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Mate-searching context of prey influences the predator–prey space race

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Predation risk is a strong driver of prey distribution and movement. However, fitness-influencing behaviours, such as mating, can alter risk and influence predator–prey space-use dynamics. In tree crickets, *Oecanthus henryi*, mate searching involves acoustic signalling by immobile males and phonotactic movement by females. Space-use patterns in tree crickets relative to their primary predators, green lynx spiders (*Peucetia viridans*), should therefore depend on their current mate-searching state; whether males are calling or non-calling and whether females are phonotactic or non-phonotactic. We first measured the degree of spatial anchoring of crickets to specific bushes in the field and determined whether that influenced the probability of broad-scale spatial overlap with spiders. In the absence of spiders, all crickets, independent of sex or male calling status, were found to be spatially anchored to specific types of bushes and not uniformly distributed on the landscape. At the broad spatial scale, spiders were more likely to be found on bushes with female crickets and, to a lesser degree, calling male crickets. At a finer spatial scale within a bush, movement strategies of crickets not only varied depending on the presence or absence of a spider, but also on their current mate-searching state. Phonotactic females showed clear predator avoidance, whereas calling and non-calling males moved towards the spider instead of away, similar to predator inspection behaviour seen in many taxa. As the strongly selected sex, males are more likely to undertake risky mate-searching activities, which includes inspection of predator positions. Overall, we found that all crickets were predictably anchored at the landscape scale, but their sex and mate-seeking behaviour influenced the degree of overlap with predators and their antipredator movement strategies. Reproductive strategies within a prey species, therefore, can alter predator–prey space race at multiple spatial scales.

1. Introduction

Predation risk is a strong driver of how prey distribute themselves across multiple spatial scales. Many theoretical models [1–3] and numerous empirical studies on a range of taxa (e.g. rodents [4], frogs [5], deer [6] and fish [7]) explain the patterns and drivers of predator–prey space-use dynamics. Landscape attributes [8], prey abundances [9] and predator hunting mode [10] are among the many factors that can influence the outcome of predator–prey spatial distributions at the population level. What is often overlooked is the degree of variation within prey species, as individuals of the same species can differ in spatial overlap with predators and thereby vary in susceptibility to predation risk. One key context that can alter predation risk, and consequently predator–prey space-use dynamics, is mate searching [11].

Mate searching is a critical fitness-influencing behaviour that has resulted in the investment of complex traits and strategies which increase the probability of encountering and acquiring mates. For example, mate-searching effort includes the evolution of communication strategies, such as visual displays, advertisement calls and pheromones, as well as the ability to locate and move towards

potential mates [12]. In animals that communicate for the primary purpose of mate searching, one sex typically signals while the other sex searches. For example, male crickets produce acoustic calls that silent females use to localize them [13], female moths release pheromones that enable localization by males [14] and female guppies sample potential mates based on the visual displays of males [15]. Communication between sexes is critical for obtaining mating opportunities, and often, greater communication effort can increase the lifetime reproductive success of an individual [16]. Hence, within the same species given a certain mating system, how individuals communicate depends on their sex, and how much they communicate depends on their ability and motivation to search for mates. Communication, however, carries a cost in the form of predation risk, as predators can eavesdrop on communicating individuals or intercept a moving responder [15,17–19]. Increased predation risk is therefore known to influence animal communication, driving signalling individuals to employ less conspicuous tactics, such as decreasing calling effort [20] and overall activity [21], altering call structure [22], or use alternative mating tactics that not only reduce conflict with competitors but also encounters with predators [23,24].

In the predator–prey space race, spatial anchors that attract either the predator or the prey strongly increase the degree of spatial overlap between them [25]. Prey spatially anchored to patchily distributed resources may lose the space race to predators that can distribute near such resources in anticipation of prey, in a phenomenon called the 'leapfrog effect' [10,21,26]. Prey may avoid predation risk by proactively evading such risky spaces, or employing antipredator movement strategies at a fine scale if they do overlap at the broad scale [27], or even choosing a temporal refugia [28]. But prey need not always be anchored to only foraging resources. Individuals that are signalling to attract mates often anchor themselves in areas that facilitate signalling. For example, males that are motivated to mate prefer positions that maximize success, such as the entrance of burrows [29] and certain positions in the lek [30], as these help optimize signal transmission or establish territoriality [31]. Concurrently, recipients of these signals are not expected to be anchored in space as they are often moving to localize signalling males. Hence, sexually signalling individuals are not only spatially anchored, but their conspicuous location on the landscape may enable predators to more easily locate and overlap with them, compared with the mobile responders of these sexual signals [32]. Whether this spatial anchoring, caused by intraspecific variation in mate-searching behaviour, alters the predator–prey response race at multiple spatial scales remains poorly understood.

The tree cricket species *Oecanthus henryi* is found in the dry scrubland of southern India and inhabits the *Hyptis suaveolens* bushes [33]. Mate searching involves males of *Oecanthus* species producing long-range, species-specific calls from *H. suaveolens* leaves and silent females localizing these calls by moving to the bush and navigating through the complex architecture of the bushes to reach males [13,34]. Cricket populations of *O. henryi* exhibit variation in mate-searching behaviour where not all males call and neither do all females respond to calls, a feature common to several cricket species [23,35]. These mate-searching strategies are not fixed and individuals can exhibit different behaviours within and across nights. When in their non-calling state,

males exhibit satellite behaviour, where they move towards calling males and position themselves on neighbouring bushes such that they can intercept and mate with phonotactic females [24]. The primary predator of tree crickets is the green lynx spider *Peucetia viridans*, which does not spin webs to hunt, but actively moves between and within *H. suaveolens* bushes to capture their prey [36]. Spiders are predators of multiple cricket species [37,38] and are capable of perceiving acoustic signals [39] as both substrate-borne vibratory cues [40] and airborne acoustic cues [41]. Spiders can also locate locomoting prey using the vibratory cues produced, while prey move on bush branches [40]. Such multimodal sensitivity not only makes these lynx spiders a major predator for tree crickets but allows us to study the effects of behavioural variation, such as movement by females and calling by males, on prey risk and response [18,19].

Here, we test whether mate-searching behaviour of prey alters the predator–prey response race at two distinct spatial scales. We first tested whether tree crickets are spatially anchored on certain bushes by estimating preferential inhabitation of bushes by females, calling males and non-calling male crickets, in the absence of predators. This spatial anchoring of prey should result in increased spatial overlapping by predators who are expected to be moving through the habitat in search of prey. Thus, we then examined whether green lynx spiders were more likely to spatially overlap with tree crickets on bushes compared with bushes with no crickets present. At this broad scale, under natural conditions, we compared the probability of spiders overlapping with females, calling males and non-calling male crickets. We then tracked the movement of crickets within individual bushes and examined whether movement decisions were affected by the presence and relative distance to a spider on the same bush, compared with typical movement decisions in the absence of a predator. At this finer spatial scale, we specifically compared the movement decisions of calling and non-calling males, as well as phonotactic and non-phonotactic females. Overall, we tested the prediction that sex and mate-searching behaviour of crickets should affect their spatial anchoring on bushes, thereby affecting the degree of predator spatial overlap at the broad spatial scale, and their antipredator movement strategies at the fine scale within bushes. Our combination of field observations and manipulative experiments allowing free movement of both predators and prey, in addition with risk-free controls, allowed us to test how intraspecific variation in prey behaviour shapes the predator–prey space use at multiple scales.

2. Methods

We examined predator–prey space use at two discrete spatial scales. Field observations of spatial anchoring and broad-scale patterns were conducted in a homogeneous patch of *H. suaveolens* bushes near Ullodu Village (13°38′27.2″ N 77°42′01.1″ E) in the Chikkaballapur district of Karnataka state in southern India. Manipulative and controlled experiments to measure fine-scaled movement were performed in semi-natural conditions in outdoor enclosures on the campus of the Indian Institute of Science, Bangalore. All observations and experiments were performed from 2013 to 2017 during the breeding seasons of tree crickets in this region, which is February–April and August–November.

(a) Spatial anchoring

We first explored whether crickets were anchored in space by monitoring the spatial distribution of crickets in the absence of spiders. This field-based experiment was performed inside two enclosures (6 m × 6 m × 2.2 m each) that were constructed with wooden stakes fastened with a stainless-steel mesh (mesh size: 0.1 cm × 0.2 cm). These enclosures were built around naturally growing *Hyptis suaveolens* bushes ($N = 47$–66 bushes per enclosure). All bushes inside the enclosures were tagged, and their height and width measured before the experiment to determine if attributes of a bush influence cricket presence. Adult crickets were collected from in and around Peresandra, Karnataka, India (13°35′25.3″ N 77°46′50.4″ E) and individually marked by tricolour codes using non-toxic paint markers (Edding 780, Edding, St Albans, UK). In each enclosure, 15 male and 15 female crickets were released and allowed to habituate for 24 h. After this, the locations of all crickets were recorded thrice a night, 60 min apart, between 19.00 and 21.30 h for 11–12 consecutive nights.

(b) Broad-scale space use

To examine broad-scale space use of crickets and spiders, field observations were carried out between 19.00 and 21.15 h in the study area when *O. henryi* are active in natural populations. We assessed whether spiders spatially overlap with crickets by comparing spider occurrences on bushes with crickets present and absent. For sampling 'cricket-present' bushes, we first localized crickets in the natural environment, either by their calls or using a combination of 5 × 5 m quadrat sampling and opportunistic searches. Once localized, all crickets were observed for a minimum of 30 min and assigned to specific categories depending on their mate-searching behaviour. Males that were calling more than 20% of the time were classified as 'calling males' ($N = 35$ found), as opposed to 'non-calling males' ($N = 42$), which did not call at all. The 20% cut-off was chosen to avoid infrequent callers. Since there was no definitive way to categorize female behaviours from field observations, we did not further classify females as 'phonotactic' or 'non-phonotactic' at this scale ($N = 43$ females found). All crickets were caught, marked using non-toxic paint markers with a unique tricolour code and released on the same bush to avoid resampling on successive nights. For sampling 'cricket-absent' bushes, we then randomly chose a bush that was at a distance (within 0.5–10 m, at multiples of 0.5 m) and angle (from 0 to 360°, at multiples of 3°) from each 'cricket-present' bush. All cricket-present ($N = 120$ total) and cricket-absent ($N = 145$ total) bushes were carefully searched for the presence of spiders after the observation period, and if found, spiders were caught and their size measured to confirm their ability to capture crickets [36]. This method ensured that we are searching for spiders in both cricket-present and cricket-absent bushes at approximately the same time in the night, avoiding any sampling errors assuming spider movement between bushes within a night.

(c) Fine-scale space use

Fine-scale space-use patterns were studied by comparing movement decisions of crickets within a bush when a spider was present (predator trials) and when absent (control) in outdoor enclosures. Crickets and spiders were collected from wild populations in and around Peresandra, Karnataka, India (13°35′25.3″ N 77°46′50.4″ E). Prior to trials, male and female crickets were housed separately in plastic boxes (6 cm diameter, 4 cm height) and were maintained on a natural diet of *H. suaveolens* leaves. Non-mated females were used for all trials since they show higher motivation to perform phonotaxis (Modak 2019). Spiders were housed in individual plastic boxes (6 cm diameter, 4 cm height) and fed *Gryllus bimaculatus*

nymphs two to three times a week. All spiders were starved for 48 h before the trials to ensure similar levels of predator motivation [36].

For all trials, one cricket was released on a bush at 15.00 h and allowed 4 h to habituate. Fine-scaled movement observations started at 19.00 h and ended at 21.00 h. As before, male crickets that called more than 20% of the time between 19.00 and 21.00 h were categorized as 'calling males' and those not calling were 'non-calling males'. To stimulate a phonotactic female, we played conspecific male calls from a speaker positioned 60 cm away from the female's position. The speaker (Capsule Speaker V1.1, Xmi Pte Ltd, Singapore) was adjusted to the observed median height of calling males in the field (42 cm), and the sound pressure level of broadcast was maintained at 61 dB (RMS re $2 \times 10^{-5}\,\mathrm{Nm^{-2}}$) at the female's initial location using a Sound Level Meter Type 2250 (Brüel and Kjær A/S, Denmark) fitted with a ½′ microphone (Brüel and Kjær A/S, Denmark, Type 4189, 20 Hz to 20 kHz). Since the carrier frequency of *O. henryi* calls changes with temperature, calls pre-recorded at the closest ambient temperature at 19.00 h every night were used for the playback [33]. Calls were played continuously during the trial and only trials in which females elicited a phonotactic response and approached within 20 cm of the speaker were included in the 'phonotactic females' category. For the non-phonotactic female category, speakers were present but silent and thus did not elicit the movement of females. Thus, the expressed mate-searching strategies of these crickets were expected to induce high mobility in phonotactic females, intermediate mobility in non-phonotactic females, and non-calling males and low mobility in calling males.

For all four categories of crickets, we measured fine-scaled movement responses in the presence and absence of a predator (details in electronic supplementary material, table S1). For predator trials ($N = 143$ total), one spider was released at 19.00 h, 4 h after the cricket. For control trials ($N = 56$ total), a spider-sized part of a bush branch was arbitrarily tagged as the reference for cricket movement measurements and will hereafter be referred to as a control reference point. The tagged location (in control trials) and the site of spider release (in predator trials) were randomly selected from the interquartile range of natural predator–prey distances that was measured during the field part of the study (*Broad-scale space use*). Similarly, the height on the bush and distance from the centre of the bush for the start location of spiders were also randomized from within the interquartile range of the uniform distribution that spiders were observed to be in the field. For the predator trials, the cricket and spider were alternately scan-sampled every 30 s, for a total of about 120 min, and all movement decisions by both were recorded as a change in the direction relative to the previous location. After each trial, points of direction changes were sequentially numbered on the bush and converted to polar coordinates from a fixed reference point. This involved measuring the height from the ground, as well as the distance and angle subtended between each tagged point and the reference point. The reference point, common for all tagged points on a bush, was the centre of a fixed and levelled survey precision compass (Survey Compass 17475780, Lawrence and Mayo, India). The subtended angles were measured using the survey precision compass, and the distances and heights were measured using a metre tape. The same procedure was followed for control trials, with the location of crickets sampled every 30 s, for a minimum of 45 min. No individual cricket was repeated in any of the experiments.

(d) Analyses
(i) Spatial anchoring

To test whether some bushes are preferentially inhabited by crickets compared with others, incidences of crickets present on

each bush during every scan sample were added to generate an overall distribution, considering each bush as a unit (details in electronic supplementary material, S1). This distribution was first compared against a uniform distribution of crickets inhabiting all bushes inside the enclosures using a Kolmogorov–Smirnov test (electronic supplementary material, figure S1). We then examined whether inhabitation of bushes by calling males, non-calling males and female crickets was influenced by bush attributes. We ran a generalized linear model for each cricket category (calling males, non-calling males and females) assuming negative binomial errors, where the collated instances of bush habitation (yes and no) were the response variable, and the height and width of bushes were the predictors.

(ii) Broad-scale space use

We compared the proportion of bushes inhabited by crickets (cricket-present) and not inhabited by crickets (cricket-absent) that held spiders for each of the cricket categories (calling males, non-calling males and females) separately. We bootstrapped these proportions 10 000 times and compared 95% confidence intervals (CIs). Overlap in CI was used to infer the statistical significance of each comparison [42]. To strengthen these inferences, permutation tests were performed to assess statistical significance with p-values [43]. All analyses were run using R, V. 3.3.3 [44].

(iii) Fine-scale space use

We examined the movement decisions of crickets within a bush in the presence and absence of spiders (see electronic supplementary material, table S1). Movement decisions were measured as the angle subtended between the current and next location of a cricket (turning angle), relative to the current location of the spider or control reference point (electronic supplementary material, figure S3; see electronic supplementary material, S4 for the R code used to extract these data). We estimated the relationship between these angles and the respective distances between the cricket and the spider/control reference point in a mixed modelling framework with a negative binomial error structure. Generalized linear mixed-effects models (GLMMs) were run separately for each cricket category with turning angles as the response variable, and the following predictors: spider presence (yes/no) and distance between the spider (or the control reference point) and cricket when movement was initiated by the cricket, as well as an interaction term between spider presence and distance. This interaction term was removed when non-significant ($p > 0.05$). Cricket identity was included as a random effect in all models to account for multiple movement decisions per individual. For statistical hypothesis testing, p-values were calculated by running permutation tests [43]. Additionally, we calculated effect sizes from bootstrapping model coefficients to measure non-parametric 95% confidence intervals, by resampling 5000 times with replacement, within the grouping variable, i.e. individual identity [43].

3. Results

(a) Spatial anchoring

Distributions of calling males, non-calling males and females on *H. suaveolens* bushes in the wild were significantly different from a null distribution of equal incidences on the bushes ($N = 127$; $p < 0.001$ for all, electronic supplementary material, figure S1). Hence, crickets prefer to inhabit some bushes more than others and were not uniformly distributed in space. From an examination of bush attributes associated with this preferential use, we found that the width of

bushes, and not height, explained the presence of calling males, non-calling males and females ($N = 126$ for each) with strong effect (width of bushes: $\chi^2 = 7.54$, $p = 0.003$; $\chi^2 = 11.52$, $p = 0.002$; $\chi^2 = 34.09$, $p < 0.001$; height of bushes: $\chi^2 = 0.95$, $p = 0.206$; $\chi^2 = 2.17$, $p = 0.167$; $\chi^2 = 1.56$, $p = 0.330$; for calling males, non-calling males and females, respectively; figure 1 and electronic supplementary material, figure S2). Hence, crickets of all behavioural categories were spatially anchored on wide bushes.

(b) Broad-scale space use

Spiders are 2.6 times more likely to be found on bushes with female crickets ($N = 43$) than on a randomly selected bush with no cricket present ($N = 145$; $p = 0.02$; figure 2). Whereas when a calling male was present on a bush, spiders were 2.2 times more likely to be present ($N = 35$) than on bushes with no cricket (N = 145), but this comparison was not statistically significant ($p = 0.076$; figure 2). The probability of finding spiders on bushes with non-calling males was not different ($N = 42$) from bushes where no crickets were present ($N = 145$; $p = 0.529$; figure 2). Thus, spiders showed greater spatial overlap with female crickets and to lesser extent with calling males, but not non-calling males, implying that, at the broad scale, spider aggregation on bushes was influenced by the sex and mate-searching behaviour of crickets. This is particularly interesting since the dimensions of cricket-absent bushes and cricket-present bushes of all three categories of crickets were similar (details in electronic supplementary material, S2).

(c) Fine-scale space use

Interaction terms for the four cricket categories were not statistically significant (at $p > 0.05$; dropped from all the models), implying that the relationship between the turning angle and inter-individual distance was not dependent on the presence or absence of the predator. However, we found that the mere presence of a spider did influence the turning angles differentially in each cricket category, regardless of the distance between the cricket and the spider. Both calling males ($p = 0.01$, figure 3a; strong support, table 1) and non-calling males ($p = 0.01$, figure 3b; strong support, table 1) had lower turning angles when a spider was present on the bush, unlike their movement in the absence of a spider. These turning angles indicate that males in both behavioural contexts were turning more towards the spiders than in control predator-free conditions at all distances from the stimulus (predator/control) (table 1). Phonotactic females ($p = 0.009$, figure 3c; strong support, table 1) turned away from the spider, whereas non-phonotactic females ($p = 0.12$, figure 3d and table 1) moved indiscriminately in comparison to their movements in control conditions. Spiders did not move more in the phonotactic female experiments compared with non-phonotactic female experiments, or in the calling male experiments compared with non-calling male experiments, indicating that the extra auditory signal did not affect spider movement (details in electronic supplementary material, S3).

4. Discussion

Studies that allow unrestricted movement of both predators and prey provide key insights into the predator–prey space
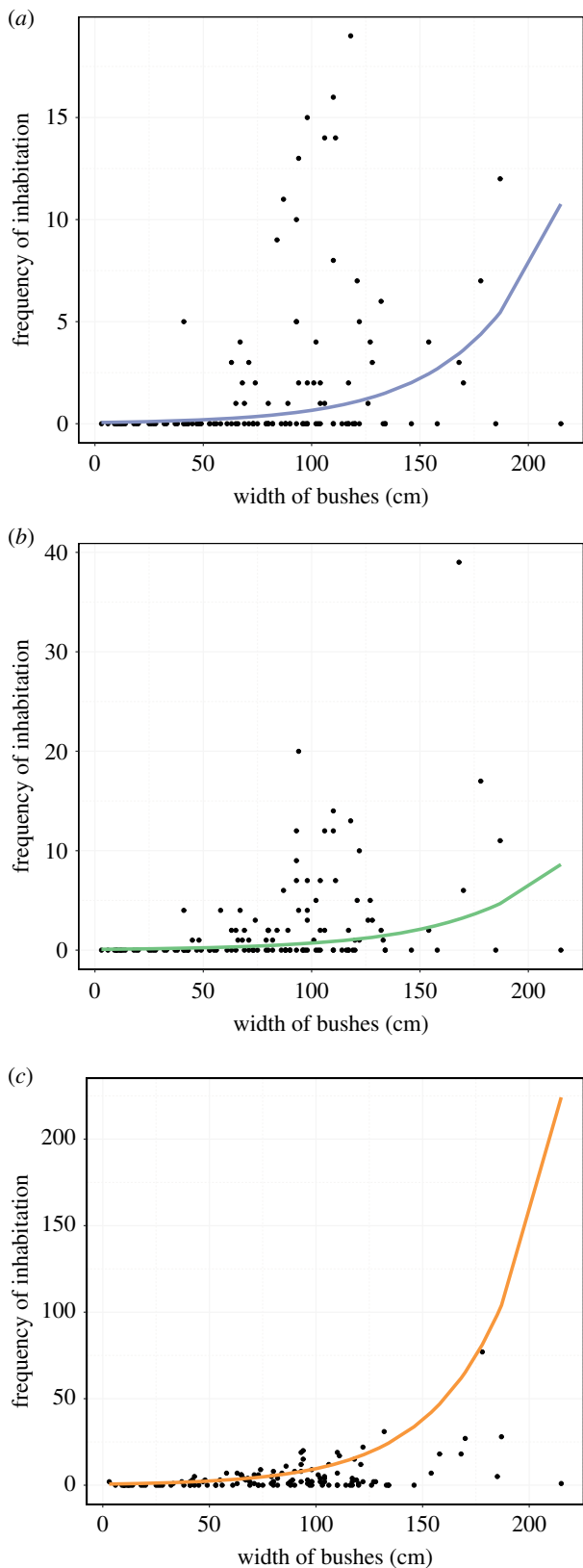
Figure 1. Bush attributes that explain the extent to which a bush was preferred by (*a*) calling males, (*b*) non-calling males and (*c*) females. Frequencies of inhabitation in all plots were incidences of cricket presence summed over hourly scans across all individuals and grouped by bush identity. Each point on the plot represents a bush and plotted lines are model fits. (Online version in colour.)

race [25,45]. Our understanding of such predator–prey spatial games, however, has largely overlooked space-use patterns when prey are spatially constrained by other fitness-influencing decisions, such as reproduction. To address this gap, we used
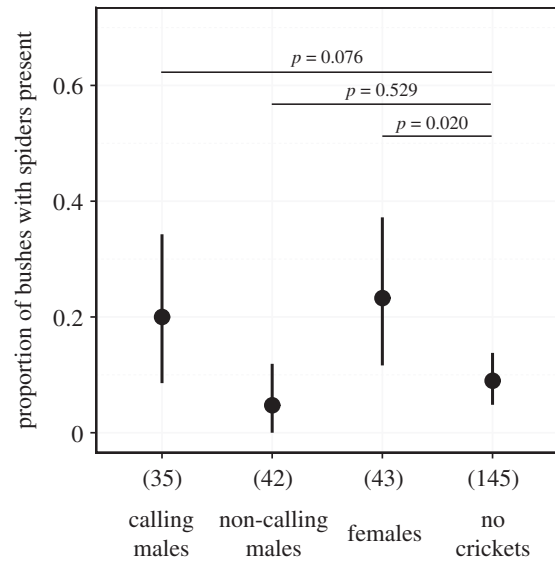
Figure 2. Broad-scale spatial distribution of green lynx spiders on bushes with tree crickets of different categories: calling males, non-calling males and females, and on bushes with no crickets. Error ranges shown are 95% confidence intervals obtained by bootstrapping proportions, and *p*-values are shown above each comparison.

spiders and the well-studied sexual signalling behaviours of crickets to determine how differences in mate-searching behaviour of crickets influence their space use and movement strategies at multiple spatial scales. We first determined whether sex and mate-seeking behaviour (calling or non-calling in males) influence the spatial distribution and anchoring of prey, and consequently of their predators. Under natural conditions, calling males, non-calling males and female crickets preferred inhabiting wider bushes. Since wider bushes tend to have more leaves and inflorescences (VRT 2014, personal observations), they could also provide better foraging opportunities, more refuges to hide from predators [37], more locations to call from and improved chances of calling through baffles [33]. Our findings thus reveal that all crickets, regardless of their sex, or whether they were in the state of calling or non-calling (for males), are anchored in space and potentially equally predictable for predators.

The expectation that spatial anchoring by prey should increase the probability of predator–prey spatial overlap has been proposed as a key driver that influences the outcome of the predator–prey space race [25,46]. We found partial support for this expectation. Despite the similarity in the type of bush inhabited by all crickets, females experienced greater spatial overlap with spiders than non-calling male crickets, with calling males showing similar trends. Thus, the selection of bushes by spiders was not random and not based exclusively on similar and independent microhabitat preferences as crickets. Relative immobility of calling males may explain higher spatial overlap with spiders. By contrast, non-calling males exhibit the more mobile satellite behaviour and orient themselves on bushes neighbouring calling males [24], thereby reducing their spatial overlap with spiders. Past work by Torsekar *et al.* [36] shows that 70% of field-caught female tree crickets do not phonotactically respond to male calls, and thus, their relatively immobile state may also explain why females show greater overlap with spiders in the wild. Although our data suggest that spiders are selecting bushes based on prey sex and behaviour and potentially bush
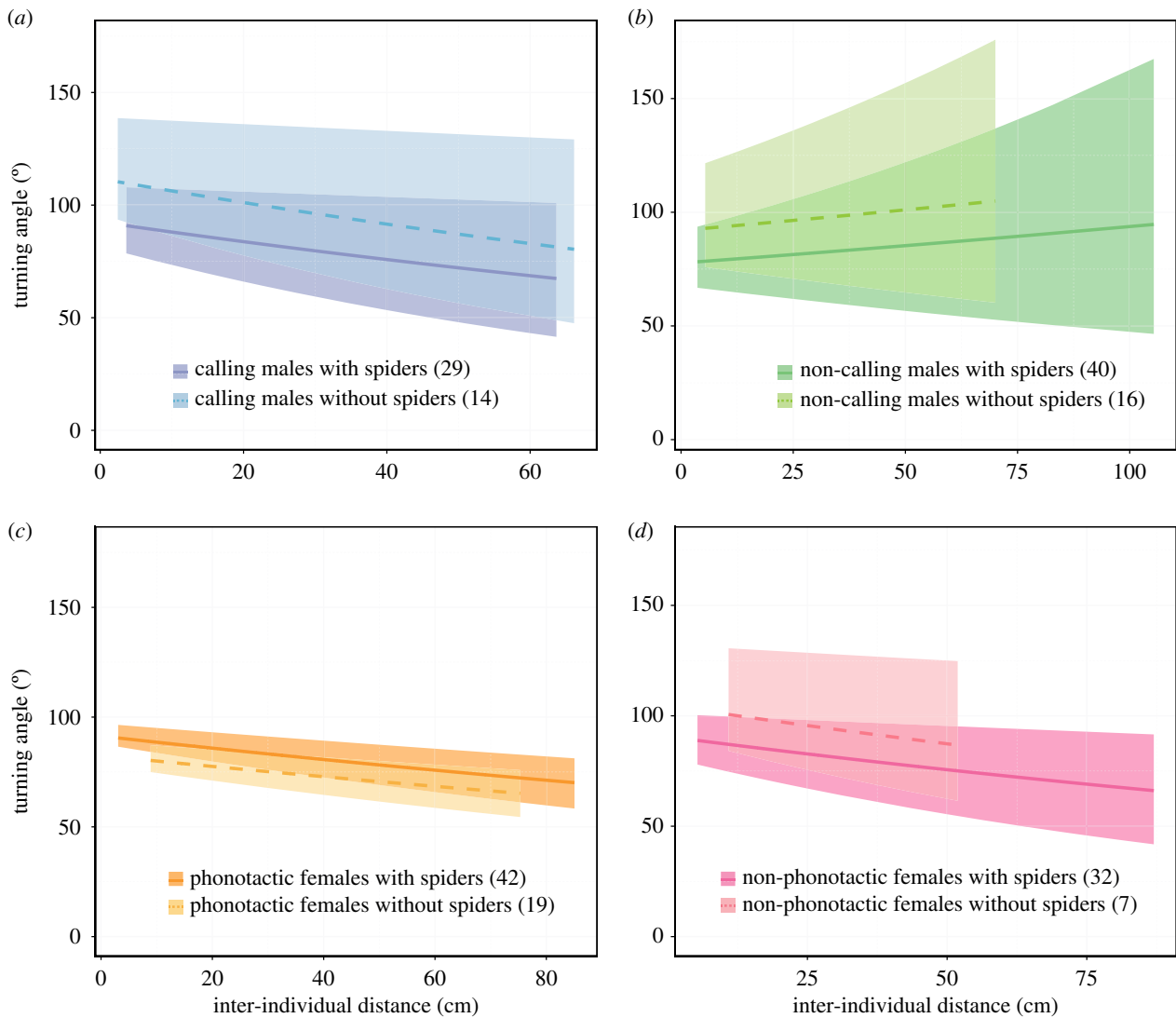
Figure 3. Distance-dependent movement decisions made by crickets in the presence and absence of spiders at the fine scale within a bush when the crickets are (*a*) calling males, (*b*) non-calling males, (*c*) phonotactic females and (*d*) non-phonotactic females. Shown are the turning angles of a cricket with respect to the location of the spider or the control reference point relative to the distance between them, referred to as inter-individual distance. Plotted lines are the model predictions with bootstrapped 95% confidence bands. Samples sizes are in parentheses in the keys. (Online version in colour.)

habitat characteristics, we cannot rule out the alternative possibility that cricket distribution may be influenced by spider distribution. However, past work in the system suggests that the broad-scale distribution of crickets changes only in extreme conditions when predation risk is artificially increased [24]. From the predator's perspective, spiders may be aggregating on bushes that predictably signal the presence of crickets, such as wide bushes with more inflorescences. Such bushes may be important for calling male crickets because they provide better foraging options and may offer better egg-laying opportunities for females. Overall, the high spatial anchoring of crickets on specific bushes does not entirely account for the degree of predator overlap at the broad scale, and future work should disentangle micro-habitat features that better explain predator distribution. Sex and the associated mobility across bushes of reproductive states in the wild population also influence the probability of predator attraction and hence the degree of predator–prey spatial overlap.

Given the differences in spatial overlap with crickets by spiders at the broad landscape scale, crickets were expected to demonstrate antipredator strategies at the fine scale that were also dependent on their mate-searching behaviour. As

before, we find notable sex and mate-searching behaviour-specific differences in movement strategies. Surprisingly, the presence of a spider on the bush was sufficient to invoke anti-predator movement decisions by crickets, regardless of the actual distance between the spider and the cricket. Phonotactic females moved away from the spider compared with control conditions, whereas the movement of non-phonotactic females was surprisingly unaffected by the presence of a spider on the bush. One explanation for this is the distance moved by females; since phonotactic females in general moved more than non-phonotactic females (electronic supplementary material, figure S4), they encountered more opportunities to avoid the actively moving spider unlike the relatively immobile non-phonotactic females. Thus, we show that within a species, antipredator responsiveness is higher for mobile individuals, a pattern typically evoked to explain the evolution of locomotive strategies across species [47,48]. Male crickets exhibited a different response to predators on their bush. Instead of turning away from the spider in a risk-averse manner, we found that turning angles of calling male crickets were oriented towards the location of the spider. Male crickets that were not actively engaged in calling also exhibited this movement pattern. Such movement

Table 1. Distance-dependent movement decisions of crickets in response to spiders when present on the same bush. Shown are the GLMMs explaining the turning angles of a cricket with respect to the location of the spider (or control reference point) as a function of the distance between the cricket and the spider/control reference point at each movement decision (inter-individual distance) and the presence or absence of the predator. Model coefficients, bootstrapped 95% CI for coefficients and p-values from permutation tests (based on 5000 iterations) are shown.

	coefficient	95% CI	p-values	coefficient	95% CI	p-value
	calling males			*non-calling males*		
intercept	4.72	4.56 to 4.93		4.52	4.35 to 4.77	
inter-individual distance	−0.005	−0.01 to −0.001	0.07	0.001	−0.004 to 0.006	0.34
predator present	−0.19	−0.33 to −0.07	0.01	−0.17	−0.30 to −0.07	0.01
	phonotactic females			*non-phonotactic females*		
intercept	4.41	4.36 to 4.49		4.65	4.52 to 4.88	
inter-individual distance	−0.0033	−0.004 to −0.002	0.004	−0.004	−0.008 to −0.001	0.02
predator present	0.10	0.04–0.17	0.009	−0.14	−0.36 to −0.03	0.12

towards predators is akin to predator inspection behaviours exhibited by a range of taxa [49–51]. Predator inspection allows individuals to gather information concerning the location and motivation of predators and deter ambush attacks, which may seem to increase the risk of an encounter and attack, but can actually increase overall survival [50], especially if the probability of capture once attacked is low. In fact, tree crickets are remarkable at escaping actual attacks by green lynx spiders, with a mortality rate of only 5% on attack and attempted capture [36]. Thus, crickets are able to undertake such risks since they can respond to attacks by fleeing successfully [52]. Males of many species are thought to be the more strongly selected sex to undertake risky mate-searching activities [53], since males show greater variance in reproductive success, thereby obtaining higher maximum potential benefits than females by mating multiply [16,54].

Overall, we show that sex and behavioural context of prey can influence predator–prey spatial interactions. Contrary to expectation, spatial anchoring by prey seeking specific micro-habitats does not directly result in higher predator spatial overlap. Instead, we show that the fitness-influencing behavioural constraints on prey that are seeking mating opportunities alter their encounter rate with predators at the landscape scale. Variation in reproductive states within females also influences their evasive movement responses at the finest spatial scale. Regardless of whether predator inspection by male crickets or direct predator avoidance by phonotactic females results in higher survival, our results demonstrate that sexual behaviour influences antipredator behaviours.

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