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# Environmental and Biological Constraints for the Evolution of Long-Range Signalling and Hearing in Acoustic Insects

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# Environmental and biological constraints for the evolution of long-range signalling and hearing in acoustic insects

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## SUMMARY

A number of insects use sound signals for the attraction of mates and in aggressive interactions between males. I discuss two constraints which may have shaped both the design of long-range signals, and the structure and physiology of the ear and nervous system of the receiver. Properties of the transmission channel for sound will impose limitations on long-range transfer of information, which may be compensated for by adapting either the signal or the behaviour of the sender or receiver. I describe properties of the nervous system which force the sender to produce more conspicuous signals. I suggest that the evolutionary past may represent a constraint on the communication system, where conservative features of the sensory and nervous system would now appear to be maladaptive for intraspecific communication.

## 1. INTRODUCTION

A sense of hearing is well developed in most groups of insects and never more so than in grasshoppers, bushcrickets and crickets: the Orthoptera. In these insects, sound is used primarily for social communication, the attraction of mates and in the aggressive displays between males. The influence of two kinds of selection pressure on the design of acoustic signals of insects form the central part of my thesis. First, the ecological constraints imposed by the transmission channel of the sound signal, and second, the phylogenetic constraints resulting from the past evolution of a species. Predation pressure is a significant constraint for both communication signals and the design of insect ears (see review by Hoy (1992)). Acoustic signals of insects would appear to be energetically costly due mainly to the low efficiency of converting muscle contraction into acoustic power; in some species metabolic rates may increase during calling by some 600% (Stevens & Josephson 1977) and although such costs represent a further constraint on signalling they will not be considered here.

## 2. CONSTRAINTS BASED ON THE TRANSMISSION CHANNEL FOR SOUND

Most physiological studies of insect hearing have been carried out – for obvious reasons – under isolated and well controlled acoustic conditions of sound proof rooms. Many sensory physiologists were surprisingly slow to realize that insects in nature do not have the luxury of listening to sound in such acoustically ideal conditions. In the field, the transmission channel for the insect's song may attenuate and degrade the signal on its way to a receiver in an unpredictable manner, thus limiting reliable long-range transfer of information. Moreover, an array of sounds from different sources and directions may complicate any assessment of signal parameters associated with an individual sender. Thus, although the insect may be able to detect a signal and distinguish one song from the other in the laboratory situation, it may fail to do so in complex acoustic conditions in the field (see Gerhardt (1982) for comments on frogs).

### (*a*) *The active space of a signal*

It is a common argument that the acoustic channel of communication has been selected for its ability to overcome obstacles to information transfer in a particular environment. However, acoustic signals of insects appear to be less well adapted for long range communication than those of birds or other vertebrates. Insects are small and usually broadcast sound with reasonable intensity in the high sonic or ultrasonic frequency range (Bennet-Clark 1970; Michelsen & Nocke 1974). At these small wavelengths there is attenuation in excess to the geometric spreading of sound, usually as a result of interactions of sound waves with vegetation (Wiley & Richards 1978; Römer & Lewald 1992). We would therefore expect that insect sound signals could only be used over short distances. Estimates of the maximum communication distance in natural habitats are difficult to obtain, simply because there are multiple physical variables that affect sound attenuation and degradation in an unpredictable way. Furthermore, there are technical

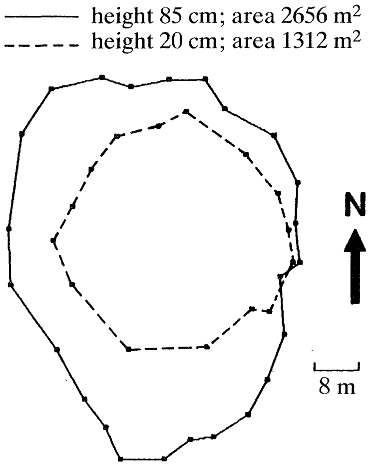

Figure 1. Polar plots of the broadcasting area of the song of two male *Mygalopsis marki*, as measured from the activity of an auditory interneuron, recorded in various directions from the singing males. Data from the two experiments are superimposed so that the position of the singing males overlaps. (After Römer & Bailey 1986.)

difficulties with high frequency sound sources and receivers which may hamper this assessment. One way to overcome some of these problems is to monitor the ear and nervous system of the insect itself, rather than a microphone, as a detector for the range of communication (Rheinlaender & Römer 1986). In this way the insect becomes a 'biological microphone', with which it is possible to study the hearing capacity of a receiver in the natural situation as well as the transmission properties of the habitat.

Measurements, using this method, suggest that bushcrickets can hear and communicate over remarkable distances, particularly in habitats with little vegetation (Rheinlaender & Römer 1986; Römer & Bailey 1986). But in habitats dominated by vegetation, the position of either sender or receiver will play an increasingly crucial role in determining the maximum hearing distances of the signal (figure 1). As the calling song determines whether males may attract a mate, or the outcome of an aggressive interaction, any mechanism to increase the broadcast range of the signal will be under strong selection.

Given that small size forces most insects to use higher frequencies, with the inherent problem of excess attenuation, we might predict that behavioural strategies (e.g. optimal broadcase positions), would be of significance in the evolution of acoustic signalling. Because scattering of sound within the vegetation seems to be the major cause of attenuation, insects should call from the top of the vegetation or close to it (Römer & Bailey 1991). Insects undoubtedly optimize their signalling strategies. For example, males of the bog katydid *Metrioptera sphagnorum* prefer to sing from isolated spruce trees close to 60 cm, although the available trees were more than twice that high. Compared to males singing from ground level, males at this height increase their broadcast range threefold, whereas there is only a minute additional advantage by singing further up the tree (H. Römer & G. K. Morris, unpublished observations). Counteracting selection pressures against a maximum broadcast range might include costs due to predation by parasitoids or bats (Cade 1975; Belwood & Morris 1987; Lakes-Harlan & Heller 1992), or increased intraspecific competition with greater risk of damage in physical contacts with rivals. It will therefore be the net profit from different, counteracting selection pressures that determines in each situation whether or not a greater broadcast range will be selected for.

### (*b*) *Signalling and information transfer*

The attenuation of sound primarily affects the receiver's ability to detect a broadcast signal. For effective communication to occur, however, the receiver must also be able to discriminate among different signals. In insects information about species identity is primarily encoded in the temporal structure of the song (von Helversen & von Helversen 1983; Doherty & Hoy 1985) and any degradation of temporal parameters would therefore impose severe limitations for long-range social communication.

Reverberations and amplitude fluctuations induced by wind or atmospheric turbulence also produce distortions particularly in the time domain. When this distortion is superimposed on amplitude-modulated patterns, it increases the difficulty to identify the signal. By using the 'biological microphone' in the field, it was possible to demonstrate that the perception of the gross temporal pattern of the song was remarkably reliable up to distances of 50 meters (Rheinlaender & Römer 1986). Broad-band signals appear to be less vulnerable to amplitude fluctuations than are pure-tone signals (Römer & Lewald 1992) and most bushcricket and grasshopper sound signals are broad-band rather than pure-tone. Such a broad-band spectrum may be an 'effect' of the structures used for stridulation; however, it may be considered adaptive for reliable long-range transfer of information on species identity. In addition, insect sounds may be extremely redundant in that short song elements are repeated, often for hours, and this redundancy counteracts the effects of degradation and attenuation of the signal. The temporal song pattern can be perceived, even when a number of song elements are lost during sound transmission (Römer & Lewald 1992).

The fine temporal structure of insect song may provide information regarding identity or status of the sender to the searching female or the competing male. However, we know very little about the ability of the receiver to resolve these details, or the behavioural relevance of this information (Michelsen 1985). It is expected that fine temporal elements (such as the tooth impact rate or small gaps in the order of a few milliseconds) will be the first to disappear as the signal passes through the habitat, primarily as a result of reverberations and scattering (Michelsen & Larsen 1983). Hence, this information may only have relevance for communication over short distances, or alternatively, it may represent a cue for estimating the distance to the sender (Simmons 1988).

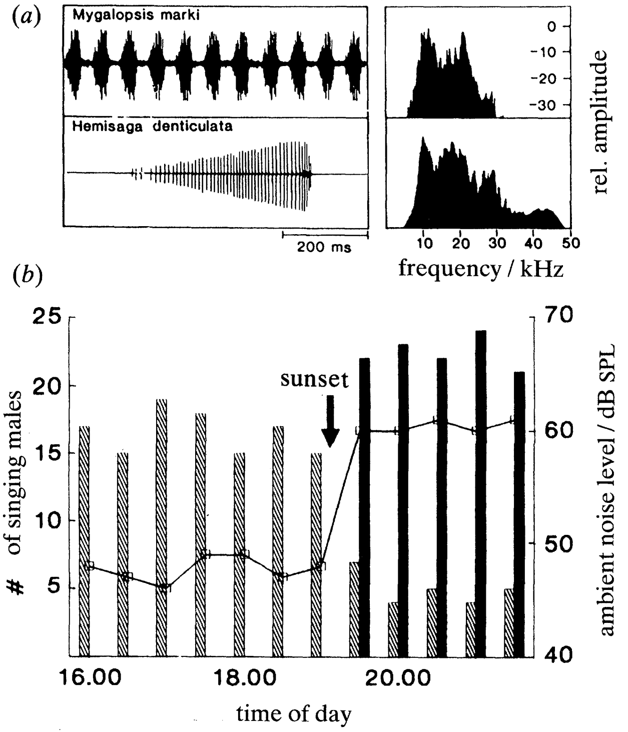

Figure 2. (*a*) Oscillograms (left panel) and spectra (right panel) of the songs of *M. marki* and *H. denticulata*. (*b*) Number of calling males of both species and mean background noise level between 16.00 h and 22.00 h in the habitat. Note the inhibition of singing activity of *H. denticulata* with the onset of singing activity of *M. marki* (black bars). (After Römer *et al.* 1989.)

### (*c*) ***Sound localization***

In most biological situations a receiver must be able to both identify and localize the sound source. However, the physical properties of the transmission channel complicate sound localization for a receiver in two different ways. Within the vegetation, multiple reflections and scattering will turn the sound field around a listening insect into a diffuse sound field in which sound waves arrive with almost equal intensity from all directions. Furthermore, when insects rely on the diffraction mechanism of sound around their body to establish interaural intensity differences, particularly at high frequencies, and these frequencies suffer from strong attenuation, directional hearing at some distance from the source will be based on very poor directional cues. Physiological measurements, using directionally sensitive auditory interneurons in the field, indicate that in unfavourable receiver positions, the directional cues of a sound signal may be completely lost (Rheinlaender & Römer 1986). Hence, information about the identity of the sender (the temporal structure) is still available, but not about its location. The receiver may compensate for this loss of information by seeking better positions in the habitat from which to hear. It is expected, but not yet tested, that the height of the sender in the vegetation has similar consequences for localization of a signal as does the height of the receiver.

We may expect that directional hearing will be under strong selection in nature, for failure or delays in locating a sound source will have energetic consequences for the searching insect as well as risks of exposure to predators. It has been argued that unfavourable conditions for directional hearing in the habitat may have consequences for the evolution of neuronal networks capable of handling these difficulties in an appropriate way (Römer 1992).

### (*d*) ***Constraints on signalling and hearing due to masking sounds***

In addition to the physical processes of the transmission channel, which result in attenuation and degradation of insect acoustic signals, several sympatric species may communicate acoustically at the same time and each is presented with the problem of detecting and discriminating its own signals in the noise produced by the other species. Measures of the range of communication, or of sound discrimination abilities, are of little relevance without considering the level of masking noise in the environment.

#### (i) *Interspecific interference*

Song interference between species is a common phenomenon in insect populations (Greenfield 1990), and calling males will often modify their species' distinct temporal pattern in response to a calling neighbour of a different species. Song interference may be avoided by calling at a different time, or place, and evidence for both temporal and spatial displacement has been found in the field (Greenfield 1988; Schatral 1990). Song interference is most prominent in species which use the same broadcast frequencies. *Hemisaga denticulata* and *Mygalopsis marki* are two sympatrically occuring species of bushcricket which use broadband songs with almost completely overlapping frequencies (figure 2). A comparative study between two populations of *H. denticulata* showed that in the presence of singing males of *M. marki* (a continuously singing species), the song of *H. denticulata* was suppressed. Such inhibitory interactions have been interpreted as a by-product of temporal interactions that usually occur between individuals in one species (Greenfield 1990). Song inhibition may also be viewed as an effect of masking, where critical song elements that are necessary for a receiver to respond in an appropriate way to the signal, can no longer be detected in the noise level produced by the inhibiting species. Neurophysiological experiments conducted in the field confirm that there is substantial masking of *H. denticulata* song when *M. marki* calls at the same time (Römer *et al.* 1989).

A human engineer free to draw up plans for perfect, undisturbed insect acoustic communication, would certainly be able to avoid song interference, simply by using narrowly tuned, species-specific frequency bands in the signal, coupled with a sharply tuned peripheral auditory filtering. It is remarkable that most insects that communicate by sound have not adopted this logical solution to avoid song interference. One reason is that calling behaviour and hearing design are

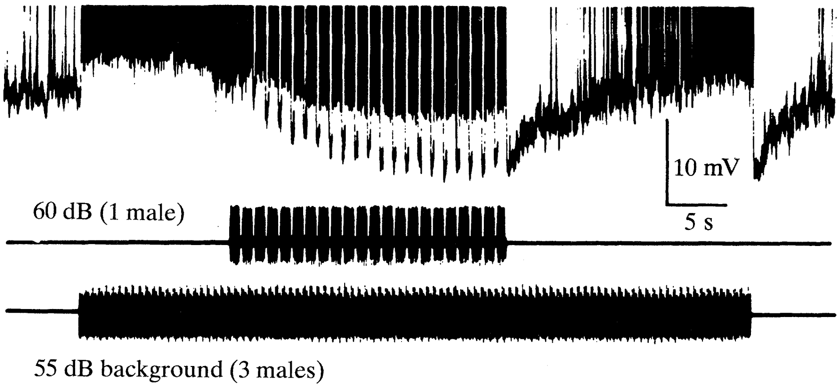

Figure 3. Intracellular recording of the activity of an identified auditory interneuron (omega-neuron) in the prothoracic ganglion of the bushcricket *T. viridissima*, in response to conspecific song at 60 dB SPL and an accoustic background of three calling males at 55 dB SPL. Note that in the presence of the more intense song the response to the background is suppressed, although there is a strong response to the background when presented alone. Membrane resting potential −45 mV; spikes are truncated. (H. Römer unpublished data.)

shaped not by the problems of intraspecific communication alone, but by many other conflicting selection pressures. For example, a broadly tuned auditory system for detecting the high-frequency biosonar of bats would be very useful as a basis for predator avoidance behaviour (Hoy 1992), but the cost for such a broadly tuned receiver, sensitive to a wide array of sounds is an increased risk of song interference and masking.

(ii) *Intraspecific interference*

Insects may also sing in dense populations of conspecifics with many senders within the hearing range of a receiver, a situation similar to that of breeding populations of frogs (Campbell & Clarke 1971; Cade 1981; Gerhardt & Klump 1988). Because masking is most effective when the spectrum of the masking sound overlaps the signal, we would expect that the background chorus of conspecifics strongly affects hearing in such populations. Furthermore, the temporal overlap of several songs arriving from different directions, may result in a severe contamination of individual temporal song patterns at the position of the receiver. The question then is, how many signals, if any, can be perceived by a receiver in these choruses?

By mimicing part of this complex hearing situation in the laboratory, Pollack (1988) discovered a neuronal mechanism that could provide a selective coding to the more intense of two sound signals presented simultaneously, analoguous to the 'cocktail party phenomenon' familiar to humans (Cherry 1966). An acoustic simulation of a natural chorus in the laboratory with four independent sound sources demonstrated a similar high selectivity in the bushcricket central nervous system (H. Römer & M. Krusch, unpublished observations; figure 3). In this case, while each auditory pathway is selectively listening to, and encoding the temporal pattern of predominantly ipsilateral sounds, each pathway also selects for the most intense of several alternative sounds. The implication for a regularly spaced population of bushcrickets is that the signals of the more distant (or the less loud) males are not present in the afferent auditory pathway of a receiver. Thus, although there may be more than ten senders within hearing range, this central nervous filter mechanism may reduce the information available for a receiver, so that it may simply be listening to two nearby calling males, one represented in the right and one in the left auditory pathway.

Based on behavioural experiments in dense choruses of green treefrogs, Gerhardt & Klump (1988) arrived at similar conclusions. Their results have implications for theoretical approaches to sexual selection theory, for if one assumes that females within a population can sample the 'quality' of many or all males, and that assessment of these males is cost-free, then these assumptions do not hold for populations of the green treefrog or the bushcricket *Tettigonia viridissima*. Our results indicate that a female *T. viridissima* can hear only a very small fraction of males from any one position, and to hear more males it would have to move throughout the population, thus increasing the risk of predation (Heller 1992).

From the viewpoint of the signalling male the existence of the intensity filter in the CNS of a receiver also has important consequences. The evolution of signals results from selection to increase their effectiveness in changing the response of receivers. The central nervous filter mechanism suggests a 'competition for representation in the CNS of a receiver', stronger than we would predict from a simple masking effect alone. If a male is unable to produce signals of reasonable loudness, or to establish and defend a preferred singing position, the representation of this signal in the auditory pathway of a receiver would be inhibited by those of other nearby males. The male would waste time and energy in calling and probably do better if it adopted an alternative strategy, perhaps acting as a silent satellite male (Cade 1975).

One may also speculate as to whether the intensity-dependent filter mechanism represents a proximate mechanism for what Parker (1983) termed passive attraction; a behaviour where females are merely attracted to the most intense, or most easily located signal, without actively choosing among males. In fact our results indicate that a female could hardly choose among a number of males, since the only remaining choice would be between the two signals represented independently in the right and left auditory pathway.

## 3. HISTORICAL CONSTRAINTS ON ACOUSTIC COMMUNICATION

### (*a*) *The design of the nervous system*

To understand why neuronal circuits, such as the auditory pathway of insects, are organized as they are, we have to consider their histories, since the nervous system has evolutionarily conservative, non-adaptive features that may constrain an underlying behaviour much in the same way as other constraints (Dumont & Robertson 1986).

Some preliminary data may highlight two possible cases of historical constraints on the acoustic communication system of bushcrickets. The first case is the heterospecific 'competition for broadcast space' between males of *M. marki* and *H. denticulata* (see figure 2). Preliminary experiments on interneurons in the auditory pathway in *H. denticulata* indicate that these neurons show the same kind of prolonged, slow inhibition in response to continuous song as do homologous neurons in *Tettigonia*. *Hemisaga*, however, produces a much shorter, discontinuous song. In *Hemisaga* the same neuronal mechanism exists as in the auditory pathway of *Tettigonia*, but it appears maladaptive for the detection of conspecific song in the presence of its heterospecific calling neighbour. Because the intensity filter mechanism appears to exist in crickets as well (Pollack 1988), it may be common to all orthopteran insects and therefore represent an evolutionarily conservative feature exploited by continuously singing species to inhibit acoustic communication in sympatric species. This hypothesis is consistent with the observation that continuously singing species of buchcricket usually inhibit the singing activity of discontinuously singing taxa (Greenfield 1990).

### (*b*) *The design of the sensory system*

In an undescribed species of bushcricket inhabiting coastal woodland of the south western part of Western Australia, there is a mismatch between the carrier frequency of the male's call and the tuning characteristic of the hearing organ. The carrier frequency is unusually low for Tettigoniids, centered at 5–6 kHz, a range at which the ear is 20 dB less sensitive than between 10–20 kHz (H. Römer & W. J. Bailey, unpublished observations; figure 4). More surprisingly, the mismatch is a consequence of an anatomical structure that guides sound from the spiracular opening in the prothorax, to the inside of the ear in the tibia of the forelegs. This acoustic trachea amplifies sound at frequencies between 8 and 30 kHz, and so causes the high sensitivity of the ear at frequencies well above the energy of the calling song (see also Lewis 1974; Nocke 1975; Seymour *et al.* 1978).

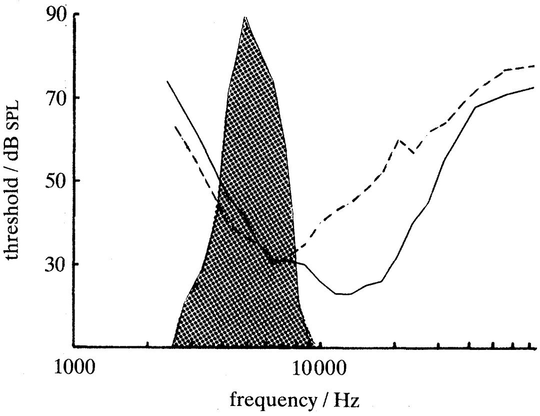

Figure 4. Spectrum of the calling song of an undescribed species of a sagine bushcricket (hatched area) and sensitivity of an auditory interneuron, representative for the tuning of the ear. As a result of the mismatch between the carrier frequency of the signal and the sensitivity of the sensory system, the unmodified ear responds more sensitive to heterospecific song of sympatric bushcricket species than to the conspecific calling song. When the spiracular opening of the acoustic trachea is closed, however, the tuning matches the carrier frequency of the conspecific signal (broken line). For further explanation see text.

This frequency mismatch results in a strong masking effect for a receiver when other sympatric bushcrickets sing in the frequency range between 10 to 30 kHz. It appears paradoxical that natural selection has favoured the development of a complicated 'hearing aid' (the acoustic trachea) that is not only useless for hearing the conspecific signal but also decreases the probability of perceiving the conspecific signal. It might be possible to argue for some adaptive value in the design of this sensory system, but from an evolutionary perspective we propose an alternative explanation. The adaptive value of increased high frequency sensitivity might have existed in the past, probably when the ancestor of this species used higher calling song frequencies in a more open habitat for intraspecific communication. Alternatively, high frequency hearing might have been adaptive for hearing sound produced by predators. The present-day species however, has adopted a cryptic lifestyle in dense vegetation, where a low frequency calling song of 5 kHz would be advantageous in that the signal is transmitted with little attenuation; it also avoids competition for broadcast space with other bushcricket species. Under present conditions, high frequency sensitivity is clearly disadvantageous in the context of social communication. The trait 'large tracheal system for amplifying sound in the ultrasonic range' might have been adaptive under past conditions, but since these conditions no longer exist, it is currently maladaptive.

The insect may adopt different solutions to this historical constraint; one strategy would be to reduce, or completely abolish, the structure causing the distracting high-frequency sensitivity. An alternative solution is to modify the existing tracheal input by some physiological mechanism to selectively remove sensitivity to higher frequencies at the right time. The animal appears to have adopted the second strategy: the spiracular opening to the trachea may be closed, changing the sensitivity of the ear so that a clear representation of the conspecific temporal calling pattern results within the afferent auditory pathway. Such a physiological mechanism would leave the animal with the option of changing the tuning of the ear, depending on the actual behavioural context.

In summary, constraints on long range acoustic signalling and hearing may exist either due to the properties of the transmission channel for the sound, or as a result of the conservative nature of the sensory and central nervous system within the receiver. Adaptations to these constraints may be difficult to separate from those features reflecting the past evolution of the auditory system.

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