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Sound Signalling in Orthoptera

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Abstract

The sounds produced by orthopteran insects are very diverse. They are widely studied for the insight they give into acoustic behaviour and the biophysical aspects of sound production and hearing, as well as the transduction of sound to neural signals in the ear and the subsequent processing of information in the central nervous system. The study of sound signalling is a multidisciplinary area of research, with a strong physiological contribution. This review considers recent research in physiology and the links with related areas of acoustic work on the Orthoptera.

1 Introduction

Many orthopteran insects are noisy, a lot are large enough for physiological and neurobiological research, and some at least are of economic significance. So, it is not surprising that orthopteran insects are popular with entomologists and much of the research on insect sound has been carried out using members of this order. Their large size relative to many other insects has enabled detailed studies of the nervous system and the ear, and analysis of hearing at the level of identifiable single neurons has been possible. As information has accumulated about the process of detection and analysis of both intraspecific and interspecific signals, from laboratory studies, it has been possible to carry out more detailed analysis of the behaviour of animals under natural conditions and this has included recording from identified interneurons in the field. Developments in the study of behavioural ecology, for example the interest in asymmetry and its role in mate choice, and the evolution of animal signalling, have opened up new areas of research, such as the degree to which the auditory system shows asymmetry at the neuronal level and the physiological costs of signals. The application of cladistic methods to the study of the evolution of the group has thrown up interesting problems, as the similarities between the auditory systems of members of the group at the neuronal level may not imply a common ancestry. As the process of integrating the results from physiological, behavioural and evolutionary studies gathers pace, it seems an opportune time to review recent advances in the study of the physiology of hearing and sound production in the Orthoptera. This is an extensive field of endeavour. In this review, we concentrate on the most recent physiological research and summarize the results and conclusions reported. In addition, we review some recent work in related areas of acoustic behaviour, physiological ecology and the evolution of acoustic systems that highlight the fact that much of the research on the acoustics of orthopteran insects is interdisciplinary. To keep this review to a manageable length, we have often provided references to other reviews that cover much of the earlier work, rather than citing earlier work ourselves.

The order Orthoptera is divided into two suborders, the Ensifera, which includes the true crickets (Grylloidea) and the bushcrickets or katydids (Tettigonioidea), and the Caelifera, which includes the grasshoppers and locusts. There are fundamental differences between the ears of the Ensifera and the Caelifera, which means that ears evolved more than once in the Orthoptera. Several unrelated taxa in the Caelifera do not produce sound and in this group the sound producing organs are not homologous. Thus there must have been multiple origins of sound production in the Caelifera (Riede, 1987; Riede et al., 1990). A recent review of the phylogeny of the Ensifera (Gwynne, 1995) suggests an evolutionary tree that satisfies multiple origins of signalling within the sub-order. He argues that both stridulation and ears have evolved independently in the Grylloidea and the Tettigonioidea basing his argument in part on the fact that his explanation is more parsimonious than one which suggests a single origin with multiple independent losses of hearing and stridulatory ability. If there had been a single origin, then there would have been four subsequent losses of tibial ears and fives losses of tegminal stridulatory organs at the family level, which seems inherently less likely. Furthermore, the raphidophorids are both deaf and mute and are the basal family in the tettigonioid clade. Thus deaf mutes are ancestral and the auditory and signalling systems we see today in gryllids and tettigoniids evolved separately after the separation of the two groups.

There is substantial evidence of homology in the neural elements that make up the auditory systems of the two groups, which might argue for a common origin, though it is possible that the auditory systems, though evolving separately, have nevertheless incorporated the same, pre-existing neural elements within the nervous system. The homologies between the neural elements of the auditory system are described in detail in Section 5.2.

The sounds of orthopteran insects are very diverse and often play a crucial role in reproduction so a substantial amount of research has been targeted on acoustic behaviour during phonotaxis and the neural bases of sound detection, localization and recognition mechanisms that underlie that behaviour (see e.g. Huber et al., 1989; Bailey and Rentz, 1990). These aspects of sound signalling will be considered in Sections 4 and 5. More recently, interest in aspects of mate choice has burgeoned (Section 6.6). However, there are other uses for sound communication such as male to male communication (Section 8), as well as unintended consequences, such as being overheard by an enemy or rival (Section 7), and these have almost certainly exerted an influence on the evolutionary history of the group.

The functions of acoustic communication and the selection pressures that have influenced the evolution of acoustic communication systems in Orthoptera have been reviewed by Greenfield (1997) and will be considered in Sections 6, 7, and 8. The structure, development and evolution of insect auditory systems has been discussed by Yager (1999) and a recent review of the evolution and function of auditory systems in insects (Stumpner and von Helversen, 2001) compares both the structure of the ear and the sound-activated interneurons in Orthoptera with other insect groups.

The study of auditory processing in the Ensifera has been extensive and has demonstrated some surprising similarities in the structure of the neuronal circuits in the central nervous system that are devoted to processing intraspecific signals (Mason and Schildberger, 1993). However, there appear to be differences in the organization of the circuits that are sensitive to ultrasound. The acoustic startle response that is triggered by the ultrasonic signals of predators is elicited via different central neuronal pathways in the true crickets (Gryllidae) and the bushcrickets (Tettigoniidae) (Libersat and Hoy, 1991). The mole crickets (Gryllotalpidae) are the most closely related ensiferan family to the true crickets but the organization of the ultrasound-sensitive auditory circuitry is different from that in the true crickets (Mason et al., 1998). The songs of mole crickets contain low frequencies only (Bennet-Clark, 1989) and the ability to detect ultrasound is likely to have evolved as a predator-detection mechanism since many mole crickets fly at night when insectivorous bats are active (Hoy, 1992a.See also Section 7.3). Auditory processing will be discussed in detail in Section 5.

2 Mating systems

2.1 Variation in mating systems

In Ensifera, the typical communication pattern between males and females is that males sing loudly and often continuously and the females locate the male by a phonotactic approach. Thus the males are speculative singers and selection tends to favour long and conspicuous song, despite the advertisement this provides to acoustically-orienting predators (see Section 7).

In the tettigoniids (reviewed by Robinson, 1990), the male produces an advertisement call. Some species also produce aggressive calls during male-male encounters and courtship songs immediately before copulation (e.g. Meixner and Shaw, 1986). In most species, the female is silent and approaches the male to mate but, in some ‘duetting’ bushcrickets, the female calls in response to the male and the singing rate of the male is influenced by whether or not a response is received (Robinson, 1980). Female song is restricted to three unrelated groups of the Tettigoniidae: it is common in phaneropterines, found in a few species of ephippigerines and may also occur in some pseudophyllines. In some duetting species, such as *Platystolus obvius*, the female still approaches the male, in others, such as *Leptophyes punctatissima* (Kilduff, 2000), the female remains stationary and the male approaches her; in yet others, such as *Steropleurus stali* and *S. nobrei*, either sex may perform phonotaxis in response to the other’s call (Hartley, 1993). In *S. stali*, it has been shown that the male approaches a responding female if she fails to perform phonotaxis; the more matings a female has had, the greater the delay before she starts phonotaxis, resulting in the male doing more and more of the approach (Bateman, 2001). Bateman suggests that the costs of phonotaxis are high for the female and/or the benefits of mating decline sharply after the first time.

Among the ephippigerines, there are two patterns of stridulatory behaviour (Hartley, 1993). Some species, such as *Ephippiger ephippiger*, call at a high rate and females do not reply but just perform phonotaxis towards the calling male. Other species, such as *P. obvius*, call sporadically and the female replies; this causes the male to increase his calling rate and the female then performs phonotaxis.

The stationary singing female system is common among the phaneropterines. In most duetting species of this type, the male call tends to be short and produced at long intervals, with the female call even shorter; only when a female response is received by the male does he increase his calling rate. In addition, the male will only perform phonotaxis if the female’s response falls within a very short time-window after his own call (Heller and von Helversen, 1986; Robinson et al., 1986). *L. punctatissima* provides an extreme example of a stationary female system: the male call is only 5-8 ms long, the female response is only 1-2 ms long, and the time-window is only 20-50 ms (Hartley and Robinson, 1976; Robinson, 1980; Robinson et al., 1986; Zimmermann et al., 1989). Such short songs are not good acoustic beacons, despite the fact that the ‘expectation’ of a response within a certain time window enhances the ability of the male to detect a female, so the selection pressures that produced them must have acted in opposition to the pressure for fast and accurate phonotaxis. The accuracy of phonotaxis in phaneropterines is thus of evolutionary, as well as physiological interest. The system may have evolved in response to predation pressure (see Robinson, 1990). It should be advantageous to the male, especially in the low-density populations found in many duetting species, not to sing unless a female is known to be present, because singing is energetically expensive (see Section 3.8) and risks attracting the attention of a predator (see Section 7).

Mating patterns among the gryllids (reviewed by Boake, 1983; Zuk and Simmons, 1997) are diverse but tend to be characterized by aggression between males, often accompanied by distinctive aggressive chirps, with possession of a burrow and large body size tending to increase the likelihood of success in male interactions. Males in most species do not invest substantially in courtship feeding (exceptions are the black-horned tree cricket, *Oecanthus nigricornis*, and *Gryllodes supplicans*: see Gwynne, 1997) or parental care. As far as mating is concerned, only male crickets sing and they may produce a number of different calls (Alexander, 1962). Males of most species send advertisement signals; the song is delivered from burrows or cracks in the ground, temporary shelters such as leaf litter, tree trunks, or in the open. Females approach calling males and, in many species, once a pair come into contact the male often produces a distinctive courtship song. Males of some species (for example in tree crickets and in the genera *Miogryllus* and *Anurogryllus*) also produce a post-copulatory call, which may function in mate-guarding.

Most mole crickets (Gryllotalpidae) call, tail outwards, from specially-constructed burrows that increase acoustic output (Walker and Figg, 1990). Some species produce a courtship song (Forrest, 1983; Hill, 2000) and/or an aggressive call (Ulagaraj, 1976) in addition to their advertisement call. Hill (1999) has argued that the prairie mole cricket, *Gryllotalpa major*, demonstrates classic lekking behaviour in that the males' burrows are spatially aggregated and serve only for sexual advertisement and mating.

The Haglidae contains only five extant species, three in the genus *Cyphoderris*. All three species of *Cyphoderris* show similar acoustic and mating behaviour in which males call and females approach to mate (see e.g.Dodson et al., 1983; Snedden and Sakaluk, 1992; Mason, 1996).

The Anostostomatidae, Stenopelmatidae and Gryllacrididae contain several relic groups of Orthoptera, including Jerusalem crickets, king crickets and wetas (the classification of these families is currently in dispute: see e.g. Johns, 1997; Gorochov, 2001; Hale and Rentz, 2001). Their mating systems are only recently becoming known (for reviews see Field and Jarman, 2001; Hale and Rentz, 2001; McIntyre, 2001; Monteith and Field, 2001; Toms, 2001; Weissman, 2001). Most anostostomatids do not have ears (Field, 2001b) and gryllacridids appear to have poor sensitivity to airborne sound (Hale and Rentz, 2001). This suggests that intraspecific sound communication is unlikely to play an important role in these groups, though there is some evidence that stridulation may be involved in courtship in some species, such as the Australian giant king cricket *Anostostoma australasiae* (Monteith and Field, 2001). Instead, many species appear to rely on vibratory communication (e.g. Jerusalem crickets: Weissman, 2001).

The New Zealand wetas are a notable exception to this general lack of sound communication. *Hemideina crassidens*, for example, not only has tympanal organs but they are tuned to the peak frequency of the conspecific song (Field, 2001b). Species of *Hemideina* (tree wetas) form 'harem' aggregations consisting of one male and several females within a refuge (Morgan-Richards and Gibbs, 2001; Field and Jarman, 2001). Males have greatly enlarged heads and jaws compared with females and use these in intense male-male aggression in defence of these harems (Jamieson et al., 2000; Koning and Jamieson, 2001). *H. crassiden*s is the only species for which a complete repertoire of sounds has been established, but observations on other *Hemideina* species suggest their acoustic behaviour is similar (Field, 2001b). *H. crassidens* males produce an advertisement call, an aggressive call in male-male encounters, and a 'mating' call after a failed mating attempt. Some females also produce aggressive stridulations. It has not yet been demonstrated, however, that females are attracted to male sounds in this or any other weta species and it is not clear whether the 'advertisement call' functions to attract females or repel rival males. Unlike other orthopteran species, the temporal pattern of advertisement calling varies enormously both within and between individuals, so much so that *H. crassidens* cannot be characterized as having a typical call type. It is even possible that each male has a unique pattern.

In contrast to tree wetas, giant wetas (*Deinacrida*) and ground wetas (*Hemiandrus*) appear to show little or no territorial or aggressive behaviour, though *Hemiandrus* males may defend their burrows (Field and Jarman, 2001). It is not clear whether communication using sound plays any part in mating (though *Hemiandrus* may use vibrational signals to attract females). In at least two species of *Deinacrida*, males are attracted to and follow females, possibly because they release pheromones. The African king cricket, *Libanasidus vittatus*, has also been shown to rely on olfaction for sexual communication; stridulation in this species is used in defence and in aggression towards other males but appears to have no role in sexual advertisement or mating (Bateman and Toms, 1998a; 1998b).

In many grasshoppers, males produce an advertisement call, which may serve in both territorial defence and sexual communication (e.g. Snedden et al., 1998). Some grasshoppers also produce a distinctive aggressive call, used in territorial defence (e.g. Greenfield and Minckley, 1993). In some species, the female approaches the male (e.g. Minckley and Greenfield, 1995), in others, notably in many of the gomphocerine grasshoppers, the female replies to the male's call and he approaches her (e.g. von Helversen and von Helversen, 1997). Males may also adopt a silent searching strategy and the ratio of time spent in acoustic advertisement compared with silent searching varies between species; when a male finds a female he may produce a courtship song (Green, 1995). The diurnal habit and often dense aggregations found in many grasshopper species allow them to make more use of visual signals than in nocturnal orthopterans; some species do not use acoustic signals at all.

Although locusts produce sounds, acoustic communication does not appear to play an important role in mating, except possibly at very close distances (Keuper et al., 1985).

2.2 Patterns of calling

Some orthopterans call mostly at night (e.g. most bushcrickets), others call mostly during the day (e.g. most grasshoppers), while others call both day and night (e.g. most crickets). Even within these broad categories, however, there are enormous differences in the diel pattern of calling. For example, Fischer et al. (1996) recognized six different patterns of calling in 14 species of grassland orthopterans during daylight hours: continuous throughout the day; peaking at noon, peaking in the morning; peaking before and after noon, only in the morning; and only in the evening. They also found that temperature and humidity can have considerable effects on the pattern shown by a species.

The variation in diel calling pattern among crickets has been reviewed by Zuk and Simmons (1997) and among nocturnal orthopterans by Walker (1983a). Both reviews argue that the time of calling should be expected to coincide with the period of maximum activity for females, i.e. when calling is reproductively more profitable than other activities. This is so in the mole crickets *Scapteriscus acletus* and *S. vicinus*: females fly during the few hours just after sunset, when predators are relatively few and temperatures are high enough to allow activity, and males call at the same time (Forrest, 1983).

Walker (1983a) points out that in nocturnal species, females mature through the day, so that there is an early evening peak in availability of responsive females; weather and predation also affect female numbers. Cold weather makes the female sluggish and more vulnerable to predation, so there will come a point where the costs of performing phonotaxis outweigh the benefits. Visually-hunting predators such as birds are probably the main reason why most crickets and bushcrickets mate at night. This is supported by the fact that species living in open vegetation (trees and bushes) mainly mate at night, while species in dense vegetation may mate during the day as well. Nocturnal predators can modify the pattern of female availability, for example if the predator is effective throughout the night but capture rates are low, females will benefit from the 'selfish herd' effect (Hamilton, 1971) of moving all together, i.e. during early evening. If, however, predators are not less lethal if all females move together, perhaps because they can temporarily specialize in that prey, then it is better for females to move when other females are not moving. If a predator threatens only for a short time, for example after dusk, then the evening peak of availability should be postponed until the earliest safe time. If females mainly perform phonotaxis at times when high numbers of males are calling (thereby enhancing their choice of mates), even higher proportions of males should call during the time of maximum calling, producing a concentration of calling in the temporal analogue of a lek, which Walker calls a spree.

As well as availability of females, profitability of calling at any particular time is also influenced by transmission conditions (for example daytime thermal gradients can create sound shadow zones in which calls are inaudible at distances they easily reach at night), the male's risk from predators, and his energetic costs (Walker, 1983a). Many species are flexible – for example, they sing at night unless the temperature is too cold, in which case they sing during the day (Zuk and Simmons, 1997). The importance of temperature can be seen from the fact that some warm-climate species of crickets and bushcrickets show a very different diel pattern of calling compared with that typical of temperate species (Walker, 1983a).

3 Songs and signals

The sounds produced by orthopteran insects not only cover a wide range of audible frequencies but extend well into the ultrasonic range. The size of most species is such that the efficiency of sound radiation is greater at higher frequencies. Size and scale effects in sound communication in insects have been reviewed by Bennet-Clark (1998). If the sound producing structures are small relative to the wavelength of the sound that they produce, there will be a mismatch in impedance between the insect and the air (Bennet-Clark, 1989; 1995). The sound source should have a diameter that is greater than one third of the wavelength of the sound produced to obtain a good impedance match (Bennet-Clark, 1999). High frequency sounds are generated by structures that act as frequency multipliers (Michelsen and Larsen, 1985). A scraper, the plectrum, rubbing along a line of teeth strikes each tooth at a rate that determines the frequency of the sound produced. Thus in *Gryllus campestris*, for example, where the sound producing apparatus is on the tegmina (forewings), an area of the wing, called the harp, is the primary resonator and the harp of the right wing is driven directly from the file of teeth. The harp on the left wing resonates in phase with the harp on the right. The size of the harp determines the resonant frequency, with larger area harps having lower dominant frequencies (Simmons and Ritchie, 1996). The frequency of wing closure is 30 Hz, but on each closure a large number of teeth are struck by the plectrum and the frequency of sound produced is 4.5 to 5 kHz (Bennet-Clark, 1999). Thus the combination of a resonant harp and a repetitive driving force from the tooth strikes produces frequency multiplication. Sound production is discussed further in Section 3.2.

The terminology used to describe the songs of orthopterans is far from being standardized. Broughton (1963; 1976) proposed a set of terms that has been partially adopted and Ragge and Reynolds (1998) have developed his terminology. However, it is not used universally and has not been adopted generally outside Europe. So, in our descriptions of recent research we have followed the terminology used by the original authors.

The structure of the songs of orthopteran insects is very diverse and in the tettigoniids often highly specialized. The length of songs ranges from under 1 ms in duration to continuous tones lasting minutes. The frequency content ranges from below 1 kHz to over 100 kHz and the intensity of sound may be as high as 95 dB SPL at 1 m. For a detailed account of the properties of the calls of orthopterans, readers should consult the recent review by Greenfield (1997). Here, we describe some examples of atypical sound communication of significance in recent research.

3.1 Intensity, distance and size

Mole crickets produce very loud sounds, achieving the high volume by the use of a second, larger acoustic resonator – the burrow that the insect lives in. The burrow is tuned to the same frequency as the primary resonator, the harp, and there is the potential for fine-tuning of the resonant frequency of the burrow. An advantage of the secondary resonator is that it is larger than the primary one and so more closely matches the impedance of the air. For the mole cricket *Gryllotalpa vineae* this give an estimated transduction efficiency of between 17 and 34% (Bennet-Clark, 1970) and the song is audible at a distance of several hundred metres.

The bladder grasshopper, *Bullacris membracioides*, signals over a very long distance, probably the longest distance so far recorded for acoustic communication in insects. From measurements of the threshold of hearing of the female and the decline in sound intensity with distance of the male call, the maximum possible communication distance is estimated at 1.9 km (van Staaden and Römer, 1997). This distance could only be achieved at night; during the day the best distance that could be achieved is 100-150 m. The explanation for this is probably to be found in the thermal conditions. The speed of sound in air decreases with decreasing temperature. During the day, temperature decreases with height and refraction of sound causes sound waves to bend upwards at boundaries of layers of air at different temperatures. At the start of the night as the ground cools a temperature inversion occurs (Larom et al., 1997) with cooler air closer to the ground. Under these conditions, sound energy is refracted downwards and there is a channelling effect that reduces the rate of attenuation of the sound.

In general, larger male orthopterans produce louder calls and the calls contain lower frequencies. In the tettigoniids, very small species generally have very high frequency calls, for example small phaneropterines where the frequencies are well into the ultrasonic range (Heller, 1984; Robinson, 1990). However, in crickets there appear to have been selection pressures to keep the frequency of the calling song low and so the sound production mechanism of one of the smallest stridulating gryllids, *Cycloptiloides canariensis*, shows adaptations that maintain a low frequency call despite the problems of the small body size. The tegmina are similar in structure, as in other crickets, with the left tegmen a mirror image of the right, but whereas tettigoniids generally stridulate with a left-over-right movement (see the review by Masaki et al., 1987) and field crickets with a right-over-left movement, this cricket has no preferred orientation. The tegmina overlap randomly at rest and during stridulation. The characteristic frequency of the song is between 5.7 and 6.1 kHz. The tegmina are minute, roughly 2.3 mm wide by 1.7 mm long, smaller than the mirror cell (see Section 3.2) of *Gryllus campestris*, and the mirror cell is about 25% of the area of the whole tegmen (Dambach and Gras, 1995). It is extremely thin, with a mean thickness of 0.2 µm. For comparison, the mean membrane thickness in *G. campestris* is 2.5 µm (Nocke, 1971). The mirror cell in *C. canariensis* functions as a resonator, in conjunction with both the lateral harp and a strip of cuticle between the mirror cell and file (Dambach and Gras, 1995). The small size of the mirror gives it a low radiating resistance and hence poor sound emission. For such small insects high sound levels could only be maintained if the frequency were higher. However, *C. canariensis* has not made such a shift and retains a call with a frequency range of other crickets. To maintain resonance at a particular frequency, a smaller membrane must be thinner and it appears that the thin membrane is an adaptation to the frequency of the song. The intensity of the song of *C. canariensis* is low (30 dB SPL at 1 m), a consequence of being an insect that is 5 to 7 mm long (Dambach and Gras, 1995) producing a sound with a frequency of 6 kHz and a wavelength of 55 mm.

3.2 Mechanisms of sound production

The mechanism by which male crickets produce sound was outlined in the introduction to Section 3. The file of teeth on each wing is a thickened Cu2 vein, which forms one side of a triangular wing cell, the harp (for a review of the physics of sound production in crickets see Bennet-Clark, 1999). As each tooth on one wing is struck by the plectrum on the anterior medial end of the other file, the vibrations in the Cu2 vein on each wing cause the harps to vibrate and radiate sound. The frequency of the radiated sound (f_C) is given by the rate of tooth impact, known as f_{PFI} (plectrum-to-file impact rate). The rate at which the wing moves clearly should effect f_C, so as temperature affects the rate of wing movement it would be expected that f_C too would be dependent upon temperature. In fact, f_C changes only slightly with temperature. This apparent paradox had been investigated by a number of workers and has produced conflicting views. Elliott and Koch (1985) proposed an escapement model to explain the paradox, known as the ‘clockwork cricket’. They envisaged the interaction between the plectrum and the file as a discontinuous process, in which the plectrum is held briefly by a tooth when it comes into contact. The vibration of the harp is in phase with the tooth strikes, so as the harp reverses its direction of movement, the plectrum is released and bounces to the next tooth where it is again held. So, it is the resonance of the harp that determines f_{PFI} and thus f_C remains roughly constant (Elliott and Koch, 1985).

This interpretation has been criticized (Stephen and Hartley, 1995b), perhaps because the analogy with a clock is less than perfect. For example, if the cricket mechanism was equivalent to a clock escapement mechanism then the song should be characterized by a single frequency, which would be relatively constant. In fact the spectrum of *Gryllus bimaculatus*, measured by Stephen and Hartley (1995b), contains a peak at 4.75 kHz and one at 5.6 kHz. Their analysis of the principal frequency component of consecutive calls showed that f_C was not constant, having a mean value of 4.65 kHz and a maximum percentage variation of 4.5%. These characteristics do not fit a clock escapement mechanism. The pulse-to-pulse variation in f_C in the cricket *Anurogryllus arboreus* is 1%, still too great to be explained by an escapement mechanism of a clock type (Prestwich et al., 2000). Stephen and Hartley reject the clockwork escapement mechanism, partly on the basis of the frequency evidence. That the escapement analogy might still be useful in describing sound production, providing it is not expected to have the precise functions of a clock mechanism, is an argument put forward by Prestwich et al. (2000).

When the tegmina are raised while a cricket is singing there is a partially enclosed airspace underneath (Bennet-Clark, 1989; Ewing, 1989). It has been suggested (Stephen and Hartley, 1995b) that singing insects can control the resonant frequency of the subalar airspace and hence f_C. A comparison of the calls of insects in air and in a mixture of oxygen and helium gases (heliox) showed that f_C had a mean value of 4.86 kHz in air but 5.15 kHz in heliox (Stephen and Hartley, 1995b). When the insects were deafened and the measurements in air repeated, the frequency of the chirps varied widely, suggesting that in the intact insect feedback from the ear might be used to adjust the subalar space and hence f_C. Measurements of f_C in *A. arboreus* in both air and heliox also showed an upward shift (Prestwich et al., 2000). Interestingly in two tree crickets, *Oecanthus celerinictus and O. quadripunctatus*, which do not have subalar spaces, a similar upward shift of f_C was observed in heliox (Prestwich et al., 2000), which suggests that frequency shifts in heliox have some other explanation. If the harps of the cricket are to function as good resonators they need to be damped by a relatively heavy air load (Bennet-Clark, 1989). Calculations by Prestwich et al. (2000) suggest that the frequency shifts observed in heliox are a consequence of a reduction in the system mass as a result of a change in the gas load portion of the system, heliox being 40% as dense as air.

In male bushcrickets, there is a file of teeth on the lower surface of the left tegmen that is struck by a plectrum on the upper surface of the right as the tegmina are rapidly opened or closed. The vein that forms the plectrum is attached to an area of the tegmina called the mirror frame, surrounding a thinned area – the mirror. The mirror and mirror frame vibrate as each tooth is struck and radiate sound, at a frequency determined by the resonance properties of the cuticle (Bailey, 1970; Bailey and Broughton, 1970). If the f_{PFI} is close to the resonant frequency of the vibrating elements of the tegmen, then a long song of high intensity can be produced, for example the 15 kHz song of *Ruspolia nitidula*, with the individual tooth impacts not being represented in the song. The song is close to a pure sine wave (Stephen and Hartley, 1995a). However, in most bushcrickets each tooth impact with the plectrum produces a set of oscillations that decay rapidly before the next impact and the tooth impact transients are visible in oscillograms of the song. Sound may be produced on the opening or closing movement of the tegmina, producing one syllable per cycle of wing movement, or on both movements of the tegmina producing either similar syllables or very different syllables. This is well illustrated by a comparative study of nine tettigoniid species (Jatho et al., 1994).

When *R. nitidula* was induced to sing in a heliox atmosphere, the frequency of the sound fell (Stephen and Hartley, 1995a) and the song became less harmonic, with irregularities that suggest that the tuning of the sound production system had been lost. Heliox does not affect the syllable repetition rate or syllable duration, but does reduce both frequency and intensity (Hartley et al., 2000). It has been suggested that the results from the heliox experiment can be explained by postulating a role for the subalar (subtegminal) space as a load on the tegminal resonator, a proposal discussed earlier in relation to the effect of heliox on gryllid song. Thus a song consisting of a series of brief transients would be amplified and filtered by the air in the subalar space (Hartley et al., 2000). However, if this is correct then heliox would be expected to raise the frequency, as observed in experiments on *Gampsocleis gratiosa*. The explanation offered for the decrease observed in *R. nitidula* is that the insect is able to regulate the subalar space (Stephen and Hartley, 1995a; b).

Clearly we are only part of the way to getting an explanation of the mechanism of sound production in gryllids and tettigoniids and further work is needed in this rather controversial area.

Acridids are distinct amongst animals that produce sound in that they utilize two organs simultaneously to generate sound. Each hindleg when rubbed against the forewing generates a sound and the sounds produced by the two legs are almost always out of phase with each other. Furthermore, in some species the phase shift is not fixed and can vary such that the leading leg in one song can become the trailing leg in the next (Elsner, 1974; Elsner and Wasser, 1994). Males and females of a particular species have essentially the same song pattern and they stridulate in the same way. The file on the hind femur of the male is homologous with that of the female, although electron micrographs show that the pegs that form the file, although derived from modified bristles in the male, are derived from the surrounding bristle cup in the female (von Helversen and von Helversen, 1997).

3.3 Pattern generation in crickets

In crickets and grasshoppers, stridulatory movements of wings or legs are generated by networks of neurons in the thoracic ganglia that produce patterns. Control of stridulatory behaviour is exerted by the brain, as the classical experiments of Huber (1960) have demonstrated. Much of the earlier work is reviewed by Huber et al. (1989). Descending neurons from the brain to the thoracic ganglia were identified initially from experiments involving stimulation of fibres in the neck connectives of crickets (Bentley, 1977) and subsequently single descending neurons that could elicit stridulation were identified in the grasshopper *Omocestus viridulus* (see Hedwig, 1994) and the cricket *Gryllus bimaculatus* (see Hedwig, 1996). The metathoracic ganglion and the first three abdominal ganglia form a complex in which the species-specific stridulatory pattern is generated (Elsner, 1994). Thus the control of stridulation is separated both in terms of function and structure within the nervous system.

Although electrical stimulation of the brain can induce stridulation (Wadepuhl, 1983), localization of regions of the brain involved in the control of stridulation have been identified using pharmacological stimuli. Injection of acetylcholine (ACh) into the medial dorsal neuropile of the protocerebrum reliably elicits continuous stridulation in *O. viridulus* and *Chorthippus mollis* (Ocker et al., 1996) and is also effective in crickets (Otto, 1978). Using microelectrodes filled with ACh, Hedwig and Heinrich (1997) were able to show that most locations in the protocerebrum were not involved in stridulation. However, injection of ACh in areas where the descending command neurons are known to arborize (Hedwig, 1994) elicited stridulation reliably. Injection of fluorescent latex particles at the same time as ACh, followed by histological examination (Heinrich et al., 1997) has confirmed that the brain areas in which stridulation is produced most reliably are posterior and dorsal to the central body in the region through which the command fibres pass. When the muscarinic agonist pilocarpine is injected into the same area (Heinrich et al., 1998) long-lasting stridulation can be elicited, lasting many minutes. A subsequent injection of GABA terminates the stridulation, demonstrating that there is a role for inhibitory mechanisms in the control of stridulatory behaviour.

Recent work on the control of stridulation in grasshoppers has demonstrated that stridulation is not a single behavioural event but that normal courtship involves the successive performance of three different stridulatory movements, all under the control of the brain. In *O. viridulus*, four types of stridulatory behaviour can be elicited by ACh stimulation, the complete sequence of courtship behaviour and three separate components. The separate components have been described as ordinary stridulation, hindleg shaking and precopulatory movements (Hedwig and Heinrich, 1997). Each appears to be under the control of a single command neuron. The picture that emerges from these results is of an area of the brain that initiates stridulation, which is then controlled through the coordinated activity of the descending command neurons. The command neurons are bilateral and elicit the stridulatory patterns in the metathoracic ganglion.

At the level of the metathoracic ganglion there is clear evidence that the pattern generation is organized separately for each leg, with the pattern generated in each hemiganglion driving the ipsilateral leg (Ronacher, 1989; 1991). Bisecting the metathoracic ganglion with a median transection in three species of grasshopper showed that in each one the phase differences between left and right legs were abolished (Heinrich and Elsner, 1997) and both legs then followed the same pattern. A difference was observed when the fast movements of *Chorthippus biguttulus* were compared with the slow rhythm of stridulation in *O. viridulus*. In the fast movements of *C. biguttulus*, the left and right leg patterns gradually drifted, showing that they were free-running. In contrast, the slow movements of *O. viridulus* remained in synchrony. This cannot be achieved through the influence of the brain since no information about rhythm is carried in the descending command fibres (Hedwig, 1994; Hedwig, 1995). Information about the slow movements is carried to the suboesophageal ganglion by ascending fibres and within the ganglion the stridulatory rhythm of the two legs is synchronized; this synchronicity is transmitted back to the metathoracic ganglion by descending fibres (Lins and Elsner, 1995).

3.4 Changes in sound signals with age

The physical structures associated with sound production are susceptible to mechanical wear and in some individuals where the number of wing closures per second is high, there may be substantial forces operating on the cuticle. This will introduce variability into the song patterns in a population. It is of great interest to determine how far such variability is acted on by sexual selection or natural selection and which properties of the song are under the greatest selection. Furthermore, as populations age, there may be shifts in the pattern of variability of the male song, consequent upon predation of a particular subset of individuals.

3.4.1 Changes with age in individuals

Age effects on mating success have been demonstrated in one bushcricket species, *Ephippiger ephippiger*, where females discriminate against the song of older males (Ritchie et al., 1995). In this study the song of males was shown to change over the course of time, as a consequence of changes in the stridulatory apparatus. When presented with simulated songs that reproduced features of the song of aged males and offered the choice of an unaltered song type typical of a young male, females showed a strong preference for the young male song. Degenerative changes in the file structure of bushcrickets occur as a result of abrasion of the teeth on the file or breaking of the teeth (Hartley and Stephen, 1989; Ritchie et al., 1995) and these influence song structure. The song produced by *Poecilimon schmidti* shortly after ecdysis is a pure tone burst at a frequency of 36 kHz (Hartley and Stephen, 1989). After a week of singing activity, the song starts to degrade, with aharmonic components appearing in the spectrum. The syllable length increases, being almost twice as long after 5 weeks. However, some other studies have not shown a relationship between calling properties and age, for example in *Gryllus pennsylvanicus* (Ciceran et al., 1994).

3.4.2 Changes with age in populations

The most comprehensive recent study of age structure and calling song within an ensiferan population is that of Allen (2000), on the Australian bushcricket *Sciarasaga quadrata*. Analysis of the song parameters showed that, relative to other males, there was a lifetime consistency in call properties of an individual. In the population, frequency showed low variability, but there was greater variability in chirp length, interchirp duration and duty cycle. Gaps in the tooth pattern within chirps were recognisable in 13 out of 55 males at the time of collection. Of 15 collected at the start of the season and held in the laboratory, 7 showed gaps by the end of the season. This may indicate the effects of wear, but the gaps are not consistently visible in syllables, with typically less than 40% of syllables in an individual’s call showing a gap. However, in the population as a whole a shift was observed towards songs with longer chirps as the season progressed, even though there was no association between chirp length and adult life span. Allen suggests that the most credible explanation for this shift lies in the effects of parasitism by the fly *Homotrixa alleni*. Only 6% of adult males escape parasitism and it would appear that shorter-chirp males are at greater risk. The songs of early season males collected in October and held in the laboratory were compared with a sample of end of season males collected in January. The surviving males had longer chirp lengths and also longer duty cycles. There was a high positive value for the selection differential for both chirp length and duty cycle, supporting the idea that shorter-chirp individuals are removed selectively from the population. The activities of acoustically-orienting parasitoid flies are discussed in more detail in Section 7.2.

3.5 Vibratory communication

Substrate vibrations can be detected by Orthoptera and a number of examples are known where vibration is related to, or replaces calling song. Rain forest tettigoniids have been reported as switching to the use of vibratory signalling in areas where bat predation is a risk (Belwood and Morris, 1987; Mason et al., 1991) (see Section 8.3). *Myopophyllum speciosum* is a pseudophylline tettigoniid from the neotropics that uses unusually high ultrasonic frequencies in its calling song, with a mean dominant carrier of 81 kHz (Morris et al., 1994). Vibrational signals with a much shorter range are used in the latter stages of pairing and this may also be the result of a selective response to bat predation.

Tettigonia cantans males perch on plant stems to sing, but through contact between the body and the stem a vibratory signal with a similar temporal pattern is produced which may be used by the female in the latter stages of phonotaxis (Keuper and Kühne, 1983). Although it has yet to be demonstrated to have biological significance, the song of the mole cricket *Gryllotalpa major* has a low frequency component that travels through the substrate and could be detectable up to 3 m away (Hill and Shadley, 1997). It is possible that this will be shown to have significance in male spacing, particularly important in mole crickets where the burrow represents a sizable investment for the male.

3.6 Sex differences

The song of the male bushcricket *Ancistrura nigrovittata* consists of a series of verses, each verse comprising several syllables forming a group and a single syllable after an interval, at the end of the verse. The final single syllable appears to act as a trigger for a female response (Dobler et al., 1994a). All these syllables have the same carrier frequency with peak energy in the range 12-17 kHz. The female song is a single syllable with maximum sound energy between 20 and 35 kHz (Dobler et al., 1994b). This sex difference in frequency spectrum is unusual and not found in other related species that have been studied.

The stridulatory apparatus of female phaneropterine bushcrickets and also some ephippigerines is not homologous with that of the male (Robinson, 1990), the plectrum being on the lower surface of the left tegmen and the file on the upper surface of the right. Once again, the diverse evolutionary origins of sound communication in orthopterans is highlighted.

3.7 Temperature effects

As orthopterans are thermal conformers, temperature can be expected to exert an influence on all the physiological processes associated with sound production. Ambient temperature and heat radiation have been shown to influence the temporal pattern of the male song in tettigoniids of the ephippigerine family (Jatho et al., 1992) and in *Orchelium* (see Walker, 1975). Chirp rate and chirp duration can both change in response to temperature in acoustic interactions between males (Latimer, 1981a; b). In *Ephippigerida taeniata* the range of temperatures over which chirp-rate and alternation is altered is 19-27 ^{o}C. The chirp rate increases over this range of temperatures, but then appears to reach a maximum as the rate at 35 °C is not significantly different from that at 27 °C (Stiedl et al., 1994). The lower temperature limit for stridulation has been measured (Stiedl and Bickmeyer, 1991) as 15-17 °C in *Ephippiger ephippiger*.

In crickets the pulse rate of the song increases linearly with temperature and this relationship has been demonstrated in a number of species (Doherty and Callos, 1991), for example the trilling cricket *Gryllus rubens* and the chirping cricket *G. fultoni*. The effect of temperature on pulse duration in *G. rubens* was less pronounced than in *G. fultoni*, but it still increased with increasing air temperature. Frequency did not show a significant link to temperature. Similar results have been reported for *G. bimaculatus*, where pulse period (reciprocal of pulse rate) was shown to decrease logarithmically with temperature (Doherty, 1985).

3.8 The energetic costs of calling

Prestwich (1994) has reviewed the energetics of acoustic signalling in insects. The energetic costs of advertisement calling in orthopterans can be very high, requiring on average a ten-fold increase in metabolic rate. In species that call rapidly and loudly, calling can use as much energy as locomotion and can form an important component of the energy budget. Repetition rate, call duration and intensity (SPL) of the call all interact to determine the total energetic cost. Efficiency of sound production (acoustic power/net metabolic power) is low, ranging from 0.05 to 6%, compared, for example, with locomotion, where efficiencies range from about 10-20%. Insects producing acoustic advertisement signals have also been shown to have higher mass-independent resting metabolic rates compared with closely related species that do not call (Reinhold, 1999). The energetic costs of calling can be particularly high in species where females tend to choose those males that call for longest, or at the highest rates, or the loudest (Burk, 1988. See also Section 6.6). In the variable field cricket, *Gryllus lineaticeps*, for example, metabolic rate increases with increasing chirp rate and pulse duration and females prefer higher chirp rates (Hoback and Wagner, 1997). Courtship song can be even more expensive than advertisement song: in *Acheta domesticus* for example, the energetic cost of courtship calling is over twice as much per unit time as the cost of advertisement calling (Hack, 1998).

In some species, there is a trade-off between locomotion and calling. Wing dimorphism, in which one morph is long-winged and capable of flight and the other is short-winged and not capable of flight, is common in the Orthoptera (Crnokrak and Roff, 2000) and in *Gryllus firmus*, for example, macropterous males call less than micropterous males and as a consequence attract fewer females (Crnokrak and Roff, 1995). Crnokrak and Roff (2000) have shown that this trade-off is an energetic one mediated by lipid stores: the energy required to maintain the flight apparatus reduces the amount of energy available for calling. Male field crickets (Gryllidae) employ alternative strategies of calling or silent searching for females dependent on population density: at higher densities, the payoff in terms of finding mates is greater for silent searching, while at lower densities, the payoff is greater for advertisement calling (Hack, 1998).

There may also be a trade-off between calling and energy investment in courtship feeding in some species. For example, *Requena verticalis* produces a large spermatophylax (Gwynne, 1990), consisting of about 20% of body weight and representing a large energy investment (spermatophore production may cost the male an average of 0.22 kJ g-1 per day: Simmons et al., 1992). *R. verticalis* males call with slow syllable rates (Bailey et al., 1993b) compared with other species of bushcricket such as the coneheads of the genus *Neoconocephalus,* which call at much higher rates but invest negligible amounts in courtship feeding (Greenfield, 1990; Prestwich, 1994). As a result, net metabolic cost of calling (total metabolic cost less resting cost) in *R. verticalis* is an order of magnitude less than the net cost for e.g. *N. robustus* (Bailey, 1995). *R. verticalis* males also control the distribution of energy reserves between calling and spermatophylax production (Bailey, 1995). After mating, they cease calling while a new spermatophore is produced. There is no difference in spermatophylax size between males on high-quality diets compared with those on low-quality diets, but the former are able to resume singing more quickly and sing for longer periods than the latter, indicating that reserves are allocated preferentially to spermatophylax production.

There is also evidence in some species that, in populations that are nutrient stressed, males reduce their calling activity, for example in *Ephippiger ephippiger* (Ritchie et al., 1998) and *Gryllus lineaticeps* (Wagner and Hoback, 1999). In *G. lineaticeps*, this appears to be because males have less energy available for calling. *E. ephippiger* may call less for the same reason but, because males produces a very large spermatophylax (up to 40% of body weight: Ritchie et al., 1998), and nutrient-deprived females compete for matings with males, an alternative explanation is that this female competition simply allows males to reduce their calling levels without suffering a reduction in mating success.

4 Hearing and ears

Hearing has evolved several times in orthopteran insects and probably in different behavioural contexts. In some grasshoppers the ability to hear is much older than the ability to communicate using acoustic signalling (Riede et al., 1990) and it seems possible that hearing may initially have developed as a response to predation, providing a predator avoidance system (Section 7.5). In the Ensifera, hearing probably developed from a communication system based on vibration and may have evolved in parallel with the sound production system for mate recognition and location. There have been later evolutionary changes, of course. For example, secondary loss of hearing is known in both bushcrickets

(Lakes-Harlan et al., 1991) and crickets (Otte, 1990). Despite the diverse origins of the auditory systems of the Orthoptera, there are a large number of features that appear to have either a common origin or a parallel development. This commonality is particularly apparent when the neuronal pathways in the segmental ganglia are compared (see Section 5.2.3). An interesting question is how hearing systems that have evolved independently turn out to look similar and function in essentially the same way.

Processing of auditory information is carried out differently in grasshoppers compared with crickets and bushcrickets, which have very similar processing. The fundamental difference lies in the degree of separation of the inputs from the two ears. In bushcrickets and crickets information from the two ears is processed separately for recognition and then subsequently a comparison is made for determining the location of the source. Thus there is discrimination of quality of song on each side. Furthermore each side has a representation of the loudest sound, improving discrimination when more than one source is present, such as when many males are calling at the same time. In grasshoppers, both directional and recognition information are processed together in parallel (von Helversen and von Helversen, 1995). Information about the patterning of the sound is received in the metathoracic ganglion and there pooled before being transferred to higher processing centres. The combination of information about pattern recognition from the two ears in ascending neurons gives poor directional information. Directional information travels in a separate channel, probably formed by the two phasic ascending neurons AN1 and AN2 (See Section 5.2.3). Parallel processing has arisen as a result of hearing and localization being older than acoustic communication in grasshoppers, with the result that evolution has overlaid an existing auditory system with adaptations for communication. In the Ensifera, hearing and stridulation probably evolved in parallel and so from early on there was selection for localization and the detection of species-specific song patterns in the nervous system. However in the haglids, a group that is probably a relict of the ancestral members of the tettigonioid clade, atympanate auditory reception evolved prior to the tibial tympanal organs. Auditory processing in the nervous system therefore predated the evolution of tympana.

There have been several recent reviews of aspects of sound reception and processing. The neural processing of acoustic signals has been considered by Pollack (1998) and the analysis of sound frequency in insects by Pollack and Imaizumi (1999), while Field and Matheson (1998) and Eberl (1999) have reviewed the physiology of insect chordotonal organs. Boyan (1998) has considered the development of insect auditory systems. However, there have also been a number of substantial studies published since these reviews, an indication of the interest that this research area has engendered, and these are described in this Section.

4.1 Structure of hearing organs

There are two parameters that are used by insects to detect sound in air. If the distance between transmitter and receiver is short, generally less than one wavelength, then a receptor that responds to the particle velocity of the incident sound can give information about the location of the source, as velocity is a vector. Close to a sound source the relative magnitude of the particle velocity is high, compared to the sound pressure. At distances much greater than one wavelength from a source, sound travels as a plane wave and sound pressure is the predominant parameter. Sound pressure receptors, such as the ears of orthopteran insects, can provide directional information if they are sufficiently far apart that there are measurable differences in either time of arrival at each ear or sound intensity at each ear. Most insects are too small for such a direct measurement to be possible. In the Orthoptera, sound stimuli can act on both sides of the tympanal membranes in the ear and thus it is a pressure gradient that the ear detects. The pathways by which sound reaches the inner side of the membrane introduce a phase shift, which may involve interaural coupling. The general effect is to enhance the difference in membrane excitation between the two ears and so provide directional information. At high frequencies, such as those used by tettigoniids, interaural differences may arise from diffraction around the body, if the wavelength is less than three times the body width.

The primary studies of the bioacoustics of orthopteran ears were carried out by Michelsen, starting with the Caelifera (Michelsen, 1971a; b; c) and subsequently the Ensifera (Larsen and Michelsen, 1978; Michelsen and Larsen, 1978; Seymour et al., 1978). In recent years there have been further studies that have expanded this work, but most attention has been focused on the tettigoniid ear (reviews by Bailey, 1990; 1993).

4.1.1 The tettigoniid ear

The hearing organs of bushcrickets are located on the tibia of the forelegs just below the joint between the femur and tibia (Sickmann et al., 1997). Although all three pairs of legs contain tibial organs comprising a subgenual organ, an intermediate organ and a crista acustica, only in the foreleg is the tibial organ adapted for sound reception. The single trachea from the prothoracic spiracle passes down the leg and divides in the tibia to give two closely adhered branches (Fig. 1) separated by a central membrane. The outer walls of the trachea are modified to form the tympana, which may be exposed, as in *Polysarchus denticauda* (Sickmann et al., 1997) or protected within a cavity that communicates with the exterior by longitudinal slits, as in *Ruspolia differens* (Fig. 1). The original morphological study of the tettigoniid tympanal organ (Schwabe, 1906) did not recognize the acoustic role played by the prothoracic spiracle and the trachea.

Since the demonstration of the role of sound entry via the prothoracic spiracle (Lewis, 1974) there has been increasing study of the tettigoniid ear in an effort to understand the sound transduction mechanism. However, while it is agreed that the spiracle is the main source of sound entry (see e.g. Nocke, 1975; Hoffmann and Jatho, 1995), there is less agreement on the transmission properties of the acoustic trachea.

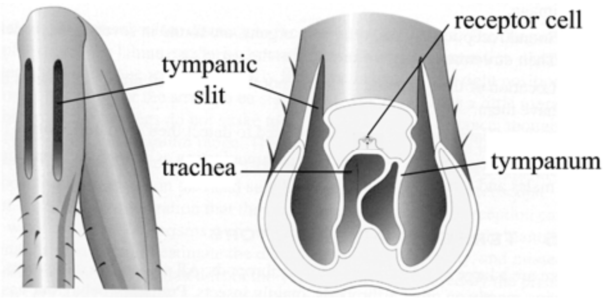

FIG. 1 Structure and location of the tibial hearing organ in a bushcricket.

The acoustic trachea approximates to an exponential horn in a number of species where morphological measurements have been made and it has been shown to have a high pass characteristic, imparting a gain of 15-20 dB (Hoffmann and Jatho, 1995). A horn of this type will have a broad-band transmission above the cut-off frequency, so it is not the trachea that provides the tuning of the ear. There are several candidates, notably the resonances in structures associated with the receptor organs (Lin et al., 1994; Hoffmann and Jatho, 1995). It has also been suggested that the individual sensilla provide frequency selectivity (Oldfield, 1985). The tympana and slits clearly have a role to play in the auditory system but what that role was remained controversial for some years (Nocke, 1975; Stephen and Bailey, 1982; Oldfield, 1984). In the bushcricket *Tettigonia viridissima,* the tympana are covered by cuticular covers, but if these are removed it is possible to measure the movements of the tympanum when stimulated with sound, using the method of laser vibrometry (Bangert et al., 1998). A small reflector attached to the tympanum reflects laser light and enables the velocity of the membrane to be measured using Doppler techniques. The addition of the reflector does not affect the measurements (Stumpner and Heller, 1992), but the removal of the covering cuticle to expose the tympana does arguably have some effect (Bailey and Stephen, 1984). When the phase of both of the sound inputs is the same, there is a measurable phase difference between the incident sound pressure and the tympanal velocity over the range of 2 to 40 kHz (Fig. 2). This is a consequence of the additional travel time in the trachea. The gradient of the line in Fig. 2 is related to the length of the trachea and the velocity of sound in the trachea. The mean gradient is constant throughout the frequency range, indicating that the propagation velocity is constant over this range also, at 260 ± 40 ms^{-1}, and there is no dispersion inside the trachea (Bangert et al., 1998).

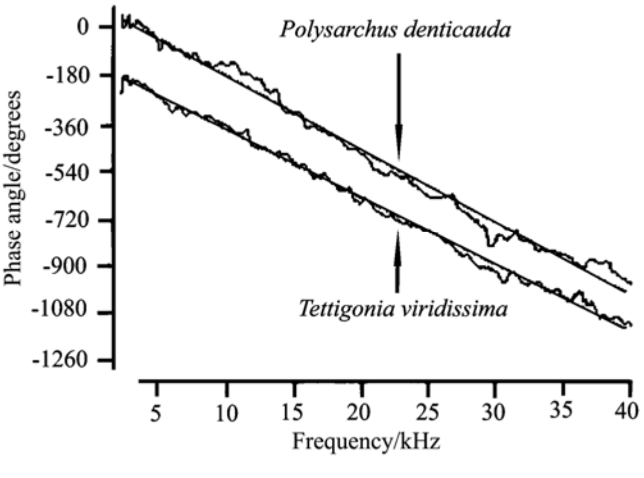

FIG. 2 The phase spectrum of the tympanic membrane velocity of two bushcrickets, in relation to the phase of the acting sound pressure. The line of the mean gradient is shown and that for *Tettigonia viridissima* has been offset by 180^{o} to separate it from the other one (Bangert et al., 1998, Fig. 2). Reprinted with permission from Elsevier Science, from *Hearing Research* **115**, Bangert, M., Kalmring, K., Sickmann, T., Stephen, R. O., Jatho, M. and Lakes-Harlan, R. (1998). Stimulus transmission in the auditory receptor organs of the foreleg of bushcrickets (Tettigoniidae) I. The role of the tympana,. 27-38.

Measurements of the phase spectra at six different points on the tympanic membrane showed that they were all effectively the same, demonstrating that the bushcricket tympanum has a single vibratory mode over the entire frequency range. This is not the case in an acridid, the locust, where the membrane of the ear has been shown to have independently vibrating areas (Michelsen, 1971b; Stephen and Bennet-Clark, 1982). Plotting velocity amplitude measurements over the surface of the tympanic membrane of *Polysarcus denticauda* showed that the maximum velocity is located at a position that is both ventral and distal (Bangert et al., 1998). This is at variance with earlier measurements on two species of *Tettigonia* (Michelsen and Larsen, 1978) which suggested that the maximum velocity occurred at the centre of the membrane, but the tympanum of *P. denticauda* is a rather different structure to that of *Tettigonia*, being between five and ten times thicker. The vibration amplitude of the tympanic membrane in *P. denticauda* increases linearly from the dorsal edge, reaching a maximum close to the ventral edge (Bangert et al., 1998). This observation suggests that the tympanum is acting like a hinged flap with the hinge along the dorsal edge (Fig. 3). The acoustic function of the hinged tympana has yet to be completely explained. From measurements made of the sensitivity of tibial organs in the midlegs and hindlegs it has been shown that the foreleg tibial organ is 50 dB more sensitive to airborne sound (Kalmring et al., 1994). Calculating the gain produced by the trachea gives a figure of 20 dB (Hoffmann and Jatho, 1995), which shows that there must be a further factor involved. It has been suggested (Bangert et al., 1998) that the tympana act together as an impedance matching transformer much in the way that the ossicles of the middle ear do in mammals, matching sound vibration in air to sound vibrations in the denser tissues of the hearing organ. Clearly this is a feasible suggestion but what particular structure of the bushcricket ear requires such an impedance match? There is as yet no answer to this question.

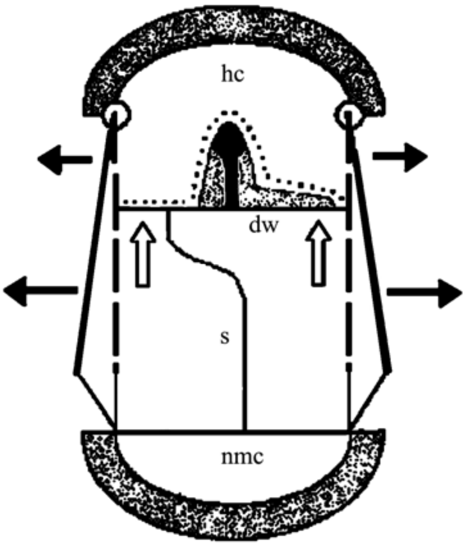

FIG. 3 Schematic cross section of the tibia of *Polysarchus denticauda* at the distal part of the crista acustica to show the hinge operation of the tympana and the effect on the translocation of the dorsal wall of the trachea. The dotted line indicates the direction of movement of the tectorial membrane and cap cell. Labels: dw, dorsal wall; hc, haemolymph channel; nmc, nerve-muscle channel; s, septum; (Bangert et al., 1998, Fig. 9). Reprinted with permission from Elsevier Science, from *Hearing Research* **115**, Bangert, M., Kalmring, K., Sickmann, T., Stephen, R. O., Jatho, M. and Lakes-Harlan, R. (1998). Stimulus transmission in the auditory receptor organs of the foreleg of bushcrickets (Tettigoniidae) I. The role of the tympana,. 27-38.

The amount of gain provided by the acoustic trachea has been linked to the size of the spiracle. In two species of *Poecilimon* with different sized spiracles, the species with the smaller spiracle had a tracheal gain of 5-6 dB whereas the species with the larger spiracle had a tracheal gain of 18-20 dB (Michelsen et al., 1994a). These gains are consistent with the dimensions of the acoustic trachea. However, in a comparison of seven species from four families (Heinrich et al., 1993), no differences in gain associated with the size of the spiracle were detected. This is perhaps because the acoustic conditions under which the measurements were made masked real differences (Michelsen et al., 1994a). The size of the auditory spiracle has been shown to determine the auditory sensitivity of female tettigoniids. In *Requena verticalis* half of the variation in sensitivity of different females to the male call could be attributed to the variation in the size of their auditory spiracles (Bailey, 1998).

Sexual dimorphism in the auditory system is unusual (Bailey and Römer, 1991), since males usually need to hear the calls of other males just as much as females do (so that they can, for example, assess, localize and interact acoustically with them; see Section 8). Where selection on male hearing sensitivity is relaxed, however, such as when male-male competition is reduced, sexual dimorphism can result. It has been found, for example, in some species of the tettigoniid *Kawanaphila* (see Mason and Bailey, 1998).

Mason and Bailey (1998) looked at the auditory systems and acoustic behaviour of *K. yarraga and K. mirla* and compared them with *K. nartee*, to test whether reduced hearing in males is associated with reduced male-male competition. In each species, female hearing is more sensitive than that of males by 10 dB, and male *K. mirla* are most sensitive at lower frequencies than females. The species also differ in the degree of dimorphism in auditory anatomy. *K. mirla* and *K. nartee* males lack some of the auditory specializations of the prothoracic tracheal system normally present in tettigoniids; these are present in *K. yarraga* but reduced in size compared with females. *K. nartee* show very low levels of male-male acoustic communication, so it is possible that reduced sensitivity is linked to reduced male-male competition in this species. *K. mirla* and *K. yarraga* males, in contrast, both interact acoustically with conspecific males to synchronize their calls (see Section 8.2). However, *K. mirla* only interact in this way over distances less than 5 m, while *K. yarraga* interact over distances of at least 10 m. Thus the nature of male-male competition in *K. mirla* and *K. yarraga* does not change with decreased hearing sensitivity, just the distance over which males are able to compete. Mason and Bailey argue that selection has favoured a reduction in male auditory sensitivity independently of the function of male-male acoustic signalling. They suggest two possible ecological factors that may have contributed to this. First, if resources are scattered and male mobility is limited, male-male communication distances would be determined by resource spacing, but competition could still be maintained within this spacing. Second, if acoustically-orienting predators or parasitoids (see Section 7) have influenced the evolution of song structure, communication distances in these species may now be limited by their ability to broadcast extremely high-frequency calls.

In *Kawanaphila nartee* it has also been demonstrated that sexual selection acts on the size of the ear in females (Gwynne and Bailey, 1999). In food-stressed populations of *K. nartee* there are more sexually receptive females than males. The male produces a spermatophore that is a nuptial gift to the female and the production requires a substantial input of food energy (Simmons and Bailey, 1990). Where food is scarce, the number of males with spermatophores is reduced but, at the same time, females too are short of food and competition for access to males is increased. In these populations, when the encounter rate with receptive females is high, males reduce their continuous calling song to an occasional brief ‘click’. As a result, those females with the greatest auditory sensitivity are the most likely to detect a calling male. In an analysis of winners and losers in competitions between females for males, the mean diameter of the auditory spiracle of the winner – the first female to hold on to the male genitally – was significantly larger than that of the loser. The size of the auditory spiracle was measured by two independent methods, one optical andthe other using video recordings and there were no significant differences between the methods. Using one of the methods, the mean diameter of the auditory spiracle of winners was 0.243 ± 0.005 mm and for the losers the mean diameter was 0.220 ± 0.007 mm. It might be thought that these differences would be correlated with the size of the individuals. Female size has been shown to be a factor in the mormon cricket (*Anabrus simplex*): at high densities, where females compete for males, larger females tend to be more successful (Gwynne, 1984). However, in *K. nartee* there was no significant difference in pronotum length, which is a measure that correlates well with size, between winners and losers. Similarly, there was no significant difference in mass (Gwynne and Bailey, 1999).

The highest communication frequency reported for an acoustically signalling orthopteran is 105 kHz (Morris et al., 1994). *Haenschiella ecuadorica* is a pseudophylline and the song consists of up to 18 pulses each less than 1 ms duration, forming a single pulse train of 51 ms duration (Mason et al., 1991; Morris et al., 1994). In pseudophyllines that communicate above 50 kHz the acoustic spiracle is reduced, relative to body size, as are the dimensions of the acoustic trachea. The area of the spiracle is also greatly reduced relative to the tympanal slits. At this very high communication frequency, sound entry to the tympanal organ is predominantly via the slits.

4.1.2 The acridid ear

In grasshoppers the tympanic membranes of the auditory organs are located on the first abdominal segment and the two membranes are acoustically coupled via closed air sacs within the abdomen. The air sacs transmit sound from one ear to the other, acting as low-pass filters (Michelsen, 1971c), such that the ear operates as a pressure gradient receiver at low frequencies but is mainly a pressure receiver at high frequencies. These biophysical findings of Michelsen, and later work by Miller (1977) were confirmed by Römer (1976), using neurophysiological techniques. Furthermore, muscle movements in the abdomen can distort the membranes (Meyer and Hedwig, 1995) and changes in air pressure in the tracheal system can alter the volume of the air sacs (Michelsen, 1971c; Meyer and Elsner, 1995). The nature of the link between changes in the tracheal pressure and movement of the tympanum has been investigated in the migratory locust (Meyer and Hedwig, 1995). Simultaneous measurements of the movement of the tympanum and the tracheal pressure were made using a laser interferometer directed at the tympanum and a digital manometer connected via a sealed tube to the mesothoracic spiracle, whose valves had been fixed into the open position. The manometer recorded the variation in tracheal pressure, relative to ambient air pressure. The movements of the tympanal membrane correspond to changes in the tracheal pressure (Fig. 4). Plotting membrane displacement against the pressure at the tympanum showed that the relationship was only linear over the range ±10 to 20 µm at best and the curve flattened out at greater displacements. At increasing displacement, the force on the membrane had to be greater to produce an equivalent deflection – the compliance of the membrane decreases rapidly with increasing displacement. The consequence of these properties is that even small displacements of the tympanic membrane resulting from pressure changes produced by breathing movements would be expected to produce modulation of the auditory information and so influence processing.

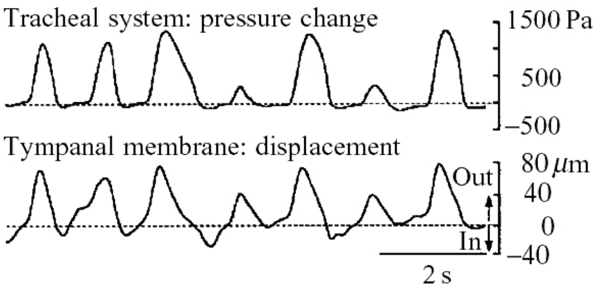

FIG. 4 Simultaneous measurements of tracheal pressure and tympanal membrane displacement in a normally ventilating locust, showing the close correlation between the pressure and the displacement of the membrane. Outward displacement of the membrane is shown as an upward deflection (Meyer and Hedwig, 1995, Fig. 1B). Reprinted with permission from the Company of Biologists.

The receptors are attached directly to the inner surface of the tympanum and the membrane shows a complex vibration pattern with different modes of vibration at the different receptor attachment sites. The vibrations have been analysed using laser vibrometry (Michelsen, 1971b) and demonstrated visually (Stephen and Bennet-Clark, 1982). The receptor attachment sites on the tympanic membrane are shown in Fig. 5. There are four distinct groups that form Müller's organ. Of these the a-, b- and c-cells are sensitive to lower frequencies than the d-cells. However, more recent analysis of the central projections of the auditory receptor cells suggests that the a and b cells are not distinct types and should be grouped together (Jacobs et al., 1999).

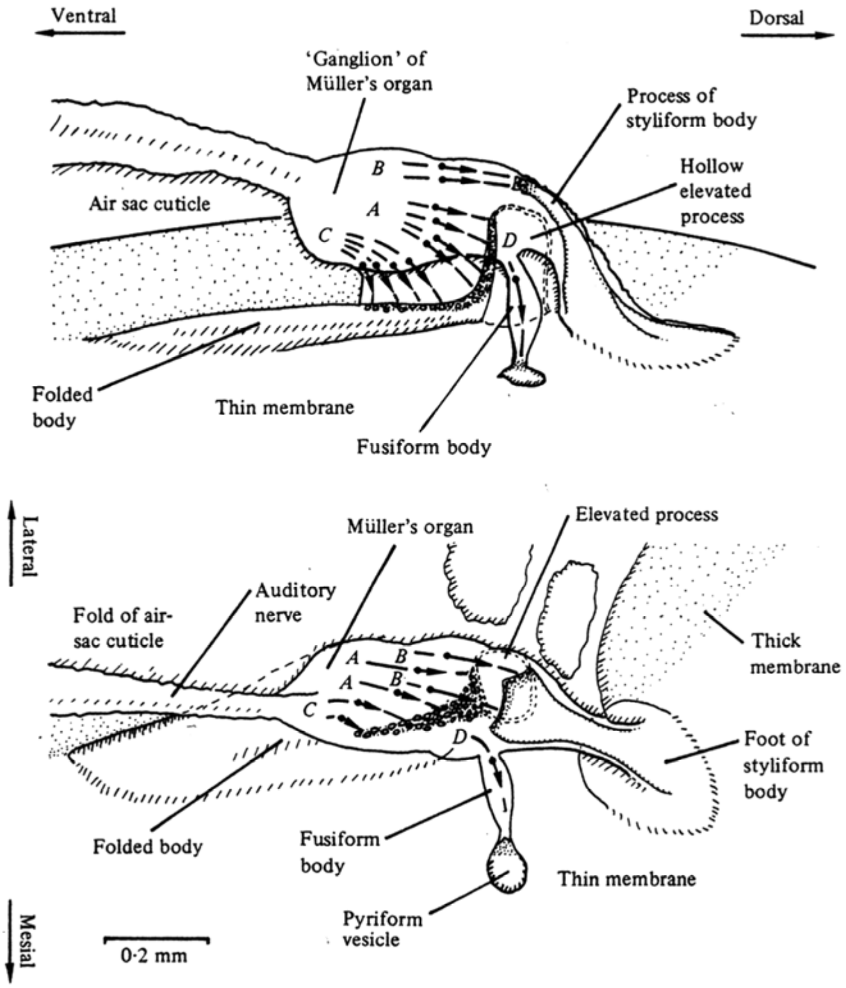

FIG. 5 Drawings of the tympanal sclerites and Muller's organ to show the trajectories of the four groups of sense cells. The points of attachment to the sclerites are shown by small circles and stippling, the approximate length of the scolopale cells is indicated by the length of the arrows and the position of the cell bodies is indicated by the letters A to D. The upper view is from about 10° above the plane of the tympanum. The lower view is normal to the tympanum (Stephen and Bennet-Clark, 1982, Fig. 4). Reprinted with permission from the Company of Biologists.

The vibrational sensitivity of the locust tympanum has been analysed for the different attachment sites of the receptors (Meyer and Hedwig, 1995). Frequency-modulated sound pulses with a band spread of 1-25 kHz were used to stimulate the membrane. The resulting vibrations, measured with a laser interferometer, were analysed using Fast Fourier Transform (FFT) analysis. The shapes of the resulting spectra showed that there were substantial differences in vibration between the elevated process (see Fig. 5) and the pyriform vesicle. Between 2 and 9 kHz the vibration patterns at both sites were similar but at higher frequencies differences emerged. At 16 kHz, there was a difference of 26 dB in the amplitude of the oscillations at the two sites, with the pyriform vesicle showing the stronger response. The maximum response from the membrane at the elevated process was observed in the range 3.5-10 kHz with peaks at 5 kHz and 8 kHz. These figures correspond well with the tuning curves of low frequency auditory receptor cells (a-cells) (Michelsen, 1971b; Römer, 1976). The membrane at the pyriform vesicle shows maximum vibrations over the range 3.5-23 kHz with a peak in the range 13-18 kHz. Once again, this corresponds well with previously measured tuning curves (Michelsen, 1971b; Römer, 1976).

Changes in the response of the locust ear to high frequencies have been investigated, following selective damage to the d-cell dendrites. A laser (Fuhr et al., 1999) was used to ablate a small area of the dendrites or their attachment to the tympanum. High energy pulses from a UV laser could produce a damage area as small as 5 µm x 5 µm. Threshold curves were produced for both the damaged and intact ears over a frequency range of 3-28 kHz and these showed a pronounced asymmetry, with the difference in threshold in the damaged ear being over 20 dB in some individuals. The asymmetry was far more pronounced at the higher frequencies, as would be expected if the damage was to the d-cells. However, it is worth noting that in control experiments where measurements of thresholds were made in intact animals, two individuals showed an asymmetry of over 15 dB at the higher frequency end of the range tested. This technique will surely find future applications in work on receptor mechanisms.

The tympanum of the acridid ear is sensitive to lower frequency sounds at the position of the d-cells. In the grasshopper *Chorthippus biguttulus,* the membrane vibration is greatest in the range 6-20 kHz and in the locust, although the greatest sensitivity is in the range 13-18 kHz, the membrane is also sensitive to sound in the range 2-9 kHz (Meyer and Elsner, 1995). In both this species and the locust, the membrane response to low frequencies may be greater at the site of d-cell attachment than at the other sites. However, as described above, the d-cells are much less sensitive at the lower frequencies. So, there is a mismatch between the low frequency properties of the membrane and the frequency response of the d-cells. There is as yet no explanation for this observation, although it is probable that the frequency response of the ear is not solely related to movement of the tympanum and that the way in which Müller’s organ responds may also have an influence (Stephen and Bennet-Clark, 1982; Brekkow and Sippel, 1985). When the tympanum vibrates, Müller’s organ vibrates as well and the driving forces that act on it produce a twisting movement described by Stephen and Bennet-Clark (1982) as being similar to a Lissajous’ figure. So, the vibration of the different areas of the tympanum, the orientation of the groups of receptor cells and the damping of the membrane by Müller’s organ, together with its complex vibration, all combine to give the response spectra of the single receptor cells.

The conclusion of studies on the effect of ventilation on hearing in the locust (Meyer and Hedwig, 1995) and in *Chorthippus biguttulus* (Meyer and Elsner, 1995) is that the changes in tracheal pressure that result from ventilation will alter auditory sensitivity and the frequency spectrum of the response of the ear. The low-frequency components of incident sound can be reduced by about 15 dB SPL while high frequencies can be enhanced by about 7 dB SPL. At incident sound pressure levels of 50 or 55 dB SPL in the locust, the auditory response to 4 kHz has been shown to be masked by the membrane displacement (Meyer and Hedwig, 1995). It is possible that the changes that the ventilatory movements make in the response of the ear would reduce the effectiveness of frequency analysis in the auditory pathways, a factor that might explain the use of broad-band sounds for communication in grasshoppers.

The leg movements of locusts have also been shown to produce responses in the tympanic nerve, as slow tympanic membrane displacements are associated with leg movements. If these occur concurrently with the high frequency oscillations of the membrane produced by sound stimulation, then the two responses in the tympanic nerve interfere strongly (Lang and Elsner, 1994). Taken together with the effects of ventilatory movements, it is clear that the acridid nervous system contends with an auditory input that may be heavily modulated by other forms of mechanical stimulation.

4.1.3 The gryllid ear

Like tettigoniids, gryllids have hearing organs on the tibia of the forelegs, with two tympana and auditory trachea that open to the exterior via auditory spiracles. Functionally, there are some differences. The small, anterior tympanum is not functional in hearing and has yet to have a role assigned to it. The larger posterior tympanum is fully functional and, in *Gryllus campestris,* vibrates in response to sound stimuli over a frequency range of at least to 1 to 30 kHz, (Larsen and Michelsen, 1978). The prothoracic spiracle provides access for sound, as in tettigoniids, but the acoustic tracheae from each side are separated by a very thin septum and there is good acoustic communication across from one trachea to the other. This gives four possible routes of sound input into each ear. Sound reaches the external face of the posterior tympanum and the internal via the prothoracic spiracle and the trachea. In addition, sound entering the opposite ear and the opposite spiracle travels across the thin septum separating the two acoustic tracheae, providing two more sound inputs. Thus, the tympanal vibration is the sum of all four inputs. The velocity and phase angle of the posterior tympanum is highly dependent upon the input from the ipsilateral spiracle but less dependent upon the input from the contralateral spiracle. The input from the contralateral tympanum has only a small effect (Larsen and Michelsen, 1978; Michelsen et al., 1994b).

During stridulation, the acoustic spiracle remains open, although crickets have the ability to close the spiracle, and the tympanic membrane responds to the pattern of the stridulatory song. There is no evidence that the responsiveness of the tympanum is altered during stridulation (Poulet and Hedwig, 2001).

4.1.4 The haglid ear

The haglids are most closely related to the tettigoniids and the tympana and the acoustic trachea are similar, although the tympana are more rudimentary as they are less well differentiated from the surrounding cuticle. There are two morphologically distinct regions of the tympanum, with an area of the dorsal margin being thicker than the surrounding membrane. This is similar to the tympana of some tettigoniids and stenopelmatids. The vibration characteristics of the tympanum of *Cyphoderris monstrosa* showed that the tuning did not match the low-frequency spectrum of the auditory nerve (Mason et al., 1999) with its best frequency of 2 kHz (Mason, 1991), but rather it matched the responses of a broadly-tuned receptor group. So the ear of the haglids appears to be functionally different from that of other members of the Ensifera in that there is a group of low frequency receptors that predominate in the auditory nerve and respond independently of the tympanal movements. Atympanate receptors for low frequency sound have been described in *Bullacris membracioides*, a representative of a relatively ancient group of Orthoptera, where it is suggested that there was an evolutionary development from stretch organs to auditory receptors (van Staaden and Römer, 1998). It seems likely that a similar evolutionary change has taken place in the haglids. *C. monstrosa* has essentially a two-channel system, with only one channel being associated with the tympana.

4.1.5 Changes with age in individuals

The auditory system in crickets has been shown to exhibit maturational changes during the first few days of adult life. By the time of the final moult all the receptor cells are morphologically complete and fully developed (Ball and Young, 1974; Ball and Hill, 1978). The posterior tympanum continues to develop after the moult is complete and the membrane thickness decreases from around 20 m to 5 m (Young and Ball, 1974; Ball and Cowan, 1978). This maturation process results in a 5-8 dB improvement in the sensitivity of the ear at most frequencies and improved directionality (Popov et al., 1994). Above 10 kHz, the decrease in threshold for phonotaxis is probably attributable to changes in the central processes, but there is no hard evidence available.

4.2 Auditory receptor organs in the tibia

All three pairs of legs in the Tettigoniidae have complex tibial organs. The arrangement of the receptor and accessory cells is essentially the same in all three pairs of legs (Schumacher, 1979; Lin et al., 1994). The postembryonic development and functional morphology of the organs has been studied in detail (Rössler, 1992a; Rössler, 1992b) in the genus *Ephippiger*. Investigation of the physiology of the complex tibial organs in the mid and hind legs of the bushcricket *Gampsocleis gratiosa* shows that the receptor cells of the complex tibial organs are mostly sensitive vibratory receptors with a frequency response that ranges from 200 Hz to over 3 kHz (Kalmring et al., 1994). The receptor cells of the intermediate organ and crista acustica in these legs do not respond to airborne sound as the structural components necessary for receiving sound are not present and the leg trachea does not appear to conduct sound to them.

The three components of the tibial organ of the foreleg of tettigoniids contain both vibration and sound receptors. The subgenual organ is extremely sensitive to substrate-borne vibratory signals and the receptors of the intermediate organ also respond to vibration. However, the receptors are probably bimodal, responding to sound signals as well. The scolopidial cells of the crista acustica are sensitive auditory receptors. The arrangement of the scolopidial cells of the crista acustica has always suggested that frequency analysis takes place in the ear. The cells are attached to the anterior trachea on the dorsal side and are arranged in a row with the largest cells at the proximal end. The cells decrease in size towards the distal end of the row. The cap of each scolopidial cell is connected to a tectorial membrane that lies over the whole of the crista acustica and the intermediate organ. In the tettigoniid *Ruspolia differens* the proximal scolopidia are tilted (Fig. 6) but the majority are aligned vertically (Figs 7 and 8). The arrangement of the crista acustica appears to be similar in *Gampsocleis gratiosa* (see Lin et al., 1993), two species of *Decticus* (see Kalmring et al., 1993), *Mygalopsis marki* (see Kalmring et al., 1995) and *Psorodonotus illyricus* (see Kalmring et al., 1993). However the number of scolopidia differs from one species to another, as do their physiological properties.

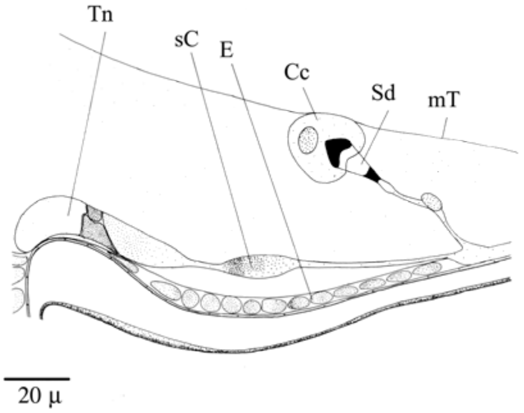

FIG. 6 The 2nd scolopidial organ (Sd) from the proximal end of the crista acustica of *Ruspolia differens* showing the inclination of the organ and the tectorial membrane (mT) stretched across the leg at an angle (compare with Fig. 5.2.2). Cc = cap cell; E = epidermal cells; sC = cell body; Tn = tympanic nerve.

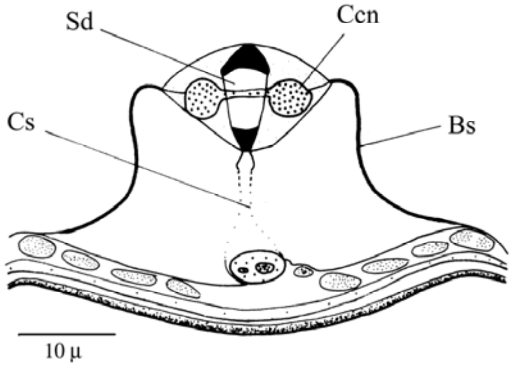

FIG. 7 A single scolopidial organ (Sd) from the distal end of the crista acustica of *Ruspolia differens*. Bs = supporting band; Ccn = cap cell nucleus; Cs = supporting column.

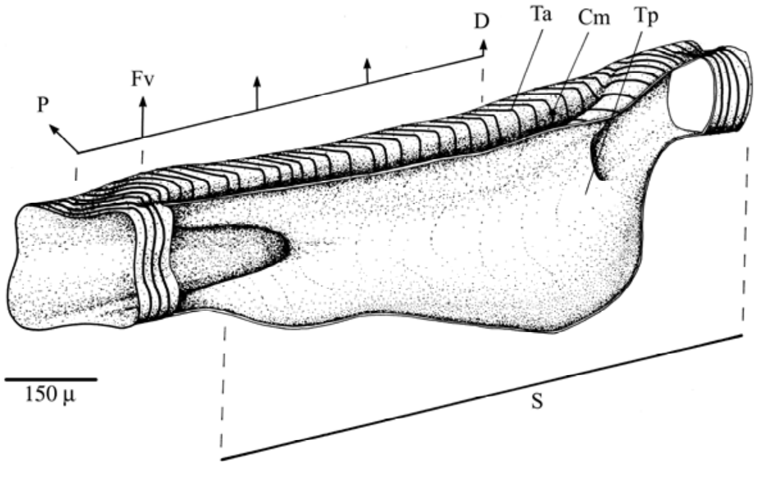

FIG. 8 A reconstruction, from serial sections, of the acoustic trachea in the region of the tympanic organ of the right foreleg of *Ruspolia differens*. The posterior trachea is shown with the outer (posterior) wall removed. Cm = central membrane; Fv = first vertical scolopidial organ; S = position of tympanic slit in tibia; Ta = anterior branch of acoustic trachea; Tp = posterior branch of acoustic trachea. The line above the trachea shows the orientation of the scolopidial organs from the most proximal (P) to the most distal (D).

There are 33 ±1 scolopidia in the crista acustica of *G. gratiosa* in a length of 700 ±30 µm whereas *M. marki* has 23 ±1 in a length of 500 ±30 µm. However it is noteworthy that despite the difference in length of the crista in the two species, if it is divided into four equally large sections, then in each species there are 17-20% of the scolopidia in each of the first two proximal sections. The third section has 21-22% and the most distal one has 42-45% (Kalmring et al., 1995). In the phaneropterine bushcricket *Polysarchus denticauda*, there are about 50 scolopidia (Kalmring et al., 1996), 30% more than in other species studied and, although the proportions in the first three sections are similar, the fourth, most distal section has proportionally more, with some of the scolopidia in pairs or even triplets (Sickmann et al., 1997). By comparison, *Tettigonia cantans*, which has a crista acustica of similar length to *P. denticauda,* has 30 to 37 scolopida (Zhantiev and Korsunovskaya, 1978) compared with 49 ±2. Both the number of scolopidia and the pairing of some of them make *P. denticauda* an unusual tettigoniid, but the significance of these observations awaits exploration.

4.2.1 Tonotopic organization of sense cells

A tonotopic organization of the sense cells in the crista acustica was first suggested by Zhantiev (1971) for *Decticus verrucivorus.* A particular problem for physiologists has been to determine whether each receptor cell itself has a frequency response determined by its internal structure or whether the frequency response is determined by its placement on the trachea. Initial work on this problem (Oldfield, 1982; 1984; 1985) suggested that each receptor cell had a centre frequency of response that was a property of the cell itself. The evidence for this came from experiments in which removal of both tympana had no effect on the tuning of auditory receptors in the crista acustica (Oldfield, 1985). Recording from the cap cells of the scolopida disrupted either the tympanum or the dorsal cuticle and this could have affected the responses of the cells. However, correlating the threshold curves of all the receptor cells in the crista acustica with the structure of the ear suggests that the frequency response of the cells could be a property of their position in the crista acustica (Lin et al., 1993; Kalmring et al., 1995). In *G. gratiosa*, there is a clear relationship between the position of each scolopidia on the crista acustica and the characteristics of its threshold curve. The characteristic frequencies are shown in Table 1. The scolopidia with the lowest frequency response are at the proximal end of the crista acustica, where the large cap cells make direct contact with the tectorial membrane (similar to Fig. 6). Moving distally, the tectorial membrane covers the smaller cap cells of the scolopidia in a V shape, restricting the area between the dorsal wall of the trachea and the membrane (similar to Fig. 7). This change in structure may be associated with the higher frequency threshold curve of these cells (Lin et al., 1993). It should be noted that these studies did not include complete staining of receptor cells, as has been achieved recently in *Pholidoptera griseoaptera*, where single cells were stained to show both their soma position in the crista acustica and their central branching pattern in the prothoracic ganglion (Stölting and Stumpner, 1998).

TABLE 1 The frequency response of individual scolopidia in the crista acustica of *Gampsocleis gratiosa*. Data from Lin et al (1993).

Scolopidia in the crista acustica (cell number)		Characteristic frequency (kHz)
Proximal	1 to7	4-5, 4-7, 5-7, 6-9, 6-12, 9
	8 to 11	6-7, 6-9, 6-12, 6-20
	12 to 16	7-18, 9-18, 10-18, 12-25
	17 to 23	16-20, 16-25, 16-30
Distal	24 to 31	Characteristic frequencies above 18 kHz and up to 40 kHz

Evidence that the scolopidia do not, in themselves, have an intrinsic frequency response comes from the comparison of the response to low frequencies of two tettigoniids (Kalmring et al., 1995). *G. gratiosa* has a broad band calling song with a fundamental frequency of 3.8 kHz and peaks at 7.6 kHz and 30 kHz.. In contrast, *Mygalopsis marki* has a narrow band song with a frequency range of 9 to 25 kHz. The threshold curves of the whole auditory organ of each species show that *G. gratiosa* is, as might be expected, much more sensitive to low frequencies below 5 kHz than *M. marki*. The important question is whether this difference is a property of the scolopidia themselves. The similarity between the structure of the crista acustica in these two species was mentioned above. Examination of the acoustic trachea reveals differences that account for the difference in response of the scolopidia (Kalmring et al., 1995). The transmission frequencies of an exponential horn depend upon the cross-sectional area and the flaring constant. Treating the acoustic trachea as an exponential horn gave a lower cut-off frequency (f_o) of 3.05 kHz in *G. gratiosa* and 7.2 kHz in *M. marki*. Thus the correspondence between thefrequency spectrum of the conspecific song and the audible range of the ear is not brought about by the presence or absence of particular receptor cell types but by the structure of the sound conducting system of the ears and a shift in the cut-off frequency of the amplifier – the acoustic trachea.

Single cell recordings from auditory receptor fibres in the cricket *Teleogryllus oceanicus* have revealed that unlike tettigoniids, where there is a single characteristic frequency (CF) for each fibre, there are additional sensitivity peaks at other frequencies (Imaizumi and Pollack, 1999). Furthermore, the CFs are not distributed over a broad range of frequencies but instead fall into three groups with the largest group centering close to the dominant frequency of the species song, 4.5 kHz (Balakrishnan and Pollack, 1996).

4.3 Tonotopic organization of receptor projections

4.3.1 Tonotopic organization of primary afferents in the prothoracic ganglion

Within the prothoracic ganglion there is a tonotopic organization in the branching pattern of the primary afferents, with low frequency receptors projecting into anterior portions of the neuropile. Higher frequency receptors have projections into more posterior parts of the neuropile. Cells tuned to the frequencies of the conspecific song appear to have a larger projection area than other receptors. In *Tettigonia viridissima* the broad spectrum song has several peaks, including one at 20 kHz, a frequency that has been shown also to be important in directional hearing (Rheinlaender and Römer, 1980). The receptor tuned to 20 kHz has the largest projection area within the auditory neuropile (Römer, 1983) and, presumably, the largest number of synaptic contacts, although no link has yet been shown between absolute number of synapses and area of projection. However, staining of complete receptors in *Pholidoptera griseoaptera* has shown no evidence for single receptor cells tuned to the frequencies of the conspecific song having larger projection areas (Stölting and Stumpner, 1998), although the general pattern of projections is similar to other bushcrickets. Proximal cells in the crista acustica project anteriorly in the auditory neuropile, medial cells project ventrally and posteriorly and distal cells project to the more dorsal regions. The termination areas of the auditory receptors overlap so there is at least a possibility that auditory interneurons do not distinguish between different receptors with different frequency responses if they have terminations in the same area. This would mean a loss of frequency information, which does not seem entirely rational, even though auditory interneurons might thus gain a greater dynamic range.

In the haglid *Cyphoderris monstrosa*, the auditory receptors fall into two groups, a low frequency tuned group and a broad frequency tuned group. The projections of the two groups differ in that the low-tuned receptors have a bifurcation near the terminal aborization whereas the axons of the broadly tuned receptors do not (Mason et al., 1999). This arrangement is quite different from that of other Ensifera, being simpler and less sophisticated and it supports the idea (see Section 4.1.4) that there are two separate hearing channels with independent evolutionary origins. The best frequency of the auditory nerve is 2 kHz but the species song is an almost pure 12 kHz tone (Mason, 1991). The mismatch between the two frequencies is marked and only the broad frequency tuned receptors respond to the species song.

4.3.2 Tonotopic organization of primary afferents in acridids

Afferent neurons from the sense cells of the tympanic organ of grasshoppers (see Section 4.1.2) enter the metathoracic ganglion complex at the first abdominal neuromere. Branches project to the neuropile of each thoracic ganglion, with the projections of the four different receptor groups separated geographically within the ganglia. In the metathoracic ganglion, the high frequency afferents project posteriorly to the other three groups of lower frequency (Römer, 1985), each of which projects to a distinct but more anterior region. There appears to be a gradient of decreasing sensitivity to low frequencies both away from the midline and anteriorly (Halex et al., 1988; Bickmeyer et al., 1992). The higher-frequency afferents have a greater anterior projection into the prothoracic ganglion than most of the lower-frequency ones, many of which do not project beyond the mesothoracic ganglion, while others only reach to the metathoracic ganglion. Although there has been substantial work on the central auditory pathways in grasshoppers (see, for example Boyan, 1999; Prier and Boyan, 2000), nobody has yet demonstrated that there is a tonotopic organization of projections within each of the four groups of receptor cells so, for the present, the tettigoniids are the group in which there is the most clearly defined tonotopic arrangement of receptor projections (see Section 5.2.5 for further discussion of the central projection of receptor cells in acridids). A comparison of the projection of receptors in tympanic organs in insects can be found in the recent review by Stumpner and von Helversen (2001).

4.4 Directional hearing

Where the body size of an animal is smaller than the wavelengths of sounds of biological significance, the sound pressure difference between the external surface of the tympana is too small to permit directional hearing. However, in the Orthoptera, directional hearing is possible as a consequence of the fact that sound arrives at both the external and the internal faces of the tympana. The phase and pressure differences between the external and internal signals produce differences between the two ears, sufficient to provide directional information. The directional dependence of tympanal vibration has been measured in gryllids (Michelsen et al., 1994b) and acridids (Michelsen and Rohrseitz, 1995).

Laser vibrometry measurements of the tympanal vibrations in acridids show that the vibrations are very much dependent upon the direction of the incident sound. The acridid ear is described as a two-sound-input model (Michelsen and Rohrseitz, 1995) because sound reaches the external surface directly or the internal surface via the air sacs (see Section 4.1.2). The amplitude of the sound reaching the internal surface of the tympanum in *Schistocerca gregaria* decreases with frequency. At 5 kHz the pressure difference across the membrane provides directionality. At 12 kHz, where there is a much smaller transfer of sound through the air sacs, there is still a significant directional effect as diffraction effects are greater at the higher frequency (Michelsen and Rohrseitz, 1995). The directional cues provided by amplitude and phase angle are not as great in small acridids. *Chorthippus biguttulus* is three to four times smaller in length and diameter of thorax and abdomen than *S. gregaria*. The amount of delay in the sound transmitted between the two ears is therefore much less and directionality is poor at 5 kHz (Michelsen and Rohrseitz, 1995). This effect would not be the same in small crickets, as the acoustic trachea provides a dramatic phase shift, though only at a restricted frequency range, providing crickets with excellent directionality at the dominant frequency of the species song.

The finding of poor directionality in *C. biguttulus* at 5kHz does not match behavioural observations which show that males have excellent lateralization. For example the orientation turn during phonotaxis by the male is made on the basis of whether the sound source is on the left or the right and such distinction can be made with 100% accuracy when the sound amplitude differences are as little as 1 to 2 dB (von Helversen and Rheinlaender, 1988; von Helversen, 1998). The results obtained by Michelsen and Rohrseitz (1995) have been challenged by Schul et al. (1999) who suggest that the phase delay between the external sound signal and that reaching the internal side of the tympanum is approximately 40^o above that measured by Michelsen and Rohrseitz. Thus the internal pathway produces a considerably larger delay, resulting in good directional hearing at low frequencies and matching the behavioural observations.

Using the ‘biological microphone’ experimental design (Rheinlaender and Römer, 1986) in which recordings are made in the field from identified nerve cells, the directional hearing ability of *C. biguttulus* has been examined in the natural habitat (Gilbert and Elsner, 2000). In sparse vegetation the overall pattern of directionality was similar to measurements made in the laboratory under free-field conditions, with only a small degradation. Correct lateralization would be expected at all angles of incidence between 20 and 160^o in the laboratory, figures that match those obtained in behavioural studies. Over gravel, directionality was much more degraded and, over dense vegetation, there were several angles of incidence of sound where the difference between the two ears would have been less than 1.5 dB, no longer providing good lateralization of the sound source, particularly if the animal is horizontal. These field neurophysiological observations have yet to be confirmed by field behavioural studies.

Gryllids use relatively low frequencies for communication and the differences in sound intensity at the two ears as a consequence of diffraction are small. At 4-5 kHz the presence of the cricket distorts the sound field such that there is a 1-2 dB difference in intensity at tympana and thoracic spiracles, compared with the undistorted field (Kleindienst, 1978). However the sound pressure and phase differences due to the four inputs to the cricket ear (see Section 4.1.3) provide directional information. There is a delay imposed by the medial septum upon information from the contralateral side, which contributes to the pressure gradient across the tympanum. With a sound source at 90^o to the cricket the difference in pressure between the two ears may be up to 15 dB (Michelsen et al., 1994b). Central processing enhances directionality (see Section 5.2.2).

At high frequencies, diffraction effects are more marked and tettigoniids, which generally communicate in the range of 10 kHz up to 102 kHz, are able to gain directional information in a similar way to acridids. The gain produced by the exponential horn shape of the acoustic trachea has been measured as 10-15 dB in some species (Heinrich et al., 1993) so the primary source of tympanal stimulation is via the spiracle. In experiments with *Gampsocleis gratiosa*, blockage of the spiracle markedly influenced the auditory threshold and directionality of the ipsilateral auditory neurons, but had very little effect on contralateral auditory neurons, while blockage of the tympanal slits had only a small effect on directional hearing (Shen, 1993). It has been pointed out, however (Michelsen et al., 1994b), that blocking sound inputs can change the radiation impedance of the tympanum and so influence the results observed. A change in membrane impedance was observed when the ipsilateral spiracle of *Gryllus bimaculatus* was blocked (Michelsen et al., 1994b). The role of the sound entering via the tympanal slits in directional hearing has been demonstrated by (Bailey and Stephen, 1978) and it is clear that the slits do have a function in hearing. The air cavity, formed by the cuticular cover over the tympanum that forms the slits, may have resonance properties that, under certain conditions and at certain frequencies, modify the pressure across the tympanic membrane. Some tettigoniids even possess structures by the slits that may act in a similar way to the pinna of mammals (Bailey, 1993).

5 Analysis

There are four key pieces of information that most orthopterans glean from acoustic signals: the amplitude modulation pattern, the frequency, the intensity of the sound and the location of the sound source. For example, males of the grasshopper species *Chorthippus biguttulus* produce a calling song to which the female replies. The male uses the female song as a signal for phonotaxis and so retrieves from the song the information that the caller is a conspecific. When the female sings, the male turns towards her, on the basis of a simple decision about whether to turn left or right. After turning, the male sings again and then, when the female replies, makes a new decision (von Helversen, 1972; von Helversen and von Helversen, 1983). When males were given a choice between two speakers playing female calls, it was found that they selected the speaker with the loudest sound, even if the difference in intensity between the two sounds was only 1-2 dB (von Helversen and Rheinlaender, 1988). The acoustic cues that orthopterans use and the neural mechanisms by which the information is analysed are the subject of much research and there has been considerable recent advance in our understanding. In addition to the purely physiological interest in the mechanisms, there is now sufficient information available for us to start to work out the evolutionary stages in the development of auditory processing in the nervous system.

5.1 Song analysis

The environment of most orthopterans is a noisy one and their communication systems would be expected to show adaptations that favour signal transmission and signal detection. The use of signals for species recognition implies a level of sophistication in the analysis of signals and yet the signals must survive degradation in the natural environment without losing their information content. Where the signals are used for location of potential mates, the signals must maintain their directional information, even in the complex environment that a meadow or hedgerow presents.

The use of the fundamental or carrier frequency of the song to convey information can provide a measure of resistance to masking (Römer and Bailey, 1998). This may be enhanced if parallel selection has matched the best frequency of the receiver and the carrier frequency of the song (Endler, 1992) and in most Orthoptera there is such close matching, although in some species there is a mismatch (Bailey and Römer, 1991).

A recent study of a southern Australian sagine tettigoniid, *Sciarasaga quadrata*, illustrates the selection pressures that may operate on a species in maximizing the effectiveness of acoustic communication (Römer and Bailey, 1998). The carrier frequency of the call is 5 kHz, which is very low by comparison with other tettigoniids. The intensity of the song is also lower than bushcrickets of comparable size, being 60 dB SPL at 1m. The sensitivity of the ear to sound in the range 3-70 kHz was measured by analysing the discharge in the tympanal fibres and the omega neuron. At the carrier frequency of the male call (5 kHz) the ear is approximately 20 dB less sensitive than it is between 10 and 20 kHz. The difference implies that the ear and call are not matched. It also implies that if there are other species in the same environment utilizing the frequency band between 10 and 20 kHz, the response of the ear to their calls might mask the 5 kHz calls of conspecifics quite effectively. Römer and Bailey found three such species with long duration calls, *Mygalopsis pauperculus*, *Hemisaga denticulata* and *Metaballus litus*. Field recordings suggested that the calls of *S. quadrata* would be masked by the calls of other species. This was demonstrated neurophysiologically by using a portable preparation of the omega cell in the field, first described by Rheinlaender and Römer (1986). The preparation was firstly positioned with conspecific males at distances of 1m and 6m and a microphone 5 cm away. The record from the omega neuron (Fig. 9A) shows that both males are detected. A second measurement was made with a conspecific male at a distance of 4 m and a male *Mygalopsis pauperculus* at 6 m. The continuous song of *M. pauperculus* masks the response in the omega cell to the conspecific (Fig. 9B). Moving the male *M. pauperculus* closer (3.5 m) increased the masking effect. In this case (Fig. 9C) another heterospecific was also singing, from slightly further away.

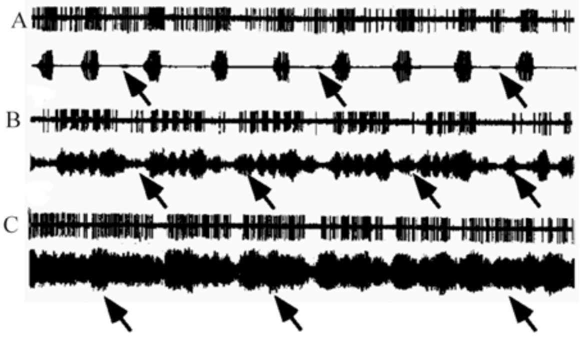

FIG. 9 Masking of the response to conspecific male calls of *Sciarasaga quadrata* by heterospecific bushcricket species in the field, using the response from the omega cell as a measure (upper trace) and a microphone by the preparation to record the calls (lower trace). A. The response in the omega cell is shown to the calls of two conspecific males, one 1m away and one (arrowed) 6m away in the same direction. B. Masking of the call of a conspecific male (arrowed) 4 m away by a male *Mygalopsis pauperculus* 6 m away. C. Increased masking when the male *M. pauperculus* is 3.5m away. Another heterospecific is calling at a distance of around 5 m. (Römer and Bailey, 1998, Fig. 5). Reprinted with permission from the Company of Biologists.

In Section 4.1.2 it was suggested that in grasshoppers such as *Chorthippus biguttulus*, the changes that the ventilatory movements make in the response of the ear would reduce the effectiveness of frequency analysis in the auditory pathways and that this observation (Meyer and Elsner, 1995; Meyer and Hedwig, 1995) might explain the use of broad-band sounds for communication in grasshoppers. Poor spectral resolution may preclude the use of carrier frequencies centred in frequency bands that have low noise levels, and so a combination of a broad band signal and analysis in the time domain might be expected to be a solution found in grasshoppers. The temporal pattern of the song of *C. biguttulus* is species specific and recognition prevents hybridization with species of gomphocerine grasshoppers (von Helversen and von Helversen, 1975; von Helversen and von Helversen, 1994). The song consists of a number of repetitions of stereotyped subunits (Elsner, 1974), each lasting about 80 ms. The duration of the song of females under natural conditions has been measured as 1.18 ± 0.23 s, with a range of 0.8-1.5 s (von Helversen and von Helversen, 1975). However, experiments have demonstrated that under laboratory conditions males can recognize the songs of conspecific females if the duration is as low as 250 ms (Ronacher and Krahe, 1998). Is it possible that longer duration signals might improve recognition in the field, where the levels of background noise are likely to be much higher than in the laboratory (Gilbert and Elsner, 2000)? Under natural conditions males produce calling songs. A female who is willing to mate replies with her own song, providing the male with a phonotactic cue (von Helversen, 1997). The male makes a turn towards the female and moves in that direction before singing again. The female response produces another turn. The male traces out a zigzag course towards the female because he does not turn through an angle that corresponds to the direction of the sound source. Rather, he lateralizes the sound (Rheinlaender, 1984). The ability of *C. biguttulus* males to recognize female songs amidst background noise has been tested under laboratory conditions (Ronacher et al., 2000). In the laboratory, the responses of freely moving males to songs containing differing numbers of subunits, and therefore of differing durations, were scored on the basis of the number of turns made as a percentage of the total number of presentations of the song. With a stimulus intensity of 45 dB or 50 dB and no masking noise, a male responded to 100% of stimulus songs, whether they contained three subunits or 12 subunits. As the intensity of the masking sound was increased (Fig. 10) the response percentage fell. However, the longer song was more resistant to masking than the short one.

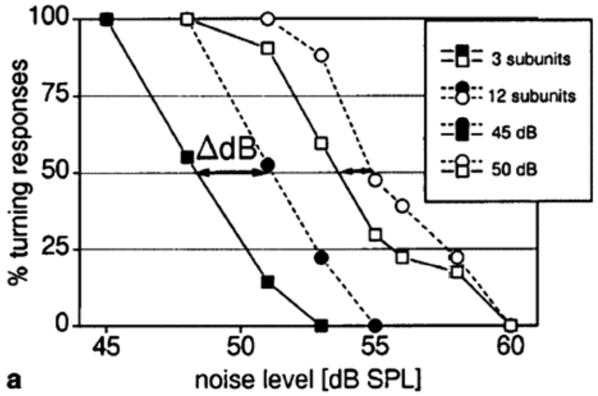

FIG. 10 Response of a male *Chorthippus biguttulus* to short (3 subunits) and long (12 subunits) female songs under masking noise broadcast from above. The percentage of turning responses relative to the total number of stimulus presentations is shown. The solid symbols represent the responses to stimuli with an intensity of 45 dB and the open symbols the response to stimuli with an intensity of 50 dB. The total number of stimuli tested was 541 (Ronacher et al., 2000, Fig. 2a). Reprinted with permission from Springer-Verlag CmbH & Co. KG.

Taking the 50% response level and comparing long and short songs showed that there was a 2-3 dB shift (ΔdB) in the response curve. An analysis of this shift for all animals tested suggested that 1 dB of added noise led to a mean value of 14.8% decrease in response to the 12-subunit signal and a 13.2% decrease in response to the three-subunit song. Additional tests were made using four-subunit and five-subunit songs, compared with the responses to 12-subunit songs. The mean values obtained for ΔdB are shown in Fig. 11 and the slope of the regression line crosses the zero line at 441 ms duration. This suggests that song lengths greater than this value do not improve significantly the detection of the signal against background noise.

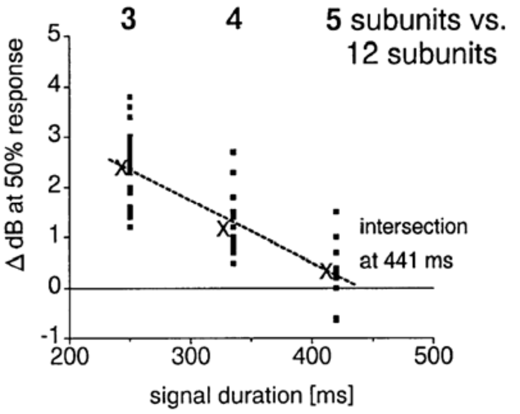

FIG. 11 The influence of signal duration upon noise tolerance. The values of ΔdB are calculated relative to the 12-subunit song (Ronacher et al., 2000, Fig. 3b). Reprinted with permission from Springer-Verlag CmbH & Co. KG.

A further feature of long signals in *C. biguttulus* is the opportunity for the male to make a correcting turn immediately after he has turned towards a female. A short song will have ended before the turning response of the male (the open-loop state), but a long song continues until after the male has completed his turn and he can therefore make a further correcting turn (closed-loop state). In a comparison of the turns performed by males in response to short and long songs, only one correcting turn was observed to the three-subunit song (n=101) whereas 55 were observed in the responses to the 12-subunit song (n=129) (Ronacher et al., 2000). The fact that females produce songs that are at least twice as long as the duration needed by the male for recognition under noisy conditions would appear to be the result of selection for a more a direct and faster phonotactic response in that the male can perform two turns in response to one burst of female song. The length of the song does not appear to be an aid to lateralization. Males have been shown to be equally effective at making correct turns to three-subunit songs as to 12-subunit ones (Ronacher and Krahe, 1997; Ronacher et al., 2000).

5.2 Identified auditory interneurons in the nervous system

The auditory receptors project into the prothoracic ganglion (crickets and bushcrickets) and the abdominal ganglion (grasshoppers) and their aborizations are entirely ipsilateral. The projections are primarily to the medial ventral association centre (mVAC) of the ganglia. Many local interneurons are small and remain uncharacterized, with most of the information we have coming from studies on a few large interneurons, for example the omega neuron. Ascending neurons generally have dendrites in the ganglion on the soma side and an ascending axon contralateral to the soma, that ascends to the brain. In comparing the identified and characterized neurons in orthopterans it is clear that there is substantial homology between the groups, for example in the T-cell. Furthermore, first order interneurons in the grasshopper have been shown to be serially homologous along the central nervous system, which suggests that the tympanal receptors are a specialized part of the general chordotonal system with a similar arrangement of projections from homologous receptors to homologous interneurons (Boyan, 1993). This developing picture of homologies between groups and serially within individuals is one of the exciting outcomes of recent neurophysiological work, which is now able to feed into discussion of the evolutionary relationships within the Orthoptera (van Staaden and Römer, 1998) and wider relationships with other insect groups (see, for example Yager, 1999; Prier and Boyan, 2000).

5.2.1 The T-cell

T-shaped interneurons (T-cells) have been identified in many groups of orthopteran insects. Since the first one was identified in the tettigoniid *Gampsocleis buergeri* (see Suga and Katsuki, 1961), their presence has been described subsequently in other tettigoniids (Rheinlaender et al., 1972; Schul, 1997; Faure and Hoy, 2000b), haglids (Mason and Schildberger, 1993), gryllids (Atkins and Pollack, 1987), acridids (Römer, 1985) and mole crickets (Mason et al., 1998). The anatomy of the T-cell was described by Kalmring et al. (1979), who identified it as part of a giant fibre system, and Oldfield and Hill (1983) who localized the cell body in the prothoracic ganglion. Information from the tympanic nerve in the foreleg reaches the prothoracic ganglion where the cell body of the T-cell passes information both anteriorally and posteriorally in the ventral nerve cord. The T-cells are paired in the prothoracic ganglion and it has been shown that responses to auditory stimuli in the ipsilateral tympanic nerve exert a strong inhibitory influence on activity in the contralateral T-cell (Rheinlaender et al., 1972). The T-cell might be expected to play a role in the detection and localization of the conspecific song. However, studies comparing the tuning curve of the T-cell with the spectral content on the species song have given equivocal results. For example in the zaprochiline *Kawanaphila nartee*, Bailey and Römer (1991) found that the T-cell in both sexes had a best frequency of 15 kHz below the peak spectral frequency of the calling song of 50 kHz. This does not preclude the T-cells from a role in detecting the conspecific song; it suggests other roles, such as predator avoidance, may have shaped the tuning curve during evolution.

The most comprehensive study of the T-cell in a tettigoniid is that of Faure and Hoy (2000a; 2000b; 2000c) who have studied the neuroethology of the cell in *Neoconocephalus ensiger*.

A typical tuning curve for a T-cell is shown in Fig. 12 and is remarkably similar to the tuning curves measured by other workers for different species of tettigoniid (Suga, 1966; Rheinlaender and Römer, 1980). The tuning curves for male and females are also similar, but the T-cell of females is slightly more sensitive to audio frequencies than in males. The best threshold for females was about 5 dB lower than in males and the best frequency was about 5 kHz lower. In both sexes, the best frequency of the T-cell was 20 kHz or higher (Faure and Hoy, 2000b). From this it appears that the female will respond better to the conspecific song than males. In tests using a simulation of the calling song, the female T-cell responded better than the male (Faure and Hoy, 2000c). The calling song of *N. ensiger* has a peak frequency at about 14 kHz with a range of 9 to 25 kHz, but there is appreciable sound energy in the ultrasonic range up to 40 kHz (Faure and Hoy, 2000d).

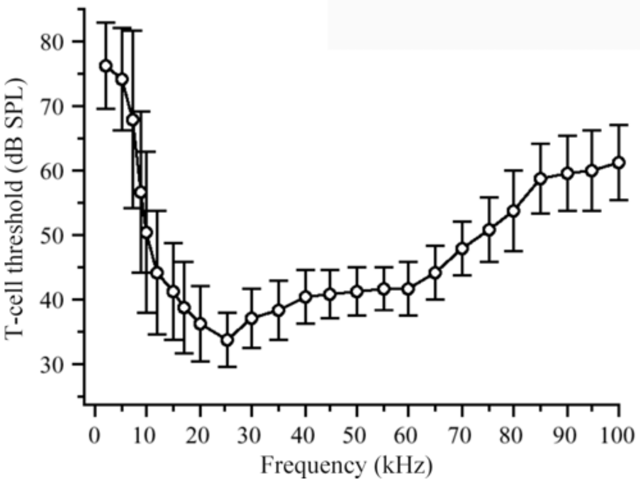

FIG. 12 The mean excitatory threshold tuning curve for the T-cell of *Neoconocephalus ensiger*, with the loudspeaker situated at 90° to the long axis of the body. Note the higher degree of variability in audiosound (7–17 kHz) thresholds (Faure and Hoy, 2000b, Fig. 2A). Reprinted with permission from the Company of Biologists.

The ability of the T-cell to follow the temporal patterning of sound was not the same at all frequencies. At a frequency of 40 kHz, with the sound source at 90°, the T-cell encoded the temporal pattern of the sound pulses over a wide range of repetition rates with almost one-to-one coding up to a repetition rate of 30 Hz. However, at a frequency of 15 kHz, which is within the maximum peak energy band of the calling song, accurate coding of the temporal pattern was degraded above a repetition rate of 5 Hz (Faure and Hoy, 2000b). The latency of the response in the T-cell also varied with frequency, being shorter at 40 kHz than at lower frequencies. Both of these findings would support the view that the T-cell is able to provide the insect with predator-avoidance information. Searching bats increase the repetition rate of their locating pulses when approaching an object and decrease their calling intensity. The T-cell with its short latency of response and an ability to follow fast repetition rates would enable an insect to detect a bat that was preparing to attack (Fullard, 1984).

The responses of the T-cells of *N. ensiger* to simulated bat calls have been compared with the responses to a simulation of the conspecific song (Faure and Hoy, 2000c). The syllable repetition rate of a calling *N. ensiger* at 25 °C is 14.25 Hz (Faure and Hoy, 2000d) and simulated bat calls used the same repetition rate. Two types of bat call were simulated, one (Bat 10) with 80 kHz to 30 kHz FM sweeps of 10 ms duration and a second (Bat 30) with sweeps of 30 ms duration, the duration corresponding to the duration of syllables in the calling song of *N. ensiger*. The way in which these simulated calls were encoded in the T-cells was not the same for each stimulus type. At 90 dB SPL the T-cell followed the Bat 10 signal perfectly and, when the sound intensity was reduced to 70 dB SPL, the ability of the cell to follow the temporal pattern was almost perfect. At 50 dB SPL the ability to follow started to break down. However, at all three sound intensities the T-cell did not follow the Bat 30 or conspecific song perfectly, with the ability to follow the pattern being poor below 90 dB SPL. However, it was clear that other neural units with smaller responses than the T-cell were following the temporal pattern of the calling song perfectly at 70 and 90 dB SPL.

The T-cell has been shown to adapt to the conspecific calling song (Kalmring et al., 1979) but it has also been reported that there is a one-to-one correspondence between syllables and responses (Suga and Katsuki, 1961). In the bushcricket *Tettigonia viridissima*, where the song is a continuous repetition of a pair of syllables, the T-cell (TN1) follows the individual syllables without adaptation (Schul, 1997). However, experiments with song analogues of different spectral composition have shown that the T-cell is responding to the ultrasonic component of the songs only. Stimulation with pure tones showed that the T-cell responded to a wide range of frequencies (4 to 60 kHz) and the spiking responses were both phasic and adapting, to ultrasonic frequencies. Regular spiking responses were not evoked by the audible range of frequencies.

A second, smaller T-shaped interneuron (TN2) has been discovered (Schul, 1997) in *T. viridissima*. It has a small axonal diameter and its responses to stimulation are not easy to detect using extracellular recordings from the connectives. The responses of TN2 are strongly phasic and adapting and the cell is primarily tuned to ultrasonic frequencies with the best response being at 30 kHz, where the threshold is below 40 dB.

The established view, or assumption, that the T-cell is primarily the agent for the detection and localization of conspecifics has now been challenged. It appears very likely, from the recent evidence (Schul, 1997; Faure and Hoy, 2000b; c), that the role of the T-cell in tettigoniids is not the detection of the conspecific song. Instead, the T-cell detects frequencies in the ultrasonic region and mediates predator avoidance and escape mechanisms. Where the conspecific song contains ultrasonic components these are detected by the T-cell (Schul, 1997) but it remains to be seen how significant this is in the identification and location of conspecifics.

5.2.2 The omega neuron

The omega neuron is shaped like the Greek letter Ω (Fig. 13) and is a first order interneuron that receives auditory input from the receptors in the tibial tympanic organ and connects the auditory neuropiles in each half of the prothoracic ganglion. Omega neurons are found in both major groups of the Ensifera, the Grylloidea (Casaday and Hoy, 1977; Wohlers and Huber, 1982) and the Tettigonioidea (Römer et al., 1988) and there is evidence that they are homologous (Schul, 1997). The neurons are paired in tettigoniids but there are two pairs in the Gryllidae (Wohlers and Huber, 1982; Stiedl et al., 1997). Each of the paired omega neurons has branches in both halves of the prothoracic ganglion, with the processes on the same side as the cell body being mostly postsynaptic, receiving excitatory inputs from the receptors in the ipsilateral ear. The processes of the neuron in the contralateral side of the ganglion are mostly presynaptic and exert inhibitory control of auditory neurons receiving input from the other ear and the other omega neuron of the pair (Watson and Hardt, 1996). Thus the pair of omega neurons enhances the contrast between the two ears and so improves the ability of the insect to localize the source of sound.

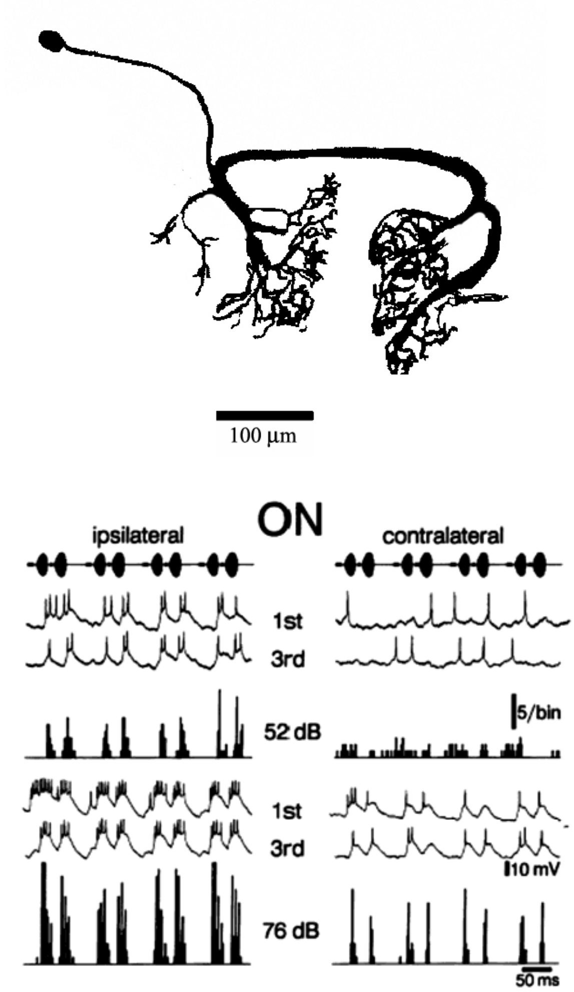

FIG. 13 (upper)An omega cell in the prothoracic ganglion of the bushcricket *Tettigonia viridissima* (Schul, 1997, Fig. 3A). (lower) The response of the omega neuron 1 (ON) to stimulation from models of the conspecific calling song. Dendritic recordings from ON and PSTHs to stimulation delivered from the soma-ipsilateral (left) and soma-contralateral side (right). The stimulus intensities are indicated. The top traces correspond to the first stimulus sweep, and the bottom traces to the third one, demonstrating the pronounced responses to the first syllables of a song. PSTH: 15 repetitions, bin width 2 ms (Schul, 1997, Fig. 4). Reprinted with permission from Springer-Verlag CmbH & Co. KG.

5.2.2.1 The omega neuron 1 (ON1)

The omega neuron ON1 responds to sound over a wide frequency range but has been found to be most sensitive at the carrier frequency of the conspecific calling song, for example in *Gryllus bimaculatus* (see Popov et al., 1978) and *Gryllus campestris* (see Wohlers and Huber, 1982). A typical response to a conspecific calling song model, recorded in

Tettigonia viridissima, is shown in Fig 13b (Schul, 1997). On the ipsilateral side the response is tonic and has a threshold of about 40 dB. The EPSPs and the spikes match the syllable structure of the song and do not show long-term adaptation over the duration of the song models (up to 20 s), although the spike response to the initial syllables of the stimulus is somewhat greater than for subsequent syllables. The responses to stimulation from the contralateral side were weaker than those on the ipsilateral side, but there was variability in the level of response between different individuals (Schul, 1997).

In the cricket *Teleogryllus oceanicus* the omega neuron ON1 is most sensitive to the frequency of the conspecific song (4.5 kHz) but the latency of the response is longer than for other frequencies (Pollack, 1994; Faulkes and Pollack, 2000). Latency decreases as sound intensity increases but the response at 4.5 kHz remains longer than at other frequencies. The difference in latency is 5-10 ms. This latency is observable not only as a delay in the onset of spikes but also of the EPSP. The functional reason for the longer latency at the species-specific frequency is not yet clear, although it is linked to inhibitory inputs onto ascending auditory interneurons (see Section 5.2.3).

The possible mechanisms that might account for the increased latency have been investigated by Faulkes and Pollack (2001). The possibility that auditory receptors might have different conduction velocities, based upon their frequencies of response was examined by Pollack and Faulkes (1998) and they found no evidence to support the idea. However, unpublished results from Imaizumi and Pollack, quoted by Faulkes and Pollack (2001) indicate that there is a sub-population of low frequency auditory receptor neurons that has lower conduction velocities than other auditory receptor neurons. Whether this fact contributes to the latency of response of ON1 at the frequency of the conspecific song is not known as the difference in conduction velocity is only 2-3 ms. A possible mechanism for the production of the latency is postsynaptic inhibition that precedes or is simultaneous with the excitation produced by the sound stimulus. When intracellular recordings were made (Faulkes and Pollack, 2001) using microelectrodes filled with potassium acetate (to avoid the use of chloride ions and thus hyperpolarization of the cell), no early IPSPs were detected. There was no reduction in the rate of firing or of the height of the spikes prior to the response evoked by the stimulating sound. EPSPs that are evoked by ultrasound have a faster rise time than those evoked by the species-specific frequency of 4.5 kHz and also a shorter latency. This demonstrates that at least part of the explanation for the longer latency at 4.5 kHz must lie in events that are presynaptic to ON1. Faulkes and Pollack (2001) argue that the likely explanation is that there is a polysynaptic afferent pathway to ON1 that is specific to 4.5 kHz, in addition to a monosynaptic one. They cite as evidence that fact that a very brief 5-kHz stimulation generates two EPSP peaks 12 ms apart but a short ultrasonic stimulus elicits a single peak. The first peak would be evoked via the monosynaptic pathway and the later one via the polysynaptic pathway. An explanation of the functional significance of this arrangement of the inputs to ON1 for species recognition and localization will be of great interest. There is some evidence that the latency is linked to the relationship between ON1 and the ascending neurons 1 and 2 (AN1 and AN2) (see Section 5.2.3).

A slowly developing inhibition of ON1 has been observed in *Tettigonia viridissima*. It has been shown that when two conspecific songs of differing intensity are presented together from the same direction, the louder song (60 dB SPL) was represented as spikes in ON1, while the representation of the weaker song (45 dB SPL) was completely suppressed (Römer and Krusch, 2000). The weaker song, when presented on its own, was effective at generating a response in ON1. The explanation for this observation came from further intracellular work, which showed that the synaptic events had two components: excitatory EPSPs encoding the train of syllables and a slowly developing hyperpolarization of the cell. This inhibitory hyperpolarization could take as long as 10 s to develop fully and as long as 15 s to disappear and for the resting membrane potential to become re-established. The effect of the hyperpolarization is to reduce the gain of the cell such that only the more intense signals produce a spiking response. One consequence of the gain control is a sharpening of the directional response, such that two sound sources at an angular separation of as little as 7.5^{o} either side of the midline axis will be represented significantly better in the ipsilateral ON1. Thus the auditory field around the bushcricket is divided sharply into two hemispheres. A further point that arises from this study is the very long time course of the development of inhibition. This inhibition is effective in *T. viridissima* because the males sing for very long periods. In a species with short songs, this gain control mechanism would be ineffective. Thus there could be a link between the evolution of long duration signals, chorusing (see Section 8.2) and this inhibitory mechanism. It will be interesting to see what comes out of future studies of long-term inhibition in ON1 and the pattern of distribution of the phenomenon in tettigoniids and gryllids.

5.2.2.2 The omega neuron 2 (ON2)

The morphology of the omega neuron ON2 in crickets has been described in *Gryllus campestris* (see Wohlers and Huber, 1982; 1985) and its acoustic responses have been reported (Lewis, 1992), but the only detailed study of its physiology is the recent one of Stiedl et al. (1997). The morphology of ON2 is very similar to that described for ON1 (Fig. 13). However, unlike ON1, there are one or more crossover branches that connect the anterior ring tracts in each hemiganglion. A small diameter ascending axon is sometimes present. It was found in six out of 41 preparations of *Acheta domesticus* and all six were from females less than eight days old (Stiedl et al., 1997). This is similar to the situation in ON1 in the cricket *Teleogryllus oceanicus* where ascending axons are found in young females (Atkins and

Pollack, 1986). The absence of evidence of ascending axons in males and older females suggests that degeneration occurs during development and that there is an interesting story about the function of these axons still to be researched.

ON2 in *A. domesticus* is a spiking neuron with a frequency response that is about 20 dB more sensitive at 16 kHz than it is at 5 kHz (Stiedl et al., 1997), similar to *T. oceanicus* (see Lewis, 1992). It receives both excitatory and inhibitory inputs from both ears and does not have a directional hearing function. The role played by ON2 in the auditory system of the cricket is speculative at present. The response to high frequency might suggest a role in predator avoidance, although there is no directional response. In combination with other auditory interneurons it could produce patterns of inhibition that enhance syllable pattern processing, although the lack of GABAergic or serotonergic immunoreactivity found in ON2 in *G. campestris* suggests otherwise (Hardt et al., 1994; Watson and Hardt, 1996). The courtship song in crickets is produced by the male when very close to the female, so it will be received at a high intensity. There remains a possibility that despite the tuning curve being most sensitive at 16 kHz, the response to the courtship song is mediated in some way via ON2.

5.2.2.3 Omega neurons in acridids

Experiments in which fluorescent tracers were injected into the afferent neuropile of the metathoracic ganglion of the locust showed the presence of omega-shaped neurons in the prothoracic and mesothoracic ganglia (Lakes-Harlan et al., 1998). These were presumably labelled trans-synaptically, although a descending axon, observed in some preparations, may have carried the label. Labelled cell bodies were found on both sides of the ganglion, indicating that input synapses occur on both sides of the aborizations, as observed in ensiferans (Watson and Hardt, 1996). The questions of whether these omega neurons are homologous with those found in ensiferans and whether they have an auditory function remain unanswered.

5.2.3 Ascending auditory interneurons

Ascending auditory interneurons have been described in a number of species. In crickets, the neurons AN1 and AN2 have been identified (Wohlers and Huber, 1982; Hennig, 1988) and their roles in phonotaxis investigated (Harrison et al., 1988; Schildberger and Hörner, 1988). In tettigoniids a number of authors have described auditory interneurons and some of them at least can be identified as being homologous with those in crickets (Stumpner, 1997). Two pairs of ascending neurons have been described (Schul, 1997) in *Tettigonia viridissima* and in both morphology and physiology are similar to AN1 and AN2 in crickets. AN1 is tuned to low frequencies and receives inhibitory input during stimulation by ultrasound, while AN2 predominantly receives information about ultrasonic signals and does not display frequency dependent inhibition. These characteristics are also found in crickets. AN2 in *T. viridissima* responds tonically to the species song and encodes the syllable pattern, unlike AN2 in crickets which does not normally resolve the syllable pattern (Hennig, 1988; Schul, 1997).

The most complete characterization of an ascending neuron in tettigoniids has been carried out in the phaneropterine bushcricket, *Ancistrura nigrovittata* by Stumpner (1997). AN1 has a cell body (soma) in the anterior dorsal region of the prothoracic ganglion. An ascending axon runs through the suboesophageal ganglion, without branching, until it reaches the protocerebrum of the brain (Fig. 14). The dendritic branches arise from the primary neurite, in the hemiganglion that is contralateral to the cell body, though some of the branches cross back into the ipsilateral side.

FIG. 14 A ventral view of the AN1 neuron in the prothoracic ganglion of *Ancistrura nigrovittata* (Stumpner, 1997, Fig. 1). Reprinted with permission from the Company of Biologists.

Acoustic communication in *A. nigrovittata* has been described by Dobler et al. (1994a) who showed that the hearing range extended from 2 kHz to well into the ultrasonic range, with the best frequencies being in the range 20 to 25 kHz, where the sensitivity was 30 dB SPL. The male song has peak energy at 15 kHz. Like other phaneropterines studied *A.*

nigrovittata females produce a song in reply to the male and they are most sensitive at 12 and 16 kHz. The peak frequency of the female song is 28 kHz. AN1 is most sensitive at 16 to 20 kHz and the sensitivity falls off rapidly between 20 and 30 kHz (Stumpner, 1997). The tuning curves are similar for males and females, although males are slightly more sensitive at 20 and 24 kHz. At 16 to 20 kHz, AN1 is more sensitive than the female behavioural thresholds for responses over the same frequency range that were measured by Dobler et al. (1994a). At frequencies in the range 4 to 10 kHz and in the range 24 to 50 kHz there are prominent IPSPs, but between 10 kHz and 20 kHz there are no subthreshold IPSPs and the first response to a stimulus is an excitatory one (Stumpner, 1997). In general, AN1 is more sensitive to stimulus from the soma-contralateral side and the IPSPs are still present when the input from the soma-ipsilateral side is removed by lesion of the tympanic nerve. At intensities up to 55 to 65 dB the soma-contralateral stimuli evoke more spikes than the soma-ipsilateral stimuli and the maximum difference is equivalent to a left-right difference of 30 dB. However, at higher intensities the difference is less and at some frequencies the ipsilateral stimuli may evoke a greater response. The asymmetry in the response implies that there is inhibitory input that is soma-ipsilateral. This was demonstrated by cutting the soma-contralateral tympanic nerve, which eliminated all spiking responses but displayed IPSPs coupled to the stimuli (Stumpner, 1997). In *T. viridissima*, white noise stimuli of increasing intensity generated an IPSP that reduced and delayed the spiking response of AN1 (Schul, 1997). This inhibitory input is tuned to ultrasonic frequencies, with stimulation of 7 and 12 kHz producing purely excitatory responses. Above 12 kHz the IPSPs appear and have a greater effect in delaying and reducing spiking as frequency increases until, at 30 kHz, only the inhibitory response is present.

The source of the inhibitory inputs acting upon AN1 have yet to be determined in *A. nigrovittata*, but experiments on the cricket *Teleogryllus oceanicus* suggest that ON1 is the main, and perhaps the only, source of contralateral inhibition to AN1 (Faulkes and Pollack, 2000). When AN1 is stimulated by sound from the soma-contralateral side it receives inhibitory inputs from the ON1 on the right, which receives sound from the ear on the opposite side. The longer latency of the response of ON1 at the species song frequency of 4.5 kHz means that the first spiking response of AN1 is not influenced by inhibition from ON1. This might be interpreted as being a mechanism that enhanced interaural differences and hence directional hearing but by adjusting the timing of the stimuli to each ear it was possible to remove artificially the latency of ON1 and show that this increased rather than decreased the latency of AN1 (Faulkes and Pollack, 2000). The function of the latency in the response of ON1 still awaits an explanation, although Faulkes and Pollack (2000) suggest that a possible reason might be the fact that ON1 is tuned to frequencies that evoke two different behaviours, positive and negative phonotaxis. The delay in the response of ON1 to the cricket song frequency might be a consequence of other unrelated requirements of the nervous system.

5.2.4 Auditory interneurons in the mole cricket

In a comparison of two mole cricket species, one winged (*Scapteriscus borellii*) and one flightless (*S. abbreviatus*), differences in the responses to high frequency sound were found in identified neurons. The auditory interneurons are similar in anatomy to those found in other ensiferans. Two classes of omega neurons (Wohlers and Huber, 1982; Römer et al., 1988) are found in the prothoracic ganglion though they are not distinguishable morphologically. Anatomically, they resemble the ON1 neurons of the true crickets. The two types differ in their frequency responses. While both have a peak sensitivity at around 3 kHz, one type has a second peak in the 20-30 kHz range (Fig. 15).

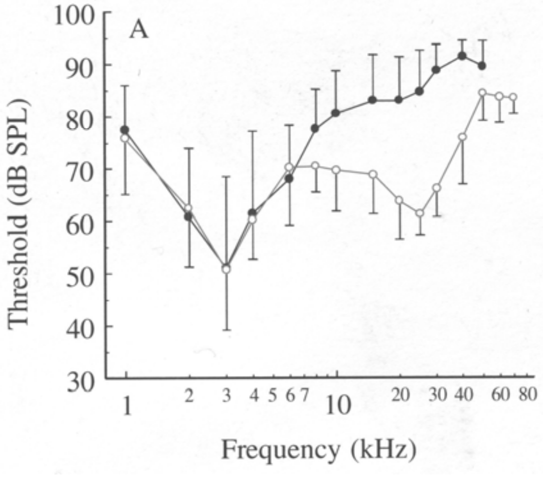

FIG. 15 The response characteristics of 2 types of omega neuron in *Scapteriscus borellii*, showing the difference between a low-frequency tuned neuron and a high frequency tuned one (Mason et al., 1998, Fig. 3A). Reprinted with permission from the Company of Biologists.

One auditory unit was recorded (Mason et al., 1998) that had a single peak of sensitivity in the ultrasonic range. This was a high frequency T-neuron, which had a low threshold between 20 and 30 kHz but with a wide range, showing strong responses at 70 kHz (Fig. 16).

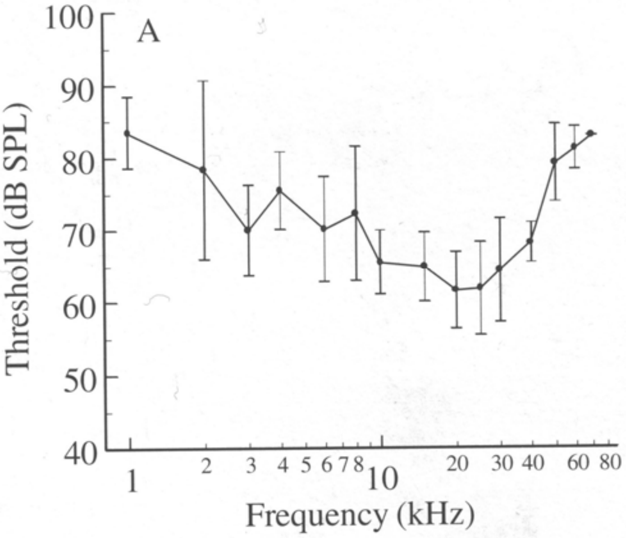

FIG. 16 The mean response characteristics of high frequency T-neurons in *Scapteriscus borellii* (Mason et al., 1998, Fig. 6A). Reprinted with permission from the Company of Biologists.

Recordings from the cervical connectives showed short-latency responses (15-20 ms) to both audio and ultrasonic acoustic signals, when signal averaging techniques were used. The responses to audio stimuli (3 kHz) were of greater amplitude and duration than those to ultrasonic stimuli (25 kHz), suggesting that multiple units carried the audio frequency information but that only one or at most a few units carried the ascending ultrasonic responses. Longer latency responses were detected to ultrasound, but these were likely to be in the descending fibres and related to the ultrasound startle response (Hoy et al., 1989).

In *S. abbreviatus*, which is flightless, the omega neurons had similar tuning and response properties to those observed in the low frequency omega neurons in *S. borellii*. One example of a high frequency T-cell was recorded and it was homologous with the high frequency T-cell in *S. abbreviatus*, but with thresholds of greater than 80 dB SPL over the whole range of frequencies tested. The presence of responses to high frequency in the night-flying *S. borellii* but not in the flightless *S. abbreviatus* suggests that the auditory system in *S. borellii* plays a part in the avoidance of predators. (see Section 7.3).

The two pairs of omega neurons found in the mole crickets are probably homologous with those of crickets, where two pairs are also found (Wohlers and Huber, 1982). Two pairs of omega neurons are also found in haglids (Mason and Schildberger, 1993), in contrast to the tettigoniids where only one pair has been found in the species studied so far (Römer et al., 1988; Schul, 1997).

5.2.5 Auditory interneurons in grasshoppers

The auditory pathways in the nervous system of grasshoppers have been studied extensively. There have been a number of reviews of auditory processing that include sections on the auditory interneurons, notably those of Stumpner and von Helversen (2001), while the auditory processing of information from chordotonal organs is reviewed by Field and Matheson (1998). Excitatory and inhibitory inputs to two ascending interneurons were identified by Marquart (1985). Subsequently, Boyan (1991; 1992) showed that there was a common synaptic input from one of the cells recorded by Marquart onto other ascending auditory interneurons. One of these postsynaptic cells was the G neuron, also known as neuron 714, and this neuron is perhaps one of the best-characterized neurons in insects. A recent study of this morphologically prominent neuron by Boyan (1999) has demonstrated that the level of excitability of the neuron depends upon the gating of modulating inputs, including auditory and vibratory sources. Eight auditory interneurons are known to be presynaptic to neuron 714 and all are excitatory. However, it is not yet known how many of the receptors in the ears themselves connect synaptically with neuron 714. Those that do ascend to the metathoracic ganglion to synapse with neuron 714 seem to be predominantly high frequency (15 kHz) ones (Halex et al., 1988). The connections between identified cells in the metathoracic ganglion and neuron 714 in the mesothoracic ganglion are summarized by Boyan (1999) and shown in Fig. 17. Neuron 714 is one of several interneurons that provide multimodal outputs in the form of combined information from more than one sensory source and it is part of the neuronal chain that triggers jumping in locusts (Gynther and Peerson, 1989). The extensive range of both inputs and outputs to this neuron highlight its importance as a component of the locust nervous system and it is clearly a neuron which will repay deeper study in the future.

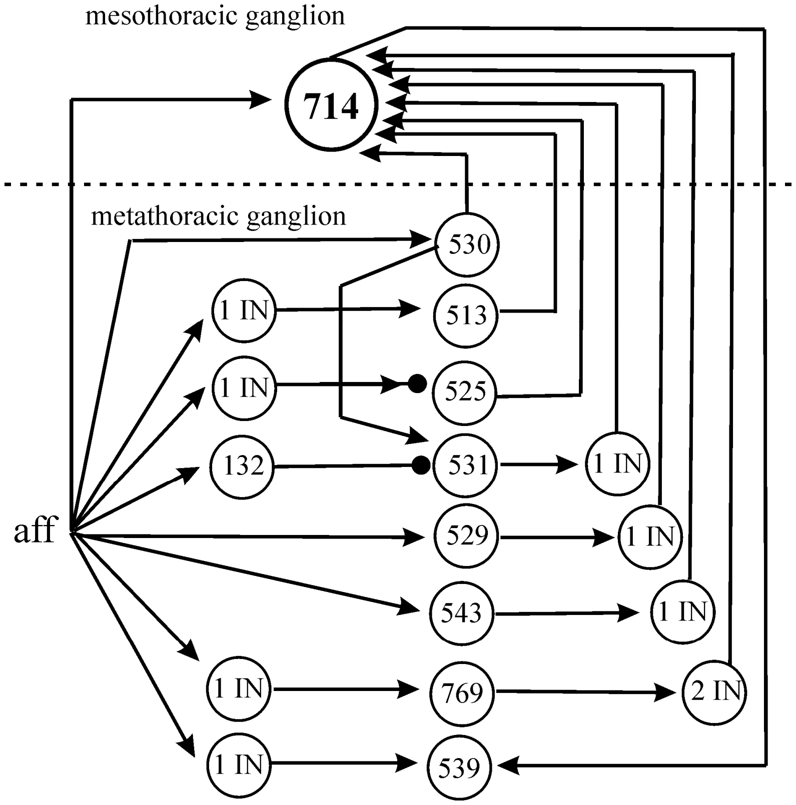

FIG. 17 A summary of the synaptic connections to neuron 714 in the locust mesothoracic ganglion, from cells in the metathoracic ganglion. The numbers in the circles refer either to identified interneurons or to the likely number of interneurons that make up the pathway, based on the measurement of synaptic delays. Arrows indicate an excitatory connection, filled circles an inhibitory one. Auditory afferents make a monosynaptic connection with neuron 714 (Boyan, 1999).

5.3 Symmetry and asymmetry

The sound producing apparatus in Orthoptera shows asymmetry both in anatomy and in motion (for examples see Ewing, 1989). However, orthopteran ears would be expected to be symmetric as directional information would be derived from the differences between the signals from the left and right ears. However, Rheinlaender and Römer (1980) found asymmetry in the ears of the bushcricket *Tettigonia viridissima* when they investigated the responses of the T-cells, particularly at frequencies below 12 kHz and above 20 kHz. Of the pairs of T-cells whose thresholds they measured, 53% showed some degree of asymmetry, explained in their view by a loss of function in single primary afferents. Boyan (1979) found an even larger proportion of individuals showing asymmetry of spiking responses in neurons in his study of *Teleogryllus commodus*. These results are puzzling when considering the importance of directionality, particularly in phonotaxis, and a recent study (Faure and Hoy, 2000a) has revisited the problem of the degree of asymmetry in the T-cell response, using *Neoconocephalus ensiger*. Of 32 males tested with a loudspeaker at 0° or 90° to the long axis of the animal, only three showed an asymmetry in their thresholds that was significantly greater than variation due solely to measurement error, all at 90°. Of 16 females tested, only three showed significant asymmetry, two at 90° and one at 0°. Overall, this study found that 87-92% of individual pairs of T-cells were bilaterally symmetrical and that the symmetry covered the whole frequency range of the ear. In contrast, Rheinlaender and Römer (1980) suggested that within the key frequency range for detecting the species song, symmetry was greatest. The reason for the difference between the two studies probably lies in the treatment of measurement error, although the studies were of different species. Rheinlaender and Römer (1980) were conservative in their analysis, excluding animals where there was a difference of greater than 2 dB between two measurements of threshold under the same conditions. Faure and Hoy (2000a) found that the measurement error was 2-3 dB in their study. Thus excluding animals at the 2 dB level may have reduced the apparent size of the measurement error and thus enhanced asymmetry.

An additional piece of evidence supporting the idea of symmetry comes from a study of the omega neuron (ON1) of *Tettigonia viridissima*, which showed that of ten pairs of neurons studied, eight had thresholds that did not deviate by more than 2 dB from each other at any frequency. It appears, from the more recent study of Faure and Hoy (2000a), that symmetry may indeed be a feature of the auditory system, but we must await confirmation from other species that is a widespread feature of orthopteran hearing.

6 Information content of signals

‘Communication can be defined as the transfer of information from one organism to another, detectable to an outsider only through the appearance of an observable response in the receiving individual’ (Alexander, 1967).

Johnstone (1997) has recently reviewed the evolution of animal signals. The most important factor in signal evolution has probably been the reciprocal nature of selection: the properties of the receiver exert strong selection on signal design and signal design in turn exerts strong selection on receiver behaviour. Thus, on one hand, selection favours signallers who elicit favourable responses while on the other it favours receivers who can accurately interpret the nature and intentions of senders from their signals. To be effective in eliciting favourable responses, a signaller must use displays that are well-suited to detection by the sensory and neural mechanisms of intended receivers (called sensory exploitation by Ryan, 1990), but at the same time unsuitable for detection by unwanted eavesdroppers such as predators. All members of the ‘audience’, not just intended receivers, can therefore influence the evolution of signalling behaviour. As far as the signaller is concerned, the signal may be a way of manipulating others, for example a means of stimulating a female to mate, but as far as the receiver is concerned, it is solely a source of information. Selection will favour receivers who can best relate their behaviour to the information contained in the signal and at the same time ignore signals that do not provide relevant information. As a result of the selection pressures on signallers, displays will be designed to produce a response efficiently; as a result of the selection pressures on receivers, displays will be designed to prevent them being ‘dishonest’ (i.e. unreliable). Many display properties can thus be explained in two ways. The high cost of some extravagant signals, for example, can be explained because they make the signal more detectable or stimulating to receivers. On the other hand, if signals are costly to produce, then only signallers of high quality or signallers who stand to gain a lot by getting a favourable response should produce them. According to this ‘handicap principle’, therefore, honesty can be maintained by costly signals (Zahavi, 1975). From the evidence so far, Johnstone concludes that the detailed design of a signal is more dependent on the environment in which communication takes place, and the audience to which it is directed. In other words, signals must be both efficient and reliable but the need for efficiency appears to place the greatest constraint on their design.

Producing a costly signal may also increase the efficiency of communication; even in an apparently cooperative signalling system where signallers gain by producing a response and receivers gain by responding, there will be conflicts because signallers have to balance efficient communication against the possibility of attracting eavesdroppers, while receivers have to balance the efficiency of responding against the possibility of responding inappropriately, for example to an extraspecific signal (Johnstone, 2000).

An orthopteran trying to obtain a mate using acoustic signals must provide information about its species, its location and its suitability as a mate. The physical environment through which its signal has to pass affects the transmission of information to the recipient. The signals of other conspecifics or other species may also obscure the sender’s signal. In addition, the sender has to avoid the attentions of unwanted eavesdroppers, for example rival males or predators. The problems of eavesdroppers and interference from other signallers are considered in Sections 7 (predators and parasitoids) and 8 (competition with conspecifics); the information content of the signal and the effects of the physical environment are considered here.

6.1 Components of sound signals

A sound signal has five main parameters: amplitude (i.e. loudness, measured as sound pressure level); frequency or wavelength spectrum (frequency is equal to the reciprocal of the wavelength); frequency modulation (e.g. a sound may rise in pitch and then fall again); amplitude modulation (e.g. a sound may start loudly, then fade away); and temporal patterning (length of pulse, length of interpulse interval, number of pulses, bout length of a series of pulses, etc). The various parameters of signals reveal different things about the sender, some of which are not under the sender’s control (Endler, 2000). For example, dominant wavelength and wavelength spectrum are determined by the biomechanics of the sender, and biomechanical properties are related to size. The energetic cost of the signal is also directly related to its components: for example, costs increase the louder the call, the faster the frequency or amplitude modulation, the longer the pulse length, the shorter the interpulse interval and the longer the bout length (see Section 3.8). The signal received by the recipient may differ from the sender’s original because of changes that occur during transmission through the environment. Some of the resulting call features can also provide information about the sender. For example, the greater the distance between signaller and recipient, the less coherent the received call is likely to be (i.e. the more echoes it is likely to have that are out of phase with the original: see Section 6.2).

6.2 Effects of the environment on sound signals

Sound waves propagate from their source and, in open air, spread spherically and attenuate by the inverse square law (Bennet-Clark, 1998). They travel faster at higher temperatures. The effects of the environment on signals have recently been reviewed by Endler (2000). Earlier reviews include those by Forrest (1994), Römer (1992) and Michelsen (1985), while Pye (1979) has considered the particular problems and advantages associated with the use of ultrasound in signalling.

The environment has two main effects: it modifies signals and masks or distorts them by adding noise (any unwanted sound that interferes with the detection of a signal and the transmission of the information it contains, including environmental noise such as wind and turbulence and biological noise such as sounds from other animals: see Forrest, 1994). Environmental noise is usually low frequency, with most energy below 2 kHz (Forrest, 1994). The signal-to-noise ratio (in its simplest sense, this is the difference in dB, between the level of the background noise and the level of the signal: see Forrest, 1994) will therefore be higher for signals over 2 kHz, so high frequency signals are inherently easier to detect. However insects, being small, are less efficient sound radiators of low frequency sound. There is thus a trade-off between producing low frequency signals that travel farther and high frequency signals that are produced more efficiently.

The problems of added noise can be eliminated to some extent by the tuning of the receiver's auditory system. Some orthopteran signals are confined to narrow frequency bands and if the auditory system is tuned to the specific frequency of the signal, the actual signal-to-noise ratio for the receiver will be higher than that measured in the field using a broad-band microphone (Forrest, 1994).

If the environment contains objects, such as plants, which reflect the signal and these reflections reach the recipient after various delays, the combination of original and reflected signals can be so different from the original, both in frequency spectrum and in temporal pattern, that it is unrecognizable (Michelsen, 1985; Endler, 2000). For example, Simmons (1988) showed that the temporal pattern of the calls of the field cricket *Gryllus bimaculatus* became significantly degraded over distances of only 2 m. The intervals between pulses and between chirps decreased because echoes filled in the parts of the call that should be silent. The only parameter transmitted reliably in such a reverberating signal may be the start time of each pulse (Endler, 2000). Reverberation is more of a problem at higher frequencies (shorter wavelengths) because objects reflect wavelengths that are the same size or less, and there are more small objects in the environment than there are large ones. Insects are constrained by their size to produce relatively high frequencies, and choosing a good signalling position free of obstructions may be their best solution to reverberation (Endler, 2000).

Some of the adverse effects of reverberation, noise and other interference can be countered by processing in the nervous system of the receiver, for example by averaging repetitive signals (Endler, 2000). Any noise uncorrelated with the signal cancels out if the repeated components of a signal are averaged. Because there is more noise at higher frequencies, and insects signals tend to be high frequency, insect calls tend to be repetitive (see e.g. Bennet-Clark, 1998). Amplification or filtering within the nervous system can also increase the signal-to-noise ratio and signal redundancy can reduce noise (Endler, 2000). For example, pulse length and song bout length both provide information about energy expenditure, but the noise associated with each of them is not correlated and can be removed during processing by comparison of the two parameters.

A constant sound broadcast from a speaker shows irregular amplitude fluctuations after travelling through turbulent air or past moving objects, and these fluctuations are likely to be greater the higher the frequency of the sound (see Römer, 1992). Römer has shown, however, that such amplitude fluctuations decrease with increasing bandwidth. Many orthopterans use broad-band signals simply as a consequence of the sound production mechanism they use, but the broad frequency spectrum may also enable them to communicate information reliably using amplitude-modulated temporal patterns of calling.

As a result of all the factors that cause degradation as a sound signal passes through the environment, the only cue that is likely to survive is the gross temporal pattern (Römer, 1992). It is probably because temporal patterning is the most reliable feature of a call, that species recognition (see Section 6.3) and mate choice (see Section 6.6) often rely on parameters such as interpulse interval or length of song elements.

Sound signals also suffer from attenuation as well as degradation as they travel through the environment (see Forrest, 1994; Kalmring et al., 1997). Excess attenuation (i.e. over and above that due to spherical spreading) can be caused by atmospheric absorption, absorption by vegetation, scattering by diffraction or reflection, refraction by wind or temperature gradients, or boundary conditions. Higher frequency sounds attenuate faster than do lower frequency sounds. This degradation can be avoided to some extent by sending signals containing wavelengths that attenuate less than others or for which the background noise is minimized (as, for example, *Sciarasaga quadrata* does: see Römer and Bailey, 1998), aiming the signal in a particular direction to minimize spherical loss (as in mole crickets: see Bennet-Clark, 1998), or choosing optimal times or microhabitats for transmission (Endler, 2000). For example, bladder grasshoppers, *Bullacris membracioides*, maximize their calling range by calling at night, as described in Section 3.1 (van Staaden and Römer, 1997).

Many orthopterans call from on or near the ground, a boundary which has a large effect on attenuation (Forrest, 1994). For example 'softer' ground (i.e. more porous surfaces) attenuates a signal much more than 'harder' ground (i.e. less porous, more reflective surfaces such as water), and a given surface attenuates high frequency sounds more than low frequency ones. Elevating the signaller and/or the receiver decreases the attenuating effect of the ground. For example, Römer (1992) measured the intensity of *Tettigonia viridissima* calls at different heights in the field. A signalling male and the recording microphone were placed at the same height, 10-20 m apart. He found that, at an elevation of 1.5 m, recorded intensities were 10 dB greater than those measured at an elevation of 0.75 m. At 2 m above the ground, attenuation was even less and approximated the expected loss due to spherical spreading. Römer suggests that the boundary effect of the ground may be one of the reasons why many orthopterans prefer if possible to call from elevated perches (though another reason may be to avoid the scattering and absorption by vegetation described above).

Attenuation is not necessary disadvantageous, however. Rapid attenuation benefits the signaller if the distance between sender and intended receiver is shorter than between sender and an unwanted recipient such as a predator (see Section 7). It can also provide the recipient with information about the distance to the signaller, since the ratio of the intensities of two or more wavelengths of the signal will be proportional to the distance from the sound source (Endler, 2000).

6.3 Species recognition

In many orthopterans, male calls are species specific and species recognition often depends on the temporal pattern of the conspecific song (e.g. Dobler et al., 1994a). Auditory neurons in the central nervous system of gryllids, tettigoniids and acridids have been shown to code the temporal parameters of the song (Section 5). Rate of singing is dependent on ambient temperature: for example, the warmer it is the faster a cricket chirps (Section 3.7). If species recognition is to depend on the temporal pattern of calling, then the ability of a female to recognize a song must also be related to the temperature; in other words the pattern that a female prefers at a particular temperature must be the same as a male produces at that same temperature. Such temperature-dependent behavioural coupling has been demonstrated in several species, including *Gryllus bimaculatus* and *G. firmus* (Hoy, 1992b).

In bushcrickets, the songs of closely related species are often very similar but with some species-specific differences in temporal pattern that allow discrimination (see e.g. Schul, 1998; Stumpner and Meyer, 2001). Stumpner and Meyer found that four duetting species of *Barbitistes* bushcrickets are similar in the carrier frequency of their song and the shape of a single syllable (the sound produced by one wing closure) but that they all differ in the temporal patterning of their song. Species differ in the number of syllables in a chirp, the syllable period (length of time from the start of one syllable to the start of the next), the trigger period (length of time from the start of the last syllable of a chirp to the start of the 'trigger syllable', i.e. the single syllable that follows a relatively long time after each chirp and which elicits a female reply), in such a way that each species has a different combination of parameters. Females could therefore discriminate between conspecific and heterospecific males on the basis of the temporal pattern of their call. For males, however, the only cue that a female is conspecific comes from the fact that she replies to his call within a certain time window: female calls in the four species are all very similar in frequency, structure and latency to reply. But the system does seem to work: hybrids between sympatric species of *Barbitistes* have never been found in the wild.

The response delay of the female to the trigger syllable and the time window in which the male recognizes the female response have been measured in several other duetting phaneropterine species (Heller and von Helversen, 1986). Within each species, the delay and the window show very close matching, but between species, there is considerable variation. In other words, the coupled female response delay/male window times are species specific and incorporate into the calling system an additional species recognition feature that may compensate for the limited amount of temporal patterning that can be contained in the relatively short male call typical of these species.

Crickets tend to rely on the temporal patterning and sometimes the frequency of the advertisement call in species recognition. This has been reviewed by Doherty and Hoy (1985); see also, for example, Doherty and Callos (1991), Doherty and Storz (1992), Stumpner and von Helversen (1992) and Hennig and Weber (1997). Hennig and Weber looked at two sympatric species, *Teleogryllus commodus* and *T. oceanicus*, which both have calls containing chirps and trills (where a chirp is a series of syllables separated by relatively long intervals, a trill is a series of syllables separated by a relatively short interval, and a syllable is one wing closure). In both species, calls consist of phrases, each containing a single chirp followed by a number of trills, with both chirps and trills of constant amplitude The two species differ, however, in that they have different syllable periods (a syllable period being the time from the start of one syllable to the start of the next) in the chirp and trill parts of their calls, and a different number of syllables in their trills. Hennig and Weber found that *T. commodus* females responded only to calls containing the species-specific syllable period during both the chirp and during the trill, while *T. oceanicus* females would respond as long as the syllable period in the chirp and the frequency of the call were appropriate to their species. For *T. commodus*, repetition is also important: the chirp and trill parts of the call must each contain a minimum of three to five consecutive syllable periods to elicit a female response. *T. oceanicus*, on the other hand, can recognize a conspecific on the basis of only one or two 'correct' syllable periods. For *T. commodus*, species recognition is largely based on central nervous processing while for *T. oceanicus*, both peripheral frequency filtering and central temporal filtering are important.

Courtship song is also important in species recognition in crickets. In *T. oceanicus*, for example (Balakrishnan and Pollack, 1996), the courtship song, like the advertisement song, has a carrier frequency of 4-5 kHz and consists of chirps and trills with a chirp syllable period of about 65 ms. It is different from the advertisement song in several ways: the courtship chirp is amplitude-modulated, slightly longer (about nine compared with about five syllables) and followed by a single, very long trill with a slightly shorter trill syllable period (about 30 ms compared with about 37 ms). Females are reluctant to mount males that do not produce courtship song and, as in the advertisement call, respond only when the frequency of the song and the temporal pattern of the chirp are appropriate to their species, thus relying on the only two features that are consistent between advertisement and courtship song.

Species do vary, however, in whether recognition of the conspecific song is absolute or relative: in some cases, only the conspecific song is attractive and heterospecific songs are rejected even if there is no other choice; in other cases, both conspecific and heterospecific signals fulfil the requirements for a response but the conspecific song is usually preferred in a choice situation (Schul, 1998; Schul et al., 1998). However, in some species, the preference for conspecific song is relatively weak. In *Tettigonia cantans*, for example, a female will perform phonotaxis towards a *T. viridissima* male if he is closer and therefore perceived as being louder; hybrids are rarely found in sympatric populations, however, and reproductive isolation may be maintained by close-range mechanisms and a partial temporal separation in the breeding season for the two species (Schul et al., 1998). Gwynne and Morris (1986) have even suggested that some species achieve conspecific matings not by recognizing and responding to the conspecific song but instead by recognizing and *not* responding to closely-related sympatric species that present a risk of hybridization. *Conocephalus nigropleurum*, for example, shows little if any discrimination between conspecific calls, the calls of congeneric allopatric species, and even random noise, but will not respond at all to the call of the sympatric *C. brevipennis*, a species which shares its habitat and has a very similar life-history (Morris and Fullard, 1983).

Vibration signals may also play a part in species recognition (see review by Kalmring and Kühne, 1983). Stridulating insects produce both airborne and substrate conducted sound and, in tettigoniids and acridids, all known auditory and vibratory ventral cord neurons ascending to the brain receive inputs from both receptor systems, i.e. the tympanal organs and the vibration receptors. The coding of the conspecific song in the responses of most of the ventral cord neurons is considerably improved when the stimulus consists of both the airborne sound signals and either a maintained vibration or vibration matched to the temporal structure of the song.

Some species are unable to discriminate between conspecifics and closely related sympatric species on the basis of their songs. For example, females of the ground crickets *Allonemobius fasciatus and A. socius* show no preference between the calls of either species even though they differ in carrier frequency and chirp period (Doherty and Howard, 1996). Hybridization between the two species in areas of sympatry is rare and appears to be prevented by a post-insemination barrier to fertilization. Doherty and Howard suggest that it is to the female's advantage *not* to discriminate between conspecific and heterospecific males in these two species because there is little danger of producing a hybrid, females mate several times so will probably find at least one mate of the right species, energy expended in approaching the male and the risk of predation while doing so are both likely to be low, and the female benefits from courtship feeding by the male.

Since song has such a vital role in species recognition and reproductive isolation in orthopterans, it is likely to have played an important part in speciation. In some cases, calling songs are the only identified characteristics separating closely-related species, for example in *Oecanthus* (Toms, 1985), *Chorthippus* (Ragge, 1987), and *Laupala* (Otte, 1994), suggesting that acoustic signals can be among the first features to change during the speciation process. Such change could be due to, amongst other things, sexual selection resulting from female mate choice. For example, Shaw and Herlihy (2000) have shown that female preference for faster than average pulse rates is exerting a selective pressure on male song in the Hawaiian cricket *Laupala cerasina*. Pulse rate has been the most labile song feature in the evolutionary history of the *Laupala* genus (Otte, 1994).

6.4 Recognition of sex

In species where both males and female call, individuals have to be able to identify the sex of a caller. It is not adaptive to waste time and energy responding or performing phonotaxis to a member of the same sex. In most duetting bushcrickets this is not a problem because the female song is very different from that of the male in temporal pattern and sometimes in frequency (e.g. *Ancistrura nigrovittata*: Dobler et al., 1994b), but in many gomphocerine grasshoppers, males and females appear to have similar songs. Von Helversen and von Helversen (1997) have shown, however, in *Chorthippus biguttulus*, that in many respects the temporal patterns in the calls show no overlap between the sexes, allowing reliable discrimination of potential mates. For example male calls consist of continuous syllables longer than 30 ms, without gaps, while female calls consist of 'gappy' syllables with pulses shorter than 15 ms. Males and females also have differently tuned auditory systems and use differences in the frequency spectra between male and female calls in sex recognition. No differences with respect to frequency sensitivity, threshold, or temporal properties have been found between males and females in either the tympanal receptor elements or the ascending metathoracic neurons, so the sex recognition system in this species must lie at the level of the brain. The properties of some ascending auditory neurons indicate they are likely to play a role in this process: for example, the neuron AN3 responds more to gappy syllables than to continuous syllables (Stumpner et al., 1991).

6.5 Mate Location

The mechanisms of directional hearing described in Section 4.4 should, in theory, allow the sex that performs phonotaxis to locate the position of its potential mate so that it can move towards it. There may still be problems, however. In duetting phaneropterine bushcrickets, for example, the only cue the male has to help him locate the female is an extremely brief click, delivered at long intervals. Von Helversen and Wendler (2000) found that male *Poecilimon affinis* can locate a female on the basis of her acoustic response alone, even though each response lasts only 0.3 ms (Heller and von Helversen, 1986), but they follow a very roundabout route to reach her. However, the poor quality of the female song as an acoustic beacon is partly compensated for by the use of visual cues. When performing phonotaxis, a male typically walks for a few seconds, stops, calls, and then continues walking. When he receives a female reply, he turns to bring the sound source within his frontal auditory field. Males perform reliable phonotaxis only to female responses occurring between 40 and 170 ms after the end of their own call, demonstrating the existence of a time window in this species. Von Helversen and Wendler used a walking compensator to compare phonotaxis with and without visual cues. As the response of the female is so short, the response of the male in the absence of visual cues is an open-loop one with the male turning towards the source and usually overcompensating, then over-correcting to the next call. Phonotaxis proceeds with the path followed by the male being essentially an oscillation about the axis of the female, resulting in a course made up of circular arcs. When the male walks within a cylinder whose sides have regular stripes, his course is somewhat more direct, but when a single black stripe is provided as a visual cue, his course is much more direct. So, if the male has landmarks in the environment, the visual cues transform an open-loop response into a closed-loop response. Von Helversen and Wendler showed that this was because males used the female's first response to establish her direction and then used the visual landmarks to maintain a straight course. They suggest that a stabilizing influence on course maintenance by visual inputs could also be important in other bushcrickets and in gryllids.

In duetting bushcrickets, the basic ensiferan neuronal processing system by which song is recognized and located may also impose constraints on the ability of the male to locate his mate. *Poecilimon ornatus* males have been shown to steer an intermediate course between two females if they both respond to the same call within the time window, even if the responses differ greatly in intensity and are separated by up to 60 ms (von Helversen et al., 2001). Thus, in contrast to other ensiferan species, *P. ornatus* males do not show a precedence effect (see Section 6.6). Von Helversen et al. suggest that the poor orientation ability of *P. ornatus* males in situations where more than one female responds may represent an evolutionary trap for duetting phaneropterines. They argue that the evolution of duetting allowed females to shift the risk of phonotaxis to males and also allowed males to reduce their own risk of attack from acoustically orienting predators or parasitoids by dramatically reducing their duty cycles. Because the female response consists of only a very brief unpatterned click, however, response time became the essential feature for species recognition. Given the serial processing of recognition and localization in ensiferans, this in turn hindered the ability of the male to perform selective phonotaxis.

The ability of a female to locate her mate can be influenced by ear size: female *Kawanaphila nartee* with the largest spiracles (and therefore the greatest hearing sensitivity) have the greatest mating success (Gwynne and Bailey, 1999). In species where males sing and females perform phonotaxis, there are also different selection pressures on the hearing system in males and females. Bailey and Kamien (2001) showed that the hearing system of *Requena verticalis* is sexually dimorphic, with females having larger spiracles than males and therefore more sensitive hearing. Females also show less variation than males in hearing threshold and bulla volume, and bulla size is related to the dimensions of their thorax. Larger males, with larger wings, have proportionately more stridulatory muscles in their thorax and bulla size is not related to thorax size. There thus seems to be a trade-off in males between hearing sensitivity and sound production. For the male singing is more important than hearing because he does not perform phonotaxis. For the female, hearing is important because she needs to recognize and locate her mate; Bailey and Kamien suggest that there is stabilizing selection on ear size in females as a result.

6.6 Mate choice

There is increasing evidence in a wide range of orthopterans that mate choice contributes to individual differences in mating success and that male song can provide cues on which female choice is based. Gwynne (2001) discusses the reasons why females may mate with certain males over others and gives a number of bushcricket examples of female choice based on song. Zuk and Simmons (1997) and Brown (1999) review the evidence for female mate choice in gryllids and tree crickets (Oecanthinae) respectively. Male mate choice has been shown to occur in an acridid

(*Melanoplus sanguinipes*), a gryllid (*Acheta domesticus*) and a number of tettigoniids but is based on chemical or tactile cues; male mate choice based on female song has not yet been demonstrated (for a review of male mate choice in insects see Bonduriansky, 2001).

Mate choice based on the male song can be ‘passive’ or ‘active’ (Parker, 1983). In the former, females do not show any preferences between particular males but are simply attracted passively to the male call. As a result, the male whose signal reaches the most females, or is the most stimulating, or the easiest to locate, will attract the most mates. This could be the male who sings most often, for example, or that has the most intense or longest call, or the call that travels the longest distance, or the call frequency most closely tuned to the female auditory system, or the temporal pattern that is most stimulating. Choice that is purely passive could therefore be described as a form of male-male competition to reach females, rather than choice per se (Brown, 1999).

Females of several species, when given the choice of two otherwise identical male calls, preferentially perform phonotaxis towards the leading call, for example *Ligurotettix planum* (Minckley and Greenfield, 1995), and *Neoconocephalus spiza* (Snedden and Greenfield, 1998). *N. spiza* females prefer the leading call even when the following call is longer, or louder by up to 4 dB, which rules out passive attraction to the male that simply sings more (Snedden and Greenfield, 1998). Minckley and Greenfield (1995) suggest, however, that the preference in *L. planum* may be passive choice due to ‘sensory bias’ (Ryan and Keddy-Hector, 1992). (For a review of receiver biases and their effect on signal evolution, see Basolo, 2000.) The mechanisms involved in the preference are not clear. The transition from silence to sound at the start of a call could be a critical feature of the call’s attractiveness and/or it could aid localization of its source, and the onset of the following call could just be masked by the leading call. Snedden and Greenfield (1998) showed, however, that this could not be the only explanation for the female preference in *N. spiza*. Alternatively, the preference might result from a ‘precedence effect’ (Wyttenbach and Hoy, 1993) in which the first signal suppresses the animal’s peripheral or central response to the second. Römer and his colleagues have shown that stimulation at the ipsilateral ear may cause inhibition at the contralateral ear so that later stimuli do not reach threshold (Römer, 1993; Römer et al., 1997). Wyttenbach and Hoy (1993), on the other hand, looked at directional ultrasound avoidance behaviour in *Teleogryllus oceanicus*, which also shows a precedence effect. He found no evidence of ipsilateral-contralateral differences in the responses of a bilateral pair of ascending, second-order auditory interneurons known to initiate ultrasound avoidance, and concluded that interactions in the brain must be responsible for the precedence effect in this case.

Just because choice is passive, it does not necessarily mean that it is not adaptive. In the desert clicker, *Ligurotettix coquilletti*, males defend creosote bushes, which vary in nutritional value, against other males. Females simply approach the most intense signal and this tends to take them to bushes of high nutritional value occupied by groups of males (Bailey et al., 1993a). The females may benefit both from the good diet provided by the bush and from the easy availability of several potential mates within a small area, which decreases the costs of moving between them.

In active choice, females show a preference between individual males, rejecting some in favour of others. Choice is adaptive in that females obtain immediate benefits, either for themselves or their offspring, or genetic benefits (Andersson, 1994). Immediate benefits include food (e.g. courtship feeding) or a low-cost copulation (e.g. with reduced predation risk). Genetic benefits can result either because the male has ‘good genes’, which give his offspring a better chance of surviving, or because the female has ‘sexy sons’, i.e. her male offspring inherit the male’s attractive trait and in turn have high mating success. For orthopterans, male songs provide a useful basis for active female choice because, being both variable and costly to produce (see Section 3.8), they are likely to be good (‘honest’) indicators of the quality of potential mates. Females can also assess each call, or several calls simultaneously, from a distance, so the cost of rejecting a male should be low. Females have been shown to be less choosy when the costs of choice are higher, for example when predation risk is greater (Hedrick and Dill, 1993).

Although female choice based on song has been demonstrated in several species of orthopterans, it is difficult to show definitively that choice is active rather than passive, or whether the benefits are immediate or genetic. For example, in laboratory experiments, females of the bushcricket *Conocephalus nigropleurum* preferentially approach the tape-recorded sounds of a group of ten males, or the sound of just two males singing together, rather than a single calling male, but this could be because females discriminate in favour of groups of males per se, or because they are simply passively attracted to the most intense signal (Morris et al., 1978; Morris and Fullard, 1983). Females of some species may simply approach the nearest/most easily located male. For example, *Kawanaphila nartee* females may prefer males with higher-frequency songs because, as a result of the more rapid attenuation of higher frequencies, they perceive them as being nearer than males with lower-frequency songs (Gwynne and Bailey, 1988). Females of many species prefer the loudest call if all else is equal (see examples in Brown, 1999). This could, however, be the result of passive attraction to the loudest signal, or active choice for the nearest male or the male with the greatest power output. Approaching the nearest male benefits the female because it reduces the energy costs and predation risk associated with performing phonotaxis. The male with the greatest power output is likely to be a high quality mate because producing a louder song requires more energy (Forrest, 1991; Brown, 1999). Forrest and Raspet (1994) provide a method for distinguishing among the possible decision rules that females might use to choose between males calling at different distances and with different power outputs, but it has not yet been applied to individual species.

Female choice has been shown to depend on various parameters of the male advertisement call in different species. Some recent examples are given in Table 2.

TABLE 2 Some parameters of the male advertisement call for which female choice has been demonstrated. Results from laboratory experiments unless otherwise stated.

Parameter of call	Example of species showing female mate choice based on parameter	Reference
Lower frequency	*Requena verticalis* *Oecanthus nigricornis*	(Schatral, 1990)[a] (Brown et al., 1996)
Higher frequency	*Kawanaphila nartee*	(Gwynne and Bailey, 1988)
Loudness (Intensity)	*Amblycorypha parvipennis* *Requena verticalis*	(Galliart and Shaw, 1996) (Bailey et al., 1990)
Higher chirp rate	*Gryllus lineaticeps*	(Wagner and Hoback, 1999)
More syllables per chirp or phrase (longer chirp/phrase durations)	*Acheta domesticus* *Gryllus lineaticeps* *Scudderia curvicauda*	(Gray, 1997) (Wagner and Hoback, 1999) (Tuckerman et al., 1993)
More pulses per trill and shorter interpulse intervals	*Gryllus texensis*[b]	(Wagner et al., 1995)
Longer chirps	*Phaneroptera nana*	(Tauber et al., 2001)
Symmetry in maximum frequency and chirp duration between chirps produced by different legs	*Myrmeleotettix maculatus*	(Møller, 2001)[c]
Leading call (start of call not overlapped by another call)	*Neoconocephalus spiza* *Amblycorypha parvipennis* *Ephippiger ephippiger* *Ligurotettix planum* *Ligurotettix coquilletti*	(Snedden and Greenfield, 1998) (Galliart and Shaw, 1996) (Greenfield et al., 1997) (Minckley and Greenfield, 1995) (Greenfield et al., 1997)

[a] Field observations.

[b] *G. texensis* was called *G. integer* by the author but this population from Texas has now been recognized as a separate species (Cade and Otte, 2000).

[c] Laboratory experiments supported by evidence from the field.

In many cases, the parameters of male song preferred by females have been shown to correlate with male size, for example in *Gryllus bimaculatus* (Simmons, 1988), *Scudderia curvicauda* (Tuckerman et al., 1993), *Oecanthus nigricornis* (Brown et al., 1996), *Acheta domesticus* (Gray, 1997), *Phaneroptera nana* (Tauber et al., 2001) and *Requena verticalis* (Schatral, 1990). The benefits from mating with a large male may be direct or indirect. Larger males may provide more or better-quality courtship feeding, and the extra nutrients may increase female fecundity or offspring survival. Proteins in spermatophores have been shown to enhance the fitness of females in some orthopteran species (see e.g.Gwynne, 1988), but in others, no effect of spermatophore consumption on the female's reproductive success has been found (see e.g. Weddell and Arak, 1989). If size is inherited, females mating with a large male will have large offspring; the daughters are likely to be more fecund and the sons to be more attractive as mates. Body size has been shown to be heritable in several species: for example, *G. bimaculatus* (Simmons, 1987), *G. pennsylvanicus* (Simons and Roff, 1994), *Acheta domesticus* (Gray, 1997), and *Poecilimon veluchianus* (Reinhold, 1994).

For example, in the black-horned tree cricket, *Oecanthus nigricornis*, females prefer males with lower frequency songs (Brown et al., 1996). Brown et al. have shown that song frequency is a reliable indicator of male size and females mating with larger males have higher fecundity. Fecundity and reproductive lifespan are at least partially resource limited and larger males probably provide better-quality courtship feeding, which in this species is in the form of a glandular secretion (Brown, 1997). Females of the bushcricket *Amblycorypha parvipennis* prefer males whose call phrases are louder, longer, and leading; sound level and ability to lead are correlated with male weight (though phrase length is not) and females may benefit from mating with larger males because they produce larger spermatophores (Galliart and Shaw, 1991; 1996). Such preferences for large males may not always be absolute: Bateman et al. (2001) found that female *Gryllus bimaculatus* are indiscriminate for their first mating (when the costs of not mating could be very high) and only choose larger males in later matings.

In several species, however, there seems to be little or no relationship between size and song parameters or mating success. For example, body size is not related to song structure in a Texas population of *Gryllus integer* (now called *G. texensis*) (Souroukis et al., 1992) or in *Leptophyes punctatissima* (Kilduff, 2000). Mating success is not related to male size in sagebrush crickets, *Cyphoderris strepitans*, and seems linked instead mainly to the number of nights in which a male is able to sing (Snedden, 1996), implying that females are attracted passively to the male song.

The relationship between song parameters, size and mating success may not be simple. Field observations by Schatral (1990) indicated that mating success in *Requena verticalis* depended equally on low song frequency and male size (which are correlated with each other). Laboratory experiments by Bailey et al. (1990), however, have revealed that females show no significant preference for the larger of two calling males, nor for the tape-recorded song of the larger male, nor for the song with the lower frequency (though the sample sizes in all these experiments were small). But females do show a significant preference for the loudest call with the greatest power in the high-frequency part of the broad-frequency song of this species, even when the difference in intensity is as little as 2 dB (Römer et al., 1998). This would tend to result in the female approaching the nearest male because higher frequencies attenuate faster with distance.

Song parameters preferred by females have also been shown to correlate, in some species, with other characteristics of the male that may benefit the females that mate with them, including quality of diet, immune function, degree of symmetry and age. For example, female variable field crickets, *Gryllus lineaticeps*, prefer males who call at higher chirp rates and with longer chirp durations (more syllables per chirp) (Wagner and Hoback, 1999). Higher calling chirp rates are more energetically expensive (Hoback and Wagner, 1997) and males on a better diet chirp at a faster rate; the cost of calling is not related to chirp duration, however, and males on a better diet do not differ in this parameter (Wagner and Hoback, 1999). Females therefore select males on the basis of one nutrition dependent (chirp rate) and one nutrition independent (chirp duration) characteristic. Although they do not rule out the possibility that high chirp rates simply make males easier to locate, Wagner and Hoback suggest that females may benefit by mating with high-nutrition males if these males provide better-quality spermatophores; on the other hand, there is no clear benefit to mating with males producing longer chirps, which may just be easier to locate.

The number of syllables per chirp in male *Acheta domesticus* is a reliable indicator of immune function (ability to resist pathogens) as well as size (Ryder and Siva-Jothy, 2000). Ryder and Siva-Jothy suggest that males vary in quality and only high-quality males may be able to invest energy in both traits. The parameters of immune function that they measured are heritable, as is male size. The female may benefit directly and/or indirectly from mating with such a male because they are likely to be able to produce a second spermatophore more quickly (reducing the costs of searching for an additional mate if the female needs to mate more than once to acquire sufficient sperm or nutrients), she is less likely to acquire pathogens from him during copulation, and her offspring will inherit the favourable characteristics of her mate.

Cricket songs are characterized by almost pure tones of constant frequency. Individual male *Gryllus campestris* show varying degrees of frequency modulation, however, depending on the degree of directional asymmetry in their harps, which in turn is directly related to the degree of fluctuating asymmetry in a measure of body size (Simmons and Ritchie, 1996). Larger, more symmetrical *Gryllus campestris* males have higher mating success in the field (Simmons, 1995). In laboratory experiments, Simmons and Ritchie showed that females prefer pure tones of low carrier frequency, characteristic of large symmetrical harps. Honesty is maintained by the increased costs of symmetry for males with large harps: only males capable of developing large harps while maintaining symmetry will benefit from the increased attractiveness of low frequency song. The male song may therefore encode information about male quality.

Møller (2001) has also demonstrated that females can discriminate against asymmetrical males directly on the basis of their calls. The number of pegs per row in the two hind legs of the grasshopper *Myrmeleotettix maculatus* shows fluctuating asymmetry and the greater the peg asymmetry the greater the asymmetry in maximum frequency of chirps and duration of chirps produced by the two legs. In laboratory experiments, females preferred the calls of males with a larger and more symmetrical number of pegs. Evidence from the field also suggests that more symmetrical males have greater mating success. The reason why females choose more symmetrical males is not known, but there is considerable evidence that fitness is related to symmetry and females may benefit directly or indirectly from mating with a more symmetrical male (Møller and Swaddle, 1997).

Females of the duetting bushcricket *Ephippiger ephippiger* prefer the songs of younger males (Ritchie et al., 1995). Males accumulate damage to their stridulatory apparatus as they get older and this damage changes the structure of their song. The changes could simply impair pattern recognition by the female, or make the song less stimulating, but Ritchie et al. argue that these possibilities are not supported by the available evidence. They suggest that females could benefit from mating with younger males if they have more nutritious spermatophores, better sperm quality or higher sperm numbers. It is not actually known if any of these differences exist between younger and older males, but *E. ephippiger* does produce a large spermatophore, which could provide important direct benefits. There could be indirect benefits too:

young males have been shown to have higher-quality offspring in *Drosophila melanogaster* (Price and Hansen, 1998). The preference for younger males is not general, however: in other species, females have been found to prefer older males (Zuk and Simmons, 1997), virgin males (Snedden, 1996; Sakaluk and Ivy, 1999), or novel males (Bateman, 1998), though in most cases song does not appear to be the cue on which choice is based.

There is also evidence for female choice based on courtship song. In some cricket species, females will only mate with males that produce courtship song, for example in *Teleogryllus oceanicus* (Burk, 1983) and *Acheta domesticus* (Nelson and Nolen, 1997). In *T. oceanicus*, males fight and fighting success is correlated with mating success because dominant (winning) males are more likely to court females and to produce courtship song. Females do not discriminate among males who produce courtship song. In *A. domesticus*, Nelson and Nolen suggested that the ability to produce courtship song may depend on the male's condition. Hack (1998) has subsequently shown that courtship song in this species requires more than twice as much energy per unit time as does advertisement song, and may therefore be a more reliable indicator of mate quality.

In other species, choice is based on some parameter of the courtship song; *Gryllus lineaticeps* females, for example, prefer males with higher chirp rates in their courtship song (Wagner and Reiser, 2000). Wagner and Reiser showed that courtship chirp rates, unlike those in advertisement song, are not affected by the quality of the male's diet. Female choice on the basis of courtship song is also independent of choice on the basis of advertisement song. There is no correlation, either, between a male's advertisement chirp rate and his courtship chirp rate. The two songs may therefore provide information to females about different aspects of male quality.

Females of some orthopteran species, or under some circumstances, appear to show little or no choice based on song (e.g *Leptophyes punctatissima*: Kilduff, 2000). This can happen if the operational sex ratio (OSR: the ratio of sexually active males to sexually receptive females) is less than one. Males of some species produce a very large spermatophore (up to 40% of body weight in *Ephippiger* for example: Ritchie et al., 1998) and, having mated, need a long time to produce another one (Gwynne, 1997), so that the interval between matings is greater for males than it is for females. The rate at which a male can produce spermatophores is dependent on the quality of his diet (e.g. Simmons, 1993; Andrade and Mason, 2000; Gwynne, 2001) and in some species, the OSR can become reversed in populations with poor nutrition; under such circumstances, females compete for matings with males and their selectivity is low (Ritchie et al., 1998).

Even with an OSR of 1 or more, other factors may influence how choosy a female is likely to be. *Poecilimon ornatus* is a duetting bushcricket in which the male produces a spermatophore equivalent to about 12% of his body weight and the OSR is likely to be close to unity (Heller et al., 1997). Heller et al. have shown that female *P. ornatus* are indiscriminate and will respond to any type of acoustical signal as long as it is at least 1-3 ms in duration, has a similar frequency spectrum to normal male song, and has a sound pressure level of 70 dB or more. In this species, females do not perform phonotaxis and so their risk of predation is low. Their response to a male call is very brief and energetically very cheap. Heller et al. suggest that, in species like *P. ornatus*, the costs for the female of responding to a male's call are so low that it pays her to respond to all males. She could still show choice after the male has approached her, based on proximal cues such olfaction or visual and tactile assessment of body size. Alternatively, she could benefit from mating with as many males as possible because of the nutrition provided by the male's spermatophore. In this case, cryptic female choice may still operate if, for example, she can control which sperm fertilize her eggs (Eberhard, 1996).

7 Exploitation of heterospecific sounds

The acoustic advertisement signals that orthopterans produce travel quickly over long distances, are easy to locate and can be detected at any time of day. These features make them ideal for communicating with potential mates and conspecific male rivals but they are also likely to make the signaller easy to detect by its enemies. Non-calling females approaching a male also produce noise and vibration that make them more susceptible to predation.

Orthopterans are vulnerable to a wide range of natural enemies, including parasitoid flies, lizards, geckos, herons and other birds, bats, domestic cats, and primates such as tarsiers and howler monkeys (Bailey, 1991; Zuk and Kolluru, 1998; Kok and Louw, 2000; Gwynne, 2001). Some of these hunt visually or locate victims by the vibrations they make when moving. However, many are thought to orient acoustically to the sexual signals of their prey, though this has been demonstrated in relatively few species. For example, the lizard *Psammodromus algirus* is a predator of the bushcricket *Steuropleurus stali* and is attracted to its song. It will approach motionless singing individuals but not motionless silent individuals (Bateman, 2001).

Most diurnal birds hunt visually but some adopt different strategies to hunt orthopterans at night. For example, herons have been observed walking on land at night, tracking calling crickets to their burrows; experiments have confirmed that the birds use the call to locate their prey (Bell, 1979).

Parasitoid tachinid flies of the tribe Ormiini have a worldwide distribution. They parasitize ensiferan Orthoptera: field crickets (Gryllidae), mole crickets (Gryllotalpidae) and bushcrickets (Tettigoniidae) are known to be hosts (see Allen, 1995a). The fly deposits its larvae on the host. They burrow into it and feed on it from within. The larvae emerge after 7 days, usually killing the host in the process, and then pupate outside the host (Adamo et al., 1995). During the 7 days the larvae are developing, the host's ability to reproduce is reduced: for example, parasitized male *Poecilimon mariannae* produce fewer and smaller spermatophores and have reduced reproductive success as a result (Lehmann and Lehmann, 2000). The flies use the advertisement call of the male to locate their host. This was first reported by Cade (1975) for *Ormia ochracea* (then called *Euphasiopteryx ochracea*). He carried out experiments with dead crickets attached to a speaker, using Texas *Gryllus integer* (now called *G. texensis*). Flies were more likely to attack a cricket attached to a speaker broadcasting the crickets' song than one broadcasting a control sound. Lakes-Harlan and Heller (1992) have also shown that *Therobia leonidei* only parasitizes males and is attracted to them by their song — surgically muted males were never attacked.

Foliage-gleaning bats in Panama feed heavily on bushcrickets and use the male call to locate their prey. In a cage experiment, bushcricket species calling frequently were located more quickly by the bats than species calling rarely (Belwood and Morris, 1987). Calling crickets and bushcrickets, which produce high-frequency songs, are especially vulnerable to gleaning bats because the frequency of their calls often coincides with the bats' best hearing frequency (Bailey and Haythornthwaite, 1998).

However, predators that locate their prey acoustically do not necessarily rely on the sexual signals of their prey. Heller and Arlettaz (1994) have shown that the European scops owl, *Otus scops*, feeds intensively on bushcrickets but does not take more males than females, even though the males call. They suggest that this may be because the owl has limited sensitivity for sounds above 10 kHz so it is likely that the only song it can hear is that of *Tettigonia viridissima*, which has a peak spectrum at 10 kHz. The songs of the smaller bushcrickets are much higher, e.g. *Platycleis albopunctata* at 29 kHz, *Pholidoptera griseoaptera* at 20 kHz, and *Barbitistes serricauda* at 26 kHz. For *T. viridissima*, they found no difference in the proportion of males and females in the diet; for smaller bushcrickets such as *P. albopunctata*, the owls actually took more females than males. They conclude that owls are able to locate *T. viridissima* males by their call but otherwise rely mainly on the noise their bushcricket prey make when moving. Females, being more mobile than males because they approach the male to mate and move around to lay eggs, are more vulnerable as a result. Similarly, laboratory experiments have shown that the pallid bat *Antrozous p. pallidus*, though it uses echolocation for general orientation, locates its prey using the sounds they generate while moving (Fuzessery et al., 1993). The bats never captured stationary calling crickets (*Acheta domesticus*) but did attack silent walking crickets. The cricket song has a spectral peak between 4.4 and 4.9 kHz, and harmonics as high as 19 kHz, and is audible to the bat. Fuzessery et al. suggest that, since crickets call from protected locations where they are relatively inaccessible, the bats may learn that a walking cricket is much more vulnerable.

It is not just predators that exploit the sounds of their prey. Airborne sounds and vibrations transmitted through the air or through the substrate can betray the presence of a predator and orthopterans, like other insects, use their acoustic senses for predator detection as well as reproduction. This is evident from the structure of orthopteran acoustic systems (see review by Kalmring and Kühne, 1983). There are no neuronal filters at the level of receptor organs or in the ventral cord that are absolutely tuned to conspecific stridulatory signals and central auditory neurons are much more broad banded with respect to frequency and time parameters than would be necessary just for intraspecific communication. For example, in *Locusta migratoria*, the auditory ventral cord neurons react to sound frequencies up to 100 kHz, even though the song of this species only contains frequencies up to 40 kHz, and this allows locusts to recognize many other sounds in the environment as well as conspecific song. The habituation properties of some auditory central cord neurons make them most responsive to new or suddenly-changed signals and so suggest that these neurons have a 'warning' function. The larvae of grasshoppers have a well developed auditory system even though they have no need to find a mate. Some orthopteran species actually have two sets of auditory units: one is tuned to frequencies appropriate for listening to the calls of conspecifics, while the other is used for detecting predators (Römer and Bailey, 1998). The most sensitive vibration receptors found in insects are the subgenual organs of orthopterans (see review by Kalmring and Kühne, 1983): they react to vibration stimuli over a wide range, from less than 30 Hz to more than 5000 Hz, with maximal sensitivity between 200 and 1000 Hz. In addition, companiform sensilla react to low-frequency vibration up to about 100 Hz. Vibratory central neurons, in gryllids at least, show habituation and respond primarily to new or changed stimuli, so may also have a warning function.

7.1 Defences against acoustically-orienting predators in general

Endler (1991) described the stages of a successful predation event: encounter, detection, identification, approach, subjugation and consumption. A number of authors (including Bailey, 1991; Endler, 1991; Endler, 1992; Zuk and Kolluru, 1998; Haynes and Yeargan, 1999) have reviewed the various defences that prey can adopt to counter the predation threat. In the context of sound signals, encounters can be avoided by 'one-upmanship' – a greater detection distance of the predator by the prey than exists the other way round – or by adopting different activity times from the predator. Detection can be avoided by calling intermittently or not at all, or by confusion (making the detection of a single individual by the predator more difficult or making it difficult for the predator to fix on a single individual long enough to identify it as edible, e.g. by synchronized calling between males). It can also be avoided if the prey stays outside the sensory limits of the predator. This can be achieved by using a 'private channel', i.e. a frequency outside the range of the predator's hearing or at least frequencies that it is less sensitive to, or by switching from calling to substrate tremulation, or by using signals that attenuate rapidly with distance so that predators are less likely to overhear them, e.g. by using low-intensity courtship song instead of the advertisement call when the mate is nearby. Identification can be avoided by confusion, by aposematism (conspicuousness associated with unpalatability or ability to inflict harm) or mimicry (resemblance to unpalatable species). For aposematic prey, aggregation helps to enhance the signal or its reinforcement in the predator's brain. Approach (attack) can be avoided by startle responses such as stopping singing when a predator is detected, or aggregation (to saturate the predator). Subjugation can be avoided by producing disturbance sounds, i.e. sudden noises that make the predator hesitate and allow the prey to escape.

7.1.1 Aggregating

Males of many orthopteran species aggregate spatially and sing in choruses (Greenfield and Shaw, 1983. See Section 8.2). Aggregations can be passive, in which individuals cluster together as a result of attraction to resources such as oviposition sites, food, singing perches, etc, or active, in which males are attracted to each other. Males show positive phonotaxis to conspecific male song in many species. Males of some species aggregate *temporally* and sing in sprees (Walker, 1983a).

There may be several benefits to spatial aggregation and synchronized singing (Greenfield and Shaw, 1983; Greenfield, 1994; Allen, 1995b. See also Section 8.2). Central individuals in a cluster are less vulnerable to predators (the selfish herd effect: Hamilton, 1971). Spatial aggregations can saturate the appetites of predators and may facilitate predator detection. There may be a dilution effect, whereby the risk of attack to any one individual is reduced the greater the number of conspecifics there are close by. Synchronized calling, which occurs in several orthopteran species, e.g. *Pholidoptera griseoaptera* (Jones, 1966), may make it more difficult for the predator to locate a single singer within the chorus because sound is emitted from several locations at once. Few of these possibilities have been tested in orthopterans. It is known that bats preying on frogs are attracted more frequently to asynchronous than to synchronous calls (Tuttle and Ryan, 1982). However, Cade (1981) found no evidence for a dilution effect in a Texas population of *Gryllus integer* (now called *G. texensis*): males calling in choruses attracted as many parasitoid flies per individual as did isolated males.

Walker (1983a) has suggested that sprees may be the result of predators exerting selection pressure on females performing phonotaxis, causing them to cluster their movements in time so as to gain some of the same benefits as they would by aggregating spatially. As a result, males should condense their singing into the same time period in which females perform phonotaxis.

7.1.2 Frequency modulation

Two South American species of cricket, *Eneoptera guyanensis* and *Lerneca fuscipennis* are unusual among orthopterans in that they show significant changes in frequency within their song elements at constant ambient temperature (Desutter-Grandcolas, 1998). Desutter-Grandcolas suggests that these frequency modulations could make it more difficult for acoustically orienting predators and parasitoids to locate the singing male. The changes in frequency would confuse any predator that identifies prey from the frequency spectrum of its song. This possibility is supported by the unusual singing behaviour of *L. fuscipennis*, which may be another adaptation to make it more difficult for a predator to locate them: unlike most other crickets, which stay motionless while singing, the male jumps and turns around completely while singing, and also jumps in the leaf litter between two bursts of song.

7.1.3 Defensive sounds

Disturbance (alarm or defence) sounds produced 'by arthropods held in the hand, or disturbed in various manners such as pinching, probing or restraining are known in almost every order of insect' (Alexander, 1967). Disturbance sounds (reviewed in Masters, 1979; Bailey, 1991) are very similar between species. They are usually noise-like, and are often emitted as an unstructured hiss; if they do consist of a series of pulses, these are usually presented at an irregular or erratic rate (as, for example, in the Mexican bushcricket species Pterophylla beltrani and P. camellifolia described by Shaw and Galliart, 1987). Disturbance sounds have a very wide frequency spectrum, including ultrasound, which means that as many predators as possible will be able to hear them. They may aid insects by startling the attacking predator, by acting as an aposematic signal or by mimicking an aposematic signal. There is some experimental evidence that disturbance sounds do deter predators. For example, Sandow and Bailey (1978) showed that active secondary defence (production of disturbance sound, with raised forelegs and open mandibles), had a deterrent effect on potential predators. The disturbance sound alone may have a deterrent effect if the predator learns to associate the sound with the defensive display.

Belwood (1990) has described disturbance sounds in bushcricket species in Central and South America. Some, such as *Cnemidophyllum eximium*, flail their legs rapidly in an up and down motion when handled, which produces a loud raspy sound. Male *Steirodon careovirgulatum* and *C. eximium* and others also produce a noisy broad-band disturbance sound in the form of a loud, startling stridulation. In *Xestoptera cornea*, *Scopiorinus fragilis* and *Parascopioricus exarmatus,* females also produce disturbance sounds.

Most species of New Zealand weta show defensive stridulation (Field, 1993; Field and Glasgow, 2001). The most common type (observed in all species of *Hemideina* and *Deinacrida*) is produced once the insect has assumed a defensive posture. In response to visual, tactile or auditory stimulation, the legs are brought down rapidly in an arc and a harsh scratching sound of broad-band frequency is produced as they rub against the abdomen. All 16 New Zealand species of *Hemiandrus* stridulate by rocking forward with all legs on the ground and the hind legs pressed against the abdomen, so that the abdomen rubs against the hind legs to produce the sound. The large-tusked weta, *Motuweta isolata*, produces a sharp, loud, barking sound by rapidly opening its mandibles while its tusks are pressed against each other; at the same time it stridulates in the same way as the *Hemiandrus* species. The *Deinacrida rugosa* group of wetas contract the abdomen and extend it telescopically as their legs kick in an arc towards the source of the disturbance, producing a hissing sound. In two undescribed species of Australian Gryllacrididae belonging to the genera *Ametrus* and *Hadrogryllacris*, defensive stridulation is produced as part of an elaborate visual display, by femoro-tergal stridulation (Field and Bailey, 1997). Two rows of spines on abdominal tergites II and III of both species are rubbed by an elongate area of tubercules on the inner femoral surface of the hind legs; this motion involves a complex counter-rotation of the leg between leg and abdomen. Both sexes of some American Jerusalem crickets show abdomino-femoral defence stridulation in which the abdomen is moved past the hind femora or the hind femora past the stationary abdomen (Weissman, 2001).

7.2 Defences against parasitoids

Ormiine flies hunt at night so cannot orient to their hosts visually. For example, when song tape-recorded from a Texas *Gryllus integer* (now called *G. texensis*) population was broadcast, it attracted *O. ochracea* from sunset to dawn but not during daylight hours (Cade et al., 1996). Flies were attracted in the greatest numbers in the few hours following sunset and there was least attraction in the hours just before sunrise.

In order to located their hosts, female tachinid flies must perform the same task as a female cricket responding to the call of a potential mate. The flies have tympanate ears which, as a result of convergent evolution, resemble a cricket ear much more than they do a typical fly's ear (Lakes-Harlan and Heller, 1992; Robert et al., 1992). Some respond to ultrasound (Lakes-Harlan and Heller, 1992). The ear of the female *Ormia ochracea* is sharply tuned to 4-5 kHz (Robert et al., 1992), which is the song frequency of her main host, the field cricket *Gryllus rubens* (Walker, 1993). Hearing thresholds of the female fly are very low: 20 dB SPL at 5 kHz, which is consistent with long-range detection of their hosts (Robert et al., 1992). In the absence of visual or olfactory cues in laboratory experiments the females could locate a sound source from 4 m, and land at a mean distance of 8.2 cm away from it (Müller and Robert, 2001). Even if the stimulus is interrupted, the fly can continue on approximately the correct trajectory and land close to the target. Their performance declines the earlier the stimulus signal is interrupted, but this ability to persist in orientation after the signal has stopped suggests that a strategy of ceasing singing, such as the ASR described for *Neoconocephalus ensiger*, or producing short calls rather than long ones, may not be very effective. There is no physiological evidence yet for an ASR in Orthoptera that is evoked by the sound produced by the fly, which has a frequency of 200 to 400 Hz.

Although female *O. ochracea* are most sensitive to sound in the range 4-6 kHz, they are also sensitive to ultrasound in the 20-60 kHz range; males also have tympanal ears but they are different both in form and function from the female's ear, being relatively insensitive to the 5-kHz frequencies that characterize cricket calls but just as sensitive as females in the ultrasound range (Robert et al., 1992; Hoy and Robert, 1996). This may be because, being active at night, the parasitoid flies are themselves vulnerable to echolocating bats and the ability to hear bat echolocation calls may have evolved in response to this predation pressure.

Walker (1993) tested the response of *O. ochracea* to *G. rubens* calls with different pulse rates (where a pulse consists of a syllable within a chirp). He found that it changes with temperature, in parallel with temperature-induced changes in the pulse rate of natural songs. He varied the frequency of the call, the pulse rate, and the duty cycle independently of each other and found maximum attraction occurring at a frequency of 4.4 kHz, a pulse rate of 45 per second, and a duty cycle of 20-80%, which compares very closely with the natural song of *G. rubens* at 21°C of 4.6-kHz pulses, produced at a rate of 45 per second, with a duty cycle of 50%. Producing calls divided into chirps instead of a constant trill of pulses made little difference to fly attraction rates, showing that producing pulses in short bursts (i.e. chirps) makes no difference to the chance of being parasitized.

Despite the tight coupling between *G. rubens* song and *O. ochracea* attraction, Ormiine flies are not necessarily host specific. *O. ochracea* is attracted not only to the song of *Gryllus rubens* but to various other cricket species (though in much smaller numbers), including *G. fultoni*, *G. integer*, *G. firmus*, *Orocharis luteolira* and *Scapteriscus borellii*

(Walker, 1993). *Therobia leonidei*, the only ormiine fly in Europe, has a broad range of tettigoniid hosts in three sub-families: Ephippigerinae, Tettigoniinae and Phaneropterinae, including several *Poecilimon* species (Lakes-Harlan and Heller, 1992; Lehmann et al., 2001). The Australian species *Homotrixa alleni* has a number of bushcricket hosts, with very different call frequencies and structures, and its ear is not sharply tuned to the frequency of the host call (Allen, 1995a). How then does the fly recognize its hosts when their calls are so different? A study of the variability of the call structure of the austrosagine bushcricket *Sciarasaga quadrata* suggests that *H. alleni* may use short chirp length rather than frequency as an auditory cue when locating its host (Allen, 2000). Allen speculates that some temporal patterns may be easier to locate and/or the ear of *H. alleni* may have a sensory bias, enabling it more easily to detect shorter chirps. Certainly, shorter males were lost from the *S. quadrata* population as the 3-month calling season progressed (see Section 3.4.2).

Parasitism rates vary between different parasitoids and different hosts but can be very high — up to 87% of *S. quadrata* males can be parasitized by *H. alleni* by the end of the season (Allen, 1995a). Because the flies are attracted to the male call, females tend to be less affected though they can pick up larvae deposited near males when approaching them to mate or walking close by them (Cade et al., 1996). As a result of the difference in parasitism rates between the sexes, the sex ratio tends to become increasingly female biased as the breeding season progresses (Allen, 1995a).

In those orthopteran species susceptible to parasitism, a number of aspects of calling behaviour seem to have been affected by the heavy selection pressure imposed by the flies. Rotenberry et al. (1996) looked at the calling characteristics of field crickets, *Teleogryllus oceanicus*, throughout the Pacific, and found that they differ between populations parasitized and unparasitized by *O. ochracea*. Their analysis of calls from five geographically separate populations with differing degrees of parasitism strongly suggests that selection pressures by the fly have shaped song characteristics rather than being due to geographical variation.

Some species avoid calling in those periods of the night when the flies are most active, though this has to be balanced with pressure from other predatory species, such as diurnal birds, which may make calling during daylight or other times during the night equally dangerous. For example, in a Texas population of *Gryllus integer* (now called *G. texensis*), males call from sunset to dawn but more males call in the hours leading up to sunrise and at sunrise, when the flies are less active, than earlier; females also mate more frequently when more males are calling, i.e. when flies are less active, and this may reduce the probability that they too will become infected (Cade et al., 1996). *Sciarasaga quadrata* is unusual in that it calls in daylight, beginning 2-3 hours before sunset and continuing until at least an hour after midnight (Allen, 1995b). A population of *Teleogryllus oceanicus* introduced to Hawaii, where it is parasitized by *Ormia ochracea*, shows a more abrupt onset and cessation of calling at sunset and sunrise than do unparasitized populations elsewhere (Zuk et al., 1993). In Hawaii, *O. ochracea* is mainly active at dawn and dusk and Zuk et al. suggest that males have been selected not to call during the active periods of the fly.

Some species reduce the time they spend calling. For example, a population of *Teleogryllus oceanicus* in Hawaii, which is parasitized by *O. ochracea*, called less than an unparasitized population in Moorea (Kolluru, 1999). Seasonal variation in amount of calling related to parasitoid fly abundance has been observed in *G. rubens* (Burk, 1982). Individual male *Gryllus texensis* from Texas and Oklahoma (the author referred to this gryllid as a Texas/Oklahoma population of G. integer but it has recently been recognized as a separate species: see Cade and Otte, 2000) and *G. rubens* from Arkansas and Oklahoma call for about 3 hours per night while *G. integer* from California and New Mexico call for about 7 hours per night (Cade, 1991). Males of *G. texensis* are parasitized by *O. ochracea*; it is not known if the flies parasitize the other populations, though *G. rubens* is likely to be a host since it is parasitized by the fly elsewhere. The duration of nightly calling is heritable (Cade, 1984b) and Cade suggests that the reduced calling time may be the result of the selection pressure from the fly. The shapes of the distributions of mean individual calling duration against proportion of males are skewed for *G. texensis* and *G. rubens*, implying that directional selection of some sort has been operating on these populations, but not for *G. integer*.

Lehmann and Heller (1998) studied *Poecilimon veluchianus* and *P. mariannae* in Greece. The two species are very closely related, parapatrically distributed and similar in activity patterns, body size and population density. The former produces monosyllabic songs (1 syllable with a duration of about 80 ms, with chirps repeated at 0.4 Hz and an interchirp interval of 2.5 s) and the latter polysyllabic songs (5-11 repeated syllables per chirp with total duration of about 600 ms, with chirps produced at a mean rate of 0.4 Hz with an interchirp interval of 1.9 s). SPL and frequency of song are the same in the two species. The polysyllabic species was parasitized about three times as much as the monosyllabic species, and Lehmann and Heller suggest this is because its higher duty cycle (24% compared with 3%) makes it easier to locate.

The ability of a male to reduce his calling time may be limited, however, by the mating system of the species. Heller and von Helversen (1993) analysed the calling activity of males for several species of *Poecilimon*, representing two different communication systems. In species with mute females that approach the males, such as *P. veluchianus*, *P. mariannae* and *P. propinquus*, calling was restricted to darkness and syllable numbers per hour were high. This is probably because the male has no feedback as to whether and when a female is approaching and so must signal his position continuously. In species where females respond acoustically to male song and thus can induce the male to approach them, such as *P. affinis*, *P. artedentatus* and *P. nobilis*, males called during both day and night or during the day only, and syllable numbers per hour were low. In this situation, once a female has responded to him, the male can increase his calling rate and approach the female as rapidly as possible. *Therobia leonidei* parasitizes *Poecilimon*, but only those species that sing at night and produce high syllable numbers.

Similarly, in *Sciarasaga quadrata* there seems to be no relationship between individual male calling duration and the likelihood of being parasitized by *H. alleni* (Allen, 1998). Males show a consistent pattern of calling activity over their lifetime but there is no decline in longer-calling males in the population as the season progresses, showing that these males are no more likely to be attacked by *H. alleni* than shorter-calling males. Nor is the distribution of call durations within the population skewed, indicating that there is no history of directional selection acting on call duration. Allen suggests that this could be because the species has a long intermating interval of about 4 days. A longer-calling male is more likely to attract a female and, once he has mated, he stops calling and is no longer vulnerable to fly attack. So the increased risk of calling for longer may cancel out the decreased risk gained by mating more often. He also has some evidence that encounters with females are rare, so the advantages of calling for long periods to increase the chance of attracting a mate probably outweigh the disadvantages of attracting a parasitoid fly.

O. ochracea has been shown to orient more readily to high-intensity songs and some hosts may reduce the risk of parasitism by reducing the loudness of their call. Males from a Texas population of *Gryllus integer* (now called *G. texensis*) call at lower intensities at dawn, when the flies are active, that they do earlier (Cade et al., 1996)

Parasitoids may have a more subtle effect on calling, however, than simply reducing calling time, or the loudness of the call. The population of *Teleogryllus oceanicus* in Hawaii showed a reduction in chirp duration compared with populations unparasitized by *O. ochracea* (Zuk et al., 1993; Zuk and Simmons, 1997). The song characteristics of males that harboured parasitoid larvae also differed significantly from those of unparasitized males (Zuk et al., 1998). The song in *T. oceanicus* consists of a ‘long chirp’ of 5 to 7 pulses, followed by a series of ‘short chirps’ of 1 to 3 pulses. Males with longer long chirps containing shorter interpulse intervals were more likely to be parasitized. Zuk et al. suggest that this is because *O. ochracea* finds these males more attractive.

The intense selection pressure from parasitoids may even have resulted in a shift in the carrier frequency of the call of *Sciarasaga quadrata* (Römer and Bailey, 1998). The call, at 5 kHz, is unusually low for tettigoniids. The responses of the tympanic nerve and a first-order interneuron (omega neuron) in the afferent auditory pathway also showed that the hearing system is most sensitive to frequencies of 15-20 kHz, an effective mismatch to the conspecific call resulting in a reduced sensitivity of approximately 20 dB at the carrier frequency of the call. *S. quadrata* can occlude its spiracular opening, however, which increases the sensitivity of the ear to lower frequencies, resulting in a match between the best frequency of the ear and the carrier frequency of the call. This ability is unusual among tettigoniids - the spiracle is permanently open in most species (Bailey, 1993). By calling at 5 kHz, *S. quadrata* escapes the interfering calls of several other tettigoniid species. Low frequencies may also help sound transmission. They found that the calls of *S. quadrata* showed almost no attenuation in excess of that produced by spherical spreading alone. This compares with a species calling at 20 kHz, where loss of signal amplitude may be as much as 40 dB over 30 ms (Römer and Lewald, 1992). Römer and Bailey suggest, however, that the selection pressure from *H. alleni* may be the most important reason for the shift in call frequency. The ear of *H. alleni* is most sensitive to frequencies between 10 and 20 kHz and so is partially mismatched to the call of *S. quadrata*. Calling at 5 kHz, instead of at 10-20 kHz to match the tuning of the *S. quadrata* ear, results in the parasitoid being less sensitive to its host’s call by about 10-15 dB (Fig. 18). Reducing the call frequency also reduces call intensity by about 20 dB which makes the call even less likely to attract a fly. Matching between call frequency and sensitivity of the auditory system of the conspecific receiver is then achieved by partially closing the spiracle. The closure of the spiracle is under the individual’s control, which enables *S. quadrata* to hear at a broad range of frequencies and therefore allows it to detect, for example, approaching predators.

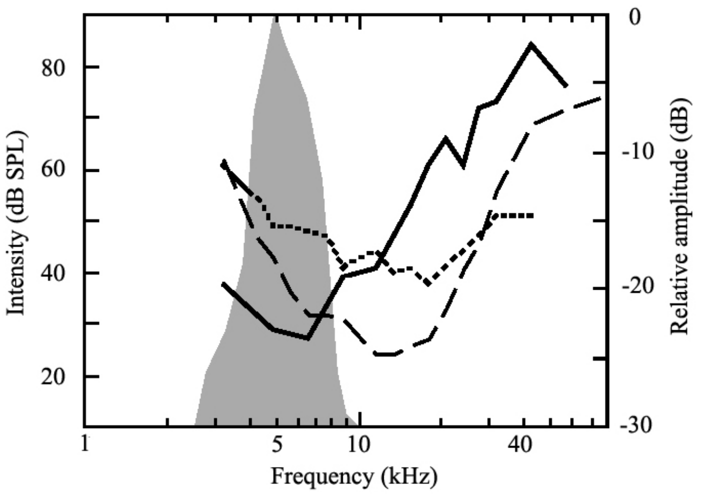

FIG. 18 Hearing sensitivity of *Sciarasaga quadrata* when the spiracle is open (dashed line) and partially blocked (solid line), compared with the sensitivity of the ear of the parasitoid fly *Homotrixa alleni*, the most common predator of *S. quadrata* (dotted line). The spectrum of the calling song of *S. quadrata* is also shown (shaded area). The ability of the fly to detect its host is much reduced for calls at a frequency of 5 kHz compared with calls at 10-20 kHz (Römer and Bailey, 1998, Fig. 9). Reprinted with permission from the Company of Biologists.

7.3 Defences against bats

There are about 700 species of insectivorous bats, most of which use ultrasonic echolocation calls when hunting. Some bats attack flying insects (aerial-hawking) while others take stationary insects from the vegetation (foliage-gleaning). Bats feed extensively on Orthoptera: 42% of the insects eaten by *Micronycteris hirsuta* in Panama, for example, are bushcrickets (Belwood, 1990). As well as the calls made by bats, ultrasound is generated by, for example, carnivorous tettigoniids, the calls of small terrestrial mammals, and disturbances to vegetation. Ultrasound therefore represents a serious risk of predation.

Many species of Orthoptera, like other nocturnal insects, have tympanal organs that are sensitive to ultrasound, e.g. in the Tettigoniidae (Libersat and Hoy, 1991), the Acrididae (Robert, 1989) and the Gryllidae (Farris and Hoy, 2000). The first evidence that orthopterans are responsive to ultrasonic was found in mole crickets by Suga (1968). He recorded from the leg nerve and thoracic connections in *Gryllotalpa hexadactyla* and *Scapteriscus didactylis* and found that neurons in both species respond to sounds up to 70 kHz. McKay (1969; 1970) found auditory neurons in *Ruspolia* (*Homorocoryphus*) bushcrickets that respond to sounds above 30 kHz. Ultrasonic sensitivity in bushcrickets, to frequencies as high as 100 kHz, has also been reported for several species in Europe, e.g. *Tettigonia viridissima* (Rheinlaender and Römer, 1980; Hutchings and Lewis, 1983) and *T. cantans* (Kalmring and Kühne, 1980). The ability to detect ultrasound enables Orthoptera to take action to avoid being captured if a bat, or other ultrasound-generating predator, gets too close.

Orthoptera show a number of ultrasound-induced startle responses (ASRs), including stopping singing or pausing, stopping flying, and flying away from the source of the sound (see review by Hoy, 1992a). Several species are known to stop singing in response to bats. Sales and Pye (1974) report that stridulating *Conocephalus conocephalus* and *C. maculatus* in Nigeria stop singing in the presence of flying bats. The creosote bush cricket, *Insara covilleae*, often calls from the tops of bushes where it is vulnerable to foliage-gleaning bats (Spangler, 1984). The call is above 20 kHz and within the bats' hearing range. Spangler recording insect singing and bat echolocation calls in the field and found that calling ceases during the high-intensity call of a bat approaching closely, but not during the low-intensity call of a distant bat. Calling resumed after the bat had passed, but only intermittently. He also observed that two other tettigoniids, *Insara elegans* and *Plagiostira albonotata*, also cease calling when echolocating bats approach.

Farris and Hoy (2000) looked at ultrasound sensitivity in *Eunemobius carolinus*, a member of the Nemobiinae (ground crickets). This species shows an ASR while flying in which the wings are closed and flight is stopped until the ultrasound stimulus ends. Extracellular recordings from the cervical connectives revealed auditory units that are sensitive to frequencies greater than15 kHz with best sensitivity at 35 kHz (79 dB SPL threshold). Stimuli in this frequency range, which is similar to that emitted by echolocating bats, also elicit the ASR.

A recent study (Faure and Hoy, 2000d) has shown that the tettigoniid *Neoconocephalus ensiger* exhibits both a non-flight and an in-flight ASR. Of 20 *N. ensiger* tested, 80% responded consistently to pulsed sounds by stopping singing or pausing. The threshold for the response was low (60-70 dB) above 30 kHz, being more or less constant up to

100 kHz. Below 30 kHz thresholds rose sharply and in the audible range below 20 kHz the threshold were above 100 kHz and most animals did not respond at all. This type of ASR in which the animal stops singing appears to be a highly stereotyped one, occurring with a short latency of 20-50 ms in this species. The response occurs only when an ultrasonic stimulus arrives during the intersyllabic period of silence, so presumably the insect's own sound masks external signals. In flight, *N. ensiger* shows a response to ultrasound that is typical of that shown by other flying insects to bat echolocation pulses. Within 50 ms of detecting a pulse of ultrasound *N. ensiger* closes all four wings (Libersat and Hoy, 1991). However, the response is not directional. A comparison of the tuning curves for the ASR cessation of singing and the ASR cessation of flying shows that they are very similar and, in shape, resemble the tuning curve of the T-cell, although the threshold for the T-cell, as might be expected, is lower (mean ΔdB≈35 dB) (Faure and Hoy, 2000d). A link between the T-cell and in-flight ASR was suggested by Libersat and Hoy (1991) and the physiology of the T-cell makes it well suited to a role as a bat-detector (Faure and Hoy, 2000b) (see also Section 5.2.1).

Unlike *N. ensiger*, *Tettigonia viridissima* does show a directional response to simulated bat calls. It responds in one of three ways, depending upon the intensity of ultrasound detected (Schulze and Schul, 2001). When simulated bat calls reached an intensity of 55-60 dB, an insect in tethered flight showed a steering response away from the sound source. At increasing intensities the insects stopped beating their hind wings but remained in the normal flight posture. Wing beats resumed 0.3 to 1 s after the bat calls stopped. At higher intensities the forewings folded into the resting position and the insect would have dived if untethered. The median threshold for the steering behaviour was 53.5 dB SPL, for the wing beat interruption 64 dB SPL and for diving 76 dB SPL. These sound intensities have been used to estimate the distance of a calling bat (call taken as 110 dB SPL 25 cm in front of the bat) from the insect at the point at which the behaviour is initiated (Schulze and Schul, 2001). Steering behaviour would occur when the bat was 18 m away. Interruption of the wing beat would occur at 10 m separation and the diving response at 5 m. The estimated distance at which the bat would first detect the echo from the bushcricket is 5 m. *T. viridissima* and *N. ensiger* are closely related and the difference in in-flight responses to bat calls suggests that the evolution of bat-avoiding strategies is shaped by different selection pressures and is not a trait that is highly conserved within the tettigoniids.

Locusts (Robert, 1989) and crickets (Lewis, 1992) also show a directional response to sound sources containing ultrasound. For example, laboratory experiments on *Teleogryllus oceanicus* in flight have shown that it will turn towards the song of a conspecific (a series of 5-kHz pulses) and away from ultrasound (sound pulses containing 40 kHz) (Moiseff et al., 1978; Nolan and Hoy, 1986a). In this species, electrical stimulation of the high frequency ascending neuron Int 1 (ANA), sufficient to produce a response rate above 180 to 220 spikes per second, results in negative phonotaxis, suggesting that Int 1 is both necessary and sufficient to elicit this behaviour (Nolan and Hoy, 1986b). Int 1 also responds to all three of the sexual songs produced by *T. oceanicus* (advertisement, aggressive and courtship) so is involved both in avoidance and courtship (Harrison et al., 1988). Nolan and Hoy (1986b) suggest that the switch between the two behaviours may be based on a difference in spike rate in the neuron. Predator avoidance only occurs if activity in Int 1 is more than 180 spikes per second while activity in response to courtship song is in the region of 35 spikes per second. Int 1 could therefore provide input to separate neural networks in the brain concerned with negative phonotaxis and song recognition.

For the ASR of ceasing to fly and thereby dropping out of the echolocation zone of the bat to work, the insect needs to detect the bat before the bat can hear the echo. Schul et al. (2000) measured the hearing range of the long-winged bushcricket, *Phaneroptera falcata*, for echolocation calls of the mouse-eared bat *Myotis myotis* in the field. Male *P. falcata* often call from exposed perches on the vegetation and, while singing, frequently change position by flying, so they are exposed both to aerial-hawking and foliage-gleaning bats. The echolocation calls of *M. myotis* are similar in intensity, duration and frequency range to other aerial-hawking bats large enough to prey on tettigoniids, having a fundamental frequency of about 80 to 27 kHz, with strongest amplitudes around 30 kHz and durations of 5-10 ms. Schul et al. recorded the hearing responses of the bushcrickets to the echolocation calls neurophysiologically and simultaneously recorded the echolocation calls of *M. myotis* via two microphone arrays, which allowed them to reconstruct the flight path of the bat and determine the maximum distance at which the bushcricket detected the bat. They found that the bushcrickets have hearing ranges of 13-30 m. They calculate that the bushcricket has more than 1 s to recognize the predator and respond evasively before the bat hears the returning echo. The insects' sensitive hearing therefore gives them an advantage over the bat - the 'one-upmanship' described by Endler (1991).

Mason et al. (1998) used sound traps to show that the phonotactic behaviour of both sexes of the mole cricket *Scapteriscus borellii* is actually affected in the field by ultrasound that represents the possibility of bat predation. Each of two sound traps broadcast synthetic calling song with a carrier frequency of 2.7 kHz, but one of the traps broadcast at a higher sound intensity (+ 6 dB). The two traps were 10 m apart and on the basis of the difference in power output from the two traps 17% of individuals would be expected to be attracted to the quieter trap (Forrest and Raspet, 1994). Then 40-kHz sound at a number of different intensities was added to the calling song broadcast by the louder trap and the proportion of insects choosing the quieter trap was measured. 40 kHz is a typical peak frequency in the sonar pulses emitted by species of insectivorous bat in North America (Fenton and Bell, 1981). There was a significant positive relationship between the intensity of the ultrasound added to the broadcast from the louder trap and the number of individuals collected at the quieter one. With no ultrasound present, the proportion collected at the quieter trap was as predicted from earlier work (Forrest and Raspet, 1994) but as the intensity of ultrasound increased, the attractiveness of that trap declined and the proportion collected at the quieter trap increased.

Foliage-gleaning bats often use echolocation for general orientation but tend to locate their prey passively by listening for the sounds they make. Four of the six bushcricket species taken by *Micronycteris hirsuta* on Barro Colorado Island in Panama call in the 23-27 kHz range, suggesting which prey are taken depends on whether the bat can hear their call or not (Belwood, 1990). The selection pressure from bats has resulted in a number of adaptations in calling behaviour.

Some species avoid predation by calling when bats are least active (Belwood, 1990). For example, wasp mimicking bushcrickets of the genera *Aganacris* and *Scaphura* in Latin America have two active periods, one during the day and one during the night. Their mimicry protects them from predators during the day but not during the night. At night, they sing in a very narrow time band between 0300 and 0500, which coincides with a lull in the feeding behaviour of gleaning bats. The strategy appears to be effective because gleaning bats do not appear to take these species. Similarly, *Copiphora brevirostris* is active between 2300 and 0500. It is the most common bushcricket on Barro Colorado Island and Belwood has shown it to be extremely palatable to bats in laboratory feeding experiments, but is taken by gleaning bats in only small numbers.

Some species simply call less, making it more difficult for bats to locate individuals. For example, species of neotropical bushcrickets sympatric with foliage-gleaning bats call for a much smaller proportion of the time compared with species in areas where these bats are absent (Belwood and Morris, 1987). In most understory forest bushcrickets, where bat predation is high, calls are short (usually less than 1 s) and produced infrequently (every few seconds to every few minutes). One exception to the rule is *Ischnomela pulchripennis,* which sings for about 50% of the time. However, this species calls from protected sites such as large bromeliads covering in long sharp spines that could kill or injure a gleaning bat; species with short, intermittent calls call from exposed sites (Belwood, 1990).

Some or all calling may be replaced with complex species-specific tremulations that generate vibrations inaudible to bats but which reach females through the substrate; females may respond by tremulations of their own which lead males to cease audible calling (Belwood and Morris, 1987; Belwood, 1990; Morris et al., 1994). Males of most pseudophylline and copiphorine species supplement calling with tremulation. Calling and tremulation are produced independently and in a seemingly random fashion within the same block of time. Males tremulate in the absence of females so the vibrations seem to be true long-distance communication signals. For example, *Myopophyllum speciosum* is a pseudophylline neotropical bushcricket which calls for a very small proportion of its time (Morris et al., 1994). Male calls are only 148 ms long on average and are produced a considerable time apart, with intercall intervals averaging 8.7 s. Pairing is completed with tremulation signals generated at closer range. Morris et al. have shown that other neotropical tettigoniids in rainforest understory, including species of *Choeroparnops*, *Schedocentrus*, *Docidocercus*, and *Copiphora*, also employ elaborate vibratory signals and some have reduced or even eliminated their use of airborne sound. Belwood (1990) looked at tremulation in five bushcricket species on Barro Colorado Island. Four of these species (*Docidocercus gigliotosi*, *Acanthodis curvidens*, *Balboa tibialis*, *Copiphora brevirostris* and *Aganacris insectivora*) spent more than twice as much time in tremulating as they did in calling, in fact *C. brevirostris* tremulated more than 90 times as much as they called. Morris et al. (1994) suggest that predation pressure from bats is the most likely reason for the shift from calling to tremulation, this being just one of a suite of several anti-bat adaptations shown by neotropical bushcrickets, including very long antennae which may enable them to anticipate a bat strike; the ability to cling tightly to the vegetation when a capture attempt is made, and spines which may deter bats from eating them.

There are costs associated with tremulation, however. The body movements required are likely to be energetically expensive. Nor do vibrational signals free orthopterans from predators. Bushcrickets observed in the laboratory stop singing or tremulating if anything touches their cage (Belwood, 1990). Belwood speculates that this may be adaptive, especially for tremulation, because individuals are more likely to be detected by predators with vibration receptors when they tremulate. She frequently observed ctenid spiders feeding on bushcrickets in the field, but especially on *Copiphora brevirostris*, which has the longest and most complicated tremulation signal of all the bushcrickets she studied on Barro Colorado Island.

Some species have calls with unusually high carrier frequencies. For example, the carrier frequencies of the neotropical species *Myopophyllum speciosum*, *Drepanoxiphus angustelaminatus*, *Haenschiella ecuadorica* and an undescribed species of *Haenschiella* range from 65 to105 kHz (Morris et al., 1994). Attenuation and scattering of sound are frequency dependent (Michelsen and Larsen, 1978). Water vapour (Griffin, 1971; Pye, 1979) and vegetation (Römer and Lewald, 1992) can also act together to reduce the energy of ultrasonic sounds. Thus the higher the carrier frequency, the shorter the range, and the less likely the calls are to be overheard by bats. *M. speciosum*'s call at 81 kHz will attenuate from a typical level of 100 dB at 10 cm to 50 dB within 3 m, which is just at the species' hearing threshold (Mason et al., 1991). Morris et al. (1994) assess the evidence for several possible reasons why these species might use such high frequencies, such as reducing interference by other species, and conclude that the most likely explanation is bat predation.

Some species alter the components of their call. *Teleogryllus oceanicus* has a two-component call: a brief chirp followed by a trill. Males prefer to call from refuges in natural hollows or vegetation and unprotected males produce calls containing fewer trill elements than males in refuges (Bailey and Haythornthwaite, 1998). Bailey and Haythornthwaite suggest that this is the result of selection pressure from bats. They carried out laboratory experiments to test the vulnerability of *T. oceanicus* to predation from two species of gleaning bats, *Nyctophilus major* and *N. geoffroyi*, both of which use passive listening rather than echolocation to locate their prey (though neither is a natural predator). Males calling from refuges were not predated. Unprotected insects were more likely to be attacked if they had longer calls (with more elements); for calls of the same length, they were more likely to be attacked if their calls contained trills rather than chirps.

As Rentz (1975) was the first to point out, calling songs of neotropical understory forest bushcrickets differ significantly from those of temperate species. In most Latin American understory forest bushcrickets, calls are shorter and produced more infrequently, with lower song duty cycles, and emphasize higher frequencies, compared with temperate species (Belwood, 1990). These differences may be related to differences in predation pressure from bats. For example, there are fewer bat species that use the calls of their prey to locate them in the palaeotropics than in the neotropics (Heller and Volleth, 1995), so predator pressure is probably less intense. If calling behaviour is affected by the selection pressure imposed by bats, it might be expected, therefore, that the effects would be less extreme in the palaeotropics than in the neotropics. A study by Heller (1995) provides support for this. He looked at a number of Malaysian leaf-mimicking bushcricket species from the family Pseudophyllidae (*Tympanophyllum arcufolium, Promeca sumatrana, Promeca perakana, Chondroderella borneenses,* and *Phyllomimus inversus*). All three of the neotropical anti-bat adaptations described above are less well developed in these species. The number of call syllables produced per day ranged from 9000 to 42000 (giving call duty cycles of 1.4-28.2%), with one exceptionally high value of 360000 in *Chondroderella borneensis*. This compares with 200 to 2000 syllables per day (giving call duty cycles of less than 1%) in neotropical species of Pseudophyllidae. None of the Malaysian species appeared to use tremulation. The peak frequency of the call for all species was below 12 kHz, and in fact the lowest frequency long-distance signal yet discovered in insects is the 600-Hz call produced by *T. arcufolium*. The Malaysian species are closely related to the African Pseudophyllidae and Heller suggests that the differences between the Malaysian species and the neotropical species probably represent general differences between the neotropical and palaeotropical Pseudophyllidae. He compared carrier frequency in 11 species of palaeotropical and 37 species of neotropical Pseudophyllidae and found a significant difference in carrier frequency between the two groups (Fig. 19), though it is possible this is a side-effect of the different camouflage strategies adopted by the two groups rather that the result of differential predator pressure. Call frequency is negatively correlated with the length of the stridulatory file. Palaeotropical Pseudophyllidae have longer stridulatory files than neotropical species but this may be linked to the different body and wing shapes they have adopted in relation to their camouflage strategies.

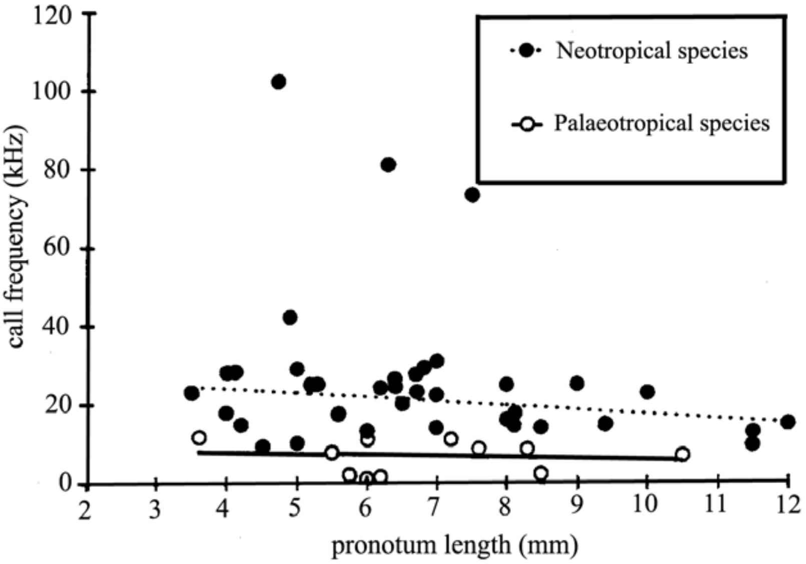

FIG. 19 Pronotum length and carrier frequency in 11 species of palaeotropical and 37 species of neotropical Pseudophyllidae (Heller, 1995, Fig. 4). Reprinted with permission from Cambridge University Press.

7.4 Sexual versus natural selection

The signals that orthopterans use to attract mates make them vulnerable to acoustically orienting predators and parasitoids. Sexual selection favouring more conspicuous calls to increase attractiveness to females will therefore be countered by natural selection favouring less conspicuous calls to decrease attractiveness to enemies. Often the features that make a call attractive to females and to enemies are the same. In *Gryllus lineaticeps*, for example, both female crickets and the parasitoid fly *Ormia ochracea* prefer male calling songs with higher chirp rates, longer chirp durations and higher chirp amplitudes (Wagner, 1996). Similarly, those male *Poecilimon thessalicus* preferred by females also have a higher risk of being parasitized by *Therobia leonidei* (Lehmann et al., 2001). Female *P. thessalicus* prefer males with the loudest and longest calls, perhaps because they are easier to detect and locate and *T. leonidei* may prefer these males for the same reason. A male preferred by a female will, if nothing else, be more likely to have a female nearby, thereby providing two potential hosts instead of one (Wagner, 1996).

In a Texas population of *Gryllus integer* (now called *G. texensis*), Gray and Cade (1999) have shown that both female crickets and *O. ochracea* prefer male calling song with average numbers of pulses per trill. Preference for the average song would minimize search costs for both conspecific females and parasitoid flies. Pulses per trill is not related either to male size or age and has a substantial genetic component. Thus female crickets exert stabilizing sexual selection on male song, which reduces genetic variation and maintains population cohesiveness, but this is balanced by parasitoid flies exerting disruptive natural selection, which promotes genetic variation and population divergence. The two opposing forces may together maintain the observed high levels of genetic variation in male song.

An alternative explanation for the persistence of genetic variation in male song characteristics in the face of natural selection from acoustically orienting predators has been put forward by Hedrick (2000). She has shown that *G. integer* males differ in their durations of uninterrupted trilling (calling-bout lengths), that these differences are heritable, and that females prefer males with longer calling bouts. However, males with longer, more conspicuous songs compensate behaviourally for their increased vulnerability to predators by acting more cautiously: they take longer to emerge from a safe shelter within a novel, potentially dangerous environment, and stop calling for a longer time when their calls are interrupted by a predator cue. There is some evidence that these differences are heritable. Genetic variation in calling bout duration could therefore be maintained because males with shorter bout lengths, although less attractive to females, may gain opportunities to mate while males with longer bout lengths are silent following disturbance by a potential predator.

7.5 Evolution of predator avoidance mechanisms

How did predator avoidance mechanisms dependent on the ability to hear ultrasound evolve? It has been argued (Gwynne, 1995) that hearing and intraspecific sound communication have both evolved independently in the Grylloidea and in the Tettigonioidea and, if this is the case, then the ability to detect ultrasound that is found in both groups must have evolved independently.

Some insects preyed upon by bats, such as moths, seem to have evolved ultrasound sensitive ears as a direct result of predation, particularly by bats (Hoy, 1992a; Hoy and Robert, 1996). In the Orthoptera, however, there is some dispute as to whether ultrasound sensitivity evolved for this reason or instead in the context of instraspecific communication. For example, Hoy and Robert (1996) and Hoy (1992a) argue that the same hearing organs serve to detect conspecific signals and also the echolocation signals of bats; they speculate therefore that the ability to hear ultrasound was added on to the ability to hear lower frequency conspecific calls. Their argument is based on evidence that the Orthoptera have existed for at least 200 million years, while the bats only appeared in the fossil record 50 million years ago, and that crickets and bushcrickets were able to stridulate (and therefore, presumably, send signals that conspecifics could hear) at least 150 thousand years ago. Their ears thus evolved in the context of intraspecific communication. They argue further that, by the time the bats appeared on the scene, orthopterans had been established for millions of years, and it is likely that they used ultrasound components in intraspecific signalling systems and had hearing organs tuned to ultrasounds, just like their modern counterparts. Hoy and Robert therefore think that in crickets, bushcrickets and locusts, the ability to hear bats was probably a simple step from the ability to hear conspecifics.

Others, such as Lewis (1992) and Römer (1992), disagree, based on the neuroethology of present day insects. For example, the auditory neuropile is organized differently in crickets, bushcrickets and acridids. Most crickets and bushcrickets sing in early morning or evening and most are heavily preyed upon by bats. Crickets show negative phonotaxis to ultrasound. Römer et al. (1988) therefore suggest that the bushcricket system evolved to mediate rapid escape behaviour and was only later incorporated into and modified for conspecific acoustic communication. The acridids on the other hand are more highly preyed on by lizards and birds and are less sensitive to ultrasound – birds and lizards can be detected by lower frequency sound, vibration and visual cues. Acridids therefore need to combine signals from more than one modality.

There is also some evidence that the tympanal organs of orthopterans were present before their sound-generating mechanisms evolved, i.e. before they started to stridulate to communicate with conspecifics (Smart, 1963). In addition, Mason (1991; 1999) has shown that song production can be uncoupled from song reception. In the haglid *Cyphoderris monstrosa*, the best frequency of the auditory system (12kHz) is mismatched to the spectral peak of calls (2 kHz) (see Section 4.1.4). Mason argues that the primary function for hearing in this species is predator detection (though not detection of a bat because 12kHz is below the typical sonar range of most bats).

8 Cooperation and competition between males

In the majority of orthopteran species, the male calls and the female does not reply. Yet the male generally has ears that are fully functional and tuned to the conspecific call (see Section 4). Males benefit not only from being able to listen for predators (see Section 7) but from eavesdropping on the calls of conspecific males in the competition to acquire mates. Features of the advertisement call relevant to females, such as those that provide information about male size or vigour, should be relevant to male rivals too since they are also likely to provide them with information about the calling male's fighting ability or his ability to attract females. Males of many species sing in choruses, and various hypotheses have been put forward as to why males should do this. Many of these explain chorusing in adaptive terms: individual males benefit in some way by singing together and so cooperate to create the chorus. Others see chorusing as the result of male competition or simply as an epiphenomenon.

8.1 Spacing, aggregating and fighting

The spatial distribution of individuals is under the control of a variety of selective forces. Aggregations can be passive, in that individuals are attracted to resources such as oviposition sites, food, or singing perches. The distribution of males of the desert grasshopper, *Ligurotettix coquilletti*, for example, is related to the distribution of the food plant most attractive to females, the creosote plant (Greenfield and Shelly, 1985). Aggregations can also be active, in that individuals are attracted to each other. In many acoustically communicating species, sound plays an important role in distribution. For example, in the bushcricket *Tettigonia viridissima*, males clump in areas where the vegetation provides higher singing perches than the surroundings, a behaviour that would enhance the distance over which the song could be broadcast (Arak et al., 1990).

Advertisement calling can act as an agonistic signal directed towards rivals as well as a signal to attract females (e.g. Simmons, 1988). In *T. viridissima*, for example, males are spaced out as far as possible from their rivals (Arak et al., 1990). In the haglid *Cyphoderris monstrosa* the song of the male is a very loud trill, almost a pure tone, at 12 kHz (Mason, 1996). At 10 cm from a singing insect the intensity is 105 dB SPL. The spacing of males in the field is such that the songs of nearest neighbours are attenuated to about 60 dB SPL (unpublished data quoted in Mason et al., 1999). The role of song in repulsing competitors was demonstrated experimentally by Bailey and Thiele (1983). They released several male *Mygalopsis marki* in the same place and found that intact males spread out from the release point while experimentally deafened males did not. They also showed that dispersal rate and the eventual distance between males is dependent on sound intensity: a population of larger males, which sing more loudly, was more widely spaced than a population of smaller males. Römer and Bailey (1986) showed, however, that males do not space themselves out on the basis of threshold sensitivity to the calls of other males. They measured the maximum hearing distance of *M. marki* in the field, using the response of an identified auditory interneuron as a ‘biological microphone’ and found that it was more than twice the mean distance between males.

Males of some orthopteran species show no evidence of territoriality and may move considerable distances between one calling session and the next, for example the haglid *Cyphoderris strepitans* (Dodson et al., 1983) and some tettigoniids such as *Leptophyes punctatissima* (M. J. Hall, personal observation). Some, however, do defend territories, and a male that calls within the territory of a neighbour is likely to become involved in a fight with the territory owner (Alexander, 1961; Greenfield and Minckley, 1993; Mason, 1996; Gwynne, 2001). In some cases the distance between territorial males is dependent on information contained in the call (e.g. Schatral et al., 1985; Römer and Bailey, 1986). Nearest-neighbour distances vary greatly, for example 2 m in *Tettigonia cantans* (Dadour, 1990) compared with 11.5 m in *M. marki* (Dadour and Bailey, 1990).

Greenfield (1990) has suggested that the necessity of hearing conspecific males calling has been an important factor in the evolution of the advertisement song. In the genus *Neoconocephalus*, for example, some species have discontinuous songs, with gaps between groups of syllables, while others have continuous songs. The former tend to live in high densities while the latter live at lower densities. Greenfield argues that discontinuous songs have evolved largely because of the importance to a singing male of being able to hear his neighbours (which he can only do when not singing himself: Hedwig, 2001), especially in higher-density populations where acoustic, spacing or territorial interactions are likely to be more frequent. Similarly, in the grasshopper *Omocestus viridulus*, there is a correlation between male density and the length of the song (Eiríksson, 1992). Males sing shorter songs at higher density, though they sing more often so that total singing time remains the same. In this case, however, Eiríksson argues that males sing shorter songs when male-male competition is high in order to increase the probability that they will hear the female's reply, since females stridulate in response to the male but do not necessarily wait for the male song to end before replying.

Male song may attract other males as well as repulse them: in some species, playback of recorded advertisement song attracts males as well as females (e.g. Walker and Forrest, 1989). As a result of the simultaneous attraction and repulsion that calling males have for each other, they may end up evenly spaced within an aggregation (e.g. Campbell, 1990). There are various possible reasons why aggregating may be adaptive for a male. For example it might make him less vulnerable to predators (see Section 7.1.1), increase his mating success if females are more likely to approach groups than single males (Alexander, 1975), or allow an unattractive male to exploit more attractive ones by intercepting females approaching preferred males (satellite behaviour: see Section 8.3). Female *Conocephalus nigropleurum* are more attracted to groups of males (Morris et al., 1978. See also Section 6.6) but studies of several other species found little or no evidence that this occurs (e.g. Otte and Loftus-Hills, 1979; Cade, 1981; Walker, 1983b). Cade (1981), for example, found that solitary male field crickets attracted just as many females as clumped males did, on a per capita basis.

The degree of separation between males may influence their relative attractiveness to females. In experiments with the cricket *Eunemobius carolinus*, the attractiveness of a male calling song for a female increased as the intensity relative to other songs increased (Farris et al., 1997). A lower intensity song lost attractiveness as the separation from a more intense song decreased. The ability of crickets to distinguish between calling songs on the basis of intensity decreased as the intensity of the calling songs increased. These findings are consistent with the conclusion from modelling (Forrest and Raspet, 1994) that dense spacing is more costly for less powerful singers. In such circumstances, the optimal strategy for weaker singers should be to search silently for females or adopt the role of a satellite male (see Section 8.3). The proportion of non-calling males does increase at higher densities in some species (e.g. Hissman, 1990). The switch from calling to satellite behaviour in *E. carolinus* would only be appropriate, however, if there was a shortage of singing sites at suitable distances from other males (Forrest and Raspet, 1994).

Males of many species of orthopteran, including most crickets, produce a distinct aggressive call during male-male aggressive encounters (Greenfield and Minckley, 1993; Zuk and Simmons, 1997; Field, 2001a). Stridulation by one male cricket during a fight usually causes the other to stridulate, though dominant males call more than subordinate males; the winning male also calls after the loser retreats while the loser rarely does so (Alexander, 1961). In tarbush grasshoppers, *Ligurotettix planum*, 80% of territorial disputes are settled without a fight by the exchange of aggressive 'shuck' calls (containing up to 60 shucks, each 25-35 ms long); the winner in most of these cases is the male with the highest rate of producing shucks (Greenfield and Minckley, 1993). Greenfield et al. argue that the shuck rate reflects an individual's strength or motivation and therefore the likelihood that he will win should a contest escalate to a fight.

In other species, such as certain bushcrickets, aspects of the advertisement song seem to function in male-male competition and may allow males to assess each other's size and strength before engaging in actual physical fighting. For example, male *Kawanaphila nartee* increase their calling rate when interacting with other males (Simmons and Bailey, 1993). Many *Orchelimum* and *Conocephalus* species have 'ticking duels' in which the tick part of the 'tick-buzz' song is extended when males interact (reviewed by Gwynne, 2001). In the common meadow bushcricket, *O. vulgare*, an intruding male is usually silent as he approaches his calling neighbour, only occasionally producing the tick part of his advertisement song. But as the two males get closer, tick sequences become more and more common from both males and eventually they may fight. In the haglid *Cyphoderris monstrosa*, the advertisement song actually seems to play a greater role in male-male competition than it does in female attraction (Mason, 1996). Males may use each other's duty cycle to assess fighting ability: winning males are more sustained singers.

Mating success can be heavily dependent on male success in aggressive encounters. In the gregarious cricket *Amphiacusta maya*, for example, the same type of chirp is used both in courtship and in male-male aggression; males that win fights have the greatest mating success, and experimentally silenced males are less able to achieve high dominance rank and are less successful at mating, not because females are less receptive but because intruding males interrupt silent courtships (Boake, 1983). In *A. maya*, courtship song appears to be mainly directed at other males: silent males are just as able to elicit mounting as males producing courtship song.

8.2 Choruses

Chorusing is found in many insects that communicate acoustically. Greenfield and Shaw (1983) defined chorusing as 'the singing of two or more conspecific males for relatively long periods of time during which there are statistically significant temporal interactions involving the acoustics signals of neighbors'. Males in orthopteran choruses are often aggregated spatially, for example near resources important to females, but they can also form temporal calling assemblies, i.e. sprees (Walker, 1983a). In many species, males respond acoustically (phonorespond) to the sounds of neighbouring males. In others, males probably do not phonorespond but may end up singing simultaneously because they respond in the same way to environmental conditions such as the onset of dusk (e.g. mole crickets and short-tailed crickets: Walker, 1983a).

Greenfield and Shaw (1983) review and define various types of chorusing. In *unison singing*, males sing during the same extended time period without showing any consistent temporal relationships between any song units. Unison singing is shown by many species with songs consisting of either relatively short or relatively long non-repeating units (NRUs), or of repeating units (RUs) at irregular intervals. Repeating units are very similar sound components of relatively uniform length at a given temperature. They can be aperiodic, in which the sound is produced at irregular intervals, or periodic, in which the sound is produced regularly so that the sound plus the following interval is a consistent length. There may be a hierarchy of sound components – song bout, chirp, syllable, etc – which may vary in repeatedness within the same species. In unison singing, individual males may phonorespond by initiating song in response to conspecifics and by singing for longer and more continuously than when singing in acoustic isolation. Examples include *Gryllus* species (Alexander, 1962), *Stenobothrus lineatus* (Haskell, 1957) and *Neoconocephalus exiliscanorus* (Fulton, 1934). *Unison bout singing* is unison singing in which collective singing is divided into bouts of irregular length separated by periods of silence of irregular length. Examples include several *Neoconocephalus* species (Greenfield, 1990), *Syrbula admirabilis* and *S. fuscovittata* (Otte and Loftus-Hills, 1979), and *Aerochoreutes carlinianus* (Otte, 1977).

In *synchronous chorusing*, the phase angles between the RUs of two or more neighbouring males are consistently very small. For example, in the snowy tree cricket, *Oecanthus fultoni*, males chirp at the rate of about 2.5 per second at 25 ^{o}C, but solitary males sing with less uniform chirp periods and lengths than chorusing males (Walker, 1969). Other species that show synchronous chorusing include *Platycleis intermedia* (Samways, 1976) and *Neoconocephalus caudellianus* (Greenfield, 1990). Leaders and followers (males that habitually initiate their RU first and second respectively) can be distinguished in some species, such as *N. nebrascensis* (Meixner and Shaw, 1986).

In *alternating chorusing*, the phase angles between the RUs of two or more neighbouring males are consistently maintained at about 180^{o} and the males do not overlap RUs (e.g. Gryllotalpa major: Hill, 2000). In some alternating species, chorusing males call more rhythmically than isolated males, i.e. intervals between RUs are more variable in isolated males. Some species call more slowly when alternating compared with solo singing (e.g. *Acanthogryllus fortipes*: Cade and Otte, 1982) while others call more quickly (e.g. *Pholidoptera griseoaptera*: Jones, 1966). Leaders and followers (where leaders are defined as males that typically initiate calling after a period of silence) can again be distinguished in some species, such as *Pterophylla camellifolia* (Shaw, 1968).

There are also choruses that cannot be described either as synchronous or as alternating but which show statistically significant relationships among RUs. For example adjacent *Amblycorypha parvipennis* males within an aggregation sing with overlapping calls such that each male overlaps his neighbour’s phrase about 70% of the time. Where phrases overlap, phonatomes (the sound produced by a single wing-stroke) are synchronized (Shaw et al., 1990). Some species vary in the type of chorusing they show: phase angles in *Orchelimum nigripes*, *O. vulgare* and *O. gladiator*, for example, are variable and at times males synchronize while at others they alternate (Feaver, 1977).

Chorusing behaviour has rarely been explored in duetting species but the existence of a time window has interesting implications for chorusing. The response latency of female *Phaneroptera nana* is about 60 ms (Tauber, 2001). Males alternate with their neighbours and their calls rarely overlap. The period of the male calls is about 700 ms (Tauber and Cohen, 1997). In experiments with synthetic calls, females were found to respond to both males of an alternating pair, providing that the calls were at least 200 ms apart. The timing of the male calls is forced into a pattern that does not jam any female reply and preserves the time window. So, in this species the male has two distinct responses to auditory stimulation by the conspecific song (Tauber, 2001). If it is a male song then the response is a delay in calling; if a female song, then phonotaxis is initiated. In this species the male and female songs differ in both temporal pattern and frequency spectrum, allowing the possibility of discriminating between male and female song, unlike *L. punctatissima* (Robinson et al., 1986) where male and female have similar frequency spectra. It will be interesting to see if male *L. punctatissima* show this discrimination.

Is participating in a chorus adaptive for males? Some possible benefits of chorusing were discussed in Section 8.1. Greenfield and Shaw (1983) give several other possibilities and Greenfield (1994) reviews the various hypotheses and studies on the evolution of chorusing, looking in particular at the possible cooperative and competitive functions of signal interactions.

Greenfield (1994) gives several reasons why chorusing might be adaptive in terms of male-male competitive interactions. Since males cannot hear while they are calling themselves, alternation may help them to assess each other on the basis of their calls, and so play a role in spacing and aggression. Synchronous calling could also result from a kind of acoustic satellite behaviour (see Section 8.3) in which a subordinate male produces short calls that are completely overlapped by his dominant neighbour, by which means he avoids detection and possible eviction. *Neoconocephalus nebrascensis* choruses may provide an example of such behaviour (Meixner and Shaw, 1986). Similarly, in duetting species, a synchronizing male may be able to ‘take over’ a female responding to his neighbour (e.g. Elephantodeta nobilis: Bailey and Field, 2000). Sprees have been explained in terms of males calling when environmental conditions are most favourable (Section 6.2), females most numerous (e.g. Walker, 1983a), or enemies least active (see Section 7), which causes them to call together by default. However, males of species that form sprees have been observed to start singing, or increase their rate of singing, in response to playback of conspecific song (e.g. Shaw et al., 1990), so sprees may be the result of competitive or cooperative interactions between males. Males may need to match or outdo other males in order to be attractive to females; the high energetic costs then limit males to singing in periods that coincide with female activity. If females are available over a long period, males may not have enough energy to sing for the whole time. They may break their calling up into bouts to cover the availability period as effectively as possible, leading to unison bout chorusing.

Greenfield and Shaw (1983) and Greenfield (1994) also list several possible reasons why males might benefit from *cooperating* to form choruses, including the reduced vulnerability to predators and increased attractiveness to females of groups compared with single males discussed in Section 8.1. In species where the call is produced at regular intervals, the period may be the most important bit of information for species recognition; if neighbouring males synchronize their calls, then any female in the area will hear the species-specific rhythm. This explanation has been suggested for the synchronous chorusing in *Oecanthus fultoni* (Walker, 1969). Where information is contained in the song itself, then alternation would preserve the information. If females select males based on relative as opposed to absolute criteria, then they may choose to mate only with members of choruses so that they can assess the attributes of potential mates. Males might also synchronize in order to maximize peak signal amplitude (the 'beacon' effect). If females are more strongly influenced by peak signal amplitude than amplitude averaged over time, tightly clustered groups of males that synchronize would be more attractive than groups that do not. In duetting species, synchronous calling would avoid masking of the female reply by other males. If female conspecifics suffer from the same confusion effects produced by many males calling simultaneously as has been suggested for predators, then males would benefit by alternating their signals. In *Ligurotettix planum*, it has been shown that females show reduced phonotaxis to overlapping calls (Minckley and Greenfield, 1995) and this may contribute to the maintenance of call alternation in this species (Minckley et al., 1995). Males may alternate to preserve signal components, such as pulse rate, which are critical features in female phonotaxis. This is analogous to the preservation of the species-specific rhythm by synchronous chorusing but assumes that males are limited in their ability to adjust pulse timing and therefore unable to synchronize pulses; call alternation is therefore selected instead of call synchrony. Finally, if females are preferentially attracted to groups with higher duty cycles, males would benefit by alternating their calls, thus maximizing the number of calls in a particular time period.

There is little or no evidence to support any of the functions that have been suggested for alternating and synchronous choruses, however. Greenfield and his colleagues (Greenfield and Roizen, 1993; Greenfield, 1994; Greenfield et al., 1997) argue instead that alternating and synchronous choruses are epiphenomena arising out of the tendency for females to prefer the leading of two male calls (see Section 6.6). They suggest that, because of the selection pressure on males imposed by this female preference, individual males compete to jam each other's signals, using mechanisms that modify the timing of their call relative to those of others so that they increase their chance of producing a leading call. For example, female *Neoconocephalus spiza* prefer male calls that precede others by 10-80 ms. A male *N. spiza* resets his calling rhythm when he hears a neighbouring male calling, which leads to him producing fewer following calls. But a synchronous chorus results when males, all using this resetting mechanism, call at similar rates (Greenfield and Roizen, 1993).

Greenfield et al. (1997) have developed a general model of rhythmic signalling in which calling is controlled by an oscillator in the central nervous system that may be inhibited and reset by a neighbour's call. This inhibitory-resetting mechanism affects one call period only, with the natural rhythm continuing thereafter. Playback experiments have shown that rhythms and signal interactions in several species fit the assumptions of their model, for example in *Pholidoptera griseoaptera* (Jones, 1966), *Pterophylla camellifolia* (Shaw, 1968), *Oecanthus fultoni* (Walker, 1969), and *Ligurotettix planum* (Minckley et al., 1995). Greenfield et al.'s simulations show that, given female choice for leading calls, the basic resetting mechanism is evolutionarily stable, as long as it includes a 'relativity adjustment' for the velocity of signal transmission and selective attention towards a subset of signalling neighbours. Greenfield et al. present data to show that relativity adjustments are incorporated into the resetting mechanisms of several species, including *O. fultoni* (Walker, 1969), *Neoconocephalus spiza* (Greenfield and Roizen, 1993), and *L. planum* (Minckley et al., 1995). Selective attention toward loud, nearby neighbours has been demonstrated in *L. coquilletti* and *L. planum* by Sneddon et al. (1998); see also Römer (1993).

Such an inhibitory-resetting mechanism can generate either synchronous or alternating choruses by default. If two neighbouring males both signal at similar rates that vary very little, phase delays tend to mutually align their rhythms within a single period and synchrony continues thereafter; alternation occurs when the rebound interval following resetting is relatively short compared with the signal period and is seen in species with slower signalling rates (Greenfield, 1994). Thus, in the genus *Platycleis*, the only species that regularly synchronizes is *P. intermedia*, the species with the highest signalling rate (Samways, 1976).

8.3 Satellite males and silent searching

Males that do not produce advertisement calls have been observed in various orthopteran species, for example in a Texas population of *Gryllus integer* (now called *G. texensis*) (Rowell and Cade, 1993), *Teleogryllus oceanicus* (Zuk et al., 1993), *Orchelimum nigripes* (Feaver, 1977), *Acanthoplus speiseri* (Mbata, 1992), and gomphocerine grasshoppers (Green, 1995). It is possible that some males do not sing because they do not have enough energy or are too badly damaged by parasites, but there is now good evidence, in some species at least, that males are adopting an alternative mating strategy by acting as a satellite male and/or silently searching for females. Satellite males stay quietly near a calling male and try to intercept females performing phonotaxis towards the caller.

The rate at which a satellite encounters females depends on the ability of the calling male to attract them, so males using this strategy could maximize their mating success by moving close to a calling male that produces the kind of song that females prefer. There is some evidence that this may happen in, for example, *Acheta domesticus* (Kiflawi and Gray, 2000).

Various hypotheses have been put forward to explain why males may adopt a silent searching or satellite role. Cade and his colleagues (Cade, 1975; Cade, 1979; 1984a) have proposed that satellite behaviour in *G. texensis* may have arisen as a genetically-determined, evolutionarily stable, alternative mating strategy to avoid the risk of attack by acoustically-orienting parasitoids (see Section 7.2). They collected calling and non-calling males in the field and found that calling males were more likely to be parasitized. More silent males were also observed in this species than in three other gryllines not known to be parasitized (Cade and Wyatt, 1984) and seasonal variation in calling related to parasitoid fly abundance has been observed in *G. rubens* (Burk, 1982). A study by Zuk and her colleagues (Zuk et al., 1995; Zuk and Simmons, 1997) of the *Teleogryllus oceanicus* population in Hawaii has shown, however, that, in this species at least, silent males do not necessarily represent a satellite class of males. Silent males are more likely to be parasitized than calling males and are probably silent because they have too much tissue damage to sing, i.e. their silence is a by-product of parasitism rather than an adaptation to avoid parasitism. On the other hand, the association between *O. ochracea* and *T. oceanicus* is more recent than for *G texensis*, so the Hawaii population may simply not have had time to adapt to the fly. However, silent males are common in non-parasitized populations of *T. oceanicus* outside of Hawaii (Zuk et al., 1993), so the adoption of a satellite strategy cannot be entirely due to the selection imposed by the fly.

Males may be opportunistic, switching between calling and non-calling depending on which strategy maximizes mating success in the prevailing circumstances. Cade (1979) has shown in *G. texensis*, for example, that non-callers may start to call if a neighbouring male is silenced. Whether males call or not may depend on their competitive status: males unsuccessful in competition with other males could avoid attracting superior competitors by staying silent. How often males call may be correlated with males' competitive ability in *G. bimaculatus* (Simmons, 1986).

The strategy a male adopts also depends on population density. At high densities, the cost of defending a territory is higher (Alexander, 1961) and there is a greater probability of encountering females simply by chance. Males may benefit in this situation from stopping singing and becoming a satellite and/or searching silently for mates. Silent searching at higher densities is found in e.g. *Gryllus bimaculatus* (Simmons, 1986), and *G. campestris* (Hissman, 1990) and the frequency of satellite behaviour increases with male population density in *G. texensis* (Cade and Cade, 1992). Cade and Cade (1992) have shown that male *G. texensis* that call more have greater mating success at low densities, whereas at very high densities there may be no difference in mating success between males who call and males who do not. Simulations of high density populations with strongly female-biased operational sex ratios, suggest that mating success for satellite males may actually exceed that of calling males in these circumstances (Rowell and Cade, 1993).

In *Orchelimum nigripes*, satellite males may be 'making the best of a bad job' (Feaver, 1977; 1983). *O. nigripes* is territorial. Larger, older males are more likely to win fights and can hold the most sought-after central territories where most females are encountered; as result they have greater mating success. Younger, smaller males are less successful in obtaining mates and, at high densities when they cannot obtain a suitable territory for themselves, often adopt a satellite strategy, staying quietly in the territory of another male and accosting females that respond to the calls of the territorial male. They have very little success, though, because females will not mate with a male who does not begin his courtship ritual by singing, and any satellite male that sings is quickly ousted by the territorial male. There is one major advantage to the satellite strategy, however: the territorial male produces a spermatophore about 10% of his body mass and, after he has mated, he cannot produce another one for some time, during which period he leaves his territory. The satellite can then take over the territory and start to sing. Feaver demonstrated experimentally that this happens by removing a territorial male.

9 New directions

Work in the different disciplines of bioacoustics has advanced sufficiently that integration of their results is providing a more coherent picture of sound signalling. For example, we now have information on directionality from behavioural and neurophysiological studies that is congruent, enabling behaviour to be explained, at least in part, at a neural level.

Studies of the structure and function of ears supports observations made behaviourally and although there is much that remains to be explored, we can provide a description of the processes involved in sound communication from the generation of a signal, its transmission through the air, its reception, its analysis and the subsequent response of the recipient. Much of the information comes, inevitably, from laboratory experiments, but the increasing ability to undertake neurophysiological, acoustic and behavioural work in the field promises to enhance the integrative approach to the study of sound signalling.

Information about the processing of auditory information in the central nervous system is now extensive and the ability to record from identified neurons has enhanced greatly our understanding of the function of the orthopteran nervous system .The absence of a large section in this review, devoted to the brain, is an indication of the greatest area of ignorance in our understanding of sound signalling. True, we know that stimulation in certain regions of the brain will induce stridulation. We also know that the brain is a centre for decision-making processes in signalling and sound reception, but we know very little indeed about how and where these decisions are made. Investigation of the brain will be perhaps the most important area of research in sound signalling in the future.

A lot of information is now accumulating about the natural and sexual selection pressures that affect the evolution of acoustic signals, including environmental effects, predation, mate choice, and competition between signallers. However there are many questions that remain at best only partially explored (Endler, 2000). For example, how much do orthopterans exploit 'beneficial' environmental effects, perhaps to avoid predation or maximize signal distance? What signal properties and parameters are best for a particular environment and, given that environment and the amount of noise associated with it, what is the best way to send information: when, say, is it better to use repetitiveness and when redundancy? When we know more about how signal parameters affect decisions made by the recipient, and how the environment degrades those parameters, it should be possible to predict much more about the details not only of signal structure but of sensory system structure and function. This is still at a very early stage.

We know a considerable amount about the effects of individual predators or parasitoids on individual orthopteran species but we also need quantitative studies that look at the effects of more than one natural enemy. There are also some unanswered questions. For example, why do neotropical bushcrickets under heavy predation from bats seem to have evolved much lower calling rates than bushcrickets attacked to a similar or even greater degree by parasitoid flies? It is possible that those species attacked by flies that have so far been studied have not been able to evolve more cautious calling behaviour because they are constrained by their shorter breeding lifetime (e.g. about 4 weeks for *Poecilimon*) compared with the neotropical species attacked by bats (Gwynne, 2001), but much more work needs to be done before we can arrive at a more complete understanding of the effects of natural enemies on the evolution of calling behaviour.

Acoustic signals have many parameters that can be used to convey information but more work needs to be done to find out which parameters are actually used, for example by females to assess male quality, or to code for such things as species, gender or age. Which parameters are inherently more honest and which can be faked? What are the trade-offs between different functions of a signal (e.g. female attraction versus repulsion of rival males) and how does this affect what parameters are used, possibly within the same call? Our knowledge of the parameters of acoustic signals that influence mating success is increasing, but distinguishing between passive and active female choice is still a big problem. And we still know very little about how female choice actually translates into male lifetime reproductive success, how individual females differ in their preferences, or how the characteristics of her mate affects a female's reproductive success. Because females mate more than once and sperm mixing is common, assigning paternity to offspring is very difficult, but DNA fingerprinting techniques should help in future research. More work is also needed, especially in the field, to see how differences between individual males in song structure, diel patterns of calling, and calling durations translate into mating success, how the calling behaviour of individual males is affected by population density and nutritional status, and how competition between signallers affects the transfer of information to females.

Finally, there is an enormous potential in the Orthoptera for divergence between populations in signalling systems. There are many ways to modify acoustic signals because there are so many different parameters that can carry information. Selection on sensory processes or preferences can also result in divergence. Thus signal divergence may play a very important role in speciation in the Orthoptera but apart from observations that different species have different signals, this area has not yet been well studied (Endler, 2000).

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