Acoustic defence in an insect: characteristics of defensive stridulation and differences between the sexes in the tettigoniid Poecilimon ornatus (Schmidt 1850)

Kerstin N. Kowalski⁎, Reinhard Lakes-Harlan⁎, Gerlind U.C. Lehmann⁎, Johannes Strauß⁎

⁎AG Integrative Sensory Physiology, Institute for Animal Physiology, Justus-Liebig-Universität Gießen, Heinrich-Buff-Ring 26, D-35392 Gießen, Germany

ABSTRACT

Many insects exhibit secondary defence mechanisms upon contact with a predator, such as defensive sound production or regurgitation of gut contents. In the tettigoniid Poecilimon ornatus, both males and females are capable of sound production and of regurgitation. However, wing stridulatory structures for intraspecific acoustic communication evolved independently in males and females, and may result in different defence sounds. Here we investigate in P. ornatus whether secondary defence behaviours, in particular defence sounds, show sex-specific differences. The male defence sound differs significantly from the male calling song in that it has a longer syllable duration and a higher number of impulses per syllable. In females, the defence sound syllables are also significantly longer than the syllables of their response song to the male calling song. In addition, the acoustic disturbance stridulation differs notably between females and males as both sexes exhibit different temporal patterns of the defence sound. Furthermore, males use defence sounds more often than females. The higher proportion of male disturbance stridulation is consistent with a male-biased predation risk during calling and phonotactic behaviour. The temporal structures of the female and male defence sounds support a deimatic function of the startling sound in both females and males, rather than an adaptation for a particular temporal pattern. Independently of the clear differences in sound defence, no difference in regurgitation of gut content occurs between the sexes.

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1. Introduction

Natural selection favours those individuals that contribute the most to further generations. One key factor contributing indirectly to individual fitness is the survival rate. In response to predation, animals have evolved a great variety of strategies to survive by avoiding to be killed by predators (Edmunds, 1990; Ruxton et al., 2004; Eisner et al., 2005; Ratcliffe and Nydam, 2008; Schmidt, 2009; Conner, 2014). These strategies have been classified into primary defences, protecting the animals from contact with a predator, e.g., by cryptic colouration and mimicry, and secondary defences, important after the contact with a predator (Robinson, 1969; Edmunds, 1974). Different secondary defences may repulse, startle, or confuse the predators (Edmunds, 1974; Gwynne, 2001) by visual display (Stevens, 2005; Vallin et al., 2005), secretion of advesive chemical components (Eisner, 1970, 1972; Whitman et al., 1990; Laurent et al., 2005; Blum, 2009) as well as regurgitation of gut contents (Eisner, 1970; Sword, 2001).

A further sensory channel used for defence is airborne sound. Alexander (1967) estimated that arthropods use sound more often for secondary defence than for any other signalling context. Insects produce acoustic defence by various mechanisms upon contact or when handled, documented from Lepidoptera, Phasmatodea, Mantidae, Coleoptera, Cicadidae, Acrididae and Tettigoniidae (Alexander, 1967; Masters, 1979; Ewing, 1989; Bailey, 1991). It is assumed that defence or disturbance stridulation startles a predator and thereby increases the possibility of escape (Edmunds, 1974; Bailey, 1991; Gwynne, 2001). An experimental study on an Australian tettigoniid showed that disturbance stridulation is indeed effective in repelling a lizard predator (Sandow and Bailey, 1978).

In the Orthoptera, sound production has evolved multiple times during evolution with a crucial function in intraspecific acoustic communication (Bailey, 1991; Robinson and Hall, 2002). For...
mate attraction, male tettigoniids produce a calling song by terminal stridulation, while females approach the male phonotactically (Bailey, 1991; Gwynne, 2001; Robinson and Hall, 2002). In most tettigoniid species, only males have stridulatory structures which are used for sound production, but females have evolved acoustic response songs in a small number of tettigoniid lineages (Heller, 1990; Robinson, 1990; Bailey, 2003).

Despite the thousands of orthopteran species using sound for intraspecific acoustic communication, disturbance stridulation and stridulatory structures have only been described for few grasshopper species (Alexander, 1967; Blondheim and Frankenfeld, 1983), a cricket species (Desutter-Grandcolas, 1998) and a restricted number of tettigoniids (Power, 1958; Bailey and Sandow, 1983; Shaw and Galliart, 1987; Belwood, 1990; Heller, 1996; Bateman and Fleming, 2009; Kowalski and Lakes-Harlan, 2011). In the brachypterous phaneropterine Poecilimon ornatus (Schmidt, 1850), both males and females produce acoustic signals for mate finding (Heller and von Helversen, 1986), which are perceived by well-developed tympanal ears (Strauß et al., 2012, 2014). Male tettigoniids have a sound-producing apparatus on the wings, which are rubbed against each other with a modified, toothed vein (the file) on the underside of the left wing which is moved against the strong edge of the right wing (the plectrum) (Robinson and Hall, 2002). In the Phaneropterinae and Ephippigerinae where females have developed a terminal stridulatory apparatus, these structures are not homologous to those of conspecific males (Nickle and Carlyle, 1975; Heller and von Helversen, 1986; Robinson, 1990; Näske, 2000).

In P. ornatus, females have a particularly complex stridulatory organ consisting of multiple files, with around ten toothed veins on the wings, which clearly differ from the single vein in the stridulatory organ of the male (Heller and von Helversen, 1986). Both sexes also produce defence sounds, the characteristics of which are investigated here. This species allows to analyse possible differences in defence sounds arising from the independent evolution of the respective stridulatory structures.

In general, insect defence sounds appear to be less structured in temporal pattern than species-specific calling songs (Masters, 1980; Shaw and Galliart, 1987; Desutter-Grandcolas, 1998; Kowalski and Lakes-Harlan, 2011). The use of defence sounds for startling a predator has been suggested to be adaptive in those species which lack other possibilities to avoid an attack, such as fast movements or spines (Heller, 1996). Disturbance stridulation is a type of deimatic (startling) behaviour, which generally aims at intimidating predators and occurs both in aposematic and cryptic species in the form of postures, visual display, or sounds (Edmunds, 1974). For tettigoniids, the adaptive use of defence sounds is apparently dependent on additional factors, as species of the African Heterodinae have strong cuticular spines on the thorax and some species also produce defence sounds amongst other secondary defences (Power, 1958; Grzeschik, 1969; Bateman and Fleming, 2009; Kowalski and Lakes-Harlan, 2010, 2013). For tettigoniids, it has also been assumed that an adaptive defence sound, efficiently serving for defence, may be produced by both females and males (Heller, 1996). While defence sounds have been reported for several tettigoniid species (see above), defence sounds in both males and females of a species are rather uncommon (Bailey and Sandow, 1983; Shaw and Galliart, 1987; Elavoa and Korsunovskaya, 2012; for summary see Heller, 1996) and have not been analysed in detail for sex-specific differences.

We hypothesise that if acoustic defence is used to startle predators, the defence sound (i) will be produced spontaneously upon contact, and independent of the site of contact by both sexes, (ii) will be less structured temporally in comparison to the calling song (as found in several other insect species, see Masters (1980) and Desutter-Grandcolas (1998)), (iii) will be more persistent (for a repulsion/startle effect) than the rather short calling song and (iv) will be produced by males irrespective of the mating history, in contrast to the calling song which ceases for several days after copulation (Heller and von Helversen, 1993). The specific function of the defence sound could result in similar characteristics of the sound and its usage in males and females. The defence sounds of males and females would not require specific temporal patterns but they might differ in length or structure, corresponding to the sex-specific differences in stridulatory structures and the calling song durations. In contrast to acoustic defence, other secondary defence mechanisms like regurgitation may be expected to be sex-independent.

2. Materials and methods

2.1. Study animals

The animals were collected as last instar nymphs in Slovenia during May and June 2012 and transferred to the University of Gießen. For the experiments, 17 males and 10 females of the species P. ornatus were analysed (Fig. 1). P. ornatus is a relatively large species of Poecilimon, showing a sexual dimorphism typical of tettigoniids, with larger body sizes in females. Body length (from head to abdomen) of animals was 29 ± 2 mm in males and 33 ± 2 mm in females. The animals were kept in individual cages (Exo Terra, 230 mm × 155 mm × 170 mm; Hagen Inc., Montreal, Canada) with a 12:12 dark:light cycle and a temperature of 24–25 °C. They were fed ad libitum on a daily basis with flowers and leaves of dandelion (Taraxacum officinale agg.), daisy (Bellis perennis) and clover (Trifolium sp.), and received water by spraying the cages once a day.

2.2. Sound recordings and analysis

For the recordings of calling and defence sounds, the animals were placed in a fly screen cage within an anechoic chamber. All recordings were made under daylight conditions, at a temperature of 24 ± 1 °C. We used a capacitor microphone (McCrew MC-18; Conrad Electronic, Hirschau, Germany) connected to a digital recorder (Tascam HD-P2; TEAC Corp., Tokyo, Japan) and a portable digital recorder (Tascam DR-100) with built-in microphones. The microphone was placed at a distance of 15–40 cm from the animals. Sound recordings were made simultaneously with behavioural experiments (see Section 2.3).

Female response sounds (for comparison with female defence sounds) could not be recorded in the lab from the individuals studied. Therefore we analysed publicly available sound recordings made by Klaus-Gerhard Heller and deposited at http://www.biologie.uni-ulm.de/cgi-bin/query_all/query_all.pl?query=poecilimon+ornatus. Recordings from two individuals were analysed (files POOR8701 and POOR8702).

The temporal structure and frequency range of the sounds were analysed with Adobe Audition 3.0 (Adobe Systems, Inc., San Francisco, USA).
Jose, CA, USA). The terminology used for syllables and impulses of the song patterns follows the definitions of Chobanov and Heller (2010). For statistical analysis, Prism 4.03 (GraphPad Software, Inc., San Diego, CA, USA) and Excel 2010 (Microsoft Corp., Redmond, WA, USA) were used.

2.3. Analysis of defence behaviours

Disturbance stridulation was evoked by grasping the animals (17 males, 10 females) consecutively at two different body sites: (i) at the pronotum in such a way that the wings could still be moved freely and (ii) at the hind legs at the joint between femur and tibia. During the experimental series, each individual was tested on six consecutive days for defence reactions (disturbance stridulation and regurgitation) upon contact to the different body sites. A positive defence reaction was registered when an individual reacted to the contact with a defence sound and/or regurgitation.

Furthermore, seven males were used to investigate modifications in defence behaviour following copulation. The individuals’ behaviour was tested for six consecutive days as described above; then animals were mated to a virgin female and tested again six times. These post-mating experiments were performed 10, 40 and 100 min as well as 4, 6 and 24 h after copulation. These time sequences were used to cover the time window after copulation up to one day without the risk of habituation. As P. ornatus was indeed found to produce defence sounds during the first day after copulation, the last test was carried out 24 h after copulation.

3. Results

3.1. Characteristics of male and female sounds

Our analysis of the male calling song showed that it contains trains of short syllables with durations of roughly 13 ms separated by intervals lasting about 10 s (Fig. 3a). The syllables are rather compact and single impulses cannot be clearly distinguished within one syllable.

Defence sound production in both male and female P. ornatus started immediately after contact and continued for a few seconds after mechanical stimulation had ended. In both sexes, the sounds produced showed a broad frequency spectrum ranging from 20 to 40 kHz (data not shown). In males, the temporal pattern of the defence sound differed from that of the calling song: in the defence sound, single impulses could be clearly distinguished within syllables, and these impulses increased in amplitude within a syllable (Fig. 3b). The females’ defence sounds were much more irregular. Most of the females produced single impulses with a high interval variation and few impulses which can be grouped together into syllables, though the temporal pattern showed high variability (Fig. 3c and d).

Quantitative analysis of the temporal features of the defence sounds showed that in males the acoustic reaction contains a significantly higher number of impulses than in females (20.25 ± 2.90 impulses in males versus 5.39 ± 1.67 impulses in females; unpaired t-test; p < 0.0001; T = 10.80; df = 19; N = 35–179 syllables per individual for the male defence sound and N = 18–87 for the female defence sound: Fig. 4a). The syllable duration in a male’s defence sound is significantly longer than in a calling song (male defence: 59.12 ± 10.01 ms, N = 13–64; male calling song: 13.38 ± 1.95 ms, N = 35–179; unpaired t-test: p < 0.0001; T = 17.37; df = 29; Fig. 4b). For females, the syllables of the defence sound are significantly longer in duration than the syllables of the response song (female defence: 24.44 ± 6.63 ms, N = 18–87; female response song: 5.35 ± 0.81 ms, N = 13–32; unpaired t-test: p = 0.0086; t = 4.193; df = 5). The male defence sound is also emitted significantly longer than the female defence sound (male defence sound: 59.12 ± 10.01 ms, N = 13–64; female defence sound: 24.44 ± 6.63 ms, N = 18–87; unpaired t-test: p < 0.0001; T = 7.260; df = 19). The irregular structure of the female defence sound did not allow a measurement of the syllable interval.

In males, interval duration between different syllables was significantly shorter in the defence sound (132.90 ± 27.54 ms, N = 24–257) than in the calling song (10.41 ± 3.13 s, N = 22–225; unpaired t-test: p < 0.0001; T = 13.15; df = 29; Fig. 4c). In addition, variation of the syllable duration was significantly higher in the defence sound than in the calling sound (defence sound: 29.43% ± 7.97; N = 35–179; calling song: 10.11% ± 4.09; N = 13–64; unpaired t-test; p < 0.0001; T = 8.357; df = 28; Fig. 4d).

Comparing the calling/response song, the variation in syllable length was higher in the male calling song than in the female response song (male: 10.11% ± 4.98, N = 13–64; female: 56.24 ± 5.78, N = 13–32; unpaired t-test: p < 0.0001; T = 17.88; df = 14; Fig. 4d). Comparing the defence sounds of both sexes, females showed a significantly higher variation in syllable duration than males (females: mean 77.89% ± 23.19; N = 18–87; males: mean 29.43% ± 7.97; N = 35–179; unpaired t-test; p < 0.0001; T = 7.220; df = 18; Fig. 4d). In males, the variation in syllable duration was higher in the defence sound than in the intraspecific song, but not so in females (defence sound: 77.89% ± 23.19; N = 18–87; response song: 56.24% ± 5.78, N = 13–32; unpaired t-test: p = 0.2706, t = 1.238, df = 5). In males, the variances of syllable duration and syllable interval were statistically significantly different for both the defence sound (male duration variation: 10.11% ± 4.09, n = 16; interval variation 57.52 ± 23.98,
Fig. 3. Temporal patterns of calling song and defence sounds of *P. ornatus*. (a) Temporal pattern of the calling song of a *P. ornatus* male. Individuals produce single syllables in which single impulses cannot be clearly separated (see magnified segment below). (b) Temporal pattern of disturbance stridulation sound in males. Syllables show an increase in amplitude, and single impulses can be distinguished from each other (see magnified segment below). (c and d) Defence sounds of female *P. ornatus* display a high variation in the temporal pattern. Some females produce single impulses (c), while others produce syllables of several impulses (d).
3.2. Analysis of defence behaviours

Our experiments showed that both sexes of the tettigonid species *P. ornatus* used both defence sound and regurgitation as defence behaviours (Fig. 2). Notable differences occurred in the display of disturbance stridulation between male and female individuals. Among males, 10 out of 17 male individuals consistently reacted with sound production in all test trials, while 50% of all tested females (*n* = 10) failed to react with a defence sound at all. In males, most individuals reacted to some degree during trials if the hindleg (15 out of 17 individuals) or the pronotum (16 out of 17 individuals) was touched. Among females, the acoustic response rate was lower, as only 5 individuals displayed disturbance stridulation upon mechanical contact to the hindleg as well as the pronotum. Within the sexes, the overall proportions of disturbance stridulation differed only slightly following contact to the hindleg or the pronotum (Fig. 2a) and were not significantly different (males: stridulation upon contact to hindleg versus pronotum: *p* = 0.545, *χ*² = 0.36565, df = 1; females: stridulation upon contact to hindleg versus pronotum: *p* = 1, *χ*² = 0, df = 1). However, the occurrence of defence sounds was statistically different between males and females following contact to the hindleg (Chi-square test; males versus females: *p* = 0.028, *χ*² = 4.793, df = 1) or contact to the pronotum (Chi-square test; males versus females: *p* = 0.008, *χ*² = 7.09, df = 1).

Both sexes showed regurgitation behaviour upon stimulation of the pronotum with a percentage similar to that of the defence sound production (males: 64.9% ± 34.3; females: 46.6 ± 30.2; Fig. 2b). Like disturbance stridulation, regurgitation was elicited easily. No reactions to mechanical contact during the experimental trials were noted for 2 out of 17 males and 1 out of 10 females. These proportions were not found to be significantly different (Chi-square test; *p* = 0.8879, *χ*² = 0.0196, df = 1).

The acoustic response to disturbance by hindleg contact depended on the sex of the individuals: defence sound production (Fig. 2a) occurred in 74.5% ± 38.3 of all male trials (*n* = 17; *N* = 112) and in 28.3% ± 36.0 of all female trials (*n* = 10; *N* = 60). The acoustic response to contact at the pronotum was nearly identical for both sexes (Fig. 2a). Contact to the pronotum elicited defence sounds in males in 72.6% ± 28.9 of all trials (*n* = 17; *N* = 112), and in females in 38.3% ± 46.5 of all trials (*n* = 10; *N* = 60). Regurgitation occurred more often in males with a mean of 64.9% ± 32.5 than in females with a mean of 46.6% ± 30.2 (Fig. 2b).

In addition, we tested the male individuals for differences in defence sound production before and after mating. The probability of defence sound production did not change after mating, though some variation between individuals could be observed.
individuals did not alter their response, while in some cases a decrease or even increase in acoustic defence during the test series was noted (data not shown).

4. Discussion

Tettigoniids use diverse primary and secondary defence mechanisms that increase survival probability when confronted with predators (Robinson, 1969; Gwynne, 2001). In the phaneropterine tettigoniid *P. ornatus*, camouflage by green colouration is the primary defence in both sexes, allowing the animals to blend into the background colouration in their natural habitat to avoid visual detection. In many tettigoniids, such camouflage by colour is the main primary defence mechanism (Gwynne, 2001), with the notable exception of Brachyptorinae and Heterodinae, the latter having strong thoracic cuticle spines and secreting haemolymph (Voseller, 1902; Gwynne, 2001; Bateman and Fleming, 2009; Kowalski and Lakes-Harlan, 2013).

4.1. Comparison of the defence sounds with intraspecific acoustic signalling

The acoustic signals of Orthoptera have an essential function in reproductive behaviour where the sexes commonly find each other by phonotaxis and calling songs show species-specific temporal structures (Walker, 1964; Gwynne and Morris, 1986; Robinson and Hall, 2002). This contrasts with the rather irregular and broad-band defence or disturbance sounds of many insects (Masters, 1980).

In many phaneropterine tettigoniids, males produce callings songs and perform phonotaxis upon an acoustic reply from the female (Heller and von Helversen, 1986; Spooner, 1995; Bailey, 2003). Thus, the males have a higher overall exposure to predation (Heller, 1992). The phonotactic behaviour of females in non-dutting species, however, might be a plastic behaviour depending on mating history: in females of the ephippigerine *Strepsileurus stylus* phonotaxis drastically decreases with the number of previous matings (Bateman, 2001).

The calling song of male *P. ornatus* consists of single syllables with long pauses in between (Chobanov and Heller, 2010). In the defence sounds of both sexes, the syllables are produced in more rapid succession and with longer duration, giving this sound a more vigorous or aggressive character. However, in males, syllable duration is longer in both the calling song and the defence sound as compared to the female response song and defence sound. In both sexes of *P. ornatus*, the variation in syllable duration is also significantly higher in the defence sound than in the calling song. These results agree with the initial hypothesis that the defence sound may be rather persistent and unstructured. These quantitative differences in the temporal patterns of calling song and defence sound have also been found for other tettigoniid species of Heterodinae (Kowalski and Lakes-Harlan, 2010, 2011) and the cricket species *Brachytrupes tropicus* (Desutter-Grandcolas, 1998). In *P. ornatus*, the calling song has evolved to rather short syllables lasting <50 ms (Heller, 1984, 1990), which is atypical even among the related species of the *P. ornatus* group (Chobanov and Heller, 2010). The longer duration of defence sounds likely makes them more effective. In sum, our findings are consistent with a deimatic function of the defence sounds to surprise or startle predators, which may allow the attacked insect to escape.

4.2. Comparison of the defence sounds between the sexes

The female defence sound has a significantly higher variation in the syllable duration than the male defence sound. This finding argues against a selective advantage for a specific temporal pattern of defence sounds in either sex. The defence sound of males, however, is more prominent because it lasts significantly longer and contains more impulses than the female defence sound. This may reflect the generally higher stridulatory activity of the males compared to the short acoustic replies of female individuals. Given the lower number of impulses per syllable in female defence sounds, the females’ higher variation in syllable duration may argue against the differences being caused purely by differences in the stridulatory structures (Heller and von Helversen, 1986). However, the experiments of the present study do not allow us to decide whether different neuronal controls underlie the stridulatory differences.

4.3. Defence behaviour in tettigoniids

Alexander (1960) reported that most of the tettigoniids producing a defence sound are relatively large, slow-moving and flightless animals. These animals are also mainly leaf mimics (cryptic) and are active at night (Heller, 1996). In contrast, *P. ornatus* is a middle-sized tettigoniid that is unable to fly as its reduced wings are only used for sound production (Heller and von Helversen, 1986). This species does not mimic leaves and produces the calling sound during the daytime. Both sexes rely on secondary defence by stridulation and regurgitation after an attack, albeit with differing frequencies. For comparison, in the Zambian armoured ground cricket *Acanthoplus spesieri* (Heterodinae), field data have highlighted the plasticity in defence behaviour of the sexes during the course of the day (Bateman and Fleming, 2013). Male individuals of *A. spesieri* may stop calling, drop to the ground, stridulate and autohaemorrhage, with the respective proportions of responses varying between daytime and night time. This species does not regurgitate when handled (Bateman and Fleming, 2013). Male defence stridulation did not differ between individuals handled during calling behaviour or while being silent (Bateman and Fleming, 2013).

Tested for the occurrence of defence sound production, both sexes of *P. ornatus* showed no significant differences with respect to the two handled body segments, while notable differences in defences depending on the direction of attack were shown to occur in the tettigoniid *A. discoidalis* (Heterodinae; Walker 1896): upon attacks from the side, aimed at the legs, the animals attempted to bite more often, and the males also increased disturbance stridulation. Upon an attack aimed at the pronotum from above, autohaemorrhage was elicited more easily while stridulation was lower in males (Bateman and Fleming, 2009). *A. discoidalis*, which uses multiple defence behaviours, can obviously be more selective when touched at different body regions than *P. ornatus*.

As an additional secondary defence mechanism, individuals of *P. ornatus* regurgitate, and males show this behaviour slightly more often than females. Among tettigoniids, stronger sex-specific differences in regurgitation occur in *A. discoidalis* where females react more often with regurgitation than males (Bateman and Fleming, 2009). In contrast to *P. ornatus*, only the males of *A. discoidalis* are able to produce sounds by terminal stridulation (Bateman and Fleming, 2009; Kowalski and Lakes-Harlan, 2011). Hence, the higher use of regurgitation in *A. discoidalis* females may be a compensation for the lack of other secondary defence mechanisms. It has been shown that regurgitation has a greater repulsive effect on smaller predators, such as skinks, spiders and ants, than on larger predators, such as terrestrial vertebrates (Lymbery and Bailey, 1980). However, the effectiveness of regurgitation also depends on the diet of the animals (Sword, 2001).

In *P. ornatus*, the male acoustic defence behaviour was not changed after mating. In *Poeciliimon* species, males reduce the production of calling songs for 24 h following mating (Heller and von Helversen, 1993). In contrast, disturbance stridulation did not differ between pre- and post-copulatory phases. This finding is
accordance with the expectation that defence mechanisms will be used upon contact independent of the mating history. In fact, acoustic defence upon contact is used independent of the mating history.

4.4. Adaptive significance of acoustic defence in *P. ornatus*

*P. ornatus* and the related *Poecilimon hoeltzeli* (Harz 1966) are the only *Poecilimon* species for which defence sounds are known. *Poecilimon ampliatu*s (Brunner von Wattenwyl 1878), another flightless species which occurs in the same habitat as *P. ornatus*, does not produce a defence sound.

The ecological or behavioural factors determining the occurrence of disturbance stridulation among *Poecilimon* species are so far not clear. However, exposure to predation may be a relevant factor. In duetting tettigoniid species, the use of sound signals during pair formation distributes the risk of detection differently compared to species in which only males sing (Heller, 1992). If the males are the main phonotactic sex (von Helversen et al., 2012), their exposition to predation during approach is increased in comparison to that of the females, as Heller (1992) found in a comparison between *Poecilimon affinis* (Frivaldsky, 1867) and *Poecilimon veluchianus* (Ramme, 1933). In *P. veluchianus*, males produce calling songs while females perform phonotaxis towards male signallers. This exposes them to a higher predation risk during movements towards the male compared to females of *P. affinis*, which produce only response songs to male calling songs upon which males perform phonotaxis. Predation risks are the highest for males if calling and moving towards the female (Heller, 1992). The acoustic defence mechanisms of *P. ornatus* might be explained by the increased risk for predation on the males, correlated to their phonotactic role. In females of *P. ornatus*, however, defensive stridulatory behaviour appears to represent their main defensive strategy. It should therefore have an adaptive value for defence in females (Heller, 1996), rather than being merely a byproduct of intraspecific signalling. The relevance for defence is also suggested by the many duetting *Poecilimon* species in which females produce acoustic signals for mate finding but lack any disturbance stridulation. The differential exposure to predation may thus shape the differences in acoustic defence between the sexes in *P. ornatus*.

Acknowledgements

The experiments reported in this study comply with the guidelines for animal care of the Justus-Liebig-University Gießen and with the current laws of the Federal Republic of Germany. Kerstin Kowalski was supported by a postdoctoral Margarete Bieber scholarship from the Justus-Liebig-University Gießen. We thank Arne W. Lehmann for his help in collecting animals and extensive comments on earlier versions of this manuscript. We thank Klaus-Gerhard Heller for directing us to the sound recordings of female response songs of *P. ornatus*. We are indebted to Andrew Warren and Michael Reichert for improving the English of the manuscript. We also thank two anonymous reviewers whose comments helped to improve the manuscript.

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