Chapter 3 Hearing and Sensory Ecology of Acoustic Communication in Bladder Grasshoppers

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Abstract Bladder grasshoppers are a small family of Orthoptera, with ear morphology and physiology, behavior, and sensory ecological features outstanding among acoustic insects. Acoustic communication is characterized by male and female duetting and male phonotaxis. The detection distance of the male signal is exceptional at about 2 km, achieved via stridulation against air-filled abdominal resonators, and exploitation of weather conditions ideal for sound transmission. In at least three species, alternate male morphs occur which are incapable of flight and sound production but copulate with females. Such alternative mating tactics constitute profound selective pressures for sexual competition and the evolution of the communication system. Auditory sensitivity is mediated by an array of six pairs of atympanate ears in abdominal segments A1–A6. The auditory organ, a pleural chordotonal organ, in A1 comprises about 2,000 sensilla, whereas ears in segments A2–A6 are less developed, making pneumorids a unique system for studying the evolution of complex ears from simple precursors.

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3.1 Introduction

Putting into the port of Simon's Town on the evening of 31 May 1836, Charles Darwin claimed that he "saw so very little worth seeing, that I have scarcely anything to say." (pp 425–426 voyage diary; Darwin and Keynes 1988). Had he arrived at the Cape of Good Hope just 8 weeks later, his initial impressions of the southern African subcontinent may have been substantially different. Several decades after, Darwin was to examine a grasshopper in the British Museum collection and recognize it as profoundly modified for the sake of stridulation "…for in the male the whole body has been converted into a musical instrument, being distended with air, like a great pellucid bladder, so as to increase the resonance." (Darwin 1871).

These bladder grasshoppers (Orthoptera; Pneumoridae) comprise an ancient family of Acridid grasshoppers, endemic to the coastal regions of Africa (Dirsh 1965; Flook and Rowell 1997). In situ, Darwin would have heard the males making "a wonderful noise during the night" (p 359; 1871) and seen them gathering around lights in large number. Besides the exaggerated nocturnal signaling of macropterous males though, it is unlikely that he would have uncovered much more in his brief visit, for the 17 currently recognized pneumorid species are highly cryptic, host plant specificity is strong, and all other micropterous individuals are confined to their food plants. A richly complex environment, much phenological specialization, and a plant diversity making it one of the most species-rich areas on earth (Linder 2003), combine to disperse bladder grasshoppers patchily, and at low densities, across space and time. Pneumorids thus face the challenge of navigating social interactions and locating mates under particularly demanding circumstances and it is unsurprising then, that their most notable morphological and behavioral features are those relating to acoustic communication.

A comparison of acoustic behavior and the related sensory system in this group with those of modern, short-horned grasshoppers reveals some striking similarities and differences. For example, in one of the best studied species of Acridid grasshopper, Chorthippus biguttulus, pair formation and mating is initiated by an acoustic duet in which males produce a song with species-specific amplitude modulation, and receptive females respond with a song used by the male to orient toward her (see Chap. 10 by Ronacher). Similarly, it is the male in bladder grasshoppers which initiates pair formation by producing a loud, stereotyped calling song at night. Males call at irregular intervals from a stationary position high up in the vegetation, and they may move distances up to 500 m between successive calls if they do not receive a female reply. Receptive females within hearing range for the male call may respond with a low-intensity call within a fixed time window 720-860 ms after the end of male call. The female response then induces a duet and male phonotaxis, where he makes a short flight, moves up to a high point on the vegetation before calling again, reorienting and repeating the procedure until finally contacting the female. Remarkably, the orientation of the male is extremely direct and accurate once he is within the hearing range of a female response. Given that adjustments must be made in both azimuth and elevation, this performance is reminiscent of the excellent orientation of the parasitoid fly *Ormia ochracea* when approaching its singing male cricket host (Müller and Robert 2001).

In contrast to Gomphocerine grasshoppers, where duetting takes place over only 1–2 m, the distance covered by bladder grasshoppers is in the range of 100 m, and hearing distance can be close to 2 km (van Staaden and Römer 1997). There are three factors contributing to the large discrepancy in the communication range between modern and bladder grasshoppers: (1) differences in call amplitude and spectrum, (2) ideal transmission of the calls under nocturnal conditions, and (3) high sensitivity of hearing organs.

This chapter addresses how bladder grasshoppers detect sounds, decipher meaning in auditory information, and use this to direct adaptive behavior. We focus first on the exaggerated acoustic signaling of duetting pairs, reviewing internal and external filtering imposed by the nervous system and the environmental transmission channel, respectively. We then consider the evolutionary impacts and constraints levied by the presence of a broader audience and finally, entertain the possibilities inherent in a perceptual allocation approach to pneumorid communication.

3.2 Combining Bladders and Acoustic Adaptation Facilitates Record-Breaking Communication Distances

3.2.1 Sound Production Using Resonators

The calling song of males is produced when a scraper with a small row of strong, transverse ridges on the proximal side of the hind femur is moved against a file of strongly sclerotized ridges on the second abdominal tergite. The abdomen of adult males is characterized by a permanently inflated bladder, giving the name to the whole family of bladder grasshoppers. The air-filled abdominal cavity acts as a resonator when the impact of file and scraper is spread across its large surface, creating a sound output of 98 dB SPL at 1 m in the best studied species *Bullacris membracioides* (van Staaden and Römer 1997). In this species, the male call consists of five short, 'noisy' syllables and a sixth long, resonant syllable with its main energy centered around 1.7 kHz, which is unusually low for acridid orthoptera. In other species, the range of carrier frequencies is between 1.5 and 3.2 kHz (Couldridge and van Staaden 2004). The SPL of the short introductory syllables is reduced by 20–25 dB relative to the final syllable.

There is a clear sexual dimorphism in the signals used for acoustic duetting, both in the mechanism by which they are produced and in the acoustic structure and loudness. The female response is rather soft compared to the final syllable of the male call (60 dB SPL at 1 m), and is produced by rubbing teeth-bearing veins on the ventral margins of the wings across raised pegs in a differentiated region of the tergum beneath the resting wing. The female call is produced in series of 1–8 syllables

(depending on the perceived SPL of the male call; see below), with a frequency spectrum from 3 to 11 kHz.

Altogether, the characteristics of male and female calls in the acoustic duet, and the roles of both sexes in pair formation are rather typical for duetting species (see review by Bailey 2003 for similar cases in duetting *Phaneropterinae katydids*): it is the male covering most of the costs associated with conspicuous signaling, as well as locomotion toward the female (Zuk and Kolluru 1998). These high costs of signaling and movement might have been important for the evolution of alternate male forms and mating tactics. Furthermore, since the signal with the smallest active range limits acoustic communication in duetting species (Zimmermann et al. 1989), it is the soft female reply and not the exaggerated male call which finally determines the range over which pair formation in bladder grasshoppers takes place.

3.2.2 Sound Transmission in the Natural Habitat

Although it is quite uncertain whether maximum range of detection is the primary selection pressure on animal vocalizations (Michelsen 1978; Richards and Wiley 1980; Römer 1998; Wiley and Richards 1978, 1982), bladder grasshoppers provide one of the best examples of how animals might use constraints imposed by the acoustic conditions of the habitat to maximize broadcast range of their signals. Observations of calling times and meteorological conditions at night revealed that acoustic communication only occurred after strong temperature inversions formed at the surface shortly after sunset, accompanied by calm wind conditions with speeds of <2 m/s. This contrasts with the super-adiabatic conditions from mid-morning to mid-afternoon, in which temperature drops rapidly with height above the hot ground surface. Strong differences were observed when signal transmission through the natural environment of the insect was determined for these two atmospheric conditions (van Staaden and Römer 1997). During the afternoon, the super-adiabatic situation produced an upward refracting of sound and a sound shadow zone, with a consequent marked drop and high variability in SPL of the male signal starting at a distance of about 50 m. By contrast, temperature inversions after sunset were downward refracting, resulting in a tunnel effect where the sound was caught between these zones of different temperature and the ground. Therefore, attenuation of the male call approached ideal values according to geometrical spreading of sound for distances up to 450 m at a nocturnal time when males and females actually communicate. Due to these rather different atmospheric conditions, hearing distances for the male signal are 120-200 m in the afternoon, but between 1.4 and 1.9 km at night, arguably the largest hearing distance yet reported for insects.

Since pneumorids' success in mate detection is entirely dependent on longdistance acoustic signaling, one may reason that natural selection should have molded signal form and transmission to maximize communication efficacy. Moreover, across the entirety of their geographical distribution range, the pneumoroidea occupy diverse biomes from open savanna and succulent karoo, averaging 0.5 m in vegetation height, to the more complex heathland vegetation ("fynbos"), and forest biomes topping out at 20 m. This combination of features provides an ideal test case for the Acoustic Adaptation Hypothesis (AAH), which predicts that the transmission efficiency of long-distance signals should be greater in native than non-native habitats (Morton 1975). The performance of male advertisement calls of bladder grasshoppers were directly compared in forest, fynbos, savanna, and succulent karoo habitats (Couldridge and van Staaden 2004). Transmission distance and signal fidelity measures indicated that the physical structure of forest and fynbos biomes imposes strong selection pressure on signal production of their native species. Additional challenges in these two habitats are posed by the highest levels of ambient/biotic noise in forests, and inconsistency in transmission efficacy/signal degradation in fynbos. Together, these selective forces have molded communication signals in forest and fynbos species which propagate with lower levels of distortion over distance in their native habitats, and in the case of fynbos taxa, have lower levels of signal attenuation over distance in all but the forested environment. Many of the design features for superior (distance/fidelity) transmission predictably accord with predictions of the AAH, e.g., repetitive syllable elements in dense habitats, and short signals with rapid rise time in open ones, though B. obliqua native to fynbos has a very gradual rise time over signals of 6 s duration. Environment-related adjustments in the structure of vocal signals appear to be constrained by additional selective forces in the succulent karoo and savannah biomes, and there is thus no overall support for AAH across all pneumoridae. This is clearly not due to constraints by call function as frequently found in anurans, mammals, and cricket assemblages (Ey and Fischer 2009; Jain and Balakrishnan 2012). However, the test is a conservative one, with transmission experiments conducted under rather narrowly defined wind/temperature conditions, and it is unclear whether the results would hold up under more variable weather conditions.

3.3 Serial, Non-tympanal Hearing Organs Provide the Sensory Basis for Sophisticated Behavior

Given the detailed duetting behavior and the sophisticated use of atmospheric conditions at night for maximizing the active range of the signal, it is a surprise to note the absence of tympana in the abdominal hearing organs, which are typical for ears of modern grasshoppers. In order to determine the neural basis underlying pair formation behavior in *B. membracioides*, van Staaden and Römer (1998) and van Staaden et al. (2003) used anatomical, neurophysiological, and behavioral analyses to define the extent to which this species possesses functional ears despite the lack of tympana.

At the same position, laterally in the first abdominal segment where in modern grasshoppers a pair of tympanal ears is located, the bladder grasshopper lacks a thinned tympanic membrane, but nevertheless, there is a pear-shaped pleural



chordotonal organ (plCO1) in a corresponding location as the Müller's organ (Fig. 3.1a). The receptor organ in Bullacris is much larger in size and houses about 2,000 sensilla, compared to only 80 in the locust (Gray 1960; Jacobs et al. 1999). A striking similarity between plCO1 and Müller's organ is the attachment to the

◄ Fig. 3.1 a, b Location and structure of the pleural chordotonal organ (plCO1) in abdominal segment 1. a Dissection of the A1 segment, a pair of pleural chordotonal organs is located in air-filled cavities (*arrows*), where the attachment cells of the scolopidia attach directly to the cuticle of the abdomen, without tympanal specializations. b Retrograde cobalt backfill of plCO1 *B. membracioides* through the sensory nerve labels axons, cell bodies, and dendrites of the sensory cells. Note one small group of sensory cells (*arrow*) with a connection to the cuticle via a separate thin bundle of attachment cells. c–g Bladder grasshopper species and morphs. c From left to right: adult forms of *B. membracioides* uninflated, alternative male, female, inflated male. d Adult male *Physemacris variolosus*. e Female *Pneumora inanis*, f adult male *B. discolor*, g alternate male and adult female *B. unicolor*

pleural cuticle of A1 via a thick and a thin bundle of very long attachment cells separated by more than 1 mm (Fig. 3.1b). In Müller's organ as well, one group of sensory cells (d-cells) connects to the tympanum via a thin bundle of attachment cells to a site different from the majority of receptor cells. Only about 30 sensilla in Bullacris have their attachment cells within the thin bundle. This morphological arrangement suggests that this small group of sensilla may well represent the ancestral precursors of the 12–14 high-frequency d-cells in modern grasshoppers, although the frequency tuning of these sensilla is currently unknown. Each sensillum comprises a bipolar sensory cell, a scolopale cell, an attachment cell, and a glial (Schwann) cell. At the ultrastructural level, sensilla in Bullacris conform to the basic structure of scolopidial sensilla as in other insects and mechanoreceptive organs (Yack and Fullard 1993). In Bullacris, five further pairs of plCOs exist in abdominal segments A2–A6, suspended between the sternal apodeme on one side and their site of attachment to the lateral body wall on the other. The plCOs 2–6 contain up to 11 sensilla per organ.

Extracellular multiunit recordings from the afferent nerves carrying the axons of pleural organs in A1–A6 revealed their nature as functional, serial homologous ears. All receptors responded to acoustic stimulation within a biologically meaningful intensity and frequency range, but with differences in tuning and thresholds. The best frequency of plCO1 was 4 kHz, and thus mismatched to the male song's carrier frequency of 1.7–2 kHz. Surprisingly, despite the absence of an overt tympanum, the organ is extremely sensitive at its best frequency with an average threshold of about 13 dB SPL in normal males, and about 20 dB SPL in alternate males and females. By contrast, receptors in plCOs 2–6 had best frequencies that matched the carrier frequency of the conspecific male signal (Fig. 3.2), but were significantly less sensitive with thresholds ranging from about 60–75 dB SPL.

The physiological background for the tuning of the pleural organs in the segments A2–A6 "matched" to the male call is currently unknown, but cannot be attributed to the mechanical resonance properties of the inflated abdomen since (1) the same tuning is present also in females lacking the inflated abdomen and (2) male and female pleural organs do not differ significantly in their thresholds. By comparing a number of atympanal chordotonal organs in other insects, we suggested that tuning to mechanical oscillations close to 2 kHz is a common property of such organs rather than an adaptation to the carrier frequency of the male call in *B. membracioides*. The list includes chordotonal organs on various body parts



Fig. 3.2 Power spectra of male–female duetting signals (*shaded areas*) and neurophysiological tuning curves in *B. membracioides* for plCO1 (*bold line*) and plCO of A2–A6 (fine lines, not to scale) for a receiver of the opposite sex. **a** Male sender, female receiver; **b** female sender, male receiver (n = 10 individuals). **c** Adult male with strongly inflated abdomen. Location of stridulatory file arrowed; location of plCOs in A1–A6 indicated by rectangles. The oscillogram shows a male–female duet in *B. membracioides*

in different taxa (Pflüger and Field 1999; Yack and Fullard 1990; Cokl et al. 1995; Shaw 1994; Cokl and Virant-Doberlet 1997; Yager 1990). The organs exhibit also variable thresholds from 55 to 80 dB SPL, similar to the range of thresholds covered by the plCOs in segments A2–A6 of the ancestral insect studied here. This suggests that mechanical tuning is unlikely and favors an explanation intrinsic to the sensory neurons, as discussed for the tuned afferents in the crista acustica of katydids (Oldfield 1985). If this is the ancestral condition of chordotonal organs for the detection of airborne sound in acridids or pneumorids, it would represent a preadaptation for the evolution of a long-distance male call at a frequency where the female organs are most sensitive (see Chap. 2 by Strauß and Lakes-Harlan).

3.4 The Functional Significance of Pleural Hearing Organs in Male–Female Duets

The data in the previous sections demonstrate, on the one hand, a sexual dimorphism in the signals used in the acoustic duet between male and female bladder grasshoppers, and on the other hand a difference in tuning and sensitivity in the serial homologous ears in A1 compared to A2-A6. As indicated in Fig. 3.2, plCO1-afferents are not tuned to the main CF of the male call, but would be most sensitive to components of the female reply. Indeed, in behavioral playback experiments with receptive females using model songs of males with carrier frequencies either at 1.7 or 4 kHz, almost no female reply was elicited with the higher frequency, but close to 100 % with the lower one. Since the playback intensity was 75 dB SPL for both frequencies, the plCO1 was stimulated more than 40 dB above its threshold, in contrast to only 15 dB for the pleural organs in A2–A6. Even after the ablation of plCO1-receptors on both sides, the behavioral response of females was unaffected, indicating that their reply in duetting is mediated on the afferent side only by these less sensitive pleural organs (van Staaden and Römer 1998). A further indication for the direct role of the pleural ears in A2-A6 comes from the observation that females add approximately one syllable to their acoustic reply with each 3 dB increase in SPL of the male song above the threshold of the behavioral response at about 60 dB SPL, which is also the threshold of the pleural organ in A2. Apart from this strong correlation between activation of more pleural organs with increasing SPL of the male call and the increase in the behavioral response, this system is also remarkable in that the female, via the number of syllables in her reply, appears to signal to the male very reliably her proximity.

For males it is tempting to speculate, based on the overlap of call energy and tuning of plCO-sensory neurons in A1, that their function is the detection and discrimination of the much softer female call. In this context, it would indeed be rather adaptive for males to evolve the high sensitivity as observed in the physiological responses, in order to detect a responding female at the greatest possible distance. However, in order to demonstrate a causal relationship between the plCO1 activity and the acoustic duetting and possible phonotactic behavior of males, this would require a similar ablation experiment as in females, but this time the ablation of all five pairs of pleural organs in A2–A6, which has not been done so far.

3.5 Frequency and Intensity Discrimination may Provide Distance Estimation

Members of the Pneumoridae are the only known insects with serially repeated, functional ears which differ in their tuning (if we exclude those taxa with tympanate hearing and additional sensitivity to low frequency sound of wind-sensitive hair sensilla on the cerci). So far we do not know whether the 2,000 receptors in plCO1

are tuned to the same or different frequencies. But given the homology in structure with the Müller's organ of modern grasshoppers, the few receptors with their attachment site far away from the main bundle could be tuned to higher frequencies, as the d-cells in locusts and other grasshoppers (Michelsen 1971; Römer 1976; Jacobs et al. 1999). The fact that females do not respond to song models with a carrier of 4 kHz (the best frequency of plCO1-receptors) indicates some kind of frequency discrimination, although this is not as elaborated as the categorical perception of sound frequency in crickets (Wyttenbach et al. 1996; Moiseff et al. 1978), or the discrimination of the sexes by spectral differences in the signals in some grasshoppers and katydids (Dobler et al. 1994; von Helversen and von Helversen 1997).

Probably, more important than the tuning of receptors and corresponding frequency discrimination is the evaluation of actual sender-receiver distances during duetting. Females modify their reply with distance from the calling male, adding about one syllable per 3 dB increase in loudness (van Staaden and Römer 1998). The sensory basis for this behavior could be the general intensity-response characteristics of receptors, firing at a higher rate with increasing stimulus amplitude. The fact that in Bullacris all plCOs in A2-A6 are tuned to the same frequency of about 2 kHz, but differ in their absolute thresholds (Fig. 3.2) offers a more likely solution (see Fig. 3.3): depending on distance and thus loudness of the male call, more and more hearing organs are stimulated, and within the population of 11 afferents in each organ, the firing increases as well. Thus at a distance of 30 m plCOs in A5 and A6 do not respond at all to the male call, whereas those in A4-A2 respond only to the last, final syllable (Fig. 3.3). Closer to 8 m, the final syllable is suprathreshold even for the least sensitive A6 receptors, and in addition even the soft introductory syllables of the male call are faithfully encoded in the discharge of neurons in A2 and A3. Thus, the number of pleural organs activated, and the degree of activation within each organ provides the female with reliable information about distance to the male. Such a coding scheme, where the number of receptor neurons being suprathreshold increases with increasing stimulus amplitude is known as range fractionation (for review see Hedwig and Pollack 2008). But in contrast to other insect species where more afferents in a single organ are recruited for encoding the distance to the signaler (Roeder and Treat 1957; Römer

Fig. 3.3 Neural responses of pleural hearing organs and distance perception. Extracellular multiunit recording of the activity of female plCO in A2–A6 in response to a male call perceived at distances of 8 m and 30 m



1987; Oshinski and Hoy 2002; Römer et al. 1998), in Bullacris additional serial repeated ears are recruited for this task.

Interestingly, observations in the field indicate that the SPL of the male call is not always close to 100 dB, in particular when the male has established reliable duetting with the female, when both are within the active range of their signals. In these cases, males often down-regulate the SPL of their call, with the consequence that the above-described activation of pleural receptors in the female decreases again. However, the decrease in loudness of the male call happens at close range (distance about 10 m) when all pleural organs are activated, and apparently is not strong enough to interrupt the duet. One selection pressure for this behavior might be the competition by "unintended receivers" from conspecific males, particularly alternate male morphs (Zuk and Kolluru 1998; McGregor 2005).

3.6 A Diversity of Signals and Receivers: What is Being Signaled and to Whom?

The nature of the duetting and the similarity of all female responses across pneumorid taxa indicate that females are responsible for the recognition/choice continuum in an intersexual context. However, short-term adjustments of male signals to social conditions allude to the presence of additional selection pressures. In all cases though, the challenges of communicating at a distance requires a bladder grasshopper to (i) detect signals against background noise, (ii) identify signals as stemming from a conspecific, and (iii) rate the attractiveness of signals.

Long-range signaling results in significant call degradation along the transmission channel, and the expectation is that signals will become less distinguishable and therefore less attractive at greater distances. Playback of degraded male calls in the absence of intensity cues indicated that both signal quality and amplitude are important determinants of preference for pneumorid females. Although females responded to signals with degradation levels equivalent to a male calling 150 m away, but intensity equivalent to one at 25 m, suggesting that call amplitude is a limiting factor, responses to conspecific calls decline significantly with decreased signal quality (Couldridge and van Staaden 2006). Unlike Ch. biguttulus (Einhäupl et al. 2011), pneumorid males have not solved the problem of retaining attractiveness cues in the face of signal degradation. Specific identity, on the other hand, is contained in the male call of at least some taxa. In interspecific preference tests with sympatric congeners B. intermedia and B. serrata, B. membracioides females discriminate only against the calls of B. serrata (Couldridge and van Staaden 2006). They also exhibit preferences for the songs of particular conspecific males in a typical sexual selection scenario where males provide females no resources or direct benefits (Couldridge and van Staaden 2006). However, it is difficult to identify the precise call features that are responsible for these differences in attractiveness. In playbacks to female B. membracioides, multiple regressions identified all but one of eight measured call features (intersyllable interval)

as significantly correlated with female preference. Enhanced female responses appear to be driven by short/high-frequency introductory syllables, and longer/low frequency final syllables, it would be interesting to know whether this is a step function, and at what combination of features (i.e., duration, frequency, or rise time) the differential female response saturates.

3.7 Alternate Males

In at least three species of pneumorid, there are alternate males which are incapable of flight and sound production because they lack macropterous wings and the inflated abdomen, but retain the strong host-plant philopatry of nymphal stages and can be found in the field in copula with females (Alexander and van Staaden 1989; Fig. 3.1). Despite the fact that inflated and alternate morphs follow distinctly different developmental trajectories in attaining their final forms (Donelson and van Staaden 2005), tuning and sensitivity of their hearing organs is identical (van Staaden et al. 2003). Costs and benefits for polyphenic males differ strongly though, with adult longevity of small, uninflated males twice that of the larger inflated ones (Donelson et al. 2008). Both morphs exhibit positive phonotaxis to conspecific female calls in playback experiments, but differ markedly in their response to male signals. In this situation, primary males move perpendicular to the stimulus source, whereas alternates remain stationary (Donelson and van Staaden 2005). Rather than actively searching for mates over great distances then, alternate males eavesdrop on duets and intercept responsive females before the normal, flighted male arrives. Such satellite tactics exacerbate the already intense intrasexual selection posed by calling males.

The sensory and communication system is subjected to antagonistic selective forces emerging from the production of shorter range acoustic signals including female responses (ca. 50 m), disturbance signals (ca. 5 m), and putative territoriality signals emanating from the mouth and functional at very short range (<0.1 m) as well.

3.8 Acoustic Energy Catch and Perceptual Allocation

The complexity of pneumorid acoustic communication in terms of sensory infrastructure, signal range and transmission characteristics, repertoire size and potential audience raises many questions, which might best be characterized as interaction effects. Perceptual allocation approaches attempt to mimic the basic features of sensory systems, and have been used to explore the key mechanisms underlying sensory detection and recognition as well as the hidden preferences that may emerge as a byproduct of such mechanisms (Enquist and Arak 1993; Phelps et al. 2001). As such, they may provide a useful complement to sensory ecology for understanding how the contingencies of the evolutionary process shape nervous systems to accommodate conflicting demands.

3 Hearing and Sensory Ecology of Acoustic Communication

We find intriguing the suggestion by Phelps (2007) of an acoustic equivalent for the quantum catch concept, which has been exceptionally useful to those in the quantitative visual sciences (Anderson and Laughlin 2000; Stavenga 2004). In visual systems, the perception of chromatic signals can be approximated using quantum catch models that predict the absolute or relative amount of available light a sensory system can "catch," and this is done regularly, e.g., in aquatic visual ecology (reviewed briefly by Smith et al. 2012). However, it is important to note that the general principles underlying quantum catch models can be extrapolated to the acoustic realm via the replacement of analogous variables (Phelps 2007) to estimate the sound energy captured by a receiver. As such, we can use the following equation to investigate auditory systems (Eq. 3.1):

$$AC_{abs,S} = \int_{x}^{y} S(f) T_{e}(f,d) R(f) df$$
(3.1)

Where AC_{abs,S} is the absolute energy transduced from a given signal (henceforth called acoustic catch), *x* and *y* are the bounding frequencies for the signal calculation, S(f) is the energy available in the signal at a given frequency, $T_e(f, d)$ is the transmission of the signal through the environment at distance *d*, and R(f) is the neural sensitivity for the acoustic signal. This equation can be modified to yield the relative acoustic catch of the auditory system for any given signal (Eq. 3.2):

$$AC_{rel,S} = \frac{AC_{abs,S}}{\int_x^y S(f) T_e(f,d)}$$
(3.2)

Using these equations, we can effectively predict the ability of an acoustic organ to transduce the energy of any sound signal with four pieces of information: (i) frequency tuning curves for receptors in the organ, (ii) spectral characteristics of the signal in question, (iii) frequency-specific attenuation measures for the transmission through the environment, and (iv) background noise measures. In the pneumorids, we have one of the few insect systems where information is available on all of these elements.

Although for most insects it is the temporal structure of calls that is critical, we argue that acoustic catch is a reasonable approach for pneumorids because (1) of the importance of frequency and intensity discrimination (demonstrated in 3.6 above), (2) the frequency shifts observed when two calling males interact acoustically (unpublished data), and (3) due to the extent that the female acoustic response depends on a match between ear tuning and stimulus frequency (van Staaden and Römer 1998). Here, we make a first pass in simplified form using *B. membracioides* tuning curves obtained by recording the auditory nerve, male signal characteristics, and signal transmission (van Staaden and Römer 1998) without frequency-specific attenuation information, i.e., assuming the shape of the signal is unchanged with distance, which it most certainly is not. Some pneumorid taxa share overlapping geographic distribution throughout their range, so signals from heterospecifics can form a substantial part of their natural acoustic environment. To explore the power of the AC approach, we thus compared the relative



Fig. 3.4 a Relative acoustic catch (AC) of *B. membracioides* pleural hearing organs in A1–6 for conspecific (*open circles*) and heterospecific (*filled squares*) male calls. Relative acoustic catch represents the total acoustic catch of each plCO normalized to the total acoustic energy of the call for which the AC was calculated. Heterospecifics include taxa native to savanna (*B. intermedia, B. serrata*), forest (*Pneumora inanis*), fynbos (*B. obliqua, Physemacris variolosus*), and succulent karoo (*B. unicolor*). b Comparison of AC estimates for the auditory system of *B. membracioides* and a conspecific call (*open circles*) or a conspecific call shifted by 1.5 kHz toward higher frequencies (*open squares*)

stimulation of *B. membracioides* hearing organs for a conspecific male signal, as well as for signals of six heterospecifics.

For *B. membracioides*, plCOs catch proportions of available signal energy in the male call ranging from a high of 72 % in plCO1, through 44 % plCO2; 50 % plCO3; 52 % plCO4; 52 % plCO5, to 33 % in plCO6. Given the critical importance of acoustic signaling in mate detection and acquisition, it is also instructive to explore the catch of *B. membracioides* for heterospecific signals namely *B. intermedia*, *B. unicolor*, *B. serrata*, *B. obliqua*, *Physemacris variolosus*, and *Pneumora inanis*. Interestingly, whereas the plCO1 is equally sensitive to the calls (70–75 % "catch") of all these taxa, plCO2–6 perform better for the conspecific call than for any of the other taxa (Fig. 3.4). This is somewhat surprising given the relatively large overlap in frequency spectra of the different species' calls (see Figs. 3.1 and 3.2 in Couldridge and van Staaden 2004; 2006, respectively). Thus

whereas *B. membracioides* hear female calls of all taxa equally well with the high sensitivity plCO1 receptors, a subset of hearing organs (plCO2–6) appear to be selective for conspecific signals. To explore how changes in signal characteristics might affect catch of the auditory organs, we shifted the sample *B. membracioides* call 1.5 kHz toward higher frequencies and found that the response of the auditory system decreased such that it closely matched the response to heterospecific signals (Fig. 3.4).

As an initial validation of the acoustic catch approach, these preliminary analyses demonstrate considerable potential, and suggest that the boundaries of signal plasticity within species may be rather narrowly delineated in the frequency domain. Combined with measures of frequency-dependent attenuation and tuning curves from additional taxa, such analyses could be used to test hypotheses concerning signal evolution, and both internal (sensory) and external (environmental) sources of filtering (for cases in crickets see Schmidt et al. 2011; Schmidt and Römer 2011).

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