Is the predation risk of mate-searching different between the sexes?

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Abstract

In animals that communicate for mate searching, typically one sex signals and the other searches. Differential predation risk of mate searching between the sexes is hypothesised to determine which sex invests more effort in mate searching. However, relative levels of risk posed by the two mate searching strategies remain largely unexplored. Furthermore, higher risks of signalling compared to responding to signals have been hypothesised to drive reduction in asymmetry of mate searching effort between the sexes in orthopterans, but rarely tested explicitly. Hence, we estimated the relative predation risk experienced in natural populations by signalling males and responding females. We did this by quantifying predation risk as a probability of mortality in the context of acoustic communication in a tree cricket, *Oecanthus henryi* from its ecologically relevant predator, a lynx spider, *Peucetia viridans*. Probability of mortality was quantified by partitioning it into three spatial components at which crickets and spiders interact, using a combination of extensive field observations and manipulative experiments in a semi-natural setup. We found no differences in predation risk faced by calling males and responding females, supporting the hypothesis that similar sex-specific costs can explain shared mate searching responsibilities. Our findings also suggest that direct benefits offered by males to females upon pair formation may better explain females contributing towards mate searching effort in orthopterans.

Keywords

Communication, sex roles, sex-specific costs, sex-biased predation, crickets

Introduction

Searching for mates typically involves some physical activity for pair formation. Mate searching effort is defined ‘as a costly investment in traits that facilitate encounters with potential mates, including mobility, advertisement calls or displays, and pheromone production’ (Fromhage et al. 2016). Several factors have been proposed to determine which of the two sexes contributes more towards mate searching (McCartney et al. 2012; Fromhage et al. 2016). However, sex differences in costs from predation risk, proposed as a potential determinant (Fromhage et al. 2016), has rarely been tested in natural populations (Heller 1992; Raghuram et al. 2015).

Sex differences in benefits of multiple matings, differential gametic and parental investments, and time- and predation-related costs have been proposed to determine which of the two sexes invests more effort in mate searching (Trivers 1972; Hammerstein and Parker 1987; Fromhage et al. 2016). Since males typically get higher maximum potential benefits from multiple matings than females (Bateman 1948; Rodríguez-Muñoz et al. 2010; Byers and Dunn 2012), and females are predicted to be the limiting resource to males by investing more in offspring (Andersson 1994), males are expected to be the searching sex. Contrary to this expectation, in a classic paper, Hammerstein and Parker (1987) showed that either sex can potentially search, arguing that sex differences in relative parental investment do not determine which sex searches for mates. But in most animals, males searching for mates is the fundamental mode of pair formation (Darwin 1871; Thornhill 1979). Among other factors, the cost of mate searching has been suggested as a potential determinant of this asymmetry (Fromhage et al. 2016). Fromhage et al. (2016) proposed that higher costs for females could explain the prevalence of male searching,

calling it the ‘sex-specific hypothesis’. One of the ubiquitous costs experienced during mate search is predation (Gwynne 1987; Magnhagen 1991; Heller and Arlettaz 1994; Zuk and Kolluru 1998; Zuk et al. 2006; Raghuram et al. 2015). Predation risk as a cost of mate searching, however, has not been widely studied between the participating sexes.

Although mate searching by males is prevalent in most animals, in orthopterans and some other taxa females physically move to localise signalling males who are predominantly sedentary (Darwin 1871; Thornhill 1979). Thus, females share mate searching responsibilities, thereby reducing the asymmetry between the sexes observed in most animal taxa. What factors explain this reduction in asymmetry and its maintenance? Thornhill (1979) attributes this to two potential factors: direct benefits provided by males to females on pair formation and/or the risks associated with signalling. In many species of orthoptera, on pair formation, males provide direct benefits such as a burrow for safe shelter (Gwynne 1995) or courtship nuptial gifts (Arnqvist and Nilsson 2000). McCartney et al. (2012) examined the interspecific mate searching differences across 32 taxa from a katydid genus, using theory and observational data. Their findings provide comparative evidence for the hypothesis that mate searching by females can be explained by the direct benefits offered by males if these are substantial. The alternative hypothesis states that since males benefit more from multiple mating, they should be selected to perform risky mate searching activities; hence, males are expected to face higher risks while signalling (Thornhill 1979; McCartney et al. 2012). The relative risk of signalling versus responding as a potential determinant of reduction in sexual asymmetry in mate searching effort between the sexes, has however rarely been tested.

Predation risk in the context of mate searching communication has predominantly been studied from the signaller's perspective (Zuk and Kolluru 1998). Many studies have demonstrated how sexual advertisement in the form of conspicuous calls makes signallers vulnerable to predation (Walker 1964; Bell 1979; Ryan et al. 1982; Belwood and Morris 1987; reviewed in Zuk and Kolluru 1998). However, studies analysing predator diet found evidence for responding females being at an equal, if not higher predation risk, in comparison with signalling males (Heller and Arlettaz 1994; Raghuram et al. 2015). Thus, both signalling and responding to signals entail predation risk, since signalling attracts eavesdropping predators (Zuk and Kolluru 1998) and movement towards a signal increases exposure to predators (Gwynne 1987; Heller and Arlettaz 1994; Raghuram et al. 2015). There is however, a paucity of studies that attempt to estimate the relative predation risk of signallers and responders (but see Heller 1992; Raghuram et al. 2015).

We examined the mate searching costs from predation risk in tree crickets by estimating predation risk experienced by calling males and responding females. We studied predation risk using an approach novel to the field of communication, though commonly used in ecology (Holling 1959; Lima and Dill 1990; Hebblewhite et al. 2005; Brechbühl et al. 2011). We partitioned risk into constituent parts, each characterised by a discrete spatial scale at which predator and prey interact: co-occurrence, encounter and being eaten. At each scale, the binary response of prey either succeeding or failing to avoid the predator helped estimate probabilities. Predation risk was estimated as a product of these probabilities (represented in Fig. 1). Such a comprehensive approach is critical to determine any trade-offs across different

scales that might not reflect in the total predation risk if studied only at the scale of proportion of sexes in predator diets, predator visitations in playback experiments, or predator preferences of certain prey behaviours in a controlled environment (Tuttle and Ryan 1981, Heller and Arlettaz 1994, Alem et al. 2011).

To summarise, the sex-specific cost hypothesis attributes ubiquitous male mate searching in most animal taxa to higher costs of searching in females (Fromhage et al. 2016). But unlike in most animal taxa, both sexes in orthopterans share mate searching effort, with sedentary males signalling, and silent females localising these signals. Hence, given these reduced sexual asymmetries of mate searching effort, we expect costs to be similar between the two sexes in orthopterans. Whereas, explicitly testing whether higher costs explain this reduced asymmetry in mate searching in orthopterans, we expect the costs of male signalling to be higher (Thornhill 1979).

Methods

We carried out our study on a tree cricket species, *Oecanthus henryi* whose major predator is the green lynx spider, *Peucetia viridans*. *Oecanthus henryi* is found extensively in the dry scrubland of southern India, predominantly on bushes of *Hyptis suaveolens*. *Oecanthus* species exhibit a mating system typical of true crickets (Gryllidae), where the males produce a long-range species-specific call and females do not call, but detect, recognize and locate males of their species (Walker 1957). Males of *O. henryi* typically call from *H. suaveolens* leaves and the females negotiate the complex architecture of the bushes and approach the calling males (Bhattacharya 2016). *O. henryi* male calls are made up of rhythmic chirps (Metrani and Balakrishnan 2005). *P. viridans* (family Oxyopideae) is commonly observed on

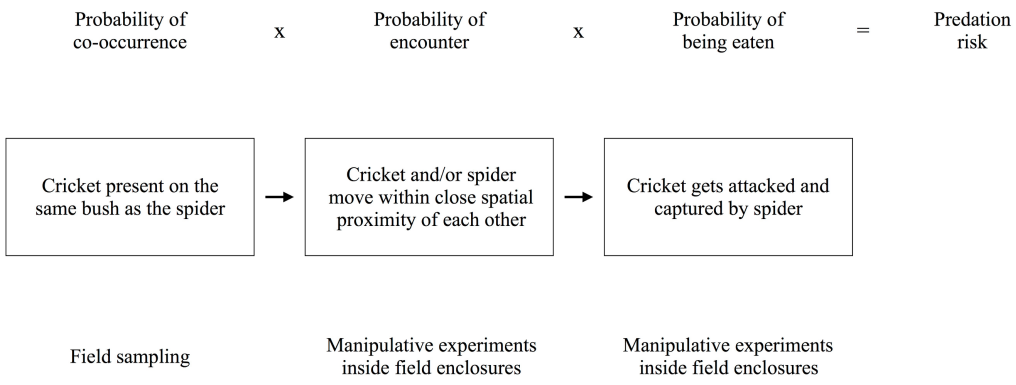

Fig. 1 Graphical representation of experimental design employed in the study to estimate predation risk. Each box represents a cricket interacting with its predator, a spider, at a particular spatial scale. Each arrow represents transition to the next spatial scale. Text above each box indicates what constituent of predation risk is studied and text below indicates how it was estimated. Probabilities from each spatial scale were multiplied to estimate predation risk.

Hyptis suaveolens bushes and has been observed preying upon tree crickets and honeybees (VRT and RB, personal observations).

All field surveys, sampling sessions and experiments were carried out in a homogenous patch of *H. suaveolens* on unused farmland, near Ullodu village (13°38'27.2"N 77°42'01.1"E) in Chikkaballapur district of Karnataka state in southern India. Laboratory experiments were performed on the campus of the Indian Institute of Science, Bangalore. All experiments in semi-natural conditions were carried out in an outdoor enclosure, constructed with a steel frame of dimensions 6m x 6m x 3m and

142 fastened with a fibre mosquito mesh (mesh size: 0.1cm x 0.2 cm), on the campus of
143 Indian Institute of Science, Bangalore.
144
145 We measured predation risk as a product of three probabilities: 1) probability of co-
146 occurrence of *O. henryi* and *P. viridans* on a bush (POC), 2) probability of *O. henryi*
147 encountering *P. viridans*, given their co-occurrence (POE), and 3) probability of *O.*
148 *henryi* being eaten by *P. viridans*, given an encounter (POBE).
149
150 Predation risk = POC x POE x POBE
151
152 The study was carried out in four parts. First, we performed extensive sampling to
153 investigate who the major predators of *O. henryi* were in the field. Second, we
154 sampled a population of *O. henryi* in the field to estimate the probability with which
155 they co-occur with their major predator species, considering a single *H. suaveolens*
156 bush as a unit (POC). Then we conducted two experiments in a semi-natural outdoor
157 enclosure to obtain the probability of encounter between *O. henryi* and *P. viridans*
158 when both co-occurred on the same bush (POE), and the probability with which *O.*
159 *henryi* are eaten by *P. viridans* upon encounter (POBE, represented in Fig. 1). The
160 sampling and experiments to measure the probabilities were carried out on two
161 different treatment regimes: calling males and responding females of *O. henryi*.
162
163 *Predator sampling*
164 Playback experiments were carried out in the field to determine acoustically orienting
165 aerial predators of *O. henryi*. Visitations by aerial predators were compared at
166 speakers playing back *O. henryi* calls with paired silent speakers for a total of 40

hours (details in supplementary information). For discovering arboreal predators of *O. henryi*, relative abundance sampling sessions and predation experiments were carried out. The extensive relative abundance sampling helped determine who the potential predators of *O. henryi* were. To establish whether these potential predators are real predators, detailed predation experiments were conducted in the lab and field. Experiments were also conducted to understand how body size and starvation period of the predator affects predation so as to better design further experiments (details in supplementary information).

Probability of co-occurrence

To determine the probability of co-occurrence between *O. henryi* and its major predator *P. viridans*, incidences of *O. henryi* co-occurring with large *P. viridans* on the same bush were recorded in the field between November and May. Between 1900hrs and 2115hrs, calling males were located using their calls, whereas females were localized using 5x5m quadrat sampling or opportunistically. Once localized, these crickets were focally sampled for at least 30 minutes, allowing time for males to call, to help distinguish callers from non-callers. The bush or bushes, on which these crickets were observed while sampling, were thoroughly searched for the presence of *P. viridans* at the end of the sampling session. If a spider was present, distances between the cricket and the spider and whether they were present on the same or different branches was recorded. Post sampling, crickets and spiders were collected and brought back to the field station for marking and sizing, respectively. Crickets were marked with a unique tricolour code using nontoxic paint markers (Edding 780, Edding, St Albans, U.K.), to avoid resampling; spiders were sized to confirm their ability to predate on crickets, and both were released back into the field. Male *O.*

192 *henryi* were considered as callers based on whether or not they called more than 20%
193 of the time they were observed. 20% of the calling effort was chosen as a cut-off so as
194 to avoid choosing infrequent signallers as callers. Since there was no intuitive way to
195 categorise communicating and non-communicating females during field observations,
196 observed females were randomly classified as responding and non-responding based
197 on a supplementary experiment (that estimated the relative frequency of
198 communicating (phonotactic) females in the same population). This random sampling
199 involved computationally segregating (sampled for 10,000 iterations) the observed
200 females into responding and non-responding females, using the proportion of wild-
201 caught females known to be responsive (experiment details in supplementary
202 information).
203

204 *Probability of encounter given co-occurrence*

205 To determine the probability of encounter between *O. henryi* and *P. viridans* given
206 their co-occurrence on a bush, experiments were carried out in semi-natural
207 conditions, inside a large outdoor enclosure. Crickets and spiders were collected from
208 wild populations from in and around Peresandra, Karnataka, India (13°35'25.3"N
209 77°46'50.4"E), a few days before the experiment. Crickets were maintained on *H.*
210 *suaveolens* bushes and spiders were provided *Gryllus bimaculatus* nymphs 2-3 times
211 a week, both in the laboratory. Female crickets were collected as nymphs from the
212 field and fed on an apple diet till they eclosed into adults after which they were
213 maintained on *H. suaveolens* bushes. This exercise ensured virginity of all tested
214 females, which increases the propensity of females to perform phonotaxis. Male and
215 female crickets were maintained separately. Spiders were maintained in individual
216 plastic boxes (6 cm diameter, 4 cm height). Spiders were starved for 48 hours prior to

a trial and crickets were transferred to *H. suaveolens* bushes in outdoor cages at least a day before a trial to acclimatise them. No cricket was repeated across or within treatments and no spiders were repeated within treatments.

Each trial involved releasing one cricket and one spider on a *H. suaveolens* bush and observing the interaction for about 120 minutes. Crickets were released on bushes at least 4 hours before the trial was started. The spiders were released at 1900 hours, marking the beginning of a trial. They were released on the bush at a height and distance from its centre, picked randomly from the interquartile range of their respective uniform distributions that were obtained from field data (refer to earlier section). Spiders were released on either the same or on a different branch as the cricket at 1900 hours with the proportion with which they were observed in the field. On the same or different branch, the distance at which spiders were released from crickets was drawn randomly from the interquartile range of a uniform distribution of distances at which crickets and spiders were observed in the field. Once the spider was released at 1900 hours, the interaction between the cricket and spider was observed for about 120 minutes by scan sampling each individual alternatively every 30 seconds. An encounter was defined as any spatial proximity between the cricket and spider, within 4 cm of each other, on the same branch. This distance was the outer range from which *P. viridans* attacked *O. henryi* and also the distance at which the cricket could potentially antennate the spider (VRT, personal observations).

Any male that called for more than 20% of the time it was observed was classified as a calling male. Females were played back conspecific male calls from a speaker (X-mini Capsule Speaker V1.1, Xmi Pte Ltd, Singapore) placed 60 cm away, across the

bush from the female's position at 1900 hrs. A trial was considered only if the female performed phonotaxis and reached within 20 cm of the speaker. The speaker was fixed on a stand, which was adjusted to the median height at which calling males were observed in the field (42 cm). The SPL of each call broadcast from the speaker was adjusted to be 61 dB (r.m.s. re. 2 x 10^{-5} Nm^{-2}) at the female's location with the help of a ½" microphone (Brüel and Kjær A/S, Denmark, Type 4189, 20 Hz to 20 kHz) fitted on a Sound Level Meter Type 2250 (Brüel and Kjær A/S, Denmark). Since the call carrier frequency changes with temperature in *O. henryi*, the choice of call to be played back was based on the temperature recorded at 1900 hours every evening. The call was chosen from among 3 representative calls that were recorded at 22°C, 24°C and 26°C (calls recorded by Rittik Deb, Deb 2015), whichever was closest to the recorded temperature. This call was played back in a loop using Audition software (Adobe, Version 5.0.2) on a MacBook Pro (2011) laptop using X-mini (Capsule Speaker V1.1, Xmi Pte Ltd, Singapore) speakers, for the entire duration of the experiment.

Probability of being eaten given encounter

The probability of *O. henryi* being eaten by *P. viridans* once encounter occurs was examined empirically in the same outdoor semi-natural setup. *O. henryi* and *P. viridans* were collected and maintained using the same protocol mentioned in the earlier section. The same two treatments were maintained for this experiment. Crickets were released at least 4 hours before the commencement of the experiment at 1900 hours on the bush at a height and distance from its centre as explained in the last experiment. From 1900 hours onwards, focal observations were made for at least 45 minutes to allow males to call and to allow females to perform phonotaxis. Following

these observations and based on whether the male called and female performed phonotaxis, a spider was gently released within close proximity of the cricket, not more than 6 cm away from it, using a *H. suaveolens* stick. A trial was considered only if the spider attacked, which was confirmed by videotaping all interactions. A spider capturing the cricket was scored as the cricket being eaten by the spider.

Analyses

Since comparing estimates of rare and non-normally distributed events can be challenging, we employed non-parametric bootstrapping and permutation tests (Manly 2006). These are robust methods for obtaining confidence intervals and *P*-values, respectively, since they make few assumptions about the underlying distributions (Manly 2006; Nakagawa and Cuthill 2007). Bootstrapping was used to generate 95% confidence intervals around each probability. This process involved sampling with replacement, for 10,000 iterations, from the original vector of success/ failures used to calculate the probability. Overlap in confidence intervals was used to infer statistical significance for each relevant comparison (Cumming and Finch 2005). Additionally, permutation tests were carried out to assess statistical significance (Manly 2006). We used software R, Version 3.3.3 (R Core Team 2017) to run all analyses, and the 'ggplot2' package (Wickham 2009) to plot all graphics.

Results

Not much is known about the identity of predators of *Oecanthus* species (Ponce-Wainer and Del Castillo 2008, but see O'Neill and O'Neill 2003). We conducted a series of experiments and sampling sessions to elucidate the predators of *O. henryi*. Playback experiments were carried out in the field to observe if there are any

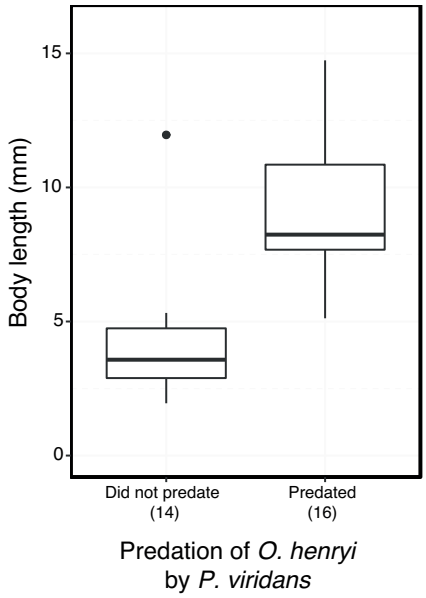

Fig. 2 Size distinction between *P. viridans* individuals that predated on *O. henryi* and the ones that did not. All spiders that captured crickets were larger than 5.12mm in body length.

acoustically orienting aerial predators of *O. henryi*. Bats (species unknown) flew past the playback speaker on 4 separate occasions, and past the control speaker on 5 occasions out of a total of 40 hours of observation. Approaches to both speakers by bats was very similar (4 and 5 times in 40 hours, respectively). Also, a praying mantis approached a broadcast speaker once. In relative abundance sampling to investigate arboreal predators, 15 5x5m plots were sampled, amounting to 1083 bushes. A total of 127 *P. viridans* individuals, 129 spiders belonging to the web-building guild, and 1 praying mantis were observed, along with many beetles, roaches, termites and moths which were not enumerated since they are not potential predators of tree crickets. Of these, *P. viridans* and spiders belonging to the web-building guild were categorized as potential predators. In the field predation experiment, 16 out of 30 *P. viridans* that were offered *O. henryi*, captured and consumed them. All *P. viridans* that captured *O. henryi* were larger than 5.12 mm in body length (n=14) (Fig. 2). In similar sets of

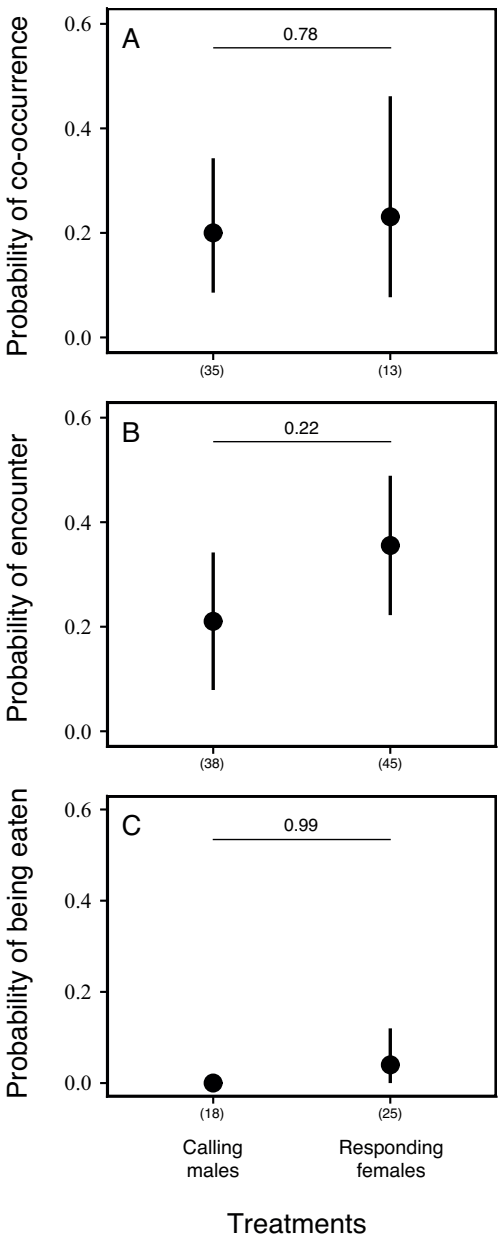

Fig. 3 Constituent probabilities of predation risk faced by *O. henryi* from its predator, *P. viridans*. Predation risk experienced by communicating crickets was partitioned into three spatial scales: probability of (a) co-occurrence, (b) encounter and (c) being eaten. Pairwise comparisons between calling males and responding females at the 3 spatial scales are represented with associated *P*-values. Values in parentheses are sample sizes.

Treatments	Probability of co-occurrence	Probability of encounter	Probability of being eaten	Predation risk
Calling males	0.2 (35)	0.211 (38)	0.0 (18)	0.0 (91)
Responding females	0.232 (13)	0.356 (45)	0.04 (25)	0.0033 (83)

Table 1. Probability values of calling males and responding females listed for 3 different scales and the total predation risk. Values in parentheses are sample sizes.

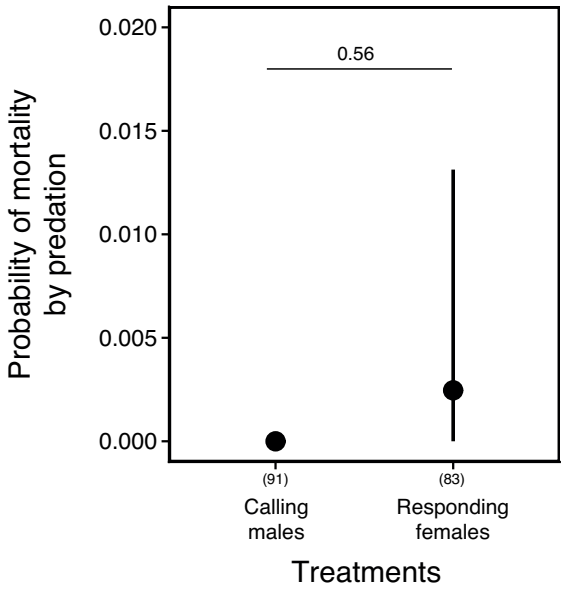

Fig. 4 Predation risk faced by *O. henryi* from its predator, *P. viridans*, as calling males and responding females. Probabilities are bootstrapped values represented as 95% confidence intervals. Values in parentheses are sample sizes. Pairwise comparison is represented with associated *P*-value.

experiments, spiders belonging to the web-building guild, were found not to be major predators of *O. henryi* (details in supplementary information).

The probability with which crickets co-occur with large spiders was similar between calling males and responding females ($P = 0.779$; Table 1, Fig. 3a). These results did not qualitatively change even when all sampled females (n = 43) were considered instead of only the randomly sampled segregate classified as responding females ($P = 0.790$). Once co-occurring on the same bush, both calling males and responding females encountered spiders with the same probability ($P = 0.221$; Table 1, Fig. 3b). When an encounter was forced between the spiders and crickets, relatively few individuals, whether calling males or responding females were captured and eaten by *P. viridans* (Table 1). Thus, on encounter, the probability of being eaten by the spider is similar for both ($P = >0.999$; Table 1, Fig. 3c). Consequently, the product of these probabilities, the predation risk, is also similar between calling males and responding females ($P = 0.558$; Table 1, Fig. 4).

Discussion

Our study investigated the relative predation risk of communicating individuals, signallers and responders, in natural populations on a within-night time scale. Observing interactions at various spatial scales allowed a comprehensive quantification of predation risk by taking into account predator-prey dynamics. Our choice of predator was justified using extensive field surveys and acoustic sampling sessions to determine all potential predators and carefully pruning that list using predation experiments to select a predator that is ecologically relevant to our system of choice. We found that the green lynx spider *P. viridans* was the primary predator of

O. henryi. Spiders have been observed to be predators of several species of crickets (Hedrick and Kortet 2006; Dangles et al. 2006; Storm and Lima 2010). Spiders are sensitive to both long-range acoustic (Shamble and Hoy 2016) and substrate-borne vibratory cues (Barth 2002). Such multimodal sensitivity could allow them to perceive both acoustic calls and locomotory cues, making spiders good model predators for studying costs of communication that involves calling by males, and movement by females.

Predation risk of calling in males and responding to calls in females was similar across all spatial scales relevant to predator-prey dynamics. We examined and compared the probability of communicating crickets co-occurring on bushes with spiders. This probability was similar, indicating that risk faced from distribution of spiders at a broad-scale is not influenced by whether the cricket is a signalling male or a responding female. While co-occurring on the same bush, the probability of encountering a spider was similar between the predominantly sedentary calling males and mostly mobile responding females. A possible explanation for this result is that communicating individuals are taking similar necessary evasive measures to spatially avoid predators (reviewed in Sih 2005). It will be interesting to investigate whether the two sexes spatially avoid predators while communicating. In addition, we investigated the probability with which crickets were captured by spiders when attacked and found no differences. This probability was extremely low for both sexes in comparison with the earlier two probabilities. This result is not unexpected since crickets are known to have high escape success against spider attacks, attributable to their air-sensing systems (Dangles et al. 2006). Although probability of calling males being eaten by spiders was zero, it was statistically similar to the non-zero probability

of responding females. Since almost certainly the probability of calling males being captured by spiders in nature is not zero, this probability was interpreted as being very low. Finally, the resultant product of the three probabilities, considered as predation risk, was similar for calling males and responding females, suggesting the cost from predation was comparable for mate searching crickets. Also, this probability was extremely low for the two sexes, primarily due to high escape probabilities exhibited by crickets when attacked by spiders.

The sex-specific cost hypothesis predicts sex differences in mate searching effort if searching is more costly for females than for males. Since in orthopterans this asymmetry in mate searching effort is reduced, we expected costs from predation risk between the sexes to be similar. Our results, that costs of mate searching from predation risk are similar for the signalling males and responding females, support the sex-specific cost hypothesis as an explanation of shared mate searching responsibilities in orthopterans. More such examinations of mate searching costs between the sexes are important to determine whether searching costs indeed are systematically higher for females than males. Furthermore, it will be interesting to test whether the extent of sexual asymmetry in mate searching corresponds to the differences in sex-specific costs, across different taxa.

We also tested one of the two factors proposed to explain females sharing mate searching responsibilities with males in long distance signalling taxa: high risk of signalling (Thornhill 1979). Risk associated with signalling has been shown in several taxa in which males signal for mate searching (Walker 1964, Bell 1979, Ryan et al. 1982, Belwood and Morris 1987, reviewed in Zuk and Kolluru 1998). But, we suggest

403 when studies test this hypothesis, they should not only provide evidence that the risk
404 is high for signalling males, but also that this risk is higher than that for responding
405 females. Very few studies have estimated risk of signalling in comparison with
406 searching. Our findings, in corroboration with two other studies (Heller 1992,
407 Raghuram et al. 2014), refute the hypothesis of signalling males facing higher risks
408 than responding females to explain the reduction in mate searching effort (Thornhill
409 1979) in long distance signalling taxa. The hypothesis that direct benefits offered by
410 males drives evolution of female mate searching was however supported by
411 theoretical and observational results in katydids (McCartney et al. 2012). In addition,
412 courtship feeding as observed in *Oecanthus* species (Houghton 1909; Fulton 1915),
413 has been shown to be an ancestral trait in the orthopteran suborder Ensifera,
414 suggesting that males of most Ensiferan genera will offer direct benefits to their
415 female counterparts on pair formation (Gwynne 1997). Hence, reduction in sexual
416 asymmetry in mate searching efforts in orthopterans can perhaps be better explained
417 by provision of resources by males to females rather than invoking higher risk of
418 signalling.
419
420 In conclusion, although predation risk of signalling in males has been considered to
421 be high (Zuk and Kolluru 1998), when compared with risk of responding, our findings
422 show these risks to be similar. It is only by addressing predation risk between the
423 communicating sexes across several relevant spatial scales that we could compare
424 risks faced by the two mate searching strategies. More such detailed comparisons of
425 predation associated costs between the mate searching sexes would help update our
426 understanding of whether at all there are systematic cost differences in mate searching
427 strategies. Finally, we also show that overall predation costs of communication per

night are low and that a predation event is very rare, which raises questions on the importance of predation as a major selection pressure on the evolution of communication.

Author contributions

VRT participated in conceptualising and designing the study, carried out data collection and analysis and wrote the manuscript. KI contributed to data analysis, interpretation and writing the manuscript. RB contributed to conceptualising and designing the study, interpretation of data and writing the manuscript.

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