Acoustic signalling in Orthoptera

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Abstract

Acoustic communication is one of the most well-known behavioural traits of the Orthoptera. Orthopteran insects and the sounds they produce are both extremely diverse, and species-specific sounds are an extremely important tool in orthopteran taxonomy and systematics. For most species, acoustic signalling is the most important means of communication. It plays a vital role in mating, mate choice, intrasexual competition, interspecific interactions with predators and parasitoids, and the divergence of populations and species. The enormous diversity of the orthopterans has provided researchers with a wealth of model systems for studying anatomy, physiology, neurobiology, bioacoustics, communication, life-history traits, behaviour, evolutionary ecology, and speciation, all areas in which acoustic communication is important. We first reviewed orthopteran sound signalling nearly 20 years ago (Robinson and Hall, 2002), since when there has been an enormous amount of further work. This second review will look mainly at research published since that first review.

Abbreviations

AN	ascending neuron
CNS	central nervous system
CPG	central pattern generator
CF	characteristic frequency
CHC	cuticular hydrocarbon
EP	elevated process
EPSP	excitatory postsynaptic potential
FM	frequency modulation
IID	interaural intensity difference
ITD	interaural time difference
LN	local interneuron
MR	metabolic rate
ON	omega neuron
RU	repeated unit
SPL	sound pressure level
SB	styliform body
TN	T-fibre neuron

1 Introduction

The order Orthoptera is extremely diverse biologically, morphologically, behaviourally, and ecologically, with more than 26,000 species occupying every possible terrestrial habitat, and some semi-aquatic ones, outside the polar regions (Song, 2018). It is divided into two main branches: the Caelifera and the Ensifera. The Caelifera mostly consist of the 12,000 or so species that make up the grasshopper family (the acridids) and the ground-hopper family (the tetrigids). The Ensifera consist of about 15,000 species, of which around 7000 are bush-crickets, or katydids as they are called outside Europe (the tettigoniids) and about 5000 are 'true' crickets (the gryllids); there are also several other smaller families such as the mole crickets in the gryllotalpid family. The classification of the orthopteran insects is much disputed and often revised but here we will follow the taxonomy used in the online Orthoptera Species File database (Cigliano et al., 2021).

Acoustic communication is one of the most well-known behavioural traits of the Orthoptera. The sounds produced by orthopterans are very diverse and, for most species, the most important means of communication. They play a vital role in mating, mate choice, intrasexual competition, interspecific interactions with predators and parasitoids, and the divergence of populations and species. They are an extremely important tool in orthopteran taxonomy and systematics and differences in song are often key to separating otherwise morphologically identical, cryptic species (e.g. Liu et al., 2020; Tan et al., 2020; Tian et al., 2019; Weissman et al., 2021).

Orthopteran species are of huge importance to humans. They include several crop pests such as grasshoppers and locusts (Fig. 1) but on the other hand they provide a major source of nutrition, with well over 250 species known to be consumed by humans (Song, 2018). The enormous diversity of the orthopterans has also provided researchers with a wealth of model systems for studying anatomy, physiology, neurobiology, bioacoustics, communication, life-history traits, behaviour, evolutionary ecology, and speciation. Acoustic communication is important in all these areas.

Fig. 1 The Egyptian grasshopper *Anacridium aegyptium*, which can be a pest of fruit trees.

Since we published our review of sound signalling in Orthoptera nearly 20 years ago (Robinson and Hall, 2002), there has been an enormous amount of research in this area, which has not only greatly expanded knowledge in previously existing areas of study but has also developed several exciting new topics. We therefore felt the time was ripe for this second review, which will look mainly at research published since 2002.

2 Mating systems

2.1 Variation in mating systems

In the typical orthopteran mating system, males are speculative singers. Using airborne sound they produce a long-distance *calling song*, in the absence of the female, to advertise their presence to potential mates. The calling song is usually loud and often continuous over long periods. In most species, females are silent. They are attracted to the male's song and locate him by moving towards the source of the sound (*phonotaxis*). Some species use vibrational advertisement signals, as well as or largely instead of calling song (e.g. Römer et al., 2010; Sarria-S et al., 2016). Most ensiferan males provide a nuptial gift during mating that the female eats (see review by Vahed, 1998). This is usually the spermatophore (Fig. 2) but can be in the form of other body parts (e.g. tegmina), haemolymph, or secretions from external glands.

Fig. 2 The male (underneath) transfers a spermatophore to the female during mating in the bush-cricket *Leptophyes punctatissima* (left) which the female then eats (right).

However, there is a lot of variation in this basic pattern (summarized in Table 1). The female often sings as well as the male. Apart from the calling song, several other songs relating to the mating system have been identified, with crickets having a particularly rich repertoire (reviewed by Centeno et al., 2020). Once the pair meet, there may be a courtship phase before copulation with a specific *courtship song*. Where species copulate several times within a single mating event, there may be an *inter-copulation song*. In some species the male guards the female for a time after copulation and this sometimes involves a specific *post-copulation song*. Some males produce a *courtship interruption song* after a failed mating attempt. In some species, males may also produce a *territorial song* that functions in male–male spacing and either sex may sing an *aggressive song* directed at rivals during intrasexual encounters. We use the term 'song' here only for signals that use airborne sound; vibrational signals are referred to as such.

This terminology is based on that found most commonly in the recent literature. However, usage varies greatly (though attempts have been made to standardize it: see e.g. Baker and Chesmore, 2020). For example, call is frequently used instead of song, advertisement song or mating song instead of calling song, mating song instead of courtship interruption song, and rivalry or agonistic song instead of aggressive song. The distinction between aggressive song and territorial song is not always clear.

Table 1 Summary of mating systems found among Orthoptera[a] (reviewed in Robinson and Hall (2002) unless otherwise referenced).

Orthopteran group	Mating system (all involve male calling song to which silent female performs phonotaxis unless otherwise stated)	Songs or vibrational signals other than calling song found in at least some species
Suborder Ensifera		
Gryllidae (true crickets)	Diverse but tends to involve aggression between males Common for there to be several copulations within a single mating event (e.g. deCarvalho and Shaw, 2010; Narvaez and Robillard, 2012)	Courtship song Courtship vibrational signal Inter-copulation song Male aggressive song Post-copulation song See e.g. Brown (2016); Narvaez and Robillard (2012); Singh and Jain (2020)
Mogoplistidae (scaly crickets)	Female usually approaches but male may also approach female Usually several copulations within a single mating event See e.g. Glen-Worrall (2003); Saidy and Gray (2004)	Courtship song Courtship vibrational signals Inter-copulation song See e.g. Glen-Worrall (2003); Saidy and Gray (2004)
Phalangopsidae (spider crickets and relatives)		Courtship song Courtship vibrational signals by either male or female Male aggressive song See e.g. Acosta et al. (2020); Fianco et al. (2018); Zefa et al. (2008)
Trigonidiidae (sword tailed crickets)	Some species have several copulations within a single mating event (Centeno et al., 2020; Funk, 2016; Tan, 2020)	Courtship song Courtship vibrational signal Courtship interruption song Post-copulation song Post-copulation vibrational signal Male aggressive song See e.g. Centeno et al. (2020); Funk (2016); Mays (1971)
Gryllotalpidae (mole crickets)	At least one species (*Gryllotalpa major*) has lek mating system (Howard et al., 2011; Keane et al., 2018)	Courtship song Male aggressive song Territorial song (Zhantiev et al., 2003) Female song; function unclear but possibly aggressive (Ulagaraj, 1976)

Orthopteran group	Mating system (all involve male calling song to which silent female performs phonotaxis unless otherwise stated)	Songs or vibrational signals other than calling song found in at least some species
Prophalangopsidae (haglids, humped-wing crickets or grigs): *Cyphoderris* species	In *C. monstrosa*, female approaches singing male but hearing sensitivity does not match frequency of song and unclear if females perform phonotaxis as such (Morris et al., 2002) In *C. strepitans* females do perform phonotaxis to male calling song (Ower et al., 2013)	Male song in *C. monstrosa* may be territorial song and/or it may signal fighting ability (Morris et al., 2002) In *C. strepitans* it may function as an aggressive song as well as a calling song (Ower et al., 2013)
Anostostomatidae: New Zealand tree wetas (*Hemideina* species; Fig. 3)	Male has calling song but unclear whether functions to attract females or repel males	Courtship interruption song Aggressive song by both males and females Territorial song See Ewers and Cowley (2005)
Anostostomatidae: New Zealand ground wetas (*Hemiandrus* species) and giant wetas (*Deinacrida* species)	*Hemiandrus* unlikely to be able to use sound in mating but is sensitive to vibrations (Strauß et al., 2017a) *Deinacrida* do not appear to use sound or vibrational signals in intersexual encounters. Usually several copulations within a single mating event. See e.g. Kelly and Gwynne (2016); Watts and Thornburrow (2011) In both, males are attracted to females and follow them, possibly via pheromones	Male *Hemiandrus* use vibrational signals ('drumming') to attract mates and females may also drum (Gwynne, 2004) In *Deinacrida rugosa* (Fig. 4) aggressive vibrational signals by both male and female (Howard et al., 2018)
Anostostomatidae: Indian weta (*Gryllacropsis* species)	Both male and female sing, often at same time. Unclear if both sexes have independent calling songs or whether they are duetting (Diwakar and Balakrishnan, 2006; Tomar and Diwakar, 2020)	
Anostostomatidae: King crickets of Australia and South Africa	Most species do not have ears and males rely on vibrational or chemical signals to attract females	Courtship song (possibly) Male aggressive song
Gryllacrididae (leaf-rolling or raspy crickets)	Can produce sounds but poor sensitivity to sound so unlikely to play important role in mating (Scholtz et al., 2018) Male produces vibrational signal to attract mates; in some species the female responds in a duet. Unclear which sex approaches (Field and Bailey, 1997)	Courtship vibrational signals by both male and female (Ingrisch and Rentz, 2009)

Orthopteran group	Mating system (all involve male calling song to which silent female performs phonotaxis unless otherwise stated)	Songs or vibrational signals other than calling song found in at least some species
Stenopelmatidae (Jerusalem crickets)	Able to stridulate but unclear if sound used in mating. Instead both male and female use vibrational signal to attract mates (Weissman et al., 2021)	Courtship vibrational signal (Weissman et al., 2021)
Tettigoniidae (bush-crickets/katydids): Bradyporinae: Bradyporini and Zichyini	Either male or female can produce a calling song and the other sex then performs phonotaxis (Elaeva and Korsunovskaya, 2012; Korsunovskaya, 2008)	
Tettigoniidae: Bradyporinae: Ephippigerini	Some species perform duets similar to those in Phaneropterinae, see below (Pfau and Pfau, 2015)	Aggressive song by both males and females (Hartley, 1993)
Tettigoniidae: Phaneropterinae	Most species perform a duet in which the male sings and the female responds (Bailey, 2003). Males may change the content or pattern of their song once they get a reply from a female (Heller et al., 2021) Sex that approaches varies between and within species: can be male, female, either or both. Which sex approaches may depend on the size of the nuptial gift the female receives (McCartney et al., 2012) or on the balance of risks incurred by moving (e.g. predation) for each sex (von Helversen et al., 2012) Stationary female system is common; in these species the male usually only performs phonotaxis if female response falls into narrow time-window after his song See review by Heller et al. (2015)	Male aggressive song (Spooner, 1964) 'Ticking' song that may function as territorial song (Spooner, 1968)
Tettigoniidae: Phyllophorinae	Males of *Siliquofera grandis* do not have a calling song; the same may apply to other species (Korsunovskaya et al., 2020)	Courtship song Courtship vibrational signals by both males and females Post-copulation vibrational signal Territorial vibrational signal
Tettigoniidae: Tettigoniinae		Territorial song Courtship song See Zhantiev and Korsunovskaya (2019)
Tettigoniidae: Zaprochilinae	The male's calling song may also serve to repel other males (Simmons and Bailey, 1993)	

Orthopteran group	Mating system (all involve male calling song to which silent female performs phonotaxis unless otherwise stated)	Songs or vibrational signals other than calling song found in at least some species
Suborder Caelifera		
Acrididae (true grasshoppers): acridid grasshoppers other than locusts	Male calling song may function both in sexual communication and territorial defence In some species, especially gomphocerine grasshoppers, female replies to male song and male then approaches (e.g. Wirmer et al., 2010) Male also approaches in some other species (Garcia et al., 2015)	Courtship song (Vedenina et al., 2020) Courtship vibrational signals by both males and females (Benediktov, 2015) Male aggressive song used in territorial defence Possible female aggressive song used in interactions with other females and when rejecting a male (Larrosa et al., 2008) Vibrational advertisement signal instead of calling song (Ingrisch and Rentz, 2009)
Acrididae: locusts (*Schistocerca gregaria* and *Locusta migratoria*)	Mate location relies on visual/chemical cues rather than acoustic signals (Ely et al., 2006) Courtship minimal but signals exchanged while male mounted before actual copulation, especially in solitary phase compared with gregarious phase (2018a; Golov et al., 2018b; Wang et al., 2014)	Courtship song and courtship vibrational signals by both male and female (Golov et al., 2018b)
Pamphagidae (stone grasshoppers)	Males and/or females can produce sounds but unknown how or if sound used in mating system (Massa, 2012; 2020) In at least some species, males do not sing at all; females sing to advertise their reproductive receptivity to males (Lopez et al., 2008)	
Pneumoridae (bladder grasshoppers)	Females respond to calling song of male in a duet. Male performs phonotaxis and female always remains stationary. No courtship before copulation (Couldridge and van Staaden, 2006)	
Tridactylidae (pygmy mole crickets)	At least some species can produce sound and vibrational signals but unknown how these are used in mating system (Benediktov, 2012; Woo, 2020)	

[a]For those taxonomic groups not included in this table, we have been unable to find any evidence that sound signals are used in their mating system apart from, in some groups, the existence of a calling song.
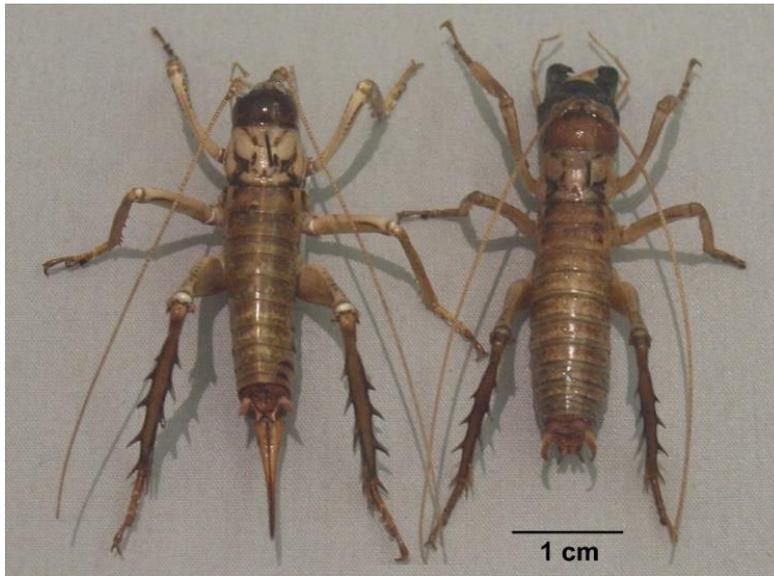
Fig. 3 Tree weta *Hemideina thoracica* (female left, male right).

Fig. 4 Giant weta *Deinacrida rugosa.*

2.2 Alternative mating tactics

Not only do orthopteran species vary in their mating systems, many also show differences in mating behaviour within species, with individual behaviour depending on, for example, their stage of life, their condition or, in polymorphic species, their morphology. Individuals do not necessarily show consistent behaviour, instead switching tactics depending on their circumstances. As summarized in Rotenberry et al. (2015) and Torsekar and Balakrishnan (2020), such alternative mating tactics are widespread across the animal kingdom and may result from factors such as predator pressure (see Section 8) or intrasexual competition (see Section 7).

Orthopteran males commonly adopt alternatives to singing for at least some of the time, including switching to vibratory signals (see Section 2.3). Males may search

silently for females and/or show satellite behaviour, whereby they move towards and stay near a singing male to try and intercept any females approaching him. Examples include the tree cricket *Oecanthus henryi* (Torsekar and Balakrishnan, 2020) and the field crickets *Teleogryllus oceanicus* (Bailey et al., 2010; Balenger and Zuk, 2015) and *Gryllus texensis* (Bertram et al., 2006); for other examples see Robinson and Hall (2002). A study of 16 Panamanian species of katydid showed a trade-off across species between the number of calling songs produced per day and the number of males silently searching (Symes et al., 2021). In duetting species, males may eavesdrop on duetting pairs and perform phonotaxis towards the responding female without singing themselves, as in the phaneropterine bush-crickets *Caedicia* (Hammond and Bailey, 2003) and *Scudderia pistillata* (Villarreal and Gilbert, 2014). Females may also adopt related alternative tactics in which, instead of performing phonotaxis, they remain stationary and rely on silently searching males to find them (Torsekar and Balakrishnan, 2020). In *Poecilimon affinis*, the female replies to a distant male with a soft response that he is unable to hear: such responses may be aimed instead at closer eavesdropping males, by which strategy the female avoids having to approach to within hearing distance of the calling male (von Helversen et al., 2015).

Males of several foliage-dwelling cricket species have been observed using baffles made of leaves to amplify the sound of their calling song (Forrest, 1982). Studies in *Oecanthus* tree crickets (reviewed in Deb et al., 2020) have shown that males modify leaves to make baffles more efficient and that the use of baffles is an alternative mating strategy used by smaller males and/or those with lower-intensity songs. Males in poor condition and/or with low dominance status can increase their mating success by using baffles; for more attractive males, using baffles makes no difference to their mating success.

Similarly, in the cricket *Anurogryllus muticus*, some males use anthropogenic sites such as small depressions in a wall instead of singing from their natural grassland habitat, allowing them to produce a louder calling song without using more energy (Erregger and Schmidt, 2018).

Wing dimorphism is common among Orthoptera and different wing morphs represent alternative mating tactics. In the cricket *Macroanaxipha macilenta*, a rare narrow-forewing male morph is almost silent, allowing energy saved from singing to be put into producing a second spermatophore for each female; despite its lack of song, its mating success is equal to the singing wide-forewing morph that only produces one spermatophore per female (Elias-Quevedo and Cueva del Castillo, 2020). In several other species such as the crickets *Velarifictorus ornatus* (Zhao et al., 2017) and *Gryllus firmus* (Mitra et al., 2011), flying long-winged and flightless short-winged morphs are found in both males and females. Long-winged males can disperse from unfavourable environments but must allocate more resources to maintaining flight muscles, leaving less energy to produce attractive song and spermatophores. Short-winged males have greater mating success in favourable environments because they can put more effort into singing, but cannot escape unfavourable environments.

Bladder grasshoppers (Pneumoridae) also have two distinct male morphs, each showing alternative mating tactics (Donelson et al., 2008). Most males are 'inflated': large, fully-winged and with a bladder — a conspicuous inflated abdomen that hugely amplifies their calling song. The rest are 'uninflated': small, flightless and without the bladder. Inflated males engage in long-distance duets with females and can perform phonotactic flight over a large area; uninflated males adopt an eavesdropping strategy in which they intercept responding females before the inflated male arrives.

Inflated males mate more frequently but use a lot of energy in singing, inflating their bladder and flying; they are probably also more prone to predation. Bladderless males have lower energy costs and predation risks and live twice as long so have more opportunities to mate over their lifetime. The two morphs arise during development and the proportion of uninflated males increases at high population density: uninflated males should do better at high densities and inflated males at low densities.

2.3 Relationships between sound and other signal modalities

Until relatively recently, work on orthopteran mating has often focused solely on the sound signals involved in mate attraction, location and courtship. The relationships between sound and other types of signal, such as those visual, chemical or vibrational cues that may also be necessary if mating is to be successful, have been less frequently studied. Sound and vibrational signals in particular have often been studied in isolation despite the close functional and evolutionary links between them (Stritih-Peljhan and Virant-Doberlet, 2021) and the fact that it is almost impossible, as Benediktov (2018) has pointed out, to draw a clear boundary between them, since sound signals themselves cause vibrations in solid media.

Before 2000, work in this area was relatively limited, with the possible exception of grasshoppers. But, for example, in crickets, it was shown by Bell (1980) for *Oecanthus nigricornis* and by Balakrishnan and Pollack (1997) for *Teleogryllus oceanicus* that, while the female will not mount the male at all if he does not produce courtship song, the likelihood of her mounting also depends on the presence of appropriate chemical cues from the male. Studies on bush-crickets showed that vibrational signals can be important: for example *Copiphora rhinoceros* males sing only until they make contact with the female, then switch to vibrational signals (Morris, 1980). In many grasshoppers, courtship can be prolonged and complex, consisting of elaborate visual displays in combination either with courtship song, as in *Gomphocerus rufus*, or vibrational signals, as in *Galidacris variabilis* (Riede, 1987). This complex courtship is thought to play an important role in stimulating the female to change from a semi-receptive to a fully receptive state (e.g. *Myrmeleotettix maculatus*: Bull, 1979), probably mediated by the release of juvenile hormone (see review by Heinrich et al., 2012).

More recently, however, the amount of research looking at the relationships between sound signals and other types of signal has expanded greatly. Courtship behaviour has been described in much more detail, especially in grasshoppers (e.g. Berger and Gottsberger, 2010; Ostrowski et al., 2009; Vedenina et al., 2020). Additional signalling modalities have been identified in courtship, for example vibration in the crickets *Adelosgryllus rubricephalus* (Zefa et al., 2008), *Cranistus colliurides* (Centeno and Zefa, 2019) and *Ornebius aperta* (Andrade and Mason, 2000), chemical cues in the grasshoppers *Chorthippus biguttulus* and *C. mollis* (Finck and Ronacher, 2017), and probably chemical and tactile cues in the bush-cricket *Mecopoda elongata* (Dutta et al., 2018). In bush-crickets visual cues can be important during phonotaxis. In *Poecilimon affinis*, if the male's only cue is the female song, his course towards her is meandering but if visual landmarks are available that he can integrate with the acoustic cues, his course is much more direct (von Helversen and Wendler, 2000). In *Requena verticalis*, the female performs phonotaxis towards the male. If another male sings while she is approaching she may switch to him, but if she has a visual cue she is much more likely to stay faithful to the original male, even if he stops singing (Bailey et al., 2003). This benefits the

female because it reduces the time she spends in getting to the male and the predation risk associated with movement.

Signals in different modalities may simply send different messages. For example, in *T. oceanicus* (Simmons et al., 2013), the male's cuticular hydrocarbon (CHC) profile and his courtship song have equal weight in predicting his mating success but they are not correlated with each other. Song may signal the male's quality while the chemical cue from CHCs may signal genetic compatibility. However, things are not quite so simple. Thomas et al. (2011) showed that the expression of a male's CHCs is affected by his acoustic experience – if he does not hear other males singing, he increases his concentration of those CHCs that are attractive to females. Similarly, a *Gryllus integer* male signals his quality (e.g. ability to provide a spermatophore) via his calling song but his fighting ability via his CHC profile (Leonard and Hedrick, 2010). Female responses to the two cues are not correlated, but if she is previously exposed to the calling song of an attractive male, she accepts a courting male more quickly, regardless of whether he has an attractive calling song or not. So signals encountered earlier in the whole mating sequence may bias females' assessment of later close-range cues.

Sound and vibration are often used as alternative signals, especially in bush-crickets. In *Docidocercus gigliotosi* (Römer et al., 2010), males use either sound or vibration for long distance signalling. They switch between the two modalities frequently, moving from sound to vibration when for example the risk is high from predators who eavesdrop on sound signals, or there are high levels of background noise that mask calling songs. In *Ephippiger bitterensis* and *E. ephippiger* (Busnel et al., 2019), the female performs phonotaxis towards the male's calling song. But once the female gets close and he perceives vibrations caused by her movements, he starts to alternate sound signals with very brief vibration signals. The female then responds with similar vibration signals. She only actually moves towards the male when he signals, whether by sound or vibration.

In the bush-cricket *Onomarchus uninotatus* (Rajaraman et al., 2015) and in lebinthine crickets such as *Ponca hebardi* (Benavides-Lopez et al., 2020), male and female perform a multimodal duet, where the female responds to the male's calling song by tremulating (making body movements that create vibrations in the substrate). These are true duets, with a clear phase relationship of alternation between the chirps of the male's song and the female's vibrational response. In lebinthine crickets, the female does not perform phonotaxis at all and instead the male performs vibrotaxis towards her. In *O. uninotatus*, if the female is some distance from the male, she will begin phonotaxis after tremulating but if she is within about 4 m of the male, and on the same tree, she never performs phonotaxis and then the male performs vibrotaxis towards her. He can only locate the source of her vibrations, however, if he can hear his own sound element of the duet (Rajaraman et al., 2018).

Singing and vibrational signals are not always used as alternatives but may instead send different messages. While a *P. hebardi* male is singing in his duet with the female, he also simultaneously tremulates in response to the songs of other males, sending a vibrational signal similar to that of the female (Benavides-Lopez et al., 2020). The male's vibrations probably serve to mask the female response so that rival males cannot respond to it. Similarly the bush-cricket *Nesonotus reticulatus* sings and tremulates simultaneously (Stumpner et al., 2013). Again the vibrational signal may be directed mainly at other males, since other males tremulate in reply.

The interactions between signals sent via different modalities can also play an important part in maintaining reproductive isolation between species (e.g. Finck and Ronacher, 2017; Moran et al., 2019; Mullen et al., 2007).

Given the increasing evidence, not only in Orthoptera but across many taxa, that multimodal signals are common, that females often base their choice of mate on several different cues, and that individual components of such signals may interact in a functional way, a number of authors have addressed the general issue of how and why such signals have evolved. Greenfield (2002) argued that multimodal mate recognition signals could have originated in arthropods by default because of an inherent preference shown by some females for complex songs per se (though see Reichert et al., 2017). Candolin (2003) and Hebets and Papaj (2005) both reviewed the various hypotheses that had so far been proposed and proposed a framework for future research. Candolin concluded that, while there was some evidence for other hypotheses, there was good evidence that multiple cues provide additional information and send different messages that either indicate general male quality or allow females to choose the most suitable mate for them. The extra costs of sending multiple signals may be counterbalanced by the saving in time and energy spent assessing potential mates.

3 Songs and signals

The Orthoptera Species File Online contains 28,899 valid species (as of May 2021) a substantial number of which produce sound (Cigliano et al., 2021). Studies of the sounds reveals a rich diversity covering a wider range of frequencies than those audible to humans. Songs produced as part of sexual and intrasexual behaviour contain a sub-structure that requires a descriptive terminology. Such a terminology has yet to be formalized and although individual attempts to set out a standard exist, there is no universally agreed set of terms.

In their comprehensive description of the sounds of 170 European species of Tettigoniidae and Acrididae, Ragge and Reynolds (1998) suggest a terminology based on movements of the sound-producing apparatus. Thus, the sound produced by one complete to-and-fro movement of the stridulatory apparatus is a *syllable*. They adopt the proposal of Broughton (1976) that a discrete group of syllables should be described by a new term, *echeme*. A few authors have embraced the new term, for example Garcia et al. (2014), Heller et al. (2011), Hershberger (2021) and Pfau and Pfau (2015). The term *pulse*, which Broughton (1963; 1976) criticized, continues to be used in song descriptions, but it does not have a consistent definition. For recent use of the term see Cole (2010) and ter Hofstede et al. (2020).

Recently a standardized terminology, together with controlled vocabularies, has been proposed for insect bioacoustics, driven in part by the development of automated identification systems (Baker and Chesmore, 2020). Their terminology structure is based on three major components: echeme sequence, echeme and syllable. This matches the structure used by Ragge and Reynolds (1998). Using this terminology, a song consists of one or more echeme sequences, each echeme being composed of syllables. The sound produced by each unidirectional movement of the stridulatory apparatus (opening, closing, upward or downward), is a *hemisyllable*. If sound is produced by both opening and closing movements, the syllable is described as a *diplosyllable*.

In this review we generally follow the terminology used by the original authors since it is often not possible to indicate the relationship to the terms used by Baker and Chesmore (2020) and Ragge and Reynolds (1998).

3.1 Components of signals

The five main parameters of a sound are: intensity; frequency (the reciprocal of the wavelength); frequency modulation (rise or fall in frequency, FM); intensity modulation (increase or decrease in intensity); and temporal patterning (length of syllable, length of interval between successive syllables, number of syllables, etc.). A sound signal may contain a combination of sounds at different frequencies (the frequency spectrum).

Sound intensity may be measured in units of energy or work, or in units of power. Although loudness is related to sound intensity, it is subjective and depends on the perception of the receiver. Sound intensity on the other hand is objective, being independent of a receiver's hearing, and can be measured. However some authors refer to the loudness of a sound rather than to its intensity so we also use loudness as a general term in this review.

Sound pressure level (SPL) is the average variation in atmospheric pressure caused by the sound. It is measured in decibels (dB), the ratio of the absolute sound pressure against a reference level of sound in the air of 0.00002 pascals. So, sound intensity is expressed as dB SPL.

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. In general, larger male orthopterans produce louder songs and the songs contain lower frequencies. In the tettigoniids, very small species generally have very high frequency songs, for example those of small phaneropterines where the frequencies are well into the ultrasonic range (Heller, 1984; Heller et al., 2015; Robinson, 1990), defined as anything higher than 20kHz. The signal received by the recipient may differ from the sender's original because of changes that occur during transmission through the environment.

3.2 Intensity and distance

The songs of orthopteran insects are very diverse, covering a wide frequency range from below 1 kHz to over 100 kHz. The duration of the songs ranges from under 1 ms to several minutes and their intensity can be very high. Some of the loudest songs recorded are produced by members of a genus of neotropical Tettigoniidae, *Supersonus*. The male calling songs are ultrasonic and are the highest frequency so far recorded for an arthropod at 150 kHz (Sarria-S et al., 2014). These ultrasonic songs are also very high intensity and can exceed 110 dB SPL at 15 cm. For comparison, typical sound intensities in tettigoniids are 70–100 dB SPL at 10–15 cm (Montealegre-Z and Morris, 2004; Montealegre-Z et al., 2011b).

Mole crickets are also able to produce loud sounds that travel over significant distances. For example, *Gryllotalpa major* has an advertisement song which attracts flying females for mating. In a study of 750 field recordings, Hill (2000) found that the absolute maximum intensity measured at 20 cm from the burrow opening is in the range of 90–104 dB. The song is audible up to 400 m from the male's burrow (Walker and Figg, 1990) and produces low frequency seismic vibrations that are

detectable at distances of up to 3 m from the focal male (Hill and Shadley, 1997). The song of *G. vineae* is audible on a still night from at least 500 m (Ragge and Reynolds, 1998).

The longest distance over which acoustic communication has been recorded is 1.9 km. The calling song of the male bladder grasshopper *Bullacris membracioides* travels 100–150 m during the day but at night the change in thermal conditions enables the song to travel a greater distance (van Staaden and Römer, 1997). There is a disparity between the effective communication distances of the male and female, 2 km and 50 m respectively. The males and females duet (Donelson and van Staaden, 2005) but the female only responds if the intensity of the male song is 65 dB SPL or above, which corresponds to a communication distance of 50 m (van Staaden and Römer, 1998).

3.3 Sound production

The production of sound through frictional methods is characteristic of most tettigoniids, gryllids and acridids. Gryllids stridulate by the elytro-elytral method, in which the closing movement of the tegmina (wings) produces sound when a file on the ventral side of a modified vein (Cu2) of the right (upper) tegmen moves over the plectrum sited on the inner edge of the left (lower) tegmen. The file is made up of a number of hooked teeth and, as each tooth is struck by the plectrum, a single cycle of the song is produced (Bennet-Clark, 1999). The catching and then release of each tooth by the plectrum appears similar to the escapement in a clock mechanism and this observation led to Elliot and Koch proposing a 'clockwork cricket' model for sound production in gryllids (Elliott and Koch, 1985; Koch et al., 1988). The harp region of the forewing has been shown to resonate at frequencies similar to those that form the song. This resonance of the harp is analogous to the regulator of a clock. If the clockwork cricket model is valid, it should be possible to analyse the 'ticking' sounds made by the 'escapement' and examine the relationship between them and the dominant sounds produced by the harp 'regulator' when driven by the escapement. Bennet-Clark and Bailey (2002) made a detailed comparison between a clock mechanism and the sound production mechanism in the Gryllidae, validating and extending Koch's studies, thus demonstrating the anatomical features that make the cricket clock tick. However, in a subsequent study, Bennet-Clark (2003) investigated resonance in the wings of *Teleogryllus oceanicus*. He concluded that the harp is not the resonator; the major elastic component of the resonant system is the file plus the first anal vein and the mass component is the combined mass of the file, anal area and harp. A detailed account of the mechanics of cricket stridulation has since been given by Montealegre-Z et al. (2009).

Stridulation in grylllids usually produces pure tones at low frequencies of 2–8 kHz but some species have morphological and mechanical specializations that allow them to produce higher frequencies with rich harmonic content (e.g. some members of the Eneopterinae: Robillard et al., 2013). It has also been shown in *Gryllus bimaculatus* that calling song and aggressive song are produced by similar wing movements, indicating that both song types are probably generated by the same neuronal network, but courtship song is produced using a different wing movement and is probably under different motor control (Lin and Hedwig, 2021b).

Male tettigoniids also stridulate using the tegmina but, in contrast to gryllids, a file of teeth on the lower surface of the left tegmen is struck by a plectrum (the scraper) on the upper surface of the right tegmen. Generally, the sound is produced on the closing stroke of the wings (Montealegre-Z and Mason, 2005), though at least one

species, unusually, produces sound on the opening stroke (*Ischnomela gracilis*: Montealegre-Z, 2012). The muscle contractions that move the wings are too slow to generate sounds in the kilohertz range but the rate of impact between the scraper and the teeth on the file generates a vibration in the wings substantially above the frequency of the wing movements. The vibrations produced by the tooth strikes are further amplified by an area of cuticle attached to the scraper which frames the thin cuticle on the right forewing, called the mirror (Baker et al., 2017).

There are three common methods of stridulation used by tettigoniids (Baker et al., 2019). In the first of these the wing and scraper move at an almost identical velocity, maintaining resonance of the mirror and frame by each subsequent tooth strike (Montealegre-Z and Postles, 2010). This method has an upper frequency limit of 40 kHz, so for higher frequencies a more complex process is used (Montealegre-Z et al., 2006). Elastic tissue can store energy when deformed and then release it at a much faster rate than a working muscle (for more detail on storage of energy in elastic tissue see Burrows, 2003).

In the second mechanism of stridulation, during wing closure, when the scraper is caught behind a tooth, it stops and bends, gathering elastic energy. On release from the tooth the elastic energy is suddenly released, and the scraper moves at a greater velocity relative to the wing. Therefore, the scraper can impact on teeth at a much higher frequency, compared with the previous method which has a coupled scraper with the same velocity as the wing (Montealegre-Z et al., 2006).

The third method of stridulation has been termed 'roll-trigger' (Baker et al., 2019; Montealegre-Z and Mason, 2005). The velocity of wing closure gradually increases as the scraper sweeps the file, but the inter-tooth distance of the file is more or less constant. There is no time adjustment of velocity (by tooth density difference) to maintain a constant rate of tooth contact. A solution to this may be to produce scraper jumps that help to compensate for constant distances and increasing speed. A massive vein backs the scraper and serves to trigger its release every time the scraper has reached its maximum bend. This mechanism has only been observed in a few species of Pseudophyllinae and Phaneropterinae (Baker et al., 2019).

Bush-cricket species produce a range of songs from resonant, tonal songs to non-resonant broadband ones, at a huge range of frequencies, from 600 Hz to 150 KHz. Phylogenetic studies of 94 katydid species by Montealegre-Z et al. (2017) showed that, rather than body size per se, frequency is most strongly related to components of the sound generation system: the file and the left-wing and right-wing mirrors. A further phylogenetic study of 40 bush-cricket species by Chivers et al. (2017) showed that parameters of file tooth density and file length are the best-fitting predictors of tonality.

Amongst animals that produce sound, acridids are distinctive in that they utilize two organs simultaneously to generate sound. Each hindleg has a file with a series of pegs (visible in Fig. 1) which, 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). Stridulation in many gomphocerine grasshoppers is characterized by specific phase shifts between the hind legs as well as different movement patterns produced by the left and right leg. If the metathoracic ganglion is transected, these differences are abolished and the hindlegs then produce the same pattern (Heinrich and Elsner, 1997).

3.4 Symmetry and asymmetry

The sound producing apparatus in Orthoptera shows asymmetry both in anatomy and in motion. Male crickets produce their calling song by rapid closure of the wings, which induces resonances in the harp and associated wing parts, as described in Section 3.3. The size of the harp influences the mass, and hence the resonant frequency of the wing components that produce sound. The possibility that directional asymmetry may convey information about male quality, encoded in the song, was shown by Simmons and Ritchie (1996).

In a study of four species of cricket, Moradian and Walker (2008) investigated the relationship between the body size of males and the size of the harp. In comparing species, they found consistent directional asymmetry in harp area, but not in total wing area. Within species, larger males typically have larger harps.

Analysis of the song of *Gryllus campestris* showed that each syllable has two parts, starting with a period of sustained frequency generated primarily by the left harp, followed by a period when the right harp takes over, during which the frequency falls (frequency modulation, FM). The greater the difference in area between the left and right harp, the greater the degree of frequency modulation. There is a possibility that females may detect asymmetry in males by the degree of downward FM at the second half of each syllable (Simmons and Ritchie, 1996), though this has been disputed by Montealegre-Z et al. (2011a) in their detailed analysis of sound production and the resonances of the left and right wings. Their measurements of wing resonance and the FM pattern recorded from coupled wings showed that the two wings are simultaneously involved in controlling the frequency of acoustic radiation during stridulation, but that the left wing dominates, particularly in the magnitude of the deflection. So, these findings do not support Simmons and Ritchie's conclusion that the contributions of the two wings take place at different times and at different frequencies.

The role of asymmetry in cricket song has been investigated in *Gryllus bimaculatus* (Hirtenlehner et al., 2013). Using a trackball, female crickets were offered two choices of song model. They only distinguished between the songs of symmetrical and asymmetrical males at a carrier frequency (i.e. the principle frequency in the frequency spectrum) of 4.4 kHz and a large modulation depth of 600–800 Hz and exhibited a preference for the pure tone calling song. No preference was observed at carrier frequencies of 4.9 and 5.2 kHz. A pair of ascending neurons, AN1 (see Section 5.2) are tuned to an average frequency of 4.9 kHz (Kostarakos et al., 2008), which correlates with the preferences in the choice experiments.

3.5 The energetic costs of singing

Studies prior to 2000 of the energetic costs of singing have been reviewed by Robinson and Hall (2002). In species that sing rapidly and loudly, the energetic cost can be at a similar level to that of locomotion. Studies of gryllids and tettigoniids have shown that producing a calling song is energetically costly. For example, in the katydid *Plangia graminea*, metabolic rate during singing is 60% higher than resting metabolic rate (Doubell et al., 2017). In *Mecopoda* sp. and *Anurogryllus muticus*, singing leads to increases in the CO_2 production rate over resting levels of 12 and 16 times respectively. Moreover, singing increases thorax temperature, on average by 7.6 and 5.8°C respectively (Erregger et al., 2017). Sound production is relatively inefficient at around 1%, with most of the energy input being converted to heat (Prestwich, 1994). The increase in temperature may convert the acoustic signal to a

bimodal one in which the energy invested in sound production is not 'wasted' but, instead, is reflected in the elevated thoracic temperature of a male. This thermal cue could provide important, reliable information for females choosing a mate, as it could allow them to evaluate how much cumulative energy has been invested by the male (Erregger et al., 2017).

Male mole crickets excavate a burrow, from which they sing. The shape of the burrow is horn-like and the resonant frequency matches the resonant frequency of the harp, producing amplification of the calling song, which can be heard at a distance of several hundred metres (Bennet-Clark, 1970). The mole cricket burrow has provided an opportunity to study the metabolic cost of singing for an undisturbed insect because the burrow can be used as the respiratory chamber needed for measuring oxygen consumption (Prestwich and O'Sullivan, 2005; White et al., 2008). In their experiments with *Gryllus monanka*, White et al. (2008) showed that the singing metabolic rate (MR) is on average 13.5 times higher than standard MR and 2.2 times higher than MR measured during burrowing in the laboratory. The singing MR of *G. monanka* is similar to that measured for other singing insects but is only 10% of that predicted on the basis of allometry for a similarly sized insect (0.89 g) during flight. A male mole cricket is estimated to consume 0.4 ml of oxygen during construction of a singing burrow and 5.5 ml during a one-hour singing bout; by comparison, a flying female searching for a male would consume a similar volume in less than 6 min.

The energetic cost of producing courtship song in *Gryllus bimaculatus* males has been investigated by Mowles (2014). If a singing male exceeds his aerobic capacity and switches to anaerobic respiration, lactic acid accumulates in the haemolymph and can be assayed. Males that had performed 5 min of courtship were found to have higher amounts of haemolymph lactate relative to the controls. Males who produce more rapid song with shorter intervals between each signal component have higher amounts of lactate in their haemolymph. So sound production in courtship is also an energetically costly behaviour. Males that are compromised physiologically are not likely to be able to maintain as vigorous a courtship as a healthy male (Tregenza et al., 2006).

3.6 Relationship between singing and the immune system

Immunocompetence is used to describe the ability of an individual to resist pathogens and parasites through the response of their immune system. In insects, immunocompetence can be assessed by measuring the size of the encapsulation response to a standardized antigen such as a nylon filament (Rantala and Kortet, 2003).

The encapsulation process involves the coating of pathogens and other non-self objects with haemocytes. Ryder and Siva-Jothy (2000) looked at immunocompetence in *Acheta domesticus* and, using the relatively simple process of measuring haemocyte load in the haemocoel, showed that haemocyte load is correlated with the number of syllables per chirp, a sexually selected component of the calling song. By selecting males that produce more syllables per chirp females may also be selecting males for higher resistance to pathogens (see Section 6). In *Gryllus campestris*, inducing an immune response leads to reduced daily rate of singing (Jacot et al., 2004).

Singing in turn can affect the immune response: *Teleogryllus oceanicus* males exposed to song during rearing show stronger immune responses as adults than

males reared in silence (Bailey et al., 2011). This suggests that such signals play a role in conveying information about population density and the associated risk of pathogen and parasite transmission.

3.7 Effects of age and diet

Mechanical wear in the sound producing organs can cause changes in sound signals related to the age of the individual, though in some species (e.g. *Teleogryllus oceanicus*: Walker and Cade, 2003) there is no evidence of age-related changes in calling song.

For example, males of the field cricket *Gryllus pennsylvanicus* show significant changes in their song with age (Judge et al., 2008). Males at 21 days of age (days since the adult moult) have shorter pulse periods, shorter pulse durations, lower pulse peak frequency, more pulses per chirp and more variable pulse periods than when they are younger (Judge, 2011). There is no evidence that males increase their singing effort with age. For a detailed summary of other studies that have looked for age-related changes in field cricket calling song see Judge (2011).

Given the high energetic costs of singing, it is not surprising that diet can affect singing effort (i.e. the proportion of time spent producing calling song). Males on a high-quality diet generally show greater singing effort, as in *G. pennsylvanicus* (Judge et al., 2008) and *Gryllodes sigillatus* (Houslay et al., 2017). Hunt et al. (2004) found that female *T. commodus* on a high-protein diet live longer than those on a low-protein diet whereas the reverse is true for males. This is because males on a high-protein diet invest more energy in singing. Hunt et al. (2004) argue that the relationship between longevity and singing may be either positive or negative depending on local conditions, such as food availability.

In some species, females may choose their mates on the basis of age or condition (see Section 6).

3.8 Patterns of singing

The songs of orthopterans are usually species specific, each having a particular temporal pattern of syllables which may be overlaid with modulations of frequency and intensity (e.g. Korsunovskaya, 2009; Kowalski and Lakes-Harlan, 2013; Zefa et al., 2013; Zhantiev et al., 2017). However, this pattern can still vary to some extent within species. The temporal pattern of syllable intervals may differ, for example, depending on whether the song is produced during the day or at night (Hershberger, 2021; Ivkovic et al., 2017). The cricket *Gryllus veletis* often produces so called 'gap' pulses where intensity drops near the middle of the pulse. Gap pulses are increasingly produced through the night and in the morning; they are produced less in the afternoon and evening (Thomson and Bertram, 2014).

A study of male calling songs in 50 species of neotropical katydids (ter Hofstede et al., 2020) found that songs vary greatly in duration, temporal pattern, peak frequency, and bandwidth, both across and within subfamilies. On the whole, katydid species within the subfamilies Pseudophyllinae and Phaneropterinae produce short songs of less than 250 ms at long intervals whereas species in the Conocephalinae produce highly repetitive songs over longer periods of time. However, there are some exceptions to this pattern: a few species in the Conocephalinae produce very short songs at long intervals, and some species in the Phaneropterinae produce relatively long songs of 1–6 s in duration, or sing frequently. A study of 16 Panamanian species of katydid showed a trade-off across species between the

number of signals per day and the duration of sound in each signal (Symes et al., 2021).

Symes et al. (2016) looked at the singing patterns of eight neotropical katydids. They found that their calling songs are irregular and extremely short, with an average of around 80 songs per night totalling on average only 6.3 s. Singing may be affected by the acoustic environment, however. In some species males sing more often in response to singing by conspecifics; males in some other species respond similarly to heterospecific singing.

Species usually show diel and seasonal patterns of singing (e.g. Singh and Jain, 2020). Diel patterns can vary greatly between species (e.g. Tan and Robillard, 2021b). In *Phaneroptera falcata*, singing activity peaks about three hours after sunset and decreases from midnight onwards (Samietz et al., 2014). The start of singing activity may be triggered by decreasing light intensity while the post-midnight decline may be related to a decrease in temperature. Fergus and Shaw (2013) showed that diel singing patterns in the Hawaiian swordtail crickets *Laupala cerasina* and *L. paranigra* result from a circadian rhythm generated by a daily cycling of the *period* gene transcript; they also identified amino acid differences in the *period* gene between the two species which, they suggest, may be responsible for interspecific differences in singing pattern.

Diel singing patterns can vary to some extent depending for example on weather or temperature (e.g. Franklin et al., 2009). The amount of singing activity may also be correlated with the availability of mating opportunities (e.g. Bertram et al., 2013) and/or the risk of attack from predators or parasitoid flies (e.g. Bertram et al., 2004).

Individuals within a species may also differ in their diel singing patterns: in *G. rubens*, for example, total signalling time, trilling bout duration, and hourly bout number are highly consistent within individuals but there is a lot of variation between individuals (Bertram and Bowen, 2006).

In bivoltine species, patterns of singing may differ between spring and autumn generations. For example, the song of the cricket *G. rubens* (Beckers, 2020) differs in frequency, pulse rate, pulse duration and interval duration between seasons. Female preferences shift in parallel. These differences appear to be the result of seasonal differences in temperature during the juvenile phase.

3.9 Environmental influences on signals

Singing and hearing can be affected by environmental factors such as vegetation, temperature, weather and noise. Studies up to 2000 on the effects of the environment on signals were reviewed by Endler (2000) and more recently there has been a wide ranging review of acoustic communication in noise (Brumm and Slabbekoorn, 2005).

The types of vegetation in the habitat affect the degree to which songs become attenuated and distorted with distance, and there is evidence in some species that species adapt their signals to local conditions (e.g. Couldridge and van Staaden, 2004).

In *Teleogryllus oceanicus*, almost every feature of the male calling song is affected by temperature (Walker and Cade, 2003). In the cricket *Acanthogryllus asiaticus* the frequency and temporal pattern of the male song is affected both by ambient temperature and the temperature experienced during development (Singh et al., 2020). In the mole cricket *Gryllotalpa africana*, which signals from a burrow, the

syllable period, inter-syllable interval and duty cycle all vary with soil temperature (De Graaf et al., 2005). In tree crickets the frequency of the male's calling song changes with the ambient temperature; females, however, use active mechanical and neural processes to ensure that auditory tuning stays matched to the male's frequency, despite change environmental conditions (Mhatre et al., 2016). Because of the effects of temperature on physical and chemical processes, neurophysiological mechanisms that allow the receiver to process a song are also affected by temperature. It has been shown however, that the auditory system is able to compensate for changes in temperature (e.g. Korsunovskaya and Zhantiev, 2007; Roemschied et al., 2014).

The effects of both weather and anthropogenic noise were studied in the bladder grasshopper *Bullacris unicolor* at two sites close together but differing in noise levels. Passive acoustic recorders were used to monitor calling song from sunset to sunrise over a 3-week period and to record weather conditions. The results show that, as levels of anthropogenic noise increase, *B. unicolor* increases song interval (period between successive songs), decreases song rate, and sings at a lower peak frequency. On the noisier site the total number of songs recorded decreased, and the timing of the songs shifted to later in the night when noise levels are lower (Sathyan and Couldridge, 2021).

4 Hearing and ears

The orthopteran insects have a long history in the fossil record, with the earliest evidence suggesting stridulation coming from the structure of wings found in Triassic strata (Senter, 2008). In a large-scale macroevolutionary study using phylogenomic data, to understand how both hearing and sound production evolved, Song et al. (2020) showed that the Ensifera and Caelifera followed different pathways in the development of sexual communication through sound signals. In the Ensifera, hearing and sound-producing organs co-evolved. By contrast, in the Caelifera, sound-producing structures and hearing organs evolved independently. The ears of Ensifera are sited in the tibia of the forelegs, but in the Caelifera the ears are often in the first abdominal segment (Yack, 2004).

4.1 Structure of hearing organs

4.1.1 The acridid ear

The ears of acridids are located in the first abdominal segment. The anatomy of the ear has been described for a number of species (Jacobs et al., 1999; Yack, 2004). On each side of the abdomen is a tympanic membrane, which is coupled acoustically by air sacs to the contralateral ear. So, each tympanum receives an acoustic input on both the external and internal sides. The tympanal chordotonal organ, named Müller's organ, contains 60 to 100 scolopidia. The organ is attached to a number of sclerotized parts of the inner surface of the tympanum. The scolopidia can be divided into four groups, based on their points of attachment to the tympanum. However, in a study of tympanal receptor cells in the locust *Schistocerca gregaria* using intracellular recordings, Jacobs et al. (1999) showed that the receptor cells can be divided into three functional groups with different characteristic frequencies (CFs). Group 1 contains 20 receptor cells with their dendrites attached to the folded body. Their CFs lie at 400–700 Hz or at 1.5–2.0 kHz. Group II consists of 12–14 high frequency receptor cells (CFs 12–25 kHz) whose dendrites are attached to the pyriform vesicle. Group III receptor cell dendrites are attached to

either the elevated process (EP) or to the styliform body (SB); their CFs lie at 3–4 kHz. There are no differences in physiology and central arborizations between those receptor cells of Group III whose dendrites are attached to the SB and those whose dendrites are attached to the EP.

4.1.2 The tettigoniid ear

The ears of a tettigoniid are situated in the tibia of the forelegs. Each ear has two tympanic membranes which often differ in size and shape. The tympanum may be partially covered by a flap of cuticle, giving an external appearance of being sunk into a slit (Fig. 5). Sound enters the large prothoracic spiracle and a pressure wave passes down the trachea to the femoro-tibial joint, where the trachea splits into an anterior and posterior branch that reach the inner surfaces of the anterior and posterior tympanum respectively.
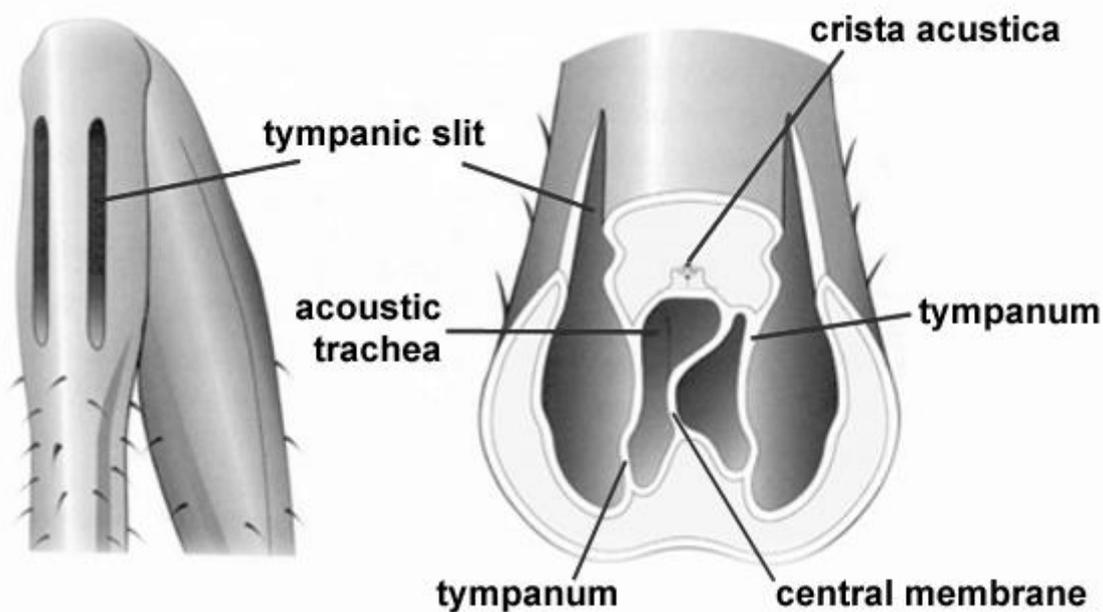

Fig. 5 Structure and location of the tibial hearing organ in a bush-cricket.

In many species this large trachea is the primary route by which sound reaches the tympanic membranes. The trachea may also act as an exponential horn, amplifying the sound signal. In some other species the prothoracic spiracle is reduced in size and the slits may play a greater role in establishing the pressure difference across the tympanic membranes.

The sense cells of the ear are attached to the dorsal surface of the anterior branch of the trachea and are arranged in a line along the long axis of the trachea branch, forming the crista acustica. Unlike the auditory organ in acridids, that of most gryllids and tettigoniids is not attached to the tympanum directly. The auditory sensilla, of which there are between 12 and 116 in tettigoniids (Strauß, 2019), are attached proximally to the anterior trachea, and distally to the tegument of the tibia by one or more attachment cells linked to the tectorial membrane (Yack, 2004). The auditory organ of tettigoniids is part of a complex tibial organ that has three parts, the crista acustica, intermediate organ and the subgenual organ. Each of these contains scolopidia.

There have been a number of studies of the complex tibial organ. For details of the neuroanatomy see Rössler et al. (2006) and Strauß (2019).

The scolopidia of the crista acustica are tuned to specific frequencies and are arranged tonotopically, with those tuned to high frequencies at the distal end of the crista. The dendrites of the receptors project into the prothoracic ganglion. The tonotopic structure in the hearing organ is preserved as central neural tonotopy (Stölting and Stumpner, 1998). Strauß et al. (2012) used cobalt chloride backfills of the tympanic nerve to compare the arrangement of auditory receptors in six species in the Tettigoniidae. They found that although the auditory receptors in the crista acustica are generally arranged in a line, some of the auditory receptors deviate from a strictly linear arrangement and are organized as double rows of receptors in two axes: anterior–posterior and dorso-ventral. The proportion of parallel somata is as high as 52% in *Poecilimon ampliatus*. The functional significance of the double row of receptors for frequency tuning is not yet fully understood (Strauß et al., 2012). It is possible that the double row of parallel somata could enable shorter distances between dendrites, which would give a higher resolution of frequency over a smaller frequency spectrum.

The number of auditory sensilla is species-specific and in general closely related species have similar numbers. The variation in number between individuals of the same species is usually very low. However, the number of auditory sensilla is not directly related to the length of the crista (Strauß et al., 2017b). In most species there is no sexual dimorphism in the number of auditory sensilla (Strauß, 2019), but in the phaneropterine *Ancylecha fenestrata* males have a longer crista acustica than females and a larger number of auditory sensilla:116 in males and 86 in females (Scherberich et al., 2016; 2017).

In a study of the neotropical bush-cricket *Cophipora gorgoensis*, Jonsson et al. (2016) investigated the role of the acoustic trachea, using micro-scanning laser Doppler vibrometry. The male calling songs of *C. gorgonensis* are short pure tone syllables at a frequency of 23 kHz (Montealegre-Z and Postles, 2010). They measured the velocity of sound propagation in the acoustic trachea and found that over the frequency range 10–40 kHz the velocity remained constant. Sound velocity inside the trachea was 255 m s^{-1}, reduced by a factor of 1.35 compared with free field measurements. Thus, the internal sound wave is delayed with respect to the sound wave on the external pathway. The acoustic trachea provides a gain of approximately 15 dB SPL, suggesting that the trachea is acting as an exponential horn. In a study of the outer ear of *Copiphora gorgonensis* using numerical modelling and real 3D geometry of the acoustic trachea, Celiker et al. (2020) showed that the most important factor in generating the gain of 15 dB is the geometry of the acoustic trachea, confirming the function of the trachea as an exponential horn.

Similar measurements carried out on gryllids are described in the next section.

4.1.3 The gryllid ear

Crickets have one of the most complicated hearing organs known (Michelsen and Larsen, 2008). The ears are located in the forelegs, just below the joint between the femur and tibia. The structure of each of the acoustic systems is similar to that of the tettigoniids. Sound acts on the external surface of the tympanum but also reaches the internal surface of the tympanum via the prothoracic spiracle and acoustic trachea. Unlike the tettigoniids, where the two ears are separate, the two ears in gryllids are linked (Fig. 6). Each acoustic trachea has a transverse extension, and these extensions meet in the midline and are connected by a thin septum, formed from a double membrane. The septum is contained within an acoustic vesicle. There is considerable diversity in the morphology of the acoustic tracheal system. A study

of 40 ensiferan species (Schmidt and Römer, 2013) revealed that those species using intraspecific acoustic communication and possessing tibial tympana have an acoustic vesicle and septum, whereas species that have lost acoustic communication, or that never use acoustic calling songs, lack an acoustic vesicle. The size of the acoustic vesicle varies between species, with field crickets having the smallest vesicle relative to their size (measured as pronotum width), compared with rainforest crickets.
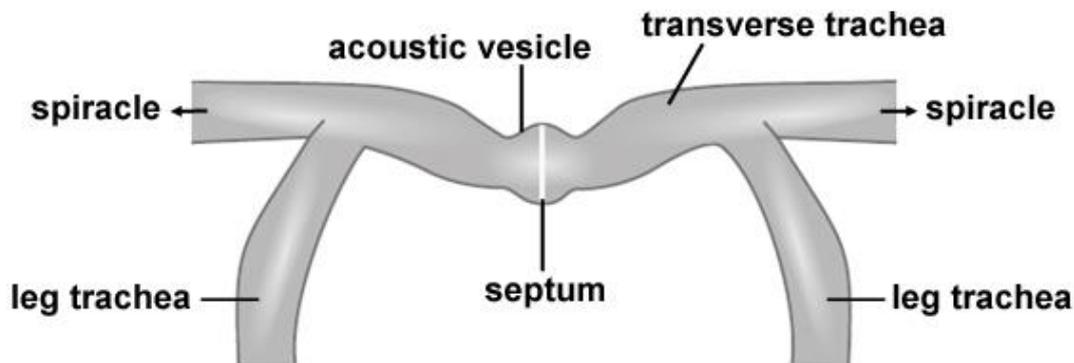

Fig. 6 Schematic diagram of the arrangement of the acoustic trachea in gryllids.

So the two acoustic tracheae are linked both anatomically and, via the thin membrane, acoustically. This connection adds two more sound inputs to the ear from the contralateral ear and from the contralateral spiracle. The cricket ear is thus an acoustic four-input device (Michelsen and Larsen, 2008; Michelsen et al., 1994) and, while the sound inputs from the spiracles and tympana are similar in some respects to those found in tettigoniids, the interactions between the four inputs in crickets adds complexity for researchers too.

The properties of the acoustic trachea have been studied as they have in tettigoniids. The propagation velocity inside the acoustic tracheal tubes has been measured in *Teleogryllus commodus* by Larsen (1981) as 263 m s^{-1} and in *Gryllus bimaculatus* by Michelsen et al. (1994) as 264 m s^{-1}. These figures are in very close agreement and are well below 344 m s^{-1}, which is the velocity of sound in adiabatic propagation (Michelsen and Larsen, 2008).

4.2 Directional hearing

The functional significance of the arrangement of the trachea described above lies in the ability to provide directional hearing. The environment in which Orthopteran insects live will always have background sounds and the function of the auditory system is to enable the insect to pick out the biologically significant sounds from the soundscape and react appropriately. For an individual avoiding predators or seeking mates, locating the source of those sounds is vital. In many species of insect, the body is smaller than one wavelength of the carrier frequency of the calling song. The carrier frequency of the calling song of *Gryllus campestris* is usually between 4.0 and 5.5 kHz (Ragge and Reynolds, 1998) which corresponds to wavelengths of 8.58–6.24 cm. The adults are 1.8–2.3 cm in length (Benton, 2012). The distance between the tympana is small, around 1 cm or less in crickets. A consequence of this small separation is that both the difference in arrival time of a sound at each ear (the interaural time difference, ITD) and the difference in intensity of the sound arriving (the interaural intensity difference, IID) are very small. Comparing the smallest and

largest crickets measured, the ITDs have been calculated as 5–23 µs (Schmidt and Römer, 2013).

In insects that are large in comparison with the wavelength of sounds, the body can cause diffraction. A consequence is that the sound intensity at the contralateral ear is lower than that at the ipsilateral ear, producing an IID. If that difference is large enough to be detectable, sound localization is possible. To measure the minimum IID necessary for determining the location of a sound source, Rheinlaender et al. (2006) examined phonotaxis in the large Asian tettigoniid *Gampsocleis gratiosa*, which has a body length of 50–55 mm and a pronotum width of 0.8–0.9 mm. They used a walking belt to maintain a female in a constant position relative to a loud-speaker playing chirps of natural song. Females that performed phonotaxis were then fitted with a back pack containing two miniature speakers connected to the auditory spiracles by plastic tubes. The intensity of the sound reaching each ear could be independently controlled, allowing the researchers to determine the smallest IID that would enable a phonotactic approach. The results revealed a sensitivity to small IIDs of 1–2 dB.

A study of phonotaxis in *Gryllus bimaculatus* (Schöneich and Hedwig, 2010) showed that ITDs could deliver information about sound direction. The difference in sound intensity on either side of the insect's body is 1.3 dB, when stimulated from 30° (Michelsen et al., 1994). Schöneich and Hedwig (2010) used an open-loop track-ball system to measure the accuracy of female orientation to male song. The sound source was positioned at a range of angles between +30° and −30° to the insect's long axis. At angles of incidence of 1°–6° the females walked precisely towards the sound source. In separate experiments, movements of the posterior tympanic membrane were measured using a laser vibrometer and activity in the tympanal nerve was recorded. An IID corresponding to 12.8 dB at 30° sound incidence was demonstrated. These experiments show that IIDs are reflected in the response latencies of the auditory afferent activity. The overall bilateral latency difference at ±30° was 1.28 ms whereas the actual interaural difference in sound arrival time was less than 15 µs. The results reveal the acoustic orientation of the cricket *G. bimaculatus* as one of the most precise among invertebrates (Schöneich and Hedwig, 2010).

5 Neural control and processing

The cricket, and particularly members of the genus *Gryllus*, has been used as a model organism in neuroethological studies for over 60 years. The cricket continues to serve that function, as exemplified by studies of the neurons and networks underlying singing behaviour (Schöneich and Hedwig, 2017) and of the auditory pathway for processing acoustic signals (Pollack and Hedwig, 2017). Studies up to 2000 are reviewed by Robinson and Hall (2002).

5.1 Control of singing activity

Sound production in crickets and grasshoppers is controlled by descending brain neurons (Hedwig, 2001). The dendritic arborizations of these neurons occupy different brain regions in the two groups. In crickets, the dendrites project within the anterior protocerebrum, between the alpha-lobe and the pedunculus, whereas in grasshoppers the dendrites form a profuse arborization within the posterior dorsal neuropil (Hedwig, 2001).

The motor programmes that drive the wing movements for stridulation are generated in the thoracic and abdominal ganglia of the ventral nerve cord. Recordings of activity in hundreds of brain neurons of *Gryllus bimaculatus* revealed a pair of descending interneurons that are command neurons, in that they are both sufficient and necessary for production of the calling song. There is no activity in these command neurons when the cricket is in a resting state. In active stridulation, there is a linear relationship between the spike frequency of the interneurons and the chirp repetition rate. The soma of the command neuron is on the dorsal surface of the protocerebrum and it has a dendritic aborization located in the ventral protocerebrum. The descending axon runs through the contralateral connective and into the prothoracic ganglion (Hedwig, 2000).

The rhythmic movements involved in stridulation are, like many other repetitive actions in animals, driven by neural networks in the central nervous system (CNS) that form discrete functional units, termed central pattern generators (CPGs). For a description of research on CPGs in animals in a historical context see the review by Mulloney and Smarandache (2010). The idea of innate acoustic behaviours in Orthoptera has been pursued in the search for CPGs that control the stridulation patterns of acridids, gryllids and tettigoniids. Innate releasing mechanisms and fixed action patterns in Orthoptera have been reviewed by Ronacher (2019).

Early work on the production of sound in grasshoppers used lesions of the connectives between ganglions in the ventral nerve cord to determine the location of the CPG (Hedwig, 1986; Huber, 1960). It was suggested that the CPG for calling song in the cricket and grasshopper was sited in the second or third thoracic ganglion. Longitudional lesions of the third thoracic ganglion in the grasshopper *Chorthippus bigutulus* suggested a hemiganglion organization for the CPG (Ronacher, 1989). In the cricket it was proposed that the mesothoracic ganglion is the site of the CPG, co-located with the motor neurons that innervate the wing muscles (Huber, 1960). Subsequently, a number of studies have implicated the abdominal nervous system in generating motor activity that produces the calling song. In *Gryllus bimaculatus*, lesions to the abdominal nerve cord showed that the abdominal ganglia each have a different role in defining the song structure (Jacob and Hedwig, 2016). Data derived from intracellular recordings of activity in singing interneurons provide support for the results obtained by lesioning (Jacob and Hedwig, 2019; Jacob and Hedwig, 2020; Schöneich and Hedwig, 2011; 2012).

The organization of the singing CPG in crickets has been studied in four species (Lin and Hedwig, 2021a) with different species-specific calling songs (Table 2). Recordings of the normal calling song pattern were made for each species.

Table 2 Normal calling song pattern of four species of cricket as described by Lin and Hedwig (2021a).

Species	Description of calling song	Reference
G. rubens	long trills	Gray and Cade (2000)
G. assimilis	chirps repeated at rather long intervals	Pollack and Kim (2013)
Teleogryllus oceanicus	phrases composed of one chirp and several trills	Bailey et al. (2017); Zuk et al. (2008)
T. commodus	phrases with one chirp, followed by a few trills	Bailey et al. (2017); Simmons et al. (2005)

The effects on the calling song of lesions to the connectives between abdominal ganglia were compared in the four species. Lesion of the connectives between the metathoracic ganglion complex T3 and the third abdominal ganglion A3 abolished singing activity in all four species. Males were still able to raise their wings to the singing position. These results are consistent with those of previous lesion experiments (Jacob and Hedwig, 2016; Schöneich and Hedwig, 2011).

Lesion of the connectives between A3 and A4 affected all four species in similar ways. The males showed large decreases in singing activity and loss of song structure. Lesion of the A4 to A5 connectives in *G. rubens* did not change the calling song pattern and neither did lesion between A5 and A6. In *G. assimilis* the effect of lesion between A4 and A5 was that singing activity continued but with extended chirps and a tendency to reduce the chirp interval. The number of pulses (syllables) per chirp increased. No change was observed after lesion between A5 and A6.

The effect of the A4–A5 lesion in the two *Teleogryllus* species was dramatic as it abolished the trill and chirp structure of the song. Instead, males produced repeated short sequences of a variable number of sound pulses. There was no change in singing pattern in either species when lesioned between A5 and A6.

The results of these lesion experiments show a conserved organization of the calling song CPG network, with the generation of pulses controlled by the A3 ganglion and timing information coming from A4 and A5 (Lin and Hedwig, 2021a).

5.2 First order auditory interneurons

In many orthopterans the temporal pattern of the male's song, and especially the relative durations of individual elements, are important in conveying meaning. It has been shown however, that a small set of auditory neurons is sufficient to reliably decode the acoustic signal and predict its behavioural relevance (e.g. Creutzig et al., 2009; Meckenhauser et al., 2014).

The auditory receptors project into the prothoracic ganglion of the crickets and bush crickets and into the abdominal ganglion in grasshoppers. The cricket ear has about 65 receptor neurons. In *Teleogryllus oceanicus* these auditory receptor neurons can be classified into three groups based on their frequency response (Imaizumi and Pollack, 1999). Two of the groups can be linked to behavioural traits. One group contains neurons with a centre frequency of 3.0–5.5 kHz and appears to be involved in acoustic communication. The second group contains neurons with a centre frequency of ≥18 kHz and is probably involved in predator detection. Low frequency receptor neurons comprise about 75% of all the auditory receptors, with the rest divided about equally between these two groups (Imaizumi and Pollack, 2001; Imaizumi and Pollack, 2005; Marsat and Pollack, 2012). The role of the third group, containing neurons with a centre frequency 10–12 kHz, is not clear.

In the prothoracic ganglion the axonal terminals of the auditory afferents synapse with a small set of auditory interneurons (Imaizumi and Pollack, 2005). Auditory information is passed to the cricket brain by two ascending neurons (AN). AN1 is sharply tuned to the centre frequencies of the male song and connects with a network of brain neurons linked to recognition of the species-specific pattern of the male song (Schöneich et al., 2015). It facilitates phonotaxis. Discharge differences in the pair of AN1 neurons drives phonotactic steering behaviour (Trobe et al., 2011). It may also be involved in the recognition of the male aggressive song. There is no evidence for sexual dimorphism in the hearing system of field crickets: the auditory

responses of ascending neurons cover the same overall range of sound frequencies with similar sensitivity (Schöneich, 2020).

AN2 is most sensitive to frequencies above 10 kHz, triggering avoidance behaviour in response to bat calls (Marsat and Pollack, 2012). AN2 may also contribute to positive phonotaxis and the processing of the high frequency ticks of the male courtship song (Samuel et al., 2013; Stout et al., 2011). The pattern of the neural response in AN2 is high frequency bursts of spikes. The bursts are triggered by nearly synchronous bursts in the ultrasound receptors. Recent research on the neural basis of ultrasound avoidance in crickets has been reviewed by Marsat and Pollack (2012).

Two types of local interneurons form part of the acoustic processing network. These neurons are called omega neurons and get their name from their shape when stained. The neurons are paired in tettigoniids but there are two pairs in gryllids (Stiedl et al., 1997). ON1 in gryllids responds to sounds over a wide range of frequencies. In *Teleogryllus oceanicus* it is most sensitive to the frequency 4.5 kHz of conspecific songs (Faulkes and Pollack, 2000). The response latency is longest for this frequency by 5–10 ms. The onset of excitatory postsynaptic potentials (EPSPs) is delayed for 4.5 kHz when compared with ultrasound stimuli (Faulkes and Pollack, 2001). ON1 is strongly stimulated by input from the ipsilateral ear but inhibits the contralateral ON1, AN1 and AN2. The inhibition enhances the difference between the sound reaching the two ears, facilitating sound localization (Faulkes and Pollack, 2000; Marsat and Pollack, 2005).

In contrast to ON1, ON2 receives excitatory inputs from both ears and there is no inhibitory coupling between the two ON2 neurons. The function of the ON2 neurons is not yet clear (Zhang and Hedwig, 2019).

There are only three auditory interneurons that have ascending axons. The T-fibre TN1 and AN2 are tuned to high frequencies and do not reliably follow the pattern of the calling song. Only AN1 carries information about the calling song towards the brain (Hedwig, 2016).

5.3 Pattern recognition in the brain

In the study of pattern recognition in the brain, the cricket continues to be a model organism, providing not only specific information about crickets but also observations that are more generally applicable in the study of the principles of auditory processing at the level of identified neurons (Zorovic and Hedwig, 2011). Local brain neurons are difficult to identify individually, but systematic intracellular recordings from the cricket brain when stimulated with sound patterns revealed four neuron types that, together with AN1, form an auditory detector network for the pattern of the male calling song (Hedwig, 2016; Kostarakos and Hedwig, 2012; Schöneich, 2020).

The axonal projections of AN1 form a ring-like arborization in the frontal protocerebrum. Four local interneurons (LN2 to LN5) closely match this arborization pattern and form a similar ring-shaped auditory neuropil in the brain (Kostarakos and Hedwig, 2012). These neurons form a local auditory network that has the fundamental characteristics of a coincidence detector circuit (Schöneich et al., 2015). For a detailed account of the filtering processes in the auditory pathway shaping feature detection in crickets see Hedwig (2016). The neuroethology of acoustic communication in field crickets has been reviewed by Schöneich (2020) and a detailed section on song pattern recognition in the brain is included.

6 Choosing a mate

6.1 Recognition of sex and species

Reproductive success depends on choosing a mate of the appropriate sex and the same species. The male calling song is usually species specific (see Section 3.8), so in singing species the first stage of mate recognition usually takes place via the processing of the male's calling song by the female's nervous system (Section 5). The female's evaluation of the male's song may be based on both its temporal parameters and its frequency components (e.g. Schmidt et al., 2008).

In duetting species, the timing of the female response is often species specific too (Heller et al., 2018). Generally females show a strong preference for the calling song of their own species, as in the bush-cricket *Isophya camptoxypha* (Orci, 2007), the grasshoppers *Chorthippus biguttulus* and *C. mollis* (Finck and Ronacher, 2017) and the tree cricket *Oecanthus forbesi* (Symes, 2018), though in closely related species females are not always able to discriminate conspecific from heterospecific songs (e.g. Couldridge and van Staaden, 2006; Kowalski and Lakes-Harlan, 2011). Safi et al. (2006) have shown however that female *C. biguttulus* prefer those conspecific songs that can be more reliably discriminated from heterospecific songs, thus maximizing the efficiency of species recognition.

However, in non-duetting species the male still needs to identify the sex and species of any potential mate that responds to his calling song. In duetting species there may be considerable room for error in species recognition by males (Heller et al., 2018) and females cannot be certain that the male that approaches them is the one that was singing rather than an eavesdropper (Section 2.2). So most species have further means of mate recognition once a pair actually meet. Initial mutual antennation has been widely observed in orthopteran mating (e.g. Hall and Robinson, 2020) and the chemical cues detected in this way have been shown to be important in mate recognition. Ryan and Sakaluk (2009) for example found that antennation is required for sex recognition in the cricket *Gryllodes sigillatus*, while Finck et al. (2016) showed that males of the grasshoppers *C. biguttulus* and *C. mollis* only produce courtship song if they detect appropriate chemical cues from a conspecific female.

Courtship song can have a role in species recognition but is probably more concerned with stimulating the female to mate (see Section 2.3) and/or providing information about the male's quality; it may be particularly important in mate choice if satellite males are common (Rebar et al., 2009; Shestakov and Vedenina, 2015; Simmons et al., 2013; Zuk et al., 2008).

6.2 Sexual selection theory

Sexual selection can be defined as 'differential reproductive success due to the ability to secure matings and/or fertilizations' (Rosenthal, 2017, p. 503). Traditionally it is divided into two categories, though the two do not necessarily operate independently: intrasexual competition, where members of one sex (usually but not always males) compete with each other for access to mates, and mate choice, where one sex (usually but not always females) preferentially mates with individuals that have particular traits. Mate choice is considered in this section and intrasexual competition in Section 7.

Wagner (2011), the recent book by Rosenthal (2017), and Rosenthal's reviewers Makowicz et al. (2020) provide useful reviews of mate choice theory. Mate choice may be the result of active choice. Alternatively, females may simply be passively attracted to the male whose signal is the most stimulating, easiest to locate, or most

closely tuned to the female nervous system. Or they may show preferences just because they carry genes that are beneficial in another context but which also happen to influence their responses to male traits in the mating context (*receiver bias*, also called *perceptual* or *sensory bias*); see for example Gray et al. (2016) and Reichert et al. (2017).

In theory, mate choice can have significant effects on female fitness, either through their own reproductive success or through that of their offspring. Preferred males can provide direct benefits (material resources such as nutrients contained in the nuptial gift) and/or indirect benefits (via *good genes* that increase offspring viability or *sexy son* genes that increase the attractiveness to females of male offspring). The parasite-mediated sexual selection theory (Balenger and Zuk, 2014) proposes that females choose a male whose signals indicate his ability to resist parasitic infections, thereby providing them with benefits both direct (e.g. reduced risk of sexual transmission of disease) and indirect (e.g. offspring who inherit parasite resistance).

While it is relatively clear how selection can favour preferences for mates that provide direct benefits (though see Wagner, 2011), little evidence has actually been found in support of the good genes/sexy sons/parasite-mediated theories and there has recently been a growing body of opinion that the importance of indirect benefits may be limited (Makowicz et al., 2020; Rosenthal, 2017).

6.3 Choosing a mate based on information in male song

Studies in Orthoptera have often looked at the relationships between song features, male characteristics and female mate preferences. Some of these have shown that song features correlate with certain male characteristics, e.g. with size in the cricket *Acanthogryllus asiaticus* (Singh and Jain, 2020) and the mole cricket *Gryllotalpa major* (Howard and Hill, 2006) or age in the cricket *Gryllus veletis* (Fitzsimmons and Bertram, 2011), without demonstrating that females can perceive the differences between songs or have a preference for males with these characteristics. Others have shown that females prefer certain song features without demonstrating a correlation between song and male characteristics. For example females in the cricket *Gryllus bimaculatus* (Fig. 7) prefer courtship song with louder 'ticks' (very short chirps) and quieter pulses (Shestakov and Vedenina, 2015), but it is unclear what, if any, information about the male these features convey.

Fig. 7 A female two-spotted cricket*, Gryllus bimaculatus* (© Axel Hochkirch).

Females in many species have, however, been shown to prefer songs with features that provide information about some characteristic of the male that could, at least

potentially, affect the female's fitness. Several examples of such preferences were given in Robinson and Hall (2002); more recent examples are shown in Table 3.

There is the potential for direct benefits in several of the examples in Table 3, especially where females choose a mate that is likely to provide a larger or more nutritious nuptial gift, or more sperm, as in *G. sigillatus* (larger spermatophore with higher protein content), *Ephippiger ephippiger* (larger, more nutritious spermatophore, with more sperm), *Poecilimon zimmeri* (larger spermatophore), *Allonemobius socius* (larger nuptial gift and more sperm), and *Velarifictorus ornatus* (larger spermatophore). But of these five species, actual effects of the choice of mate on female fitness have only been demonstrated in the last two. In *V. ornatus* fertilization is more successful. In *A. socius*, immune-compromised males produce less attractive song and smaller nuptial gifts, so that females choosing mates on the basis of their song receive more resources from the male and have higher fecundity (which also provides support for the parasite-mediated sexual selection theory).

Direct benefits may also be provided via seminal fluid. For example *G. lineaticeps* females choosing males with longer chirp durations benefit from increased lifespan, even if they only receive sperm and seminal fluid and do not eat the spermatophore. This seems to be due to delayed oviposition, possibly as a result of fewer or less potent oviposition stimulants in the male's seminal fluid. The offspring of *Neoconocephalus ensiger* females who choose a leading male (i.e. one whose song precedes those of other singing males: see Section 7.5).are in better condition (heavier relative to body size), possibly as a result of the proteins provided in seminal fluid (Murphy et al., 2017).

However, even if females prefer larger males, and male size is correlated with spermatophore size, it cannot be assumed that choosy females gain direct benefits. Jarrige et al. (2013) found no evidence that song features in *Ephippiger diurnus* could predict the nutritional content of the spermatophore actually transferred during copulation. Instead males adjusted the size and quality of their spermatophores depending on the age and size of the female. Male choice in this species effectively makes it impossible for females to assess what direct benefits they will get by mating with a particular male.

Evidence for indirect benefits associated with the female's choice is also limited. In *Acheta domesticus* the female's choice results in more attractive sons, more fecund daughters, and a shorter generation time (faster maturation/earlier reproduction) for her offspring. She suffers from direct costs because her lifespan and fecundity are reduced, but these are outweighed by the indirect benefits. In *G. assimilis* females mating with more aggressive males have larger offspring: daughters lay more eggs and sons are more attractive, though there is no increase in offspring viability. In *G. bimaculatus*, successful males (i.e. those chosen by females) have male offspring that are in turn successful (Wedell and Tregenza, 1999). On the other hand, two species provide evidence against indirect benefits. In *G. campestris*, older males attract more females but once the female has approached an older male she is less likely to mate with him than she is with a younger male. There is no relationship between the male's age and the number of his offspring or grand-offspring. In *Chorthippus biguttulus*, there are no differences between females mating with attractive or unattractive males in the hatching success, viability or rate of weight gain of their offspring, or in the attractiveness of their sons. Safi et al. (2006) argue that female choice in this species is probably driven mainly by selection for species recognition.

Table 3 Species in which females show a preference for parameters of song that provide information about male characteristics.

Species	Parameter of song (refers to calling song unless otherwise stated)	Information contained in song (correlation between parameter and male characteristic)	Reference
Crickets			
Acanthogryllus asiaticus	Lower peak frequency	Larger size	Singh and Jain (2020)
Acheta domesticus	Higher proportion of 3-pulse chirps	Larger size; better immunocompetence	Head et al. (2005); Stoffer and Walker (2012);
Allonemobius socius	Longer pulse duration	Status of immune system	Fedorka and Mousseau (2007)
Gryllotalpa major	More pulses per chirp; lower dominant frequency	Larger size	Howard and Hill (2006)
Gryllus assimilis	Louder	Larger size; better condition; more aggressive; older male	Bertram et al. (2016); Bertram and Rook (2011; 2012); Loranger and Bertram (2016)
	Lower frequency	Larger size; better condition; more aggressive	
	Chirps with longer pulses; longer chirps; more pulses per chirp (i.e. higher duty cycle with more sound per unit of time)	Older male; more aggressive	
	Higher pulse and chirp rates	Older male; better condition	
G. bimaculatus	Louder song	Larger size	Verburgt and Ferguson (2010); Verburgt et al. (2011); Zhemchuzhnikov et al. (2017)
	For songs of equal intensity, higher duty cycle with longer syllables and/or shorter intervals between syllables/chirps	Younger male	
	Courtship song with higher duty cycle for high-frequency ticks (very short chirps) with longer ticks at faster rate	Better immunocompetence	Rantala and Kortet (2003)

Species	Parameter of song (refers to calling song unless otherwise stated)	Information contained in song (correlation between parameter and male characteristic)	Reference
G. campestris	Lower frequency (given priority over chirp rate)	Older male; better condition as nymph	Jacot et al. (2007); Rodriguez-Munoz et al. (2019); Scheuber et al. (2004);
	Higher chirp rate	Better current condition	
G. lineaticeps	Higher chirp rate	Better nutritional status	Wagner and Harper (2003); Wegehaupt and Wagner (2017)
	Longer chirp duration	Possibly seminal fluid contains fewer oviposition stimulants	
G. pennsylvanicus	Lower frequency, longer pulses	Larger size	Judge (2011); Ting et al. (2017)
	Lower peak frequency, faster pulse rate (shorter pulse period), shorter pulse duration, more pulses per chirp	Older male	
G. sigillatus	Shorter pulses	Larger size	Champagnon and del Castillo (2008)
G. texensis	Lower frequency; higher pulse duty cycle (longer pulses and shorter intervals)	Larger size	McAuley and Bertram (2016)
Oecanthus henryi	Higher frequency	Possibly larger nuptial gift	Mhatre et al. (2012)
Plebeiogryllus guttiventris	Faster chirp rate (shorter chirp period)	Possibly condition	Nandi and Balakrishnan (2013)
	Louder song (overrides other preferences)	Larger size	
Teleogryllus oceanicus	Courtship song with greater trill duty cycle	Better condition: can produce energetically expensive song despite inherent costs (reduced immunocompetence and lower sperm viability)	Simmons et al. (2013)

Species	Parameter of song (refers to calling song unless otherwise stated)	Information contained in song (correlation between parameter and male characteristic)	Reference
Velarifictorus ornatus	Specific parameter unknown (song of short-winged males preferred to that of long-winged males)	Larger spermatophore	Zhao et al. (2017)
Bush-crickets			
Ephippiger ephippiger	Longer chirp duration	Younger male	Wedell and Ritchie (2004)
Isophya camptoxypha	Longer syllable duration	Possibly larger size and/or better condition (longer syllables more costly to produce)	Orci (2007)
Orchelimum pulchellum	Louder song; for songs of equal loudness, greater attenuation in the higher frequency components	Larger size or one otherwise capable of more energetically costly song	Harness and Campbell (2021)
Poecilimon zimmeri	Specific parameter unknown	Larger size	Lehmann and Lehmann (2008); Reinhold (1999)
Grasshoppers			
Bullacris membracioides	Lower frequency; shorter total song duration; smaller ratio between total duration and final syllable duration	Larger size	Couldridge and van Staaden (2006)
	Longer final syllable duration	Smaller size	
Chorthippus biguttulus	Louder song	Larger size; better condition	Franzke and Reinhold (2012); Klappert and Reinhold (2007); Ronacher and Stange (2013)
	Shorter pauses between syllables (higher syllable to pause ratio); shorter gaps within syllables		
	Greater onset accentuation (syllable louder at beginning)	Larger size: better immunocompetence	
	Larger offset depth (greater decrease in loudness in pause between syllables)	Better immunocompetence	

The female choices listed in Table 3, and the benefits that may be gained from that choice, are also not always as straightforward as might seem. In the cricket *Gryllus lineaticeps*, females prefer higher chirp rates, and benefit from increased fecundity as a result, but only if the male is on a low-quality diet. For males on a high-quality diet, there is actually a negative correlation between chirp rate and fecundity. Females, however, are able to choose males on a poor diet, whatever their chirp rate, so they must be using additional cues to enable them to do so. The benefits gained by females choosing males with high chirp rates are also balanced by costs: these males are more likely to be attacked by lethal parasitoids (see Section 8) and females associating with them are in increased danger too. Females also prefer higher chirp rates in courtship song but there is no correlation between chirp rate in calling song and that in courtship song and females may prioritize courtship over calling song, being more likely to mate with a male that has a higher courtship chirp rate even if the calling song of that male has a lower chirp rate. Courtship chirp rate has no relationship to nutritional status and any benefits of selecting a mate based on courtship song are unknown (Martin and Wagner, 2010; Wagner and Reiser, 2000; Wegehaupt and Wagner, 2017). In *G. pennsylvanicus*, females who mate with a high quality male tend to lay more eggs, but they still do this even if the male they mate with is a low-quality male accompanied by recorded song from a high-quality one (Ting et al., 2017). In *A. domesticus*, females choose initially on the basis of the male's calling song but then reassess the male using proximate signals, which may be non-acoustic (Stoffer and Walker, 2012). Choice may sometimes be more to do with rejecting males that are unsuitable – e.g. heterospecifics, injured males or those with developmental problems – rather than selecting a high-quality mate (Clemens et al., 2017; Clemens et al., 2021). The costs and benefits for the female may also be affected by male manipulation of, for example, egg laying rates or longevity, via factors transferred in the spermatophore, rather than her choice of mate (e.g. Wilson and Walker, 2019).

Many studies of mate choice based on song are designed to investigate a single song feature at a time. But different song parameters are not always correlated with each other and an individual male may have a song with a mixture of attractive and unattractive characteristics. Females can, however, make a comparative evaluation of males, integrating different aspects of their song and weighing up negative versus positive features (Clemens et al., 2017; Gabel and Hennig, 2016). Wittmann et al. (2011) developed a neural network model that allows them to analyse courtship songs in *Chorthippus biguttulus* in terms of the relative contribution of different song characteristics to overall song attractiveness and female responsiveness. Bentsen et al. (2006) and Ower et al. (2013) both caution against laboratory studies that draw inferences about sexual selection based on the manipulation of single song parameters, as these underestimate the strength and complexity of sexual selection acting on male signalling characteristics. Morphological constraints are also an important consideration. During mating in haglids from the genus *Cyphoderris*, the female consumes the fleshy hind wings of the male as well as the haemolymph that flows from the damaged wing. Wing morphology is a major determinant of song structure. Sexual selection acting on song structure is much stronger than that acting on wing morphology, suggesting that the latter may constrain the evolution of the former (Ower et al., 2017).

In most of the examples in Table 3, the preferred song feature is either correlated with large male size or with the male's ability to allocate the greater amount of energy required for the production of higher-effort song containing more sound per unit of time (a higher duty cycle). Larger males may provide better direct benefits

such as a bigger spermatophore containing more sperm (Whitman, 2008). Females may be passively attracted to song containing more sound or be more likely to hear one that is louder. On the other hand, males singing with a higher duty cycle may be signalling that they are in good condition, though this does not necessarily mean they are able, for example, to provide a larger nuptial gift: high effort song and nuptial gifts are both energetically expensive and the ability to produce one affects the ability to produce the other (see e.g. Copeland and Fedorka, 2012; Lehmann, 2012; Wagner, 2005). Harrison et al. (2013) have also shown that songs with a high duty cycle are not always an honest indicator of quality.

Similarly, males who show greater singing effort (i.e. who spend a higher proportion of their time producing calling song) tend to have greater mating success (e.g. Bentsen et al., 2006; Holzer et al., 2003). This may simply be the result of passive attraction—the more often a male sings, the more likely a female is to hear him. However, calling song is energetically expensive and the amount of time a male spends singing is usually dependent on, for example, diet, condition and size (see Section 3). The singing effort of males in the cricket *Plebeiogryllus guttiventris*, for example, is not consistent from one night to the next (Nandi and Balakrishnan, 2016). In some species at least, those males whose songs have the most attractive features are also the ones that sing with the greatest effort (Bertram et al., 2011) so both the quality and quantity of song constitute an honest signal (Maynard Smith and Harper, 2003). In other species males may be able to compensate for unattractive features of their song by increasing their singing effort. In *G. texensis* for example (McAuley and Bertram, 2016), male calling songs at sub-optimal frequencies are less audible to females, have a smaller range, and induce reduced neural and phonotactic responses in females. However males with unattractive song frequencies can increase their singing effort and sing more loudly, though only if they are high-quality males able to invest the extra energy required.

Apart from the amount of effort a male puts into singing, and the specific features of his song, the timing of his song in relation to those of other males can influence his attractiveness to females. Such male–male interactions are considered in Section 7.

6.4 Variation in female mate preferences

Although females across a species may show a significant preference for male song with particular parameters, this does not mean that all females of that species necessarily show the same preference, or the same degree of choosiness (i.e. how selective they are in terms of accepting or rejecting a male whose song feature is different to some extent from their preferred value).

Preferences and choosiness often vary consistently between different females (e.g. Reinhold and Jacoby, 2002; Stout et al., 2010; von Helversen et al., 2004). In some species variation in choosiness can be related to the condition of the female: if she is in poor condition she cannot afford to spend a lot of energy in finding her preferred mate (e.g. Judge et al., 2014). Females infested with parasitoids (see Section 8) may also show reduced selectivity in choosing a mate, probably because they need to reproduce as quickly as possible before the parasitoids kill them (e. g. Beckers and Wagner, 2013). The strength of preference for leading songs also varies between females.

Individual females also show plasticity in their mate choice behaviour. In some species, older females (with low residual reproductive value) may be less choosy because the benefits gained from being selective no longer offset the costs (e.g.

Mautz and Sakaluk, 2008; Pacheco et al., 2013), though in others there is no consistent relationship between age and choosiness (e.g. Sarmiento-Ponce et al., 2021). Female choosiness may also vary with stage of oviposition cycle (Aufderheide and Ronacher, 2019).

The female's social environment, either as a juvenile or as an adult (Swanger and Zuk, 2015), can affect both her preferences and her choosiness (see review by Rodriguez et al., 2013). In the bush-cricket *Ephippiger diurnus* for example, females reared in an environment where all the male song they hear is high quality (i.e. has the preferred number of syllables) are more selective than those that only hear low-quality male song (Rebar et al., 2019). Population density can also affect choosiness: for example in *Teleogryllus oceanicus* (Bailey and Zuk, 2008; Lierheimer and Tinghitella, 2017) and *Gryllus lineaticeps* (Atwell and Wagner, 2014), females hearing sounds that simulate a high density of males are more selective than those that hear sounds simulating a low density of males. In *T. oceanicus* females reared in the absence of male songs (i.e. in an environment where potential mates are likely to be limited) are more likely to engage in risky behaviour (i.e. perform phonotaxis when the perceived risk of predation is high), especially if they have the opportunity to mate with a male with preferred song characteristics (Ghalichi et al., 2020). In *G. lineaticeps*, Beckers and Wagner (2011) have found some evidence that a female adopts different strategies for selecting a mate depending on male density at the time. When male density is low she may use a comparison strategy whereby she continues searching as long as each new male encountered is of higher quality than the previous one; once she encounters a new male that is of lower quality than the previous one, she chooses the previous male. When male density is high, she may use a fixed threshold strategy with a 'last chance' option whereby if, after some period of time, she has not encountered a sufficiently attractive male (one that meets her quality threshold), she will mate with the next available male regardless of his quality. Bailey and Zuk (2009) also showed that female *T. oceanicus* adjust their mate choice behaviour according to their specific social experience: their response to a particular male depends on what males they have already encountered and what order they encountered them in. Females hearing a more attractive male song shortly before hearing an 'average' song are more choosy (less likely to respond to the average song) than females that had previously heard a less attractive song.

There may also be constraints on the female's ability to exercise choice. In the cricket *Teleogryllus commodus*, for example, Hall et al. (2008) showed that, after copulation, females can 'choose' males whose courtship song has particular parameters by removing the spermatophore of non-preferred males earlier than those of preferred males. The male's fitness is correlated with spermatophore attachment time and he can delay spermatophore removal by harassing the female. In the presence of the male, the female's ability to exercise choice is limited, the intensity of sexual selection on male courtship song is greatly reduced and the particular song features that are selected are different compared with when the female is able to escape from his harrassment and remove the spermatophore when she chooses. Differences in environmental conditions that make it more or less likely that the female is able to escape will therefore lead to differences in both the strength and focus of sexual selection. Such fluctuations in time and space are likely to be common (see review by Miller and Svensson, 2014).

6.5 Female song, male mate choice and role reversal

Compared with the extensive literature on female male choice, there has been relatively little research on male mate choice in Orthoptera. Where it has been

demonstrated, male choice has been related to non-acoustic cues such as the female's size or age (e.g. Hare and Simmons, 2020; Jarrige et al., 2013). There is potential for male choice based on female song in those species where females sing but we have been unable to find any studies where this possibility has been investigated or which have looked for correlations between features of song and other female characteristics, such as body size or condition, that might affect the reproductive success of the male.

Female song has been found to stimulate male mating activity in general. For example, in *Chorthippus biguttulus*, females sing to show they are ready to mate and males preferentially court singing females (Wirmer et al., 2010).

In duetting species, the length of the female reply can vary between and within individuals. Longer replies may provide more locational information, allowing the male to search more effectively for the female, and may indicate a preference for the singing male (Bailey, 2003). For example, in the katydid *Scudderia pistillata*, males in better condition produce more syllables per bout of singing and females respond faster and with longer songs containing more 'ticks' (Villarreal and Gilbert, 2013).

In some species, when food is scarce, females compete with each other for nutritious nuptial gifts and males become choosy. Sexual selection may act on females as a result of this role reversal. For example in *Kawanaphila nartee*, females have more sensitive hearing than males, possibly because this benefits them during intrasexual competition when they scramble for access to acoustically signalling males (Hare and Simmons, 2020). However, selection for larger ear size in females has been shown to occur only during periods of role reversal (Hare and Simmons, 2021).

6.6 Mate choice and speciation

Divergence in acoustic mating signals has been a significant driver of speciation in Orthoptera (e.g. Wilkins et al., 2013). Sexual selection has also played an important role: divergence in the male song between populations is often coupled with divergence in female song preferences (e.g. Barbosa et al., 2016; Orci and Iorgu, 2017). One of the most detailed studies has been carried out by Shaw and colleagues on the rapidly speciating Hawaiian cricket *Laupala* (e.g. Grace and Shaw, 2011; Wiley et al., 2012; Xu and Shaw, 2021). They have shown that male song and female preference coevolve in a stepwise manner and that genetic coupling underlies this signal–preference coevolution. Female mate choice thus facilitates the establishment of sexual isolation, reduced gene flow, and population differentiation, all prerequisites for speciation.

7 Competition and cooperation

The ability to hear is important to male orthopterans, even though females in most species do not sing: it allows them to detect predators (see Section 8), locate and interact acoustically with other males, and obtain information from their songs which may be important in male–male cooperation or competition.

7.1 Aggregating and spacing

As we described previously (Robinson and Hall, 2002), orthopteran species commonly form aggregated populations, either because individuals are passively attracted to an area containing resources like food or singing sites or because they

are actively attracted to each other. Various possible benefits of aggregating have been suggested, such as reduced vulnerability to predation and increased attractiveness to females of a group of singing males compared with a single male (see e.g. Greenfield, 2015). The male calling song plays an important part in the distribution of individuals within a population, repelling or attracting other males as well as attracting females. Where singing males interact temporally with each other over relatively long periods of time, aggregated populations are defined as choruses (see Section 7.5).

Males may respond to another male that they can hear singing by moving away to maintain a space between them, by approaching the singer using their song to locate them (phonotactic response), or by adjusting their own singing behaviour (acoustic response). Chamorro-R et al. (2007), for example, showed experimentally that one of the functions of the calling song of the katydid *Panacanthus pallicornis* is to maintain spacing: a group of males that had been deafened tended to aggregate while a group of normal, hearing males spread out randomly. Where males use song to maintain a minimum distance with neighbours, distribution is likely to be random at low population densities, only becoming regular as density increases, as shown for example in the katydid *Sphagniana sphagnorum* (Morris et al., 2018). Distance estimation must however be relative rather than absolute because so many environmental factors, such as temperature and vegetation, affect the transmission of song (see Section 3.9). Morris et al. (2018) have suggested that *S. sphagnorum* males may estimate distance using the ratio between the perceived sound pressure levels of the audio and ultrasonic components of the calling song and Kostarakos and Römer (2018) have described a neuronal mechanism that would allow them to do so.

There may be advantages to keeping a distance from other males, at least to some extent. For example the mole cricket *Gryllotalpa major* forms leks in which males sing in close proximity. Females however prefer to visit smaller leks (Keane et al., 2018) and, within a lek, those males further from the centre and from nearest singing neighbours (Howard et al., 2011).

Males may perform phonotaxis for a variety of reasons: to join other males in an aggregation (e.g. in the bush-cricket *Conocephalus brevipennis*: Guerra and Mason, 2005), to get close to a more successful male so they can act as a satellite (Section 2.2), or to initiate an aggressive contest. For example, *Gryllus integer* males that are more able to win contests preferentially approach the song of a male that is more attractive to females (Leonard and Hedrick, 2009). They are more likely to be doing this to initiate a contest than to act as satellites because unattractive males do not behave in the same way. As *G. rubens* males get older they become less likely to perform phonotaxis and more likely to respond acoustically (Jang, 2011). This strategy may enable them to find singing sites as young adults and then swich to attracting females and maintaining spacing from other males.

7.2 Aggressive signals and fighting

7.2.1 Males

Aggressive song can play an important role in aggressive encounters between males. It may have a function before and/or after a contest. Before, it may mitigate the costs of aggression by allowing males to assess each other's competitive ability and so decide a contest without an actual fight. In Hawaii some *Teleogryllus oceanicus* males have lost the ability to sing (see Section 8.3). Contests between

two silent males are much more aggressive than those in pairs where at least one male can sing (Logue et al., 2010). In *Hemideina* tree weta contests, the larger male usually wins, but if both males are of similar size contests are likely to be extended and therefore costly, and in these cases aggressive song is probably used to decide the winner (Ewers and Cowley, 2005).

If males are to assess each other based on song, that song must contain information. In some species, the energy put into the aggressive song—either the duty cycle or the singing effort—is an honest signal of competitive ability. For example, the haglid *Cyphoderris monstrosa* (Chang, 2015) is territorial and sings before a fight. The duty cycle of this aggressive song is not necessarily consistent from one fight to another but reflects their competitive ability at the time. Particular parameters of the aggressive song, such as chirp length, may also be correlated with competitive ability as for example in the crickets *Gryllus veletis* (Harrison et al., 2017) and *Acheta domesticus* (Brown et al., 2006). In *A. domesticus*, temporal components of the song are correlated with body size which in turn affects the intensity and outcome of fights.

After a contest the winner may sing aggressively as a 'victory display' (Bertram et al., 2010). This may have two functions: to 'browbeat' the loser, i.e. to show them the winner is still capable of continuing or even escalating the contest, and to advertise their success to nearby prospective mates or rivals. Information in the victory display could inform decisions made by the loser about whether or not to engage the winner again in future encounters. Such victory displays are seen in several territorial cricket species that display from, and defend, burrows or crevices, including *G. veletis*, *G. pennsylvanicus*, *G. rubens*, and *T. oceanicus* but are rarely seen in non-territorial ones like *G. fultoni* or *G. vernalis* (Jang et al., 2008).

Male–male encounters can be affected by the social environment. For example in *G. assimilis*, males are more likely to initiate or escalate fights and spend less time performing victory displays if a female is present (Montroy et al., 2016). *G. veletis* males are more aggressive and perform more victory display behaviours if another male is present (Fitzsimmons and Bertram, 2013).

Songs produced during male–male interactions may not always be directed at the rival male. In the katydid *Gnathoclita sodalis* (De Souza et al., 2011) the male produces both airborne sound and vibratory signals during contests. The 'loser' (who withdraws, usually without a fight) is usually the smaller male. The number of his vibratory signals predicts the winner of the contest, but there is no apparent relationship between winning and the male's aggressive song, which may be directed at nearby females rather than at the other male.

However, it is not necessarily the case that males who are more aggressive or more likely to win contests are more attractive to females. In *G. integer*, for example, females prefer males who sing for longer but singing time is negatively correlated with aggressiveness, possibly because both require energy and there is a trade-off between the two (Hedrick and Bunting, 2014).

7.2.2 Females

Females are known to fight each other and may also produce aggressive song. For example, *Gryllus campestris* females (Rillich et al., 2009) may fight for the opportunity to mate in the presence of a courting male, though they do not produce aggressive song. Either male calling song or courtship song can induce female fighting but aggressive song rarely does. Females in the bush-crickets *Steropleurus*

stali and *S nobrei* (Hartley, 1993) may also fight in the presence of a singing male. They produce aggressive song which depresses the acoustic activity of other individuals nearby, both male and female.

7.3 Acoustic defence and attack

Males of duetting species are vulnerable to rival eavesdropping males (Section 2.2). Several strategies have been adopted among bush-crickets species to counter eavesdroppers. Most commonly, once a singing male receives a response, he reduces the interval between his songs, which enables him to exchange information with the female about her location more quickly (see e.g. Heller et al., 2020). He may also sing more quietly so he can only be heard by an individual close by, which is likely to be the female, as for example in *Anaulacomera almadaenis* and *Phaneroptera sparsa* (Heller et al., 2021). In some species, males add an element to their own calling song that masks the female reply and prevents other males from hearing it while still being able to hear it themselves (e.g. *Caedicia*: Hammond and Bailey, 2003). Others mimic a female response after their normal calling song, thereby making it more difficult for the eavesdropper to locate the actual female that is responding, for example in *Scudderia pistillata* (Villarreal and Gilbert, 2014), *Gonatoxia* (Heller and Hemp, 2017) and *A. almadaenis* (Heller et al., 2020).

Eavesdroppers may also attack singing males acoustically. *Caedicia* males for example (Bailey et al., 2006) produce a song that mimics a female response, possibly to distract the singing male away from the real female response. They also sing over the part of the male's calling song necessary for species recognition, thus reducing the likelihood that a female will respond and potentially making her available for mating with the eavesdropper.

Some species exhibit more than one of the strategies adopted by singers and eavesdroppers, giving rise to highly complex male songs. Heller and Hemp (2020) argue for the importance of sexual selection by male competition, as well as by female choice, in the evolution of male song in duetting species.

7.4 Plasticity in male behaviour

Just as individual females show plasticity in mate choice behaviour depending on their social environment (Section 6.4), individual males are able to adjust their behaviour depending on acoustic cues from other males.

It is common for males to put more effort into singing (greater singing effort or higher duty cycle) if they can hear rival males (e.g. Anichini et al., 2018; Callander et al., 2013; Mhatre and Balakrishnan, 2006; Morris et al., 2002; Noguera, 2019; Rebar et al., 2016). Males of one *Mecapoda* bush-cricket species simply start singing as soon as a rival does (Krobath et al., 2017). Males may also adjust their courtship behaviour. For example, in the cricket *Gryllodes sigillatus* males start courtship more quickly if they have been exposed to the sound of another male (Santori et al., 2020).

The amount of singing a male can hear around him is typically an indication of population density and therefore the level of sperm competition he is likely to experience, so it is unsurprising that males of several species have been found to change their investment in sperm or spermatophores if they can hear rivals singing. They may produce better quality sperm (e.g. *Teleogryllus oceanicus*: Simmons and Lovegrove, 2017) or more sperm (e.g. *Acheta domesticus* and *Gryllodes supplicans*: Gage and Barnard, 1996). Males of the bush-cricket *Ephippiger diurnus* change the

size of their spermatophore depending on the quality rather than the number of songs of rival males, i.e. the perceived level of strong competition (Rebar et al., 2016).

The potential availability of mates also depends on population density and males have been shown to adjust their mating tactics in response to the amount of conspecific song they hear. For example, *T. oceanicus* males that can hear conspecifics singing are more likely to perform phonotaxis towards other males, and therefore more likely to adopt satellite behaviour (Section 2.2), compared with males kept in the absence of song (Balenger et al., 2018).

7.5 Choruses

As we described previously (Robinson and Hall, 2002), different species show different kinds of chorusing behaviour. Recent research has concentrated however on *synchronous chorusing*, in which males sing so that the repeated units (RUs) of their songs occur at almost the same time as those of other males, and *alternating chorusing* in which males sing so their RUs occur in the spaces between those of other males. Synchrony tends to be more common in species where the rate of singing is high and alternation where it is low (Hartbauer and Römer, 2016). Most of the studies of synchrony so far have been on species that sing with regular simple rhythms and the first study of synchrony in a species with a complex song (*Mecopoda* 'Two-part caller') has only been published recently (Nityananda and Balakrishnan, 2021).

Within a synchronous chorus, leader and follower males can often be identified: leaders are defined as males that habitually initiate their RU first and followers as those that initiate their RU second. It is still unclear how these types of chorus evolved but since 2002 considerable progress has been made in understanding the possible benefits of synchrony and alternation and the mechanisms by which they may arise (see for example Greenfield, 2015; Greenfield et al., 2017; Hartbauer and Römer, 2016).

7.5.1 Leaders, followers and female choice

In some species, females are more likely to respond to leading songs in a synchronous chorus. This preference appears to result from a sensory bias (Hartbauer and Römer, 2016) that causes females to attend to leading songs and ignore songs whose onsets follow the onset of the leading song within a certain time (the *preference extent*). The preference extent can be less than 70 ms in some species or as long as 2 s in others (Greenfield and Snedden, 2003).

Studies of three *Neoconocephalus* species (Murphy and Schul, 2017; Murphy et al., 2017) found no heritability of leadership ability and no correlation between leadership ability and several possible indicators of male quality such as size, condition, chirp duration, song duty cycle, or immunocompetence. But in the one species of the three where females show leadership preferences (*N. ensiger*), there is a possible direct fitness benefit for females mating with a leader: they produce offspring in better condition, possibly because leader males provide better seminal proteins.

Males with shorter intrinsic signalling rates are more likely to become leaders (e.g. *Mecopoda*: Hartbauer and Römer, 2016; Nityananda and Balakrishnan, 2007) and leaders are expected to attract more females than followers. So why should males who are likely to end up as followers take part in a chorus? It has been suggested that by cooperating to form choruses, follower males may have greater mating

success than they would by singing on their own. This is considered in the next section.

However, leader and follower roles, and female preference for leaders, are not necessarily consistent or clear-cut. Males are able to adjust their signalling rate and in some species males switch between leader and follower roles relatively frequently, as in *Mecopoda* 'Chirper' (Nityananda and Balakrishnan, 2008) and *Ephippiger diurnus* (Party et al., 2014). In *M. elongata*, chirps of older males are longer than those of younger males so younger males more often take the leader role in male–male duets; given a straight choice between a young leader and an old follower, females prefer the young male (Hartbauer et al., 2015). But things are not so simple in more complex choice situations. In a small chorus of four males only 40% of females chose the leader and most instead preferred the male that had both a frequent leader role and longer chirps. As a result, older males are likely to be just as attractive as younger males even though they spend more time than younger males as followers.

The strength of the female preference for leading songs may also vary within a species. Greenfield et al. (2004), for example, found that different *E. ephippiger* females differ consistently in the strength of their preference and that the preference declines with age. Mate choice is also influenced not only by whether the male is a leader but by the acoustic neighbourhood: males singing in locations with more overall singing are preferred (Berg and Greenfield, 2005).

Followers may also have strategies to improve their mating success. Nityananda and Balakrishnan (2008) found that a *Mecopoda* 'Chirper' male that is generally a follower may sing more often when leaders are not singing. Also, while leaders are typically louder than followers, some quieter males are able to distance themselves sufficiently from them to become the loudest male in their local area, which compensates for their lack of leadership. Simulations by Fertschai et al. (2007) have shown that the ability of followers to attract females may be much higher than suggested by laboratory trials. Followers may also make a trade-off between a reduced rate of mating versus reduced longevity caused by infestation with parasitoid fly larvae. *M. elongata*, for example, is subject to acoustically-orienting Ormiin parasitoids (see Section 8) but these flies are more likely to attack males with leading songs (Lee et al., 2009).

7.5.2 Evolution of choruses

Alternating choruses probably arose because they reduce acoustic interference between neighbouring males (Greenfield, 2015). Because a male cannot hear as clearly while singing himself, alternation ensures that a singer can clearly evaluate a neighbour's song and adjust his own singing and location as necessary. The same applies to the neighbour, so cooperating to create an alternating chorus benefits both males. Females also benefit from being able to discriminate more easily between the characteristics of two singing males.

Explanations for the evolution of synchrony are more diverse and not necessarily mutually exclusive (for good summaries see: Greenfield, 2015; Hartbauer and Römer, 2016). Evidence for any of them is very limited.

One hypothesis is that singers that synchronize are less vulnerable to phonotactic predators and parasitoid flies, which find it more difficult to locate a single singer within the chorus. Some support for this idea has been found in *Mecopoda* (Prakash

et al., 2021), where acoustically orienting bats take longer to capture an individual singing in a chorus than one singing alone.

Many species have a calling song with a rhythm or distinct sound envelope that is species specific and females only respond to the song if they recognize that rhythm or sound envelope. By cooperating to synchronize their songs, groups of males maintain the species-specific rhythm and/or distinct sound envelope. Otherwise females would hear nearly continuous sound at fairly constant intensity and would not be attracted to the group. Some support for this idea has been found in *Neoconocephalus nebrascensis* (Deily and Schul, 2009) and *Sorapagus catalaunicus* (Greenfield et al., 2017).

Synchronization could also create a 'beacon effect' — an increase in peak signal intensity which leads to an increase in the signal-to-noise-ratio and the distance at which females can detect the group signal compared with a single singer. Computer simulations of *Mecopoda* 'Chirper' chorusing behaviour (Nityananda and Balakrishnan, 2009) show that while leaders have some selective advantage, cooperation among followers to create a beacon effect is an evolutionarily stable strategy.

The above explanations are based on cooperation between synchronizing males such that followers are able to achieve greater fitness in a chorus (more mates on a per capita basis) compared with singing alone or in a non-synchronous chorus. Other explanations see synchrony as a result of competition between males. Where female preferences for leading songs occur, selection favours males that adjust their song timing to increase their incidence of leading songs. Synchrony or alternation may then be an emergent property of this competition to become leader.

7.5.3 Mechanisms of synchrony and alternation

The male's singing rhythm is regulated by a central pattern generator (oscillator) in the nervous system (Section 5.1) and each male has an intrinsic rate of singing. But the rate is not fixed and males can adjust it. In some species *(e.g. Neoconocephalus ensiger*: Murphy et al., 2016) a male modifies the rate and phase of his rhythm so that it gradually aligns with his neighbours: slow singers accelerate and fast singers decelerate until all singers are synchronized. This can lead to very precise synchrony. In other species, rather than adjusting their intrinsic rhythm, males lengthen or shorten a single song period after hearing the song of a neighbour (e.g. *Mecopoda elongata*: Hartbauer and Römer, 2016). Both these mechanisms can lead to a kind of synchrony which has been called 'type 1 synchrony' (Greenfield et al., 2017), where the group rhythm remains stable for long periods, leaders and followers can be identified most of the time, and an individual male may sing as a leader or as a follower for a high proportion of the time within a chorusing bout.

In other species such as *Ephippiger diurnus*, synchronization emerges as the result of an 'inhibitory-resetting mechanism' (Greenfield et al., 2016). In this model, which has been called 'type 2 synchrony' (Greenfield et al., 2017), a male interrupts his own song when he hears a neighbour sing, stays inhibited from singing until the neighbour's song ends, then rebounds to produce the song that was suppressed, thereafter resuming his intrinsic rhythm. When a local group of males sing with similar intrinsic rhythms, an approximate synchrony emerges if the male's rebound phase is about the same length as the free-running song period; but if the male rebounds more quickly, he will sing out of phase with his neighbour, i.e. they will alternate. Even so, there will still be some degree of synchrony because the neighbour's neighbour will also alternate with that neighbour and as a result will be in

synchrony with the original male. The process therefore may create a series of small interlacing groups that chorus in a mixture of synchrony and alternation. Unlike type 1 synchrony, leader and follower roles switch frequently between males during a chorusing bout.

Greenfield et al. (2017) argue that type 1 synchronies should be favoured by selection when the overall characteristics of the chorus are adaptive, for example where it is critical to maintain a species-specific rhythm or to generate a beacon effect. Here males must cooperate if they are not to reduce the attractiveness of the group and ultimately their own mating success. On the other hand, because type 2 synchronies are much less regular, the inhibitory resetting mechanisms that generate them would not be favoured by selection if overall chorus characteristics are adaptive. Instead, they should be more likely where competition between individual males within the chorus is the key factor and overall characteristics such as synchrony are of little importance either to the males that produce the chorus or to the females who are listening. Here the synchrony probably emerges as an incidental property with negligible adaptive value.

Whether a species shows type 1 or type 2 synchrony does not seem to be related to its phylogeny and even two species from the same genus may have different types. Greenfield et al. (2017) compared *E. diurnus* (with its irregular type 2 synchrony arising from an inhibitory-resetting mechanism) with the related species *Sorapagus catalaunicus*, which has a steadier type 1 synchrony. They found that *S. catalaunicus* chorusing arises from a strikingly different mechanism from that in *E. diurnus*: males simply do not initiate songs during a 500–700 ms period after the end of a neighbour's song. This ensures a minimum period of silence between sound envelopes broadcast in the chorus. Chorusing in *S. catalaunicus* is therefore potentially the result of cooperation between males driven by a female's requirement to hear a distinct sound envelope while that in *E. diurnus* probably reflects male–male competition caused by female preference for leading songs. However, this is not the whole story because Greenfield et al. (2017) also found that females of both species must hear clear sound envelopes before they respond. Both species also strongly prefer leading songs, though in *S. catalaunicus* the preference extent is extremely short, at about 45 ms (compared with 150–600 ms in *E. diurnus*). Because of neuromuscular constraints, it is likely that an inhibitory-resetting mechanism would therefore not be able to prevent *S. catalaunicus* males producing following songs. There is also very little disadvantage to singing as a follower if the male's song occurs at least 45 ms after the leader, which will be the situation most of the time. They conclude therefore that an inhibitory-resetting mechanism would not have been favoured by selection and, in fact, males do not display it. The mechanism adopted by *S. catalaunicus* works perfectly for a species with a high duty cycle. However, in species such as *E. diurnu*s that have a low duty cycle, distinct sound envelopes will occur regardless of what individual males do, making cooperation to generate synchrony unnecessary. They suggest that this may have allowed the female preference for leading songs to co-evolve with competitive male singing interactions that increased an individual male's frequency of singing as a leader, culminating in the pronounced inhibitory resetting and extended female preferences for leading songs seen in *E. diurnus*.

Support for this suggestion comes from a comparative phylogenetic analysis of 17 populations of *E. diurnus* which have diverged in male song timing and female preference for leading songs (Greenfield et al., 2016). They found that male

adjustments in their song timing correlate with the preference extent, showing that male adjustments co-evolved with female preferences.

In either type of synchrony, adjustments to song timing become problematic in dense choruses. Any male trying to adjust to all of his neighbours by delaying his song each time he heard one of them could end up hardly singing himself. Males appear to solve this problem by attending only to some of their neighbours, usually the ones likely to be their most important rivals for any nearby female.

Greenfield and Snedden (2003) found evidence for such selective attention in two alternating species: the grasshopper *Ligurotettix planum* and the bush-cricket *E. ephippiger*. In the synchronizing bush-cricket *Neoconocephalus spiza*, however, they found that 40% of all males show no selective attention at all and suggested that selective attention is less necessary for synchronizing species: because many of his neighbours sing synchronously, a male does not hear most of them and is therefore unlikely to be 'reset' by them. However some synchronizing species do show selective attention, such as *Mecopoda* and *E. diurnus*.

Fertschai et al. (2007) looked at whether *Mecopoda* males restrict their attention to louder chirps neurophysiologically, behaviourally or through spacing. They found that louder leading chirps are preferentially represented in the omega neuron (Section 5.2) but the representation of softer following chirps is not completely abolished. Following chirps that are 20 dB louder than leading chirps are better represented than leading chirps. Males synchronize with leading chirps even when the following chirps are 20 dB louder. They do not pay attention only to louder chirps but are instead affected by all chirps above a particular threshold. Within the chorus males on average have only one or two neighbours whose songs are above this threshold. Selective attention is thus achieved in this bush-cricket through spacing rather than neurophysiological filtering of softer signals.

Marin-Cudraz and Greenfield (2016) showed that *E. diurnus* shows selective attention to just a few of their loudest neighbours. They also found that attention is most restricted — sometimes to only one neighbour — in populations with the highest duty cycle. In these populations males need to be more selective because indiscriminate attention would seriously interfere with their singing. Thus choruses appear to be finely tuned and controlled by feedback loops in which individual singers generate a collective chorus that, in turn, influences the singing behaviour of those same individuals.

7.5.4 Multispecies choruses

It is common for several species of orthopteran to contribute to the acoustic environment in a particular area: Diwakar and Balakrishnan (2007b) studied a community of 20 orthopteran species in an Indian evergreen forest, all singing over the same 12-hour time period each night and showing considerable overlap in both frequency and temporal patterning of song features.

In such multispecies choruses, therefore, acoustic overlap between species has considerable potential to reduce the efficiency of signal transmission between conspecifics. The amount of overlap depends on several factors, including song structure and intensity, the degree of signal attenuation caused by the habitat, receiver tuning, singer density and the species composition of the chorus. How individuals of a particular species within the chorus manage to communicate with each other despite the potential problems has been the subject of an increasing amount of research in recent years.

Balakrishnan et al. (2014) used simulations to look at the effects of the relative abundance of species and singer density on the levels of acoustic overlap among five orthopteran species from the same Indian evergreen forest mentioned above. There is greater acoustic overlap if species are equally abundant compared with when one species is dominant. Acoustic overlap also increases with singer density but the amount of increase depends on both the song structures of the species and on the relative abundance of species. Differences in acoustic overlap between species pairs are not predictable simply from song structures.

Acoustic interference may be reduced if different species occupy different acoustic spaces. Tiwari and Diwakar (2019) looked at six conehead katydid species from two areas in India and found that sympatric species with similar songs never sing at the same time or from the same location. Some forest multispecies choruses have been found to show vertical stratification in singing height, whereby different species tend to sing at different heights between the ground and the top of the canopy (e.g. Diwakar and Balakrishnan, 2007a; Schmidt et al., 2013).

Schmidt et al. (2016), however, found no evidence in a tropical forest multispecies chorus to suggest that selection pressures resulting from acoustic competition have led to divergence in songs so as to avoid masking interference: different species that sing at the same time, or are close in space, do not have less similar songs than those that sing at different times or at a distance from each other. They argue that selection pressures on sensory/neuronal mechanisms may have been more important in maintaining reliable communication. They have shown, for example, that some of these forest species have a more sharply tuned song frequency than field crickets, which do not need to compete with heterospecific singers.

Similarly, Jain et al. (2014) looked at temporal, spectral and active space overlap between species in a rain-forest assemblage of orthopterans. Although they found that species that sing over the same time period each day may avoid singing together within that time period, there was no relationship between spectral overlap and singing activity and there was little evidence that species actively use spacing to minimize acoustic overlap. A simulation of acoustic spaces integrating temporal, spectral and amplitudinal characteristics of multiple signals showed that increasing song intensity and tuning receivers could be powerful ways to minimize effective acoustic overlap and that for most individuals in the chorus this overlap may actually be close to zero. Thus, song temporal structure, intensity and frequency together provide sufficient acoustic space for several species to sing together yet communicate effectively with other conspecifics with little interference, despite the apparent cacophony of a rain-forest chorus.

8 Predators and parasites

8.1 Natural enemies: risks and defences

As we described in Robinson and Hall (2002), orthopterans are attacked by a large variety of natural enemies and have evolved various defences against them. Many of these enemies, in particular bats (e.g. Jones et al., 2011) and parasitoid tachinid flies from the Ormiini tribe (Lehmann, 2003), eavesdrop on a prey's acoustic signals and use them to home in on its position. Non-singing females approaching a singing male are also vulnerable: predators can locate them due to the noise and vibrations they make while moving or they may be attacked by parasitoids when close to a singing male. The risks associated with singing for the male have been shown to be

equivalent to risks associated with phonotaxis for the female in the tree cricket *Oecanthus henryi* (Torsekar et al., 2019). However, in some species at least, movement may actually increase the risk of bat predation for both males and females more than singing does (Geipel et al., 2020; Raghuram et al., 2015).

Each predator or parasitoid species usually attacks a variety of orthopteran and other species, but may prefer some prey species over others or find them easier to locate (Falk et al., 2015; Grant and Samways, 2015). For a particular orthopteran species, therefore, the selection pressures affecting them will be determined not only by which species of predators and parasitoids are present but by which other species of orthopteran they mix with (Goodale et al., 2019; Trillo et al., 2019).

Orthopterans in turn can detect approaching predators and parasitoids using the noises and vibrations they make (e.g. Kilmer et al., 2010) and the air disturbances they create (Lewkiewicz and Zuk, 2004). Filiform hairs located on the cerci can detect the faintest movements of the air (Jacob and Hedwig, 2015; Magal et al., 2006). Some species have auditory units tuned specifically to frequencies appropriate for detecting predators, for example the echolocation calls of bats (Section 5.2).

Orthopteran species have evolved various strategies for avoiding detection by predators and parasitoids, including reducing the time spent singing, reducing the duty cycle, avoiding singing when predators or parasitoids are active (e.g. Bertram et al., 2004), singing at a frequency that the predator or parasitoid cannot hear well (e.g. Dobbs et al., 2020), singing more quietly, switching to vibrational instead of sound signals (e.g. Römer et al., 2010), and/or singing at the same time as other conspecifics (e.g. Trillo et al., 2019). Once a predator has been detected, orthopterans may react defensively to try and avoid being captured, such as switching to low-intensity song so only a nearby mate can hear, stopping singing completely for a time (e.g. ter Hofstede et al., 2010), and/or producing a defensive sound (a noise directed at a predator that improves the chances of survival; for a review of defensive sounds see Low et al., 2021). Haglids in the genus *Cyphoderris* have an unusual stridulatory method of producing a defensive sound, probably directed at ground predators, using Ander's organ (Woodrow et al., 2021). Ceasing singing has been shown to be a successful strategy in *Neoconocephalus ensiger* (ter Hofstede et al., 2008). But attempts to avoid detection and capture are not always successful, and acoustically-orienting predators also use other methods of finding prey such as echolocation (e.g. ter Hofstede et al., 2017).

Some orthopteran species are predatory themselves and may use sound to capture their own prey. The katydid *Chlorobalius leucoviridis*, for example, preys on cicadas and can attract male cicadas by imitating the species-specific wing-flick replies of sexually receptive female cicadas (Marshall and Hill, 2009). This aggressive mimicry is accomplished both acoustically, with tegminal clicks, and visually, with synchronized body jerks.

8.2 Variation in response

Just because a species is able to hear echolocating bats does not necessarily mean that it will react defensively if a bat is detected. Symes et al. (2020) found that many of the species of neotropical katydids on Barro Colorado Island do not stop singing when exposed to bat echolocation sounds, even though they are able to hear them. Probably fewer than 10 of the 76 bat species on the island eavesdrop on singing katydids, and the other bats pose no threat. Since the katydids are unlikely to be

able to discriminate between the sounds of different bat species, stopping singing every time they hear a bat would severely disrupt their ability to attract a mate. Instead most of the katydid species show 'proactive' defence in the form of very reduced signalling rates, making them difficult for eavesdropping bats to locate. Symes et al. (2020) argue that even when they are capable of detecting predators, proactive defence has greater benefits than reactive defence when predator cues are not strongly correlated with the risk of actual attack.

Defence strategies that reduce the duty cycle, the overall amount of singing, or the distance at which the calling song can be heard, or which change the frequency or characteristics of the calling song can be advantageous in terms of reducing the selection pressure imposed by predators and parasitoids. However, they are disadvantageous both for males in terms of attracting mates (e.g. Dobbs et al., 2020) and for females in terms of perceiving and discriminating a conspecific male song against background noise (Römer et al., 2011). The balance between natural selection (predator pressure) and sexual selection (mating success) will vary between species, and between populations of the same species, depending on the particular enemy species that are present and the local environmental conditions that affect signal transmission (see Section 3.9). Differences in signalling behaviour between populations has been recorded in numerous species, for example the bladder grasshopper, *Bullacris unicolor* (Couldridge and Gordon, 2015). Hawaiian populations of *Teleogryllus oceanicus* vary in the level of risk from parasitoids and the level of risk correlates with the length of time males cease singing after a potential parasitoid is detected (Lewkiewicz and Zuk, 2004).

On the other hand, some species have been found to show no differences between populations in the total time spent singing, or the temporal pattern of singing, regardless of the level of risk, for example *Gryllus lineaticeps* (Beckers and Wagner, 2012). And some species respond to high risk by actually increasing 'risky' behaviour. Beckers and Wagner (2018) found that in *G. lineaticeps*, both females and parasitoids prefer faster chirp rates, yet males in populations with a higher risk of parasitoid attack actually produce faster, i.e. riskier, chirp rates. They suggest that, because the parasitoids attack late in the breeding season, males have increased investment in singing so as to maximize their mating success before the advent of parasitoid activity. Lehmann and Lakes-Harlan (2019) argue that, in some species of the genus *Poecilimon*, mating in aggregation might select for increased, not reduced male singing, despite the risk of attack from parasitoids. This is because, once a male has mated, he drops out of the chorus, being unable to mate for a few days while he produces another spermatophore. During this refractory period he is not vulnerable to parasitoid attack. Males preferred by females are also preferred by parasitoids but quick and risky singing might be advantageous if better singers are able to attract females before parasitoids can find them.

In some species, there are consistent differences between individuals in their behaviour in relation to predators. Wilson et al. (2010), for example, identified a 'boldness' syndrome of behaviour in *Acheta domesticus*, in which bolder individuals explore more and are more willing to emerge after a predation event. Bolder males also sing more and bolder females are more willing to perform phonotaxis.

Female mate choice behaviour (choosiness and preferences) and male singing behaviour may also vary with predation risk. In a Florida population of *G. rubens*, adults emerging in spring are not subject to parasitoids whereas those emerging in autumn are. Autumn females are less likely to perform phonotaxis and autumn males

are less likely to sing and more likely to switch to alternative strategies such as silent searching (Velez and Brockmann, 2006).

Individuals may also vary their behaviour depending on their local circumstances, for example in relation to temporal differences in predator pressure, such as in the katydid *Docidocercus gigliotosi* (Römer et al., 2010; see Section 2.3) and the cricket *Acanthoplus speiseri* (Bateman and Fleming, 2013). The likelihood of a male switching to silent searching or satellite behaviour instead of singing may vary depending on the perceived level of risk from predators, as shown in the tree cricket *Oecanthus henryiand* (Torsekar and Balakrishnan, 2020). The two phases of the locust *Schistocerca gregaria* differ in their hearing ability: solitary locusts, which are at greater risk of predation from bats because they fly at night, have hearing that is more responsive to the higher frequencies of bat echolocation calls than is the hearing of gregarious locusts (Gordon et al., 2014).

8.3 A cricket and a parasitoid in Hawaii: evolution in real time

The Australian cricket *T. oceanicus* colonized the Hawaiian islands between 150 and 2500 years ago; it shares its range on some of the islands with the eavesdropping parasitoid *Ormia ochracea* which was introduced some time before 1989 and is most common on the islands of Kaua'i, O'ahu and the 'Big Island' of Hawai'i (Tinghitella et al., 2021). The Hawaiian islands are the only place where the two species occur together (Lehmann, 2003).

In the early 2000s a sex-linked mutation ('flatwing') arose in the *T. oceanicus* population on Kaua'i (Zuk et al., 2006). This mutation reduces or eliminates sound-producing structures by feminizing wing venation and flatwing males are unable to sing. The wings of females, which do not sing, are unaffected by the mutation. The mutation has other costs for males apart from not being able to attract females with a calling song. It appears to act as a master regulatory switch during early development and has pleiotropic effects including feminization of the cuticular hydrocarbon profile (Pascoal et al., 2020). Cuticular hydrocarbons (CHCs) are sexually dimorphic in *T. oceanicus* and function as sexual signals during courtship (Section 2.3); CHCs of flatwing males are less attractive than those of normal males (Gray et al., 2014). The lack of courtship song is also a problem, since it is important in releasing female mounting and in mate choice and as a result females prefer not to mate with flatwings when they encounter them (Kota et al., 2020). Flatwing males also continue to make stridulatory movements and maintain the same degree of 'singing' effort as normal males but cannot actually produce any sound, so they still pay the energetic price of singing without the benefit of attracting females (Rayner et al., 2020).

A different mutation producing a similar flatwing phenotype was found on O'ahu in 2005; O'ahu flatwings show a less drastic loss of secondary wing structures than Kaua'i flatwings, tending to retain more of their harp and cross veins, and often having a scraper, but are still unable to sing (Bailey et al., 2019; Pascoal et al., 2014). Since 2010 the occasional flatwing has also been found on Big Island (Zuk et al., 2018). Recently two other mutations have been found that lead to song loss: 'curlywing' on O'ahu and Kaua'i and 'small-wing' on Big Island (Rayner et al., 2019).

Silent males (i.e. males with these various song-loss mutations) are rarely attacked by *O. ochracea* but cannot attract mates by singing (Zuk et al., 2018). However, silent males are able to compensate for this inability to attract females: they are much more likely than normal males to search silently for females (Balenger and

Zuk, 2015) or to show satellite behaviour (Zuk et al., 2018). The effects on male reproductive success of adopting satellite behaviour versus singing when the chances of attack by parasitoids are high have been modelled by Rotenberry and Zuk (2016). They found that satellite behaviour can compensate for the negative effects of parasitoids, though the effect is slight. However, flatwings also show a strong preference for calling songs with characteristics preferred by females, whereas normal males do not prefer any particular calling song type. Flatwings therefore tend to act as satellites to the most attractive normal males, thus maximizing their chances of intercepting females and simultaneously reducing the mating success of those singing males (Olzer and Zuk, 2018). In addition, flatwings sire more offspring per mating than do singers (Heinen-Kay et al., 2019).

Tinghitella and Zuk (2009) have shown that females from ancestral, unparasitized populations, as well as parasitized Hawaiian populations, will mate with silent flatwing males, so this behaviour must pre-date song loss. Ancestral Australian females discriminate against flatwing males more than Hawaiian females. Tinghitella and Zuk suggest that island colonization favoured females with relaxed mating requirements, which facilitated the rapid evolution of song loss in Hawaii.

However, there is still strong sexual selection favouring singing males. Both flatwing and normal genotype females prefer normal males and are more likely to mate in the presence of courtship song; normal females are especially likely to mate with song (Heinen-Kay et al., 2020). Females reared in silent conditions mimicking the population on Kaua'i are less choosy and more responsive with respect to male calling song compared with females that hear song during rearing (Zuk et al., 2018). This suggests they may be able to compensate for the reduced availability of singers by increasing their responsiveness to the few that are left. Tanner et al. (2019) also found that females are predominantly homozygous normal-wing and their offspring are sired disproportionately by singing males. Yet, overall, the benefits of song loss in terms of avoiding parasitoids must outweigh the costs because the spread of the song-loss mutations has been extremely rapid: more than 90% of males on Kaua'i and about 50% on O'ahu are now flatwings (Zuk et al., 2018). The persistence of singing males in each population reflects the large advantage they have over silent males in terms of mating success, which increases the fewer of them there are.

Very recently, yet another *T. oceanicus* variant has emerged and started to spread. Since 2017 Tinghitella et al. (2021) have increasingly been finding males that produce a novel and extremely variable song. This song, which they call purring, appears to be heritable. It is spectrally unlike the normal song and is produced using structurally different wing morphology. They first found purring males on the island of Moloka'i, in a population which otherwise only had silent males, but since then they have found five more populations on three islands, all of which also have either silent males or a mixture of silent and normal males. *Ormia ochracea* does not respond to purring song but *T. oceanicus* females do. Although females still much prefer normal males, this puts purring males at an advantage over silent males.

8.4 The role of predation in the evolution of communication systems and population divergence

Predation pressure has played an important role in the evolution of communication systems in Orthoptera. In lebinthine crickets, for example, ter Hofstede et al. (2015) argue that the duet between male calling song and female vibrational response (see Section 2.3) probably originated soon after the evolution of bat echolocation. They suggest that the frequency of the male's calling song increased until it was able to

release the female's vibrational startle response, normally triggered by bat echolocation sounds. By then performing vibrotaxis towards the female, the male was able to locate her without having to depend on her choosing him and, by remaining still, the female reduced her risk of predation. So both sexes benefited.

Evolutionary loss of traits is common in diverse taxa over evolutionary time. The selection pressures affecting sexual signals and other non-signalling traits are different. For sexual signals, persistence is favoured by sexual selection because they contribute to mating success for both males and females but loss will be favoured by natural selection if they are exploited by natural enemies. Heinen-Kay and Zuk (2019) argue that most examples of sexual signal loss come from phylogenetic studies, so it is difficult to ascertain the context and key factors responsible for their loss. Since song loss in *T. oceanicus* in the Hawaiian islands has been documented in real time over the last 20 years, they were able to use this species to identify factors that facilitated this evolution and found that losses of non-signalling traits in other taxa show important parallels. In general, a significant cost from the environment, weak selection for persistence, and alternative ways of achieving the purpose of the trait appear to be critical in the evolutionary loss of both sexual signals and non-signal traits.

Selection pressures from parasitoids may also have played an important role in the divergence of populations and ultimately, in speciation. For example, five distinct song types are found in various parapatric and sympatric populations of *Mecopoda elongata* in South India. Dutta et al. (2019) looked at three of the sympatric song types and found that there are significant differences between song types in the probability of being infected with parasitoid larvae. Parasitoid infection rates are extremely high, and Dutta et al. (2019) argue that this creates a strong selection pressure likely to drive any changes in acoustic signals that reduce the probability of detection by the flies, especially as parasitoids show preferences for some song types over others (Sakaguchi and Gray, 2011).

Bailey et al. (2019) argue that the release of cryptic variation following sexual signal loss resulting from predator pressure could have played an important role in speciation. In Hawaiian *T. oceanicus*, the wings of flatwings are morphologically very variable and produce a broad range of acoustic resonances well outside the species' normal range. This could facilitate the rapid evolution of novel songs with frequencies far removed from the narrow range around 5 kHz typical for the species. Receiver structures and physiology would need to coevolve, but on Moloka'i females already prefer to respond to signals produced by some flatwings. Female responses to novel frequencies may therefore be less of a barrier to signal evolution than are the biomechanical constraints on sound production. Widespread secondary trait losses have been inferred from fossil and phylogenetic evidence across many taxa, and Bailey et al. (2019) suggest that such reversals could have played a role in shaping historical patterns of speciation.

9 Conclusions and future work

Despite enormous advances in research on orthopteran acoustics over the last 20 years, there are still many outstanding questions. For example, to what extent is synchronous singing in a chorus adaptive, especially for followers, versus simply being an emergent property, and how do ecological and physiological factors interact to determine the structure of a chorus in the field?

Research since 2002 has also begun to move into some relatively new areas. It is becoming increasingly apparent that behaviour, such as that shown in mate choice, male signalling, and responses to predators and parasites, can be extremely plastic depending on the particular developmental, physiological, social, and environmental circumstances experienced by a species or an individual. Possibly as a result of such plasticity, field researchers or those who try to create more naturalistic protocols for their laboratory experiments are finding that there can be major differences in behaviour in simple laboratory trials compared with the real world. Similarly, it has been recognized that sound signalling cannot be considered in isolation and the interactions between acoustics and other signalling modalities must be considered if a complete picture of orthopertan communications is to be revealed. Studies in all these areas are likely to become increasingly important in the future.

There is also a growing literature on the generally adverse effects on orthopteran communication and behaviour caused by anthropogenic factors such as climate change (Cusano et al., 2016), radiation resulting from nuclear accidents (Fuciarelli and Rollo, 2021), artificial light at night (Levy et al., 2021) and urban and traffic noise (e.g. Bent et al., 2021; Gurule-Small and Tinghitella, 2019; Schmidt et al., 2014). Some species are able to adapt to anthropogenic noise to some extent at least (Gallego-Abenza et al., 2020; Lampe et al., 2014; Sathyan and Couldridge, 2021; Tan, 2020). Others may be relatively unaffected (e.g. Costello and Symes, 2014) and the effects in some cases may even be beneficial (Phillips et al., 2019). The COVID-19 pandemic has provided opportunities for natural experiments to learn how human activities affect orthopteran behaviour (Tan and Robillard, 2021a).

Studies of song loss in the Hawaiian populations of *Teleogryllus oceanicus* that have been taking place since the early 2000s have also dramatically improved our understanding of the evolution of communication systems in orthopterans, and further study of this species and its parasitoid are likely to provide invaluable data for many years to come.

Another relatively recent development is the emergence of automated methods that utilize orthopteran acoustic signalling to survey or monitor population size or density (e.g. Wang et al., 2014), species diversity (e.g. Thompson et al., 2020; van der Mescht et al., 2021), responses to environmental change (e.g. Gibb et al., 2019), or environmental health (e.g. Hill et al., 2019). With the accelerating pace of climate change, these methods can only become more important.

Orthopterans, especially crickets, have long provided model organisms for work on auditory processing in the nervous system and substantial research in this area has continued over the last 20 years. These studies are not only useful for understanding insect systems but are applicable to auditory systems in general and as such will probably continue to be widely relevant.

There are however still some continuing gaps in research. For example, there has been very little work on female song and, in particular, on questions such as whether female song contains any information or whether males choose their mates based on female song. Given the increased interest in male mate choice in recent studies, it is to be hoped that this topic will soon be addressed.

Acknowledgements

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