Sex-based differences in anti-predator response of crickets to chemical cues of a mammalian predator

Brian P. Tanis¹,², Bradley Bott¹,³ and Brian J. Gaston²

¹ Department of Integrative Biology, Oregon State University, Corvallis, OR, United States of America
² Department of Biological Sciences, Fort Hays State University, Hays, KS, United States of America
³ PRA Health Sciences, Lenexa, KS, United States of America

ABSTRACT

Anti-predator behaviors like vigilance or hiding come at the expense of other fitness increasing behaviors such as foraging. To compensate for this trade-off, prey assess predation risk and modify the frequency of anti-predator behaviors according to the likelihood of the threat. In this study, we tested the ability of house crickets (Acheta domesticus) to indirectly assess predation risk via odors from a mammalian predator, Elliot’s short-tailed shrew (Blarina hylophaga). As natural differences in encounter rates and predation risk differs between sexes, we tested if male and female crickets perceive similar rates of predation risk from the presence of shrew odor measured via anti-predator behavioral response. Crickets were placed in enclosed, cardboard-lined chambers either treated with shrew odor or control, along with a food source. Time until foraging was measured for each individual and compared across treatment and sex. We found that in the presence of shrew odor, female crickets delayed foraging while males showed no response. These results suggest adult crickets can use chemical cues to detect mammalian predators. Furthermore, we demonstrate that female crickets associate greater predation risk from shrew predators than do male crickets, which are more stationary yet acoustically conspicuous. As predation risk potentially differs drastically for each sex, changes to the operational sex ratios of wild cricket populations could be influenced by the identity of the predator community.

INTRODUCTION

Anti-predator behaviors (e.g., vigilance and hiding) are frequently associated with direct high fitness tradeoffs, including reduced time foraging or searching for mates (Brown, 1999; Lind & Cresswell, 2005). While costs of anti-predatory behaviors will always be less than mortality, lost opportunities during predator avoidance are significant enough that it benefits species to occasionally reduce or forego anti-predatory behaviors, also referred to as boldness (Main, Weckerly & Blech, 1996). Theoretical and empirical studies have shown that measuring differences in the frequency and duration of anti-predator behaviors correlates with the frequency of predation risk experienced (Lind & Cresswell, 2005; Preisser, Bolnick & Benard, 2005; Abbey-Lee, Mathot & Dingemanse, 2016).
One challenge in reconstructing the landscape of predation risk for a species is that this risk will frequently scale with variation in phenotypic traits (Werner & Peacor, 2003). Although applying to any phenotypic continuum, this pattern is exacerbated among species with pronounced sexual dimorphism (Croft et al., 2006). Sexually dimorphic traits such as coloration, body size, and ornamentation can alter the ability of predators to find, capture, and subdue prey (Brown, 1999; Croft et al., 2006). Physical attributes are not the only sexually dimorphic traits that impact predation risk; differences in behaviors will also impact the odds of predator-induced mortality. For instance, brooding behavior, specialized foraging needs, and conspicuous displays can also create unequal rates of predation between sexes (Wolfe et al., 2007).

Crickets (Orthoptera: Gryllidae) are frequently used as a model system for testing anti-predator behavior and provide a well-studied example of how sexually dimorphic behaviors can drive unequal rates of predation risk and boldness. As male crickets chirp to attract mates, they also signal acoustically-hunting parasitoids and predators. Silent females are inconspicuous to acoustically-hunting parasitoids and therefore tend to be significantly bolder than males in regions of high parasitoid density (Hedrick & Kortet, 2006). These findings have prompted insight into community ecology following novel dispersals and invasion biology (Trompeter & Langkilde, 2011; Cote et al., 2013), differentiation into adaptive behavioral suits (Wilson et al., 2010; Niemelä, DiRienzo & Hedrick, 2012; Hedrick & Kortet, 2012), and predator–prey evolutionary arms races (Zuk, Rotenberry & Tinghitella, 2006; Beckers & Wagner, 2012). However, not all cricket predators rely on acoustic signals to locate prey. Many predators, especially opportunistic generalists, rely on chance encounters while foraging (Iwasa, Higashi & Yamamura, 1981; Lucas, 1983; Bastille-Rousseau et al., 2011). Females, which must actively seek out stationary signaling males to mate, have an increased likelihood of encountering an opportunistic, mobile or sit-and-wait predator than males would. Therefore, female crickets are expected to have higher predation risk and reduced levels of boldness for non-acoustic hunters (Hedrick & Dill, 1993; Csada & Neudorf, 1995). Females, which are the more selective sex in crickets, also use a variety of other sensory cues for mate choice, including visual, chemical, and tactile (Otte & Cade, 1976; Hedrick & Dill, 1993; Adamo & Hoy, 1994; Nelson & Nolen, 1997; Gray, 1999; Thomas, 2011). In this study we set out to test the hypothesis that female crickets perceive a greater risk of predation from opportunistic mobile hunters compared with males by measuring delayed onset of foraging in the presence of indirect chemical cues from a tactile and olfactory hunting vertebrate predator, Elliot’s short-tailed shrew (Blarina hylophaga).

Elliot’s short-tailed shrews, typical of the diverse clade of shrews (Eulipotyphla: Soricidae), are small (13–16 g), voracious predators that use rapid speed coupled with a paralyzing, venomous saliva to subdue prey (Thompson et al., 2011). Given their small body size and relatively high mass-specific metabolic rate, shrews require nearly their entire body mass in food each day to avoid starvation (Saarikko, 1989). To consume this high quantity of food, shrews engage in hourly foraging excursions in which arthropods compose the bulk of their diet (Saarikko, 1989; Ritzi, Bartels & Sparks, 2005). Although able to detect chirping crickets, shrews primarily rely on tactile and olfactory senses to locate prey as they patrol established territories (Saarikko, 1989; Platt, 1976; Pernetta, 1977).
Due to their increased motile behavior, female crickets are theoretically more likely than males to be preyed upon by shrews. Given shrews are habitat generalists with abundant yet locally patchy distributions (Thompson et al., 2011), there is a potential that unequal predation risk between cricket sexes could alter sex ratios and lead to dynamic shifts in cricket metapopulations. To determine if female crickets recognize and associate a higher predation risk from mobile, non-acoustically hunting insectivores disproportionately to males, we made use of chemical cues produced by the shrew to measure indirect predation risk assessment.

Shrews possess numerous, highly odiferous abdominal glands for marking territories and deterring predators (Thompson et al., 2011). These chemical markings could be used by crickets as an indicator of shrew presence in the wild. Chemical recognition of predators has evolved in a wide variety of predator–prey systems as a mechanism for prey to indirectly assess predation risk (Kats & Dill, 1998). This behavior has previously been observed in field crickets (Gryllus integer), with experimental evidence that juveniles can recognize and avoid arachnid predators via chemotactile signals alone (Kortet & Hedrick, 2004). Additionally, adult house crickets (Acheta domesticus) have been shown to recognize centipedes via olfaction (Hoefler, Durso & McIntyre, 2012). While these patterns have never been extended to mammalian predators, we hypothesized chemical recognition of predators is likely a behavior that transcends taxonomy. By experimentally manipulating shrew odor within a habitat and measuring anti-predator response behavior, (i.e., delayed foraging) we directly tested if (1) adult crickets detect and respond to shrew odor as an indicator of predation risk and (2) if female crickets, with a hypothesized higher risk towards shrew predators, display more pronounced anti-predator response of delayed foraging than males.

**MATERIALS & METHODS**

We used commercially bred house crickets (Acheta domesticus) purchased from Fluker’s Cricket Farm (Port Allen, LA, USA). This species is native to Southwest Asia, although, it has subsequently spread throughout much of the globe through human-aided dispersal (Ghouri, 1961; Weismann & Rentz, 1977; Alexander, 1957). Within North America, large populations of feral house crickets have been established throughout the southern portion of the continent, including the southern Missouri, Arkansas, and Mississippi River basins, where populations overlap with those of Elliot’s short tailed shrews (Thompson et al., 2011). Purchased crickets were first acclimated for one week within a 50 L communal container, containing approximately 1,000 crickets. The container was filled with ample cover via egg cartons and was free of known predator stimulus. Conditions were maintained at 20 °C with a 12 h light/dark photoperiod, during which the crickets were fed sliced apples and oranges and watered ad libitum. 24 h prior to experimental trials, a subset \((n = 15–25)\) of healthy (i.e., large, no missing limbs) adult crickets were randomly selected and moved to a new container where they were deprived of food and water.

Trials were conducted in two opaque, 36 × 16 × 16 cm, sturdy plastic study chambers. Pieces of brown, 0.5 mm thick, corrugated cardboard were cut from a single source sheet
to fit into the bottom of the plastic study chamber (36 × 16 cm). Cardboard pieces were maintained within a sterile environment until needed for trials. 24 h prior to conducting trials, one cardboard sheet was infused with shrew odor by association with a captive Elliot’s shrew for 24 h. Cardboard was placed on the bottom substrate of one-half of the shrew enclosure, a 50 gallon aquaria (91 × 46 × 48 cm), so that the paws and ventral surface of the shrew, including abdominal scent glands, would have direct contact with the cardboard. This tactile interaction with the cardboard was observed while the shrew regularly patrolled its’ enclosure. Care was taken to ensure the cardboard was not placed near the shrew’s latrine sites to minimize excretion based chemical signals. The shrew was originally captured from Hays, KS (KDWP&T permit number SC-118-2011) and housed at the Sternberg Museum of Natural History for education. The shrew enclosure was held at a constant 20 °C with a 12 h light/dark photoperiod during the 24 h odor infusion period. In captivity, the shrew’s diet consisted of mealworms, crickets, oats, and peanut butter. Odor infused cardboard was ensured to be free of feces and other particulates and transferred to the chamber with clean forceps. Control cardboard pieces were transferred directly from the sterile environment to the control study chamber with clean forceps. No cover was provided within the study chambers.

At the onset of trials, a slice of fresh orange was placed in one corner of each chamber. One cricket at a time, chosen at random without regard for sex, was released in the chamber, opposite from the orange, and time to observed foraging activity was recorded with a stopwatch. Observations were done live and in-person, with care taken to not disrupt cricket behavior. In the event that a cricket did not forage within 720 s (chosen arbitrarily a priori), the trial was concluded and the individual was treated as censored (Rich et al., 2010). Following confirmed foraging or timed-out censorship, crickets were removed from the chamber along with any debris introduced by the cricket. Cardboard pieces were not replaced between each individual’s trial, instead they were replaced at semi-regular intervals following approximately 15–25 trials. Although it was possible crickets also encountered conspecific chemical cues during trials, crickets were acclimated communally, and such cues would not be considered novel. Additionally, there is evidence that conspecific chemical cues alone are not enough to induce behavioral responses in *Acheta domesticus* (Hardy & Shaw, 1983). Trials were repeated until 100 crickets (50 male and 50 female) were run through each treatment, odor and control, for a total of 200 crickets with no individual being used in more than one trial. Trials were completed over the span of 3 weeks in October of 2011. All trials were completed at 20 °C, under fluorescent lighting between 15:00 and 19:00 h. Although the lighting conditions were neither natural or reflective of when crickets are most active (typically either late afternoon or pre-dusk, Nowosielski & Patton, 1963; Cymborowski & Muszyńska, 1974), these conditions were necessary to aid in visual confirmation of foraging and other behaviors.

We conducted a Kaplan–Meier survivorship analysis to assess if time to foraging (i.e., anti-predator behavior) differed between male and female crickets in both the odor and control chambers. Specifically, we used the Gehan-Breslow-Wilcoxon log-rank method in the survival package of program R (Therneau, 2015; R Core Team, 2016) to test if the proportion of crickets foraging was different between four treatments: males and females.
within each chamber type, odor, and control. This method is appropriate due to the non-
constant rate of delayed foraging and the skew of all censored (i.e., timed-out) individuals
taking place at 720 s (Rich et al., 2010). Four pairwise comparisons, between males and
females within each chamber type and among males and females between chamber types,
were planned a priori and adjusted for multiple comparisons with a Bonferroni correction.

RESULTS
Of the 200 total crickets tested, 20 individuals were censored (10% of total sampled). This
could have been reduced by increasing the time until censorship to >720 s; however, an
adequate sample size was attained for Kaplan–Meier analysis. Censorship was unevenly split,
with six occurring in the control group (3 female, 3 male) and 14 in the odor group (nine
female, five male). The Kaplan–Meier curves showing the proportion of crickets foraging
over time for the four treatments were not identical ($\chi^2 = 26.4$, $df = 3$, $p < 0.001$), with
female crickets in the odor and control group occupying the upper and lower extremes,
respectively (Fig. 1). Cricket behaviors observed during trials predominantly included
continuous movement and antennae touching of the cardboard substrate until feeding.
Within the odor chamber, crickets of both sex would often approach food multiple times
prior to feeding. Males in both experimental treatments never made acoustic signals.
However, it should be noted these observations reflect general trends and were not scored
or quantified rigorously.

Of the pairwise comparisons, we detected no difference in the foraging curves between
females and males of the control group ($\chi^2 = 2.6$, $df = 1$, $p = 0.42$). There was a non-
significant trend for females to have a greater foraging latency than males in the shrew
odor treatment ($\chi^2 = 6.0$, $df = 1$, $p = 0.058$). We did not detect a difference between
males within the control and odor groups ($\chi^2 = 1.2$, $df = 1$, $p = 1.00$). Finally, there was a
significant difference between females within the odor and control groups, where females
displayed greater latency of foraging within the shrew odor treatment ($\chi^2 = 21.2$, $df = 1$,
$p = < 0.001$). It should be noted that the power of the Gehan-Breslow-Wilcoxon log-rank
method to detect differences between some groups is limited due to the non-constant
rate of the proportion foraging within each group, indicated by crossed foraging curves
(Fig. 1).

DISCUSSION
Once detected by predators, crickets’ primary defense strategies involve rapid-burst speed
to escape or the voluntary loss of limbs (i.e., autotomization). Given this limited arsenal
for predator defense, obtaining advanced and indirect recognition of predation risk is vital
for assessing habitats and reducing costly anti-predator behaviors. Our results provide
strong evidence that female crickets are able to detect chemical cues that correspond with
shrew presence and delay foraging for vigilance accordingly. This contributes to the already
lengthy list of prey species that use chemical signals to decrease predation risk, underscoring
the importance of chemosensation in predator–prey evolution (Kats & Dill, 1998).
Interestingly, male crickets do not appear to alter foraging rates when in the presence of shrew chemical signals. It is unclear, however, if the lack of response by male crickets indicates the inability to detect the chemical cues or indifference to the signal. This could be elucidated in subsequent studies by adding one or more negative control odors to the experimental design. Not only could this provide evidence for the range of chemical perception with male crickets, but it could also help confirm if responses from females were shrew-odor specific or more general. Few studies have explored chemosensory detection of predators within crickets; unfortunately, previous studies did not test for differences between sexes, either using juveniles of unidentified sex or adults of a single sex (Kortet & Hedrick, 2004; Storm & Lima, 2008; Hoefler, Durso & McIntyre, 2012; Binz et al., 2014; Atwell & Wagner, 2015). Male crickets have been documented to identify and respond to pheromones from females and potentially recognize differences in sympatric species (Otte & Cade, 1976), as well as use chemosensory perception for foraging (Matsumoto & Mizunami, 2000). Regardless of the mechanism, the absence of response to the chemical
signals of shrews supports our hypothesis that anti-predator behaviors would be greater within female crickets, as they have higher predation risk from non-acoustically hunting predators.

Although domestic crickets and Elliot’s shrews have experienced overlapping ranges within North America for at least half a century, the evolutionary history of domestic crickets occurred on continental Asia. While this might suggest a recent adaptation to the recognition of shrew odor as a signal for predation risk, it should be noted that the shrew family (Soricidae) has a global distribution (Fumagalli et al., 1999; Dubey et al., 2007) and scent glands are common trait throughout the group (Eadie, 1938; Hutterer, 1985). Furthermore, shrews are not unique in being highly odiferous; numerous mammalian insectivores spanning several distinct taxonomic clades and geographic distributions also possess highly pungent scent glands (Poduschka & Wemmer, 1986; Haffner, 1998; Dawley, Miller & Schnader, 1999; Jannett & Jannett, 2009). Given the near ubiquity of scent-marking among small insectivorous mammals and the evolutionary histories of both domestic crickets and Elliot’s shrews, it is highly likely that our results are not a species-specific interaction but instead a general response of crickets. Previous studies have also suggested that chemosensory recognition of predators is directly related to the individual predator’s consumption of conspecifics (Hoefler, Durso & McIntyre, 2012). Further work using a variety of mammalian and control odors would help differentiate the generality of our results across taxa and predation risk.

Although this is the first study to explicitly test cricket response to a highly mobile, mammalian predator, previous work has been done on cricket boldness using variety of other predation stimuli (Kortet & Hedrick, 2004; Hedrick & Kortet, 2006; Wilson et al., 2010; Hoefler, Durso & McIntyre, 2012; Niemelä, DiRienzo & Hedrick, 2012; Binz et al., 2014). Findings from many of these studies run counter the trends we observed. For instance, past studies reported that latency to emerge from shelter in novel environments and following simulated predation events were consistently higher among male crickets (Hedrick & Kortet, 2006; Hedrick & Kortet, 2012; Niemelä, DiRienzo & Hedrick, 2012). Likewise, Wilson et al. (2010) demonstrated that female crickets are typically more active when exploring novel areas. However, these experiments all occurred within a laboratory setting and were likely free of any predator chemical stimuli. In the absence of chemical stimuli within our study, females appeared to initially forage faster than males (Fig. 1), although the entire foraging curves did not significantly differ. This further highlights the pronounced behavioral changes among female crickets in the presence of a predator’s chemical cues.

The apparent dichotomy between the responses of either sex to different hunting strategies, observed both from our results and prior studies, suggests interesting implications for community dynamics through predator control of cricket sex ratios. Alterations to the operational sex ratio can drastically impact the amount of sexual selection and intraspecific competition within a population (Souroukis & Murray, 1994; Murray & Cade, 1995). This can lead to quantifiable alterations in population genetics and evolutionary trajectories (Bull, 1981; Souroukis & Cade, 1993).

While female crickets significantly delayed foraging in favor of increased vigilance in the presence of shrew odor, we did not test the effectiveness of this as an anti-predator
behavior. It should be noted that crickets used in this study were commercially bred and likely naive to shrew odor, meaning that the perception of predation risk and behavioral responses observed are innate rather than learned. While commercial crickets do possess similar behavioral traits to their wild counterparts (Wilson et al., 2010; Fisher et al., 2015), subsequent studies on natural populations would be necessary to firmly establish the relationship suggested here and to determine the ecological significance of our findings. Habitat choice or giving-up density experiments could provide additional value to determining how influential chemical cues from shrews, or other mammalian predators, are to crickets when making decisions about predation risk and the impact this has on broad ecological and evolutionary patterns.

ACKNOWLEDGEMENTS

We thank the Department of Biological Sciences and the Sternberg Museum of Natural History at Fort Hays State University for guidance and support, particularly Elmer J. Finck, Robert Channel, and Curtis J. Schmidt. We thank the editor and two anonymous reviewers for their suggestions which vastly improved this manuscript. Additionally, we thank Kyle Coblentz, Emily Khazan, and Erin Gorsich for insightful comments on earlier drafts. We also express gratitude to Binky, wherever he might currently reside, for help during experimental trials.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding
The authors received no funding for this work.

Competing Interests
Bradley Bott is currently an employee of PRA Health Sciences.

Author Contributions
• Brian P. Tanis conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
• Bradley Bott conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
• Brian J. Gaston conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Animal Ethics
The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):
Shrew odor was achieved by placing cardboard at the bottom of the educational shrew enclosure. No handling or other manipulation were done to the shrews. At the time of the
study, the Fort Hays State University IACUC was on prolonged hiatus and was unable to review our experiment. Discussions with previous members of the committee described our study design as not influencing vertebrate welfare and encouraged us to undergo the experiment without providing any formal paperwork.

**Data Availability**

The following information was supplied regarding data availability:

The raw data have been supplied as Supplementary File.

**Supplemental Information**

Supplemental information for this article can be found online at [http://dx.doi.org/10.7717/peerj.4923#supplemental-information](http://dx.doi.org/10.7717/peerj.4923#supplemental-information).

**REFERENCES**

Abbey-Lee RN, Mathot KJ, Dingemanse NJ. 2016. Behavioral and morphological responses to perceived predation risk: a field experiment in passerines. *Behavioral Ecology* 27:857–864 DOI 10.1093/beheco/arv228.

Alexander RD. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: Acheta). *Annals of the Entomological Society of America* 50:584–602.

Adamo SA, Hoy RR. 1994. Mating behavior of the field cricket *Gryllus bimaculatus* and its dependence on social and environmental cues. *Animal Behaviour* 47:857–868 DOI 10.1006/anbe.1994.1117.

Atwell A, Wagner Jr WE. 2015. Along came a spider who sat down beside her: perceived predation risk, but not female age, affects female mate choosiness. *Behavioural Processes* 115:143–148 DOI 10.1016/j.beproc.2015.04.002.

Bastille-Rousseau G, Fortin D, Dussault C, Courtois R, Ouellet JP. 2011. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography* 34:588–596 DOI 10.1111/j.1600-0587.2010.06517.x.

Beckers OM, Wagner Jr WE. 2012. Evesdropping parasitoids do not cause the evolution of less conspicuous signaling behaviour in a field cricket. *Animal Behaviour* 84:1457–1466 DOI 10.1016/j.anbehav.2012.09.016.

Binz H, Bucher R, Entling MH, Menzel F. 2014. Knowing the risk: crickets distinguish between spider predators of different size and commonness. *Ethology* 120:99–110 DOI 10.1111/eth.12183.

Brown J. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology and Research* 1:49–71.

Bull JJ. 1981. Sex ratio evolution when fitness varies. *Heredity* 46:9–26 DOI 10.1038/hdy.1981.2.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T. 2013. Personality-dependent dispersal cancelled under predation risk. *Proceedings of the Royal Society B: Biological Sciences* 280:Article 20132349.
Croft DP, Morrell LJ, Wade AS, Piyapong C, Ioannou CC, Dyer JRG, Chapman BB, Wong Y, Krause J. 2006. Predation risk as a driving force for sexual segregation: a cross-population comparison. *American Society of Naturalists* 167:867–878.

Csada RD, Neudorf DL. 1995. Effects of predation risk on mate choice in female *Acheta domesticus* crickets. *Ecological Entomology* 20:393–395 DOI 10.1111/j.1365-2311.1995.tb00473.x.

Cymborowski B, Muszyńska M. 1974. The effect of some psychotropic drugs on the circadian rhythm of locomotor activity of *Acheta domesticus* L. *Journal of Interdisciplinary Cycle Research* 5:362–370 DOI 10.1080/09291017409359451.

Dawley E, Miller M, Schnader J. 1999. Scaling chemosensory epithelia. In: Johnston RE, Müller-Schwarze D, Sorensen PW, eds. *Advances in chemical signals in vertebrates*. Boston: Springer.

Dubey S, Salamin N, Ohdachi SD, Barriere P, Vogel P. 2007. Molecular phylogenies of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations. *Molecular Phylogenetics and Evolution* 44:126–137 DOI 10.1016/j.ympev.2006.12.002.

Eadie WR. 1938. The dermal glands of shrews. *Journal of Mammalogy* 19:171–174 DOI 10.2307/1374611.

Fisher DN, James A, Rodrigues-Munoz R, Tregenza T. 2015. Behaviour in captivity predicts some aspects of natural behavior, but not others, in a wild cricket population. *Proceedings of the Royal Society B: Biological Sciences* 282:Article 20150708 DOI 10.1098/rspb.2015.0708.

Fumagalli L, Taberlet P, Stewart DT, Gielly L, Hausser J, Vogel P. 1999. Molecular phylogeny and evolution of *Sorex* shrews (Soricidae: Insectivora) inferred from mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* 11:222–235 DOI 10.1006/mpev.1998.0568.

Ghouri ASK. 1961. Home and distribution of the house cricket *Acheta domesticus* L. *Nature* 192:1000.

Gray DA. 1999. Intrinsic actors affecting female choice in house crickets: time cost, female age, nutritional condition, body size, and size-relative reproductive investment. *Journal of Insect Behavior* 12:691–700 DOI 10.1023/A:1020983821436.

Haffner M. 1998. The size of sebaceous glands in relation to the size of hair follicles on the heads of some small mammals (Insectivore, Chiroptera, Rodentia). *Annals of Anatomy* 180:165–171 DOI 10.1016/S0940-9602(98)80018-6.

Hardy TN, Shaw KC. 1983. The role of chemoreception in sex recognition in male crickets: *Acheta domesticus* and *Teleogryllus oceanicus*. *Physiological Entomology* 8:151–166 DOI 10.1111/j.1365-3032.1983.tb00344.x.

Hedrick AV, Dill LM. 1993. Mate choice by female crickets is influenced by predation risk. *Animal Behaviour* 46:193–196 DOI 10.1006/anbe.1993.1176.

Hedrick AV, Kortet R. 2006. Hiding behavior in two cricket populations that differ in predation pressure. *Animal Behaviour* 72:1111–1118 DOI 10.1016/j.anbehav.2006.03.018.
Hedrick AV, Kortet R. 2012. Sex based differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology* **66**:407–412 DOI 10.1007/s00265-011-1286-z.

Hoeffer CD, Durso LC, McIntyre KD. 2012. Chemical-mediated predator avoidance the European house cricket (*Acheta domesticus*) is modulated by predator diet. *Ethology* **118**:431–437 DOI 10.1111/j.1439-0310.2012.02028.x.

Hutterer R. 1985. Anatomical adaptations of shrews. *Mammal Review* **15**:43–55 DOI 10.1111/j.1365-2907.1985.tb00386.x.

Iwasa Y, Higashi M, Yamamura N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *The American Naturalist* **117**:710–723 DOI 10.1086/283754.

Jannett FJ, Jannett JA. 2009. Convergent evolution in the flank gland marking behavior of a rodent and a shrew. *Mammalia* **45**:473–482.

Kats LB, Dill LM. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* **5**:361–394 DOI 10.1080/11956860.1998.11682468.

Kortet R, Hedrick AV. 2004. Detection of the spider predator *Hololena nedra* by naïve juvenile field crickets (*Gryllus integer*) using indirect cues. *Behaviour* **141**:1189–1196 DOI 10.1163/1568539042664597.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* **16**:945–956 DOI 10.1093/beheco/ari075.

Lucas JR. 1983. The role of foraging time constraints and variable prey encounter in optimal diet choice. *The American Naturalist* **122**:191–209 DOI 10.1086/284130.

Main MB, Weckerly FW, Blech FC. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* **77**:449–461 DOI 10.2307/1382821.

Matsumoto Y, Mizunami M. 2000. Olfactory learning in the cricket *Gryllus bimaculatus*. *Journal of Experimental Biology* **203**:2581–2588.

Murray AM, Cade WH. 1995. Differences in age structure among field cricket populations (Orthoptera: Gryllidae): possible influence of a sex-biased parasitoid. *Canadian Journal of Zoology* **73**:1207–1213 DOI 10.1139/z95-144.

Nelson CM, Nolen TG. 1997. Courtship song, male agonistic encounters, and female mate choice in the house cricket, *Acheta domesticus* (Orthoptera: Gryllidae). *Journal of Insect Behavior* **10**:557–570 DOI 10.1007/BF02765377.

Niemelä PT, DiRienzo N, Hedrick AV. 2012. Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behaviour* **84**:129–135 DOI 10.1016/j.anbehav.2012.04.019.

Nowosielski JW, Patton RL. 1963. Studies on circadian rhythm of the house cricket, *Gryllus domesticus* L. *Journal of Insect Physiology* **9**:401–410.

Otte D, Cade W. 1976. On the role of olfaction in sexual and interspecies recognition in crickets (*Acheta* and *Gryllus*). *Animal Behavior* **24**:1–6 DOI 10.1016/S0003-3472(76)80091-7.

Pernetta JC. 1977. Anatomical and behavioural specialisations of shrews in relation to their diet. *Canadian Journal of Zoology* **55**:1442–1453 DOI 10.1139/z77-187.
Platt WJ. 1976. The social organization and territoriality of short-tailed shrew (*Blarina brevicauda*) populations in old-field habitats. *Animal Behaviour* 24:305–318 DOI 10.1016/S0003-3472(76)80039-5.

Poduschka W, Wemmer C. 1986. Observations on chemical communication and its glandular sources in selected Insectivora. In: Duvall D, Müller-Schwarze D, Silverstein RM, eds. *Chemical signals in vertebrates* 4. Boston: Springer.

Preisser EL, Bolnick DI, Benard MF. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509 DOI 10.1890/04-0719.

R Core Team. 2016. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/.

Rich JT, Neely G, Paniello RC, Voelker CCJ, Nussenbaum B, Wang EW. 2010. A practical guide to understanding Kaplan–Meier curves. *Otolaryngology-Head and Neck Surgery* 143:331–336 DOI 10.1016/j.otohns.2010.05.007.

Ritzi CM, Bartels BC, Sparks DW. 2005. Ectoparasites and food habits of Elliot’s short tailed shrew, *Blarina hylophaga*. *The Southwestern Naturalist* 50:88–93 DOI 10.1894/0038-4909(2005)050<0088:EAFHOE>2.0.CO;2.

Saarikko J. 1989. Foraging behaviors of shrews. *Annales Zoologici Fennici* 26:411–423.

Souroukis K, Cade WH. 1993. Reproductive competition and selection on male traits at varying sex ratios in the field cricket, *Gryllus pennsylvanicus*. *Behaviour* 126:45–62 DOI 10.1163/156853993X00335.

Souroukis K, Murray AM. 1994. Female mating behavior in the field cricket, *Gryllus pennsylvanicus* (Orthoptera: Gryllidae) at different operational sex ratios. *Journal of Insect Behavior* 8:269–279 DOI 10.1007/BF01988910.

Storm JJ, Lima SL. 2008. Predator-naïve fall field crickets respond to the chemical cues of wolf spiders. *Canadian Journal of Zoology* 86:1259–1263 DOI 10.1139/Z08-114.

Therneau TM. 2015. A package for survival analysis in S. Version 2.38. Available at https://cran.r-project.org/web/packages/survival/index.html.

Thomas ML. 2011. Detection of female mating status using chemical signals and cues. *Biological Reviews* 86:1–13.

Thompson CW, Choate JR, Genoways HH, Finck EJ. 2011. *Blarina hylaphaga* (Soricomorpha: Soricidae). *Mammalian Species* 43:94–103 DOI 10.1644/878.1.

Trompeter WP, Langkilde T. 2011. Invader danger: lizards faced with novel predators exhibit an altered behavioral response to stress. *Hormones and Behavior* 60:152–158 DOI 10.1016/j.yhbeh.2011.04.001.

Weismann DB, Rentz DCF. 1977. Feral house crickets *Acheta domesticus* (L.) (Orthoptera: Gryllidae) in southern Calif. *Entomological News* 88:246–248.

Werner EE, Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100 DOI 10.1890/0012-9658(2003)084[1083:AROTIT]2.0.CO;2.

Wilson ADM, Whattam EM, Bennett R, Visanuvimol L, Lauzon C, Bertram SM. 2010. Behavioral correlations across activity, mating, exploration, aggression, and
antipredator contexts in the European house cricket, *Acheta domesticus*. *Behavioral Ecology and Sociobiology* 64:703–715 DOI 10.1007/s00265-009-0888-1.

**Wolfe DH, Patten MA, Shochat E, Pruett CL, Sherrod SK. 2007.** Causes and patterns of mortality in Lesser Prairie-chickens *Tympanuchus pallidicintus* and implications for management. *Wildlife Biology* 13:95–104 DOI 10.2981/0909-6396(2007)13[95:CAPOMI]2.0.CO;2.

**Zuk M, Rotenberry JT, Tinghitella RM. 2006.** Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters* 2:521–524 DOI 10.1098/rsbl.2006.0539.