggested that the ancestral song was composed of intermediate-length chirps delivered at intermediate but irregular rates and that a weak evolutionary “trend” toward an increased number of pulses per chirp may have been present (Desutter-Grandcolas and Robillard 2003; see Carroll 2001 on trends in evolution). In bush crickets (Eneopterinae), a comparable analysis of the worldwide fauna also suggested an evolutionary tendency toward increased redundancy in song (Robillard and Desutter-Grandcolas 2011). But the overall picture that emerges from these various studies is one of “dynamic” evolution characterized by a high level of convergence and multiple reversals of changes in character states (Desutter-Grandcolas and Robillard 2003).

Studies on diurnal acoustic insects, in which song may represent only a small portion of a male’s signaling repertoire, have added to the aforementioned impression. In *Drosophila*, where species differ in several temporal characters of male song, evolutionary trends are not apparent within the groups that have been analyzed (Hoikkala and Mazzi 2009). Similarly, analyses of gomphocerine grasshoppers, which are noted for complex, multimodal signaling (Otte 1970), have not revealed trends toward increasing complexity in song (Nattier et al. 2011). In summary, temporal song elements, being controlled by neuromuscular factors, may be particularly labile characters (cf. Fonseca et al. 2008), subject to additions, deletions, and other modifications by chance or by selection pressure for avoiding the attraction of heterospecific mates.

Genetic analyses on interspecific (Gleason and Ritchie 2004) as well as intraspecific variation in *Drosophila* (Gleason et al. 2002) and in the acoustic moth *Achroia grisella* (Limousin et al. 2012; Alem et al. 2013) generally indicate that several quantitative trait loci (QTLs) influence male song characters. These numbers can be interpreted only as minimum values. But, more importantly, some studies indicate QTLs having very major effects on song character variation (e.g., Gleason et al. 2002; Limousin et al. 2012), which suggests that an allele change at a single locus could result in a markedly different signal.

2.6.3 Does Reinforcement Occur in the Speciation of Acoustic Insects?

Whereas there is now little doubt that some amount of reproductive character displacement occurs among acoustic animal species (e.g., Höbel and Gerhardt 2003; Jang and Gerhardt 2006; cf. Walker 1974), the role of reinforcement in the divergence of sympatric populations and their eventual speciation has been less certain (Butlin 1987). The subtle distinction between these processes demands some initial clarification. In reproductive character displacement, two populations that have diverged completely in allopatry, to the point of becoming separate species, meet later in a secondary zone of contact. Owing to the disadvantages of expending time, energy, and gametes in the pursuit of heterospecific mates with which there is no possibility of fitness through producing hybrid offspring, either signals, preferences, or both evolve greater differences in the secondary sympatric zone than in the allopatric areas, where these enhanced differences are not particularly favored by selection. A related phenomenon involves selection on singing behavior in sympatry to avoid acoustic interference. For example, species that broadcast discontinuous songs may adjust their daily singing schedule such that they are not subject to interference from species broadcasting continuous songs (e.g., Greenfield 1988). In reinforcement, as strictly defined, the two populations have not separated entirely, and a hybrid zone exists between them (Liou and Price 1994). These hybrids, although viable, do have lower fitness than individuals in either allopatric population. The critical question is whether reduced hybrid viability can "reinforce" signal and preference differences while the populations still overlap in sympatry to the extent that fully separated species eventually form.

Recent models show that the process of reinforcement as described previously in this section is theoretically possible (Kelly and Noor 1996; Noor 1999; Ortiz-Barrientos et al. 2004), and various examples where sympatric speciation via reinforcement is likely to have occurred are proposed (Servedio and Noor 2003). Several acoustic insect genera exhibit well-known hybrid zones in different geographic regions of North America (e.g., Shapiro 1998; Britch et al. 2001), and it would be most appropriate to know whether reinforcement and incipient speciation are occurring in these situations or whether the hybrid zones are impeding speciation (Servedio et al. 2013). In addition, reinforcement in the past may have led to some of the fully separate species observed in these genera today.

2.6.4 On the Role of Pleiotropy in Song Evolution

When novel male mating signals evolve owing to chance or ecological factors, it does not follow that females in the population will necessarily respond to and prefer the novel signal. Biologists therefore have long sought to reconcile the stabilizing selection that generally characterizes mate recognition in animal species with the diversification of mating signals. Initial work on this problem began in the 1960s and led to formulation of the "genetic coupling hypothesis." Mating signals and references may be controlled by the same genes such that when a novel male signal appears, there is a female audience that prefers it (Alexander 1962). But various tests of genetic coupling, some conducted with acoustic insects (Hoy et al. 1977; Bauer and von Helversen 1987), failed to provide convincing support or refutation (Butlin and Ritchie 1989; Boake 1991). Instead, these breeding experiments showed how intractable the problem could be when approached via traditional methods.

The question of signal evolution in the face of stabilizing selection did not disappear, however, and recent availability of molecular genetic techniques has led to "next generation studies" using more direct approaches. These current studies ask whether signal and preference traits are influenced pleiotropically or by loci that are tightly linked physically. One of the more thorough tests of trait-preference pleiotropy, or physical linkage, has been conducted on *Laupala* crickets, a genus endemic to Hawaii that is distinguished by recent adaptive radiation and a great many species. Here, QTL studies have revealed a broad pattern of genomic "co-localization" of loci influencing male song and female preference (Shaw and Lesnick 2009; Wiley et al. 2012). But these co-localizations, particularly where they reflect actual pleiotropy, beg the question of how two seemingly disparate traits, one a motor activity and the other a perceptual and behavioral response to that activity, can be controlled by the same genetic element? In the case of *Laupala* song, the explanation may lie in a focus on timing—pulse rhythm—common to both the male song and female response and preference.

How common are cases of co-localization of signal and preference loci as reported in *Laupala* crickets, and could this phenomenon explain much of the song diversity observed among acoustic insects? At present, there is too little information to justify a definitive statement on the prevalence of co-localization. Whereas it has been found in various animal species using different signaling modalities in mating communication (Shaw et al. 2011), some studies have failed to confirm its presence (Löfstedt et al. 1989), including in acoustic insects (Limousin et al. 2012). It would therefore be safer to claim that co-localization may account for certain cases of speciation, particularly those entailing a high rate of divergence and simple differences in song that occur along a single character axis. In this regard, it is telling that population differentiation and speciation in *Laupala* are among the most rapid reported among animals (Mendelson and Shaw 2005), and song and preference differences are restricted to changes in pulse rhythm. In other words, co-localization may be the only genetic mechanism by which such high rates of diversification can be achieved. Thus, when co-localization happens to be present, speciation is likely to be the end result when allele changes appear between populations.

2.7 Summary

Tympanal organs for hearing in the far field have evolved on multiple occasions among insects and are currently found in seven orders. Many, if not most, cases of insect hearing probably originated as a means for detecting and avoiding predators. In particular, sensitivity to ultrasound appears to have coevolved with echolocation signaling by insectivorous bats. However, on an overall scale, hearing is relatively rare among insects in comparison with other modalities of perception, including detection of substrate vibration. Sound signaling in insects, which typically occurs in the context of mating communication, is rarer still and is known in only five orders. Phylogenetic analyses suggest that acoustic communication in the Lepidoptera and in the suborder Caelifera (grasshoppers) of the Orthoptera originated via a "sensory bias" mechanism. Hearing was ancestral and sound signaling by males subsequently arose on multiple, independent occasions. On the other hand, acoustic communication in the Cicadidae and in the suborder Ensifera (crickets, katydids) of the Orthoptera may have originated via coevolution between female perception and male signaling. The diversity of songs among acoustic insects may reflect genetic drift and reproductive character displacement. There is little evidence, however, that insect songs are adapted to specific physical environments. In one clade of acoustic insects, the diversification of song is associated with an unusually high rate of population differentiation and speciation, which may be facilitated by a genomic co-localization of loci influencing female response/preference and male signaling. The extent to which co-localization is a general factor in speciation remains to be explored.

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