RESEARCH ARTICLE

Sex differences in alternative reproductive tactics in response to predation risk in tree crickets

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Abstract

1. Alternative reproductive tactics (ARTs) are variable, often discontinuous, behaviours that allow a particular sex to achieve enhanced mating success. Predation risk has been hypothesised to drive the evolution of ARTs, but few empirical studies have examined this. It is unclear whether predators affect fitness of the two sexes directly, by reducing survival, or indirectly, by altering mate searching.

2. In crickets, mate search typically involves acoustic signalling by males and acoustic-mediated movement towards males by silent females. Males and females may however employ ARTs, which includes silent searching by males, and mating without performing phonotaxis in females.

3. We empirically examined effects of increased predation risk on mate searching behaviour and survival of male and female tree crickets, and their effects on mating success, using field-enclosure experiments with tree crickets *Oecanthus henryi* and their primary predator, green lynx spiders *Peucetia viridans*. Crickets were allocated into three treatments with different levels of predation risk.

4. Increased predation risk strongly reduced survival, and thereby mating success, for both sexes. With increasing predation risk, males reduced calling and increased movement towards neighbouring callers, with negative effects on mating success. By comparing with simulated random movement, we found that male movement was significantly directed towards other calling males, implying a switch to satellite strategies. Female movement behaviour, however, remained unaltered.

5. Males and females thus differed in their response to comparable levels of predation risk, implying that the role of predation as a driver of alternative mate search strategies is sex-specific.

KEYWORDS

alternative reproductive tactics, crickets, field experiments, mate search, mating success, predator–prey interactions, satellite behaviour, simulations

1 | INTRODUCTION

Alternative reproductive tactics (ARTs) are variable, often discontinuous, behaviours that allow a particular sex to achieve mating success, and are observed in many animal species (Brockmann, 2001; Cade, 1975; Gross, 1996; Oliveira, Brockmann, & Taborsky, 2008).

Individuals may employ different reproductive tactics during their lifetime (behavioural traits), or one tactic could be fixed (morphological traits; Oliveira et al., 2008). Alternative reproductive tactics are wide-ranging across multiple taxa: for example, territorial males in side-blotched lizards that mate-guard their mates versus sneaker males (Zamudio & Sinervo, 2000). Similarly, polymorphic males of a

small African cichlid show considerable variation in brood care effort: males are either monogamous, polygynous or helpers (Martin & Taborsky, 1997). Another example is that of males of myobatrachid frogs that initiate amplexus with females versus satellite males that join mating pairs (Byrne & Roberts, 1999). Alternative reproductive tactics can be observed in all stages of the reproductive process: localising a mate, gaining access, mating and participating in post-copulatory behaviour (Brockmann, 2008; Zamudio & Chan, 2008).

Several potential selection pressures (that are not mutually exclusive), have been hypothesised for the evolution and maintenance of ARTs, including intrasexual competition and mate choice (sexual selection), and predator/parasite avoidance (natural selection; Oliveira et al., 2008), but empirical support for the role of predation is still limited. Predation risk is deemed to be important in the evolution and maintenance of ARTs because it affects the relative costs and benefits of the alternative tactics employed (Taborsky, Oliveira, & Brockmann, 2008). Examples of predation risk-dependent modification to ARTs include male wolf spiders *Rabidosa punctulata* shifting to less conspicuous courtship tactics in the presence of predatory cues (Wilgers, Wickwire, & Hebets, 2014), male solitary bees *Ptilothrix fructifera* altering their territorial behaviour in response to predator models (Oliveira, Pereira, Pimentel, & Schlindwein, 2016) and increasingly successful sneaky copulation attempts by guppy *Poecilia reticulata* males instead of conspicuous courtship display with increasing predation risk (Endler, 1987).

A typical and well-studied category of ARTs includes variable expression of sexual signals in the context of mate searching. Males of a species either call and attract females or silently search and intercept them, and these are known as calling and satellite strategies respectively (Cade, 1979; Wells, 1977). Caller/satellite strategies in crickets are a classic system to theoretically and experimentally study the causes and consequences of ARTs (Cade, 1975; Cade & Cade, 1992; French & Cade, 1989; Walker & Cade, 2003). Relative fitness of caller/satellite strategies under varying conditions such as differential densities, sex ratios and body sizes has been tested either empirically (Cade, 1975; Cade & Cade, 1992; Castellano, Marconi, Zanollo, & Berto, 2009; French & Cade, 1989) or in theoretical models (Lucas & Howard, 1995, 2008; Rotenberry, Swanger, & Zuk, 2015; Rowell & Cade, 1993; Walker & Cade, 2003). Theory predicts relative fitness of ARTs in the calling-satellite system to be dependent on varying parasitism risk, with satellite behaviour maximising fitness with increasing probability of parasitism (Rotenberry et al., 2015; Walker & Cade, 2003). The evolution and maintenance of an obligately silent *flatwing* mutation in males of a Hawaiian population of the field cricket *Teleogryllus oceanicus* due to high levels of parasitism is a particularly extreme example (Zuk, Rotenberry, & Tinghitella, 2006).

Alternative reproductive tactics have been predicted to evolve more frequently in males due to higher maximum potential benefits from multiple matings and higher investment in offspring by females (Taborsky et al., 2008). However, recent work has revealed female ARTs as well (Brockmann, 2001). Examples of female ARTs include monandrous versus polyandrous females in horseshoe crabs *Limulus polyphemus* (Johnson & Brockmann, 2012), communal breeders versus returners versus solitary breeders in female striped mice *Rhabdomys pumilio* (Hill, Pillay, & Schradin, 2015) and communal breeders versus solitary breeders in house mice *Mus musculus domesticus* (Ferrari, Lindholm, & König, 2019). In contexts such as mate searching, where both males and females contribute, it is crucial to explore responses of both sexes to predation risk. This is because a shift to less conspicuous ARTs in males may elicit a compensatory shift in female behaviour. Without studying these changes together, our understanding of how predation risk finally affects mating success may remain incomplete.

Predation risk can affect fitness of prey species not only by inducing prey into modifying fitness-influencing behaviours, but also by reducing their survival. Simulation models testing effects of parasitism risk on virtual populations of male crickets report dramatic decrease in fitness due to reduction in their life span, for both calling and satellite males (Rotenberry et al., 2015; Walker & Cade, 2003). These patterns are reflected in the field, where males from natural populations of crickets that are not parasitised, live longer (Murray & Cade, 1995; Simmons & Zuk, 1994). Given that the two sexes may employ different ARTs, it is not well understood how predation risk may affect fitness of differential reproductive tactics by influencing survival and mating success.

In this study, we examined whether predation risk affects prey fitness by reducing prey life span and/or by altering their reproductive behaviour. Our study system included the tree cricket species *Oecanthus henryi* and its predator, the green lynx spider *Peucetia viridans* (Torsekar, Isvaran, & Balakrishnan, 2019). They inhabit *Hyptis suaveolens* bushes and are found in the dry scrublands of southern India (Deb & Balakrishnan, 2014; Metrani & Balakrishnan, 2005). Tree cricket males produce long-range species-specific calls from bushes and silent females localise these calls by performing phonotaxis to reach males (Walker, 1957). *Oecanthus henryi* populations however also include males that do not call and females that do not perform phonotaxis and these alternative mate searching strategies are flexible, with individuals performing different behaviours both within and across nights (Torsekar et al., 2019). Non-calling males could be silently searching for mates or could be satellites waiting close to other calling males to intercept and mate with phonotactic females. Similarly, females that do not exhibit phonotaxis may be employing ARTs and mate with searching males they encounter, since females mate regardless of their motivation to perform phonotaxis (Modak, 2019). In parallel with studying calling in males, we therefore also tested movement in males and females as a fitness-influencing behaviour that could change in response to varying predation risk. Green lynx spiders actively move on branches to capture their prey instead of waiting for prey to encounter them (Torsekar et al. (2019); Supporting Information S1). Spiders are typical predators of multiple cricket species (Dangles, Pierre, Christides, & Casas, 2007; Hedrick & Kortet, 2006; Storm & Lima, 2010) and are capable of locating acoustic signals as substrate-borne vibratory cues (Barth, 2002) and

may also perceive airborne acoustic cues (Lohrey, Clark, Gordon, & Uetz, 2009; Shamble et al., 2016). Spiders can also sense vibratory cues generated by moving prey (Barth, 2002). Therefore, spiders are an ideal system for studying ARTs in mate searching crickets that includes movement by females and calling by males.

We conducted field-enclosure experiments for seven successive nights under variable predation risk and recorded fine-scale responses of individually marked crickets in the form of calling, movement, mating and mortality. This allowed us to carefully track changes in mate searching behaviour and survival of wild-caught individual crickets in response to the predation risk they experienced across multiple nights. Specifically, we investigated the following questions: (a) With increasing predation risk, do male crickets shift from calling to silent searching/satellite behaviour and do females alter their movement behaviour? (b) Does increasing predation risk reduce survival in male and female crickets? (c) Is mating success predicted by survival, by the extent and kind of mate searching behaviours, or both? Previous work by Torsekar et al. (2019), measuring predation risk in *O. henryi* crickets showed that calling and non-calling males experience similar probability of co-occurrence on bushes with their spider predators in the wild. In this study, we manipulated and increased predation risk by substantially raising the probability of encountering a predator on a bush. At elevated levels of predation risk, we expected calling behaviour to be at higher risk than not calling within a bush. This is because males that exhibit calling behaviour are not always stationary but also walk as much as non-calling males within a bush (Torsekar et al. (2019); Supporting Information S2) making them more vulnerable to encountering actively moving spiders. Consequently, with increasing predation risk we expected calling males to move out of risky bushes to other bushes with potentially no predator and to shift from calling to less risky satellite behaviour. Female crickets move across bushes to localise calling males. Female ARTs would involve reduced movement across bushes and continued presence on a bush searching for calling or walking males that happen to be on the same bush. However, females exhibiting this ART could co-occur with predators, thereby exposing females to increased chances of encountering predators on the bush. Therefore, female crickets were expected to not change their movement behaviour across bushes with increasing predation risk. We also predicted reduced survival with increasing predation risk for males and females, with both changes in behaviour and survival consequently influencing fitness.

2 | MATERIALS AND METHODS

We conducted field-enclosure experiments in a field of homogeneously distributed *H. suaveolens* near Ullodu village (13°38′27.2″N 77°42′01.1″E) in the Chikkaballapur district of Karnataka state in southern India, from February 2016 to May 2017. We set up these experiments inside enclosures of dimensions 6 m × 6 m × 2.2 m, constructed using wooden stakes and fastened with a stainless-steel mesh (mesh size: 0.1 cm × 0.2 cm). The enclosures were constructed around naturally growing *Hyptis suaveolens* bushes (Season 1, cage 1, $N = 59$ bushes, height ($M \pm SD$) = 84.3 $\pm$ 27.4, width = 78.3 $\pm$ 24.4; Season 1, cage 2, $N = 47$ bushes, height = 82.2 $\pm$ 30.6, width = 84.2 $\pm$ 28.3; Season 2, cage 1, $N = 66$ bushes, height = 90.4 $\pm$ 33.4, width = 84.5 $\pm$ 34.7; Season 2, cage 2, $N = 62$ bushes, height = 88.6 $\pm$ 38.8, width = 79.5 $\pm$ 51.2, with all measurements in cm). We selected patches of bushes that were homogeneously distributed, with most bushes not in contact with each other. A spatial map of all bushes in both cages in both seasons exhibits the homogeneous distribution of bushes (Figure S1). This vegetation structure was representative of the larger field site. We tagged and numbered all bushes inside the enclosures and ensured the densities and characteristics of bushes were comparable. We maintained three predation risk levels that differed in the number of spiders released inside the enclosure. 'No predation' level ($N = 2$) involved no spiders or other predators present inside the enclosure, whereas 'low predation' ($N = 3$) and 'high predation' ($N = 3$) levels included 15 spiders and 120 spiders respectively. Fifteen male and fifteen female crickets were released in each enclosure for all levels. Therefore, the no predation treatment involved 30 crickets:0 spiders (ratio of 1:0 prey:predator), low predation treatment involved 30 crickets:15 spiders (ratio of 1:0.5 prey:predator) and the high predation treatment 30 crickets:120 spiders (ratio of 1:4 prey:predator). Number of crickets and spiders to be introduced in each level was decided based on the differences in predation risk (co-occurrence of spiders and crickets on a bush) experienced by crickets in a pilot experiment. We marked crickets with unique tricolour codes using non-toxic paint markers (Edding 780, Edding) to distinguish individuals. An experiment consisted of monitoring male and female crickets for seven consecutive nights.

Adult crickets and spiders were collected from natural populations near the Ullodu field site 2 days before every experiment. Spiders were sized to confirm that they were large enough to be predators of crickets (body length > 5.12 mm; details in Torsekar et al., 2019). Body size of crickets was recorded by photographing the ventral side and measuring the body length using ImageJ software (version 2.0). Prior to the commencement of every experiment, all bushes inside the enclosures were carefully inspected and any adults or nymphs of *O. henryi*, *P. viridans* or any other potential predators (such as spiders belonging to the web-building guild) of *O. henryi* found were caught and released outside the enclosures. Twenty-four hours prior to the start of each experiment, we released marked crickets inside the enclosures on randomly chosen bushes, to let them acclimate. Spiders were released on randomly chosen bushes an hour before the start of the experiment. In accordance with the methodology of Walker and Cade (2003), we did not add new crickets through the duration of an experiment to replace dead crickets. Accordingly, as the number of crickets reduced, we removed spiders every alternate night to maintain the ratio of crickets to spiders.

We recorded the location and behaviour of crickets at two temporal resolutions from 19:00 to 21:30 hr to overlap with the

peak calling activity of *O. henryi* (Deb, 2015). Location of individual crickets and whether there was a spider co-occurring with them on the same bush was recorded every 60 min, three times every night. We recorded whether or not a male was calling or mating every 10 min, i.e. 16 times per night. Mating durations in *O. henryi* typically range from 20 to 45 min (Deb, 2015). During each 10-min scan, males were identified visually and acoustically and whether they were calling or mating was noted. These observations were made from inside the enclosures by walking between bushes while taking care to not touch any bush or disturb any animal. Past work in the same population of the study system by Torsekar et al. (2019) has employed similar techniques while observing individual crickets at length and was found to not affect natural behaviour in tree crickets.

2.1 | Measure of predation risk

We measured predation risk encountered by crickets by quantifying spatial proximity between crickets and spiders. Since the predator–prey habitat is a bush, co-occurrence of both on a bush allows us a definition of spatial proximity that is less arbitrary than a certain approximate distance between them. For an individual cricket, we averaged all such co-occurrences across all sampling points during which it was observed, to calculate its probability of co-occurrence with a predator on a bush. This provided a finer resolution and more accurate measure of risk, at the individual level, rather than considering level of predation risk as a categorical measure of risk faced by a population of crickets.

2.2 | Measure of mate searching behaviour: Females

We measured inter-bush movement of female crickets between sampling points within nights using two metrics: (a) the distance moved and (b) the likelihood of such movement. Successive sampling points were considered only within a night, discounting any change in location across nights. This is because female movement during peak calling period is mostly in the context of phonotaxis, unlike movement during other hours of the day which is unlikely to be for mate searching (Bhattacharya (2016); Supporting Information S3). For measuring distance moved within nights, we used Euclidean distances between bushes. Euclidean distances were calculated before experiments began, by carefully recording spatial location of every bush in each enclosure as polar co-ordinates, using a reference point common to each enclosure (Survey Compass 17,475,780, error ± 0.5°, conceptualised by Francis Barker and Sons Ltd., sold and serviced by Lawrence and Mayo, India). This information along with the location data of each individual was used to measure the distance moved by each female cricket. Movement was also analysed as likelihood of movement to examine whether crickets move more often as a function of varying predation risk, regardless of how much they moved.

2.3 | Measure of mate searching behaviour: Males

Calling in male crickets was measured in two ways, (a) how much a male called (calling effort) and (b) likelihood of calling. Calling effort was measured as the proportion of scans in which each male was observed calling. Calling effort of a male cricket was therefore the total sampling points it was found calling divided by the total sampling points it was scanned and not found mating. We measured likelihood of calling as whether a male called or not on a given night, regardless of how much it called. Movement of males was measured in the same way as for females (described in earlier section).

2.4 | Satellite behaviour

Increased movement may suggest a shift in male mate searching from signalling to satellite behaviour. But alternative explanations for this behavioural modification are plausible. For instance, males may move more to escape spider attacks or to search for females without performing satellite behaviour. Therefore, we explored whether movement in males was directed towards other calling males, implying satellite behaviour. We did so by combining observations of real movement with simulated movement and comparing which are closer to a calling male that the focal male could hear before moving. Every time a male moved across bushes, we listed all calling males it could hear before it moved (hearing range based on Deb, Bhattacharya, & Balakrishnan, 2012). Distances between the locations of these calling males and the focal male's new location were noted, as well as the distance to the nearest calling neighbour. To understand if this was directed movement, the focal male's new location was simulated (5,000 times, to any of the available bushes in the enclosure), distances between each simulated location and all callers it could hear before it moved were noted and all nearest neighbour distances were recorded. The median of this distribution was defined as the simulated nearest neighbour distance in the absence of orientation towards another calling male. We ran these simulations with a manually written 'for loop' code in R software version 3.3.3 (R Core Team, 2019; for code details refer to Supporting Information S5). We interpreted whether movement is directed towards a caller by comparing the real and simulated nearest neighbour distances to a caller, using permutation tests.

2.5 | Measure of survival and mating success

Survival was measured as the number of nights each individual survived. Crickets were counted three times every night. Since dead bodies of crickets were almost never found (ants immediately carried any small carcasses away), all crickets missing for more than one night and which did not reappear on subsequent nights were recorded as dead. We recorded mating success as the number of matings an individual acquired. One mating event was counted when crickets were found mating in at least one scan.

Differences in mate searching behaviour with increasing predation risk can potentially be a result of selective predation of individuals exhibiting certain phenotypes such as active calling, instead of an outcome from behavioural change. We performed two analyses to confirm that our results were not due to differential survival of individuals exhibiting active calling. First, we examined whether calling effort across the three levels of predation risk was comparable at the start of the experiments by comparing calling effort of all calling individuals between the three levels for night 1, when most individuals are present. To investigate whether active callers are under-represented at the end of seven nights, we calculated difference in mean calling effort between night 1 and night 7 for no- and high-predation levels separately, and then compared these calling effort differences with each other using permutation tests. In a second analysis, we compared mean calling effort of the lowest-calling subset of individuals (33rd percentile calling effort of all males) from the no-predation level with that of surviving individuals from the two predation levels (low- and high-predation levels).

2.6 | Statistical analyses

To confirm whether individual crickets are experiencing variable predation risk, we compared the co-occurrence probabilities of crickets and spiders on the same bushes across the duration of the experiment, in different treatments (levels of predation risk). We ran pair-wise permutation tests between the three levels of predation risk to test whether the probability of co-occurrences of crickets in each level were statistically different from each other based on p values. These analyses were also run separately for male and female crickets.

To test our predictions, we first analysed change in survival and mate searching behaviour as a function of varying predation risk in separate models. Specifically, we examined the effect of varying predation risk on the following response variables; for females: survival, distance moved and likelihood of movement, and for males: survival, calling effort, likelihood of calling, distance moved and likelihood of movement. Next, we explored the effect of survival and mate searching behaviour on mating success, separately for male and female crickets.

We analysed the effect of predation risk on mate searching separately for male and female crickets. For this analysis, we considered each night for every individual as a separate data point (males: $N = 506$; females: $N = 479$). Such fine resolution allowed for a better understanding of how individuals behave depending on the risk they face per night. We used zero-inflated negative binomial GLMMs for analysing distance moved by male and female crickets and binomial GLMMs for calling effort, likelihood of calling and likelihood of movement. We ran an additional analysis for examining how likelihood of movement interacts between the sexes with increasing nightly predation risk. Co-occurrence probabilities with spiders was the fixed effect and individual identity was the random effect for all models testing mate searching behaviour. We deliberately did not include

'treatment' ($N = 3$) or 'replicates' ($N = 2$ or 3 in each treatment) as a random factor in our models because it had very few levels. By including random factors with less than five levels, the mixed model may have trouble accurately estimating the among-population variance (Harrison et al., 2018). Furthermore, including random factors with few levels in the process of bootstrapping model coefficients while maintaining grouping variables can be problematic.

To confirm whether differences in mate searching behaviour due to increasing predation risk are not due to differential survival of individuals exhibiting certain behaviours, such as active calling, we performed permutation tests. We tested how survival changed due to predation risk for each individual cricket over the duration of the experiment using Poisson GLM with co-occurrence probabilities and sex and their interaction as the predictors (males: $N = 113$; females: $N = 111$). Mating success of individuals was analysed as a function of how long individuals survived and their mate searching behaviour, separately for the sexes, using Poisson GLMs (males: $N = 113$; females: $N = 110$). All variables of mate searching behaviour for males (calling effort, likelihood of calling, distance moved and likelihood of movement) and females (distance moved and likelihood of movement) could not be included in their respective models due to multicollinearity. We used variance inflation factors (VIF) to evaluate which variables are collinear and whether they should be removed (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We chose explanatory variables representing mate searching behaviour (calling effort and likelihood of movement for males; distance moved for females) such that VIF values of our final models were below the conservative value of 1.5, implying that multicollinearity is not a concern (Zuur et al., 2009). For all analyses, non-significant interaction terms ($p > 0.05$) were dropped from the model. We calculated p values by running permutation tests for statistical hypothesis testing (Manly, 2018) and also computed effect sizes and their associated 95% confidence intervals (CI; Nakagawa & Cuthill, 2007) based on 10,000 iterations. For interpretation, 95% CI of regression coefficients not overlapping with zero was considered to have 'strong support' for predictions; 95% CI slightly overlapping zero, up to 85% CI were considered to have 'moderate support' and greatly overlapping with zero were regarded to have 'no support' (Abbey-Lee, Mathot, & Dingemanse, 2016; Cumming, 2013). All analyses were run in ʀ software version 3.3.3 (R Core Team, 2019). Data collation and manipulation were done using the ᴅᴘʟʏʀ package (Wickham, Francois, Henry, & Müller, 2017) and visualisation using the ɢɢᴘʟᴏᴛ package (Wickham, 2009; for further details refer to Supporting Information S4).

3 | RESULTS

3.1 | Predation risk

Crickets in each level of predation risk faced significantly different co-occurrence probabilities with spiders ($p < 0.001$; Figure 1).

These results were corroborated when co-occurrence probabilities of male and female crickets with spiders in different levels were tested separately ($p < 0.001$). The two sexes did not face different co-occurrence probabilities within each level ($p = 0.99$; Figure S2).
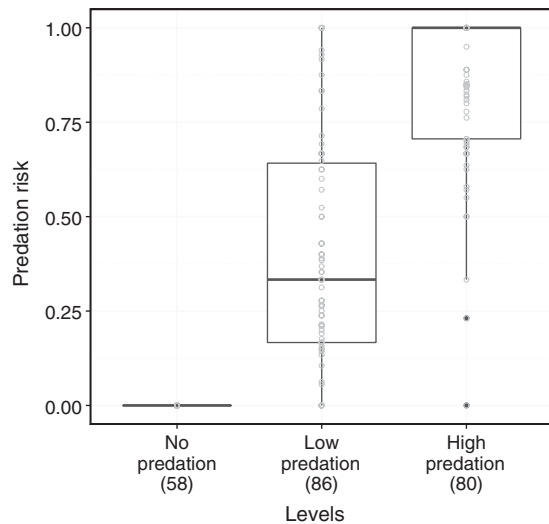

FIGURE 1 Predation risk encountered by crickets in treatments with different levels of predation risk. This comparison is shown for all crickets in the respective levels including male and female crickets (for sex-specific predation risk, see Figure S2). Predation risk is the probability of co-occurrence of a cricket with a spider on a bush across all nights it survived till the end of the experiment. Numbers in parentheses are sample sizes (number of crickets)

Therefore, crickets experienced different predation risk across levels of predation risk, whereas the two sexes experienced similar risk within the levels. The probability of co-occurrence experienced by crickets in the low predation treatment was within the range of co-occurrence probabilities observed in a natural population of crickets in the wild (0.048–0.23; Torsekar et al., 2019). We maintained a constant predator–prey ratio in the enclosures by removing appropriate number of spiders every alternate night. Although this ratio was maintained across nights, the absolute number of predators and prey reduced in number and accordingly increased the number of unoccupied bushes. This did not however affect the number of spiders that co-occurred with the remaining number of crickets across nights (Figure S3). Therefore, the predation risk experienced by crickets within any predation treatment was similar across nights.

3.2 | Mate searching behaviour: Females

In female crickets, neither distance moved nor likelihood of movement showed association with increasing predation risk (Figure 2e,f; Table 1). With increasing predation risk, there was no evidence for change in within-night distance moved ($\chi^2 = 0.174$, $p = 0.677$; Figure 2e) or likelihood of movement ($\chi^2 = 0.426$, $p = 0.514$; Figure 2f). Therefore, with increasing predation risk female mate searching behaviour was unaffected. Additionally, female body size did not correlate with their mate searching behaviour or predation
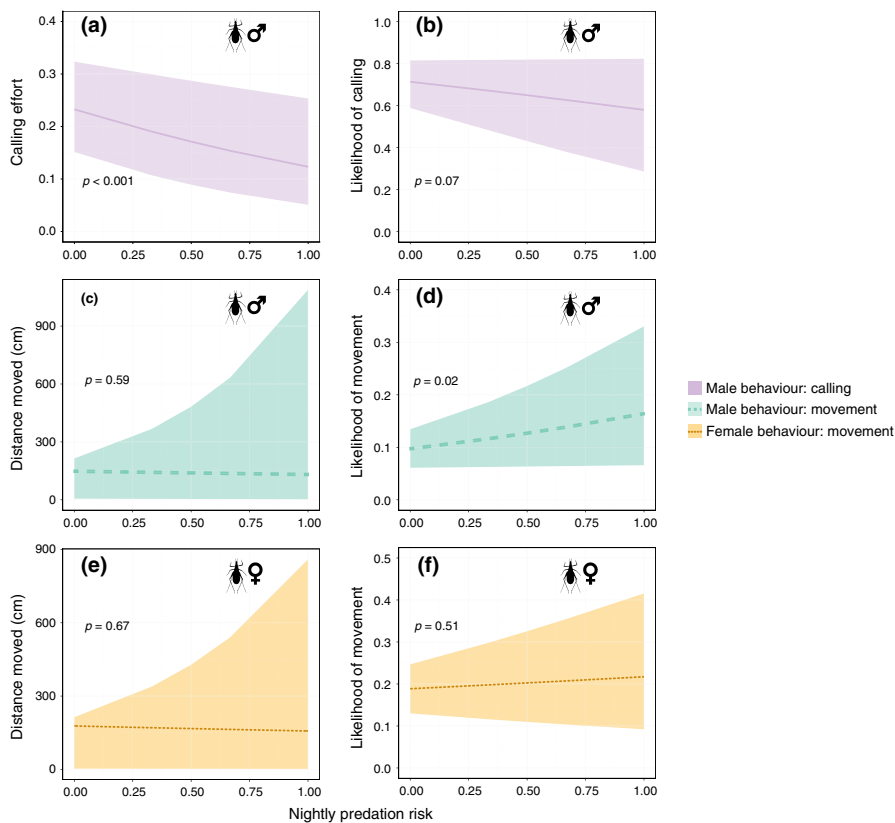
FIGURE 2 The effect of increasing predation risk on male and female behaviour including (a) the calling effort per night; (b) likelihood of calling; (c) distance moved within a night (males); (d) likelihood of movement (males); (e) distance moved within a night (females); (f) likelihood of movement (females). All X axes show predation risk experienced by crickets, represented as the probability of co-occurrence with spiders per night. The lines are predictions based on GLMMs, with shaded areas representing bootstrapped 95% CI

TABLE 1 Generalised linear mixed-effects models fitted to analyse female mate searching behaviour over increasing nightly predation risk (N = 479). Likelihood of movement was analysed using binomial GLMM and distance moved by females per night was analysed using zero-inflated Poisson GLMM. Model coefficients, bootstrapped 95% CI for coefficients and p values from permutation tests (based on 10,000 iterations) are shown

Term	Coefficient	95% CI	χ^2	p
Distance moved				
Intercept	5.180	1.120 to 5.349		
Predation risk	−0.123	−0.425 to 1.394	0.174	0.677
Likelihood of movement				
Intercept	−1.459	−1.901 to −1.117		
Predation risk	0.177	−0.386 to 0.775	0.426	0.514

risk (distance moved: r = 0.035, p = 0.718; likelihood of movement: r = 0.133, p = 0.167; probability of co-occurrence: r = 0.015, p = 0.872).

3.3 | Mate searching behaviour: Males

Predation risk affected mate searching behaviours in male crickets (Table 2). There was strong support for males calling less ($\chi^2 = 73.790$, p < 0.001; Figure 2a) and weak support for decreased likelihood of calling ($\chi^2 = 3.181$, p = 0.074; Figure 2b) at an individual level per night. Increasing nightly predation risk increased the likelihood of males moving across bushes ($\chi^2 = 4.772$, p = 0.029; Figure 2d) but did not significantly affect how far males moved ($\chi^2 = 0.291$, p = 0.59; Figure 2c). Calling effort of males was on average 15% less when there was a spider present on the same bush in comparison with when there was not. Therefore, with increasing predation risk, males reduced how much they called and increased their likelihood of movement. Body size of male crickets did not correlate with their mate searching behaviour or survival (calling effort: r = 0.128, p = 0.177; distance moved: r = −0.023, p = 0.807; likelihood of movement: r = −0.010, p = 0.911; probability of co-occurrence: r = 0.166, p = 0.078).

3.4 | Satellite behaviour

Nearest neighbour distances between new locations of moving males and calling males they could hear before they moved were significantly lower for the empirical data when compared with data simulating random movement of males (N = 62, p < 0.001; Figure 3). Male cricket movement was therefore significantly directed towards calling males that they could hear around them. Out of 62 moving males, only 11 settled on the bush inhabited by the calling male they were localising, whereas 51 settled on neighbouring bushes. To

TABLE 2 Generalised linear mixed-effects models fitted to analyse male mate searching behaviour over increasing nightly predation risk (N = 506). Calling effort, likelihood of calling and likelihood of movement were analysed using binomial GLMM, and distance moved by males per night was analysed using zero-inflated poisson GLMM. Model coefficients, bootstrapped 95% CI for coefficients and p values from permutation tests (based on 10,000 iterations) are shown

Term	Coefficient	95% CI	χ^2	p
Calling effort				
Intercept	−1.194	−1.723 to −0.738		
Predation risk	−0.768	−1.203 to −0.343	73.790	<0.001
Likelihood of calling				
Intercept	0.913	0.359 to 1.484		
Predation risk	−0.590	−1.270 to 0.055	3.181	0.074
Distance moved				
Intercept	4.413	1.778 to 5.366		
Predation risk	−0.1408	−0.640 to 1.626	0.291	0.590
Likelihood of movement				
Intercept	−2.229	−2.734 to −1.863		
Predation risk	0.601	0.0831 to 1.156	4.772	0.029
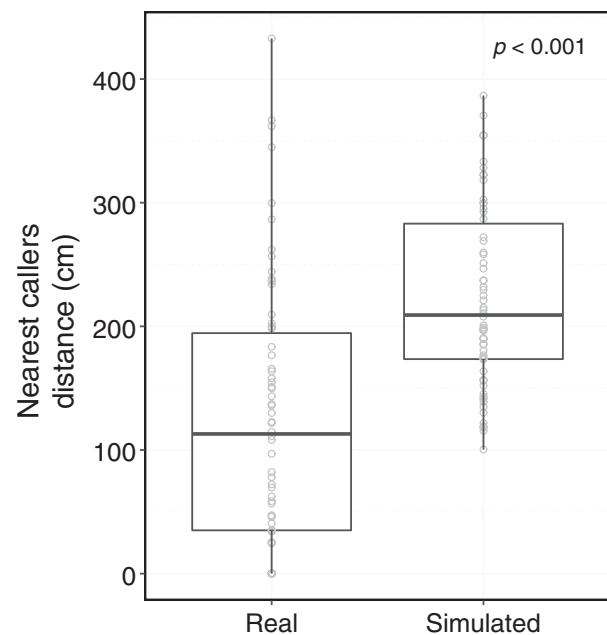
FIGURE 3 Movement as a satellite strategy. A comparison of distance to the closest caller when a male cricket moved in the enclosure. 'Real' represents the empirical data of male movement and 'simulated' represents the simulated data based on the null hypothesis of random movement to any bush. Points shown are actual distances to closest caller in the 'real' category, and medians of distributions of distances to closest caller when movement was simulated (for movement across bushes when experiencing predation risk, see Figure S4)

explicitly test whether males are more likely to move toward other singing males when predation risk was high, we ran the simulations only on males that moved across bushes when a predator was present on the bush ($N = 36$), and the results were qualitatively similar ($p < 0.001$; Figure S4), supporting the argument that this change in behaviour was a response to predation risk.

3.5 | Survival and mating success

Survival of both male and female crickets was significantly reduced with increasing predation risk (Table 3; Figure S5). This strong decrease in survival ($\chi^2 = 22.865$, $p < 0.001$; Figure 4; Table 3) was similar for both sexes ($\chi^2 = 1.796$, $p = 0.407$; Figure 4; Table 3).

Active callers did not experience selective mortality compared to non-callers. Calling effort distributions of cricket populations in the three levels of predation risk were found to be similar when compared on night 1 (no-low levels: $p = 0.21$; no-high levels: $p = 0.18$; high-low

TABLE 3 Survival in male and female crickets analysed as a function of increasing predation risk using Poisson generalised linear model. Model coefficients, bootstrapped 95% CI for coefficients and p values from permutation tests (based on 10,000 iterations) are shown

Term	Coefficient	95% CI	χ^2	p
Intercept (females)	1.774	1.679 to 1.860		
Predation risk	−0.356	−0.509 to −0.204	22.368	<0.001
Sex: males	−0.032	−0.147 to 0.085	0.299	0.584
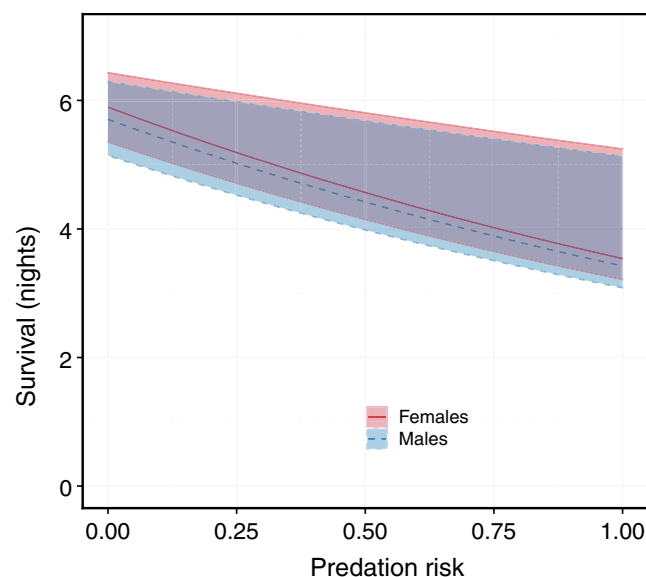
FIGURE 4 Survival as a function of predation risk for male and female crickets. The X axis is the predation risk faced by crickets, represented by the probability of co-occurrence with spiders on bushes across the nights they survived. The lines are predictions based on GLMs, with shaded areas representing bootstrapped 95% CI

levels: $p = 0.95$). The difference in mean calling effort (between night 1 and 7) of all singing males between no- and high-levels of predation risk was similar ($p = 0.64$), implying that mean calling effort of the population does not reduce across nights as a function of level of predation risk treatment (discrepancy between individual-level and population-level male calling effort responses to predation risk are explored in Supporting Information S6). Finally, the lowest-calling subset of individuals in the no-predation level over the span of seven nights (33rd percentile calling effort) comprised of non-callers (9/29, Mean calling effort = 0). Comparing the calling effort of this subset of individuals ($M = 0$, $N = 9$) with that of the individuals that survived for seven nights in the low- and high-predation levels ($M \pm SD = 0.36 \pm 0.19$, $N = 36$) showed that the surviving individuals in low- and high-predation risk levels had a higher calling effort than the lowest-calling subset of individuals from the no-predation level ($p < 0.001$). Even if we compare the calling effort of the subset of individuals from no-predation treatment that called at least on one night (from 33rd to 66th percentile calling effort, 10/29), i.e. excluding non-callers ($M = 0.19 \pm 0.12$, $N = 10$) with that of the individuals that survived for seven nights in the low- and high-predation treatments ($M \pm SD = 0.36 \pm 0.19$, $N = 36$) we find that the individuals remaining in the predation treatment have a higher calling effort than the lowest-calling subset of individuals from the no-predation treatment ($p = 0.009$, permutation test). In a separate analysis, we found that survival of male crickets and their calling effort showed a weak positive correlation ($r = 0.33$, $p < 0.001$). These results indicate that active callers were not eaten disproportionately more than non-callers.

Crickets varied widely in the number of matings they acquired during the experiment (males: 0.57 ± 0.83; females: 0.57 ± 0.90, $M \pm SD$, $N = 64$). To determine what best predicted this variation in total number of matings, we tested individual mating success as a response to propensity to mate search, and survival, separately for male and female crickets. Mating success in male

TABLE 4 Mating success in male and female crickets, tested separately using Poisson GLMs. Model coefficients, bootstrapped 95% CI for coefficients and p values from permutation tests (based on 10,000 iterations) are shown

Term	Coefficient	95% CI	χ^2	p
Males				
Intercept	−2.306	−3.600 to −1.547		
Survival	0.312	0.169 to 0.518	18.982	<0.001
Calling effort	0.716	−0.464 to 1.871	1.310	0.252
Likelihood of movement	−0.381	−0.797 to −0.068	4.758	0.029
Females				
Intercept	−1.891	−3.443 to −1.004		
Survival	0.238	0.076 to 0.470	12.111	<0.001
Distance moved	0.00011	−0.0012 to 0.0008	0.049	0.824

crickets (Table 4) increased with increasing survival ($\chi^2 = 18.982$, $p < 0.001$), decreased with increasing likelihood of movement ($\chi^2 = 4.758$, $p = 0.029$) and showed no association with calling effort ($\chi^2 = 1.310$, $p = 0.252$) when analysed together. Female mating success (Table 4) increased with increasing survival ($\chi^2 = 12.111$, $p < 0.001$) and was not influenced by how far individuals moved ($\chi^2 = 0.049$, $p = 0.824$).

4 | DISCUSSION

With increasing predation risk, male crickets exhibit ARTs from calling to movement directed towards other calling males, implying satellite behaviour. However, this had negative consequences on their mating success. Females did not alter their mate searching behaviour and moved similarly regardless of predation risk. Survival of both males and females was strongly affected by increasing predation risk but did not differ between the sexes. Although previous studies by Walker and Cade (2003) and Rotenberry et al. (2015) have simulated varying parasitism risk and predicted variable fitness for calling and satellite behaviours, to the best of our knowledge, this is the first empirical demonstration of these theoretical predictions that male crickets switch to ARTs along a selection gradient of predation.

4.1 | Mate searching behaviour: Males

Increasing predation risk not only reduced calling effort and likelihood of calling in male crickets, but also simultaneously increased their likelihood of movement, indicating that males might be employing the less conspicuous tactic of silent searching instead of calling to obtain mates. Why would males direct their movement towards other calling males if calling behaviour is risky? It is possible that by localising calling males without being on the same bush, moving males can potentially benefit from the calls without experiencing the costs. Our results revealed that a majority of moving males did not settle on the same bush as the calling male they were closest to, suggesting that moving males may be optimising their movement to reduce predation risk. By directing their movement towards other callers, moving males may benefit by intercepting any phonotactic females. An alternative explanation for this behaviour is that males aggregate in the presence of predators. Field observations however suggest that aggregation and chorusing is sparse in natural populations of *O. henryi* (Deb & Balakrishnan, 2014). Further work is however needed to examine the effect of predation risk on aggregation behaviour.

Reduced calling and increased movement directed towards neighbouring callers suggests a shift in male mate searching from signalling to satellite behaviour. Other studies simulating the caller-satellite system in virtual cricket populations show that ARTs may be both frequency- and environment-dependent (Rotenberry et al., 2015; Walker & Cade, 2003). Frequency-dependence in

this system has been demonstrated empirically in field crickets (Cade & Cade, 1992; French & Cade, 1989). Our findings provide empirical evidence for environment-dependence, where males favoured satellite over calling behaviour under the condition of high predation risk. Other examples of ARTs being affected by frequency, along with environment-dependence include 'parental' versus 'cuckolder' male in bluegill sunfish (Gross, 1997) and 'attached' versus 'satellite' males in horseshoe crabs (Brockmann & Penn, 1992).

4.2 | Mate searching behaviour: Females

Females did not alter their movement behaviour with increased predation risk suggesting that female ARTs in tree crickets are not driven by predation risk. Since females can also move to forage, lay eggs and avoid predators in addition to phonotaxis, how can we interpret movement behaviour as potential ARTs in females? Previous field and empirical observations by Bhattacharya (2016) have shown that females move primarily to perform phonotaxis towards calling males across bushes during peak calling activity in tree crickets (Supporting Information S3). Nevertheless, both phonotactic and non-phonotactic females are repeatedly found in natural populations of crickets suggesting a typical variation in female mate searching behaviour (Tanner, Garbe, & Zuk, 2019; Torsekar et al., 2019). When offered a male in laboratory conditions, female tree crickets mate regardless of their motivation to perform phonotaxis (Modak, 2019). This suggests that the female behavioural decision to either move across bushes to perform phonotaxis or stay in the same bush, not perform phonotaxis and mate with a searching male, are ARTs, since ARTs are ultimately discontinuous alternative ways to achieve reproductive success.

Given that the female likelihood of movement in the no-predation treatment is non-zero and that it does not change when experiencing increased predation risk, female movement decisions may be better explained by female physiological condition rather than as a response to predation risk. Although not dependent on environmental perturbations such as predation risk, female ARTs may be frequency- or condition-dependent. For example, unmated *O. henryi* females are more likely to exhibit phonotaxis (Modak, 2019) implying that potential ARTs in female mate searching behaviour may be influenced by intrasexual and intersexual rather than natural selection mechanisms. Overall, male and female crickets responded differently to varying predation risk, despite experiencing similar predation risk.

4.3 | Survival and mating success

Survival and satellite behaviour influenced mating success in males, whereas survival alone explained mating success in female crickets. Survival was expected to have a strong effect on mating success and this is consistent with the simulation study results, in

which the number of encountered females was strongly correlated with the life span of male crickets (Rotenberry et al., 2015; Walker & Cade, 2003). Contrary to our expectations, however, calling effort did not on its own influence mating success. A possible explanation is that since survival and calling effort show a weak positive correlation, callers are represented by individuals that survive for longer. Studies have shown that expression of sexually selected traits in males is positively correlated with their age (reviewed in Jennions, Moller, & Petrie, 2001; but see Hunt et al., 2004). In other words, males that survive longer and increase their chances for achieving mating success, also exhibit higher calling effort. On the other hand, we find that with increasing likelihood of movement behaviour, mating success reduced. We speculate that male crickets switch from calling to satellite behaviour when predation risk is high because the satellite/search strategy is safer. Even though immediate mating opportunities are negatively affected, the switch to satellite strategy may allow males to survive long enough to mate later. Although mating success has been shown to be a reliable surrogate for overall reproductive success in a field cricket (Rodríguez-Muñoz, Bretman, Slate, Walling, & Tregenza, 2010), sperm competition and cryptic female choice can influence the paternity share among mating partners and offspring quality, and ultimately their reproductive success beyond what can be measured with mating success alone.

In conclusion, our results demonstrate that males change their reproductive behaviour under increased predation risk conditions whereas females, under equivalent conditions of risk, do not. Also, fitness consequences of response to immediate environmental threats are different for the two sexes, with only direct (survival) effects in females, but both direct and indirect (mate searching behaviour) effects in males. Taken together, these effects are likely to have important implications for sexual selection dynamics, and highlight the role of predation in the evolution and maintenance of ARTs.

AUTHORS' CONTRIBUTIONS

V.R.T. participated in conceptualising and designing the study, carried out data collection, data analysis, interpretation of data and wrote the manuscript; R.B. contributed to conceptualising and designing the study, interpretation of the data and writing the manuscript.

DATA AVAILABILITY STATEMENT

All raw data are deposited and accessible at the Dryad Digital Repository https://doi.org/10.5061/dryad.b8gtht79p (Torsekar & Balakrishnan, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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