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RuiLin Guo
Western University, rguo27@uwo.ca

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The Fear Factor:
Impacts of Perceived Predation Risk and Competition on Fall Field Crickets (*Gryllus pennsylvanicus)*

RuiLin Guo

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Supervisor: Liana Zanette

Readers: Beth MacDougall-Shackleton & Lauren Des Marteaux

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ABSTRACT

Fear is a powerful force. The perceived threat of predation and competition can cause behavioural and physiological changes that ultimately affect fitness. Fear of predation may result in decreased foraging, increased hiding, or energetically-costly defense mechanisms, while intraspecific competition may lead to risky mating efforts. I investigated the impact of perceived predation and competition on the growth, behaviour, and fecundity of fall field crickets (*Gryllus pennsylvanicus*). This study is the first to manipulate both perceived predation and competition while measuring multiple impacts, allowing a holistic perspective. Using four treatments of control, predation, competition, and predation+competition, I exposed juvenile crickets to visual, chemical, and auditory cues (recordings of bird predators and male crickets) from their 4th instar to adulthood. I tracked growth measures such as mass, size, and development time until adulthood, then conducted behavioural assays and dissections to determine reproductive investment. My results showed that indirect predation and competition have substantial impacts. Perceived competition led to significantly decreased growth and food intake, while perceived predation led to anti-predator behaviour in females, which showed a trend of exiting from a vial faster. Both perceived predation and competition led to reduced reproductive investment, indicating a fecundity cost. These findings show that perceived risk alone can have wide-ranging impacts, expanding our understanding of indirect predation and competition effects.

INTRODUCTION

Predation and competition act as strong influencers of organismal behaviour, with consequences for development, survival, and fecundity (Bolnick & Preisser 2005). Failure to contend with predation and competition may ultimately affect fitness, through consequences such as limited access to resources or mates, injury, and mortality (Bolnick & Preisser 2005). Beyond the direct presence of predators or competitors, even the indirect perceived threats of predation and competition have impacts (Bolnick & Preisser 2005, Hedrick & Dill 1993, Kortet & Hedrick 2004). Individual-level factors such as behavioural patterns, growth in size or mass, developmental rate, and fecundity may all be altered by the perception of predation or competition (Bolnick & Preisser 2005, Kortet & Hedrick 2004).

Perceived Predation Risk

Predation risk imposes fitness costs on prey even when there is no immediate threat (Bolnick & Preisser 2005, Sih 1980). Studies have manipulated perceived predation risk through exposure to predators that cannot kill or through indirect chemical, auditory, or visual cues to predators' presence (Atwell & Wagner 2015, Danner & Joern 2003, Oedekoven & Joern 2000, Reader 2006, Riley & Dill 2005, Zanette 2011). Such manipulations have confirmed that perceived predation risk is as impactful as direct consumption at affecting behaviour, survival, or fecundity (Bolnick & Preissor 2005).

Predation risk may lead to increased defensive or avoidance strategies by prey, including reduced foraging time, increased escape behaviour, or less conspicuous mating displays (Adamo et al. 2013, Hedrick & Dill 1993, Reader et al. 2006). Anti-predator responses are prevalent in invertebrates: red-legged grasshoppers (*Melanoplus femurrubrum*) took off faster and jumped longer distances when exposed to disarmed spider predators (Hawlena et al. 2011), Colorado potato beetles (*Leptinotarsa decemlineata*) reduced feeding behaviour when exposed to predatory stinkbug cues (Hermann & Thaler 2014), and fall field crickets (*Gryllus pennsylvanicus*) showed greater immobility in the presence of wolf spiders' chemical cues (Storm & Lima 2008).

Though anti-predator responses can provide a survival advantage, such behaviours are costly and may result in reduced foraging, nutrition, growth, and even fecundity (Adamo et al. 2013, Pérez-Tris et al. 2004, Sih 1980, Zanette et al. 2011). As such, there exists a fitness trade-off, where the risk of predation (and potential mortality) must outweigh the energetic and fecundity costs of anti-predator behaviour (Adamo et al. 2013). A balance between natural and sexual selection also exists, as conspicuous courtship displays may attract predators, but discreet anti-predator strategies decrease reproductive success (Hedrick 2000). For example, female crickets prefer mates with long calling bouts, but males with shorter, inconspicuous displays are less likely to be eaten by predators (Hedrick 1986, 2000, Hedrick & Dill 1993, Dill et al. 1999).

Perceived Competition Risk

Intraspecific competition for mates or resources influence many species, leading to impacts on growth, body size, and reproductive investment (Iba et al. 1995, Bretman et al. 2011, Gray & Simmons 2013). My study focuses on reproductive competition, which may alter behaviour or development. In the presence of more rivals, males respond by increasing courtship displays, sperm production, and mating effort (Bretman et al. 2011, Gray & Simmons 2013). In crickets, intrasexual competition favours males with greater body size, which results in greater access to females, more offspring sired, and greater success in male-male competition (Hack 1997, Rodríguez-Muñoz et al. 2010, Saleh et al. 2014, Simmons 1986, 1988). Increases in the actual density of conspecifics also leads to greater resource competition and decreased foraging behaviour (Halliday & Morris 2013). These responses induced by competition also bear costs, from diverting resources to reproduction to physical altercations with rivals (Kortet & Hedrick

2007). For example, male crickets invest more energy into calling when in proximity to other males, to the extent that high quality males actually die sooner due to this energetic cost (Bateman & Fleming 2006, Hunt et al. 2004).

Unlike direct competition, the effects of perceived competition are not well understood. Studies indicate that even without direct exposure to conspecifics, the perception of high densities alone can act as a signal for individuals (Bolnick & Preisser 2005). Auditory cues for density have been successful at inducing competitive responses. For example, red squirrels (*Sciurus vulgaris*) increased territorial calling behaviour when exposed to recordings of conspecific territorial calls that simulated high competition (Shonfield et al. 2012). Acoustic cues signifying increased competition (i.e. recorded calls of male conspecifics) have also been used for juvenile black field crickets (*Teleogryllus commodus*), which altered their development rate based on perceived density levels (Kasumovic et al. 2011). Under high perceived reproductive competition, male crickets delayed maturity to reach greater sizes, while females developed faster (Kasumovic et al. 2011). In another species of field cricket (*Teleogryllus oceanicus*), males reared with recordings of calling males invested 10% more in reproductive tissue mass (gonads and accessory glands) (Bailey et al. 2010).

Model Species

Fall field crickets are an ideal model species as they react to both predator and conspecifics based on visual, auditory, and chemical cues (Fullard et al. 2005, Hedrick 2000, Kasumovic et al. 2011, Kortet & Hedrick 2004, Storm & Lima 2008). Fall field crickets are also fast-growing and semelparious, with only one reproductive season, so lifetime reproductive investment can be quantified at adulthood.

Project Objectives and Hypotheses

My study examines the growth, behavioural, and fecundity effects of perceived predation and competition (high conspecific density) on fall field crickets. Perceptions of competition are rarely studied, and in a review of the literature, I found no studies that manipulated both perceived predation and perceived competition. Additionally, few studies investigate multiple measures such as growth, behaviour, and fecundity within the same experiment (but see Bolnick & Preisser 2008 for a modeled approach). My research will therefore provide a more holistic view of indirect effects on insects, expanding our understanding of perceived predation and competition. Knowledge of developmental, behavioural, and reproductive effects can help us better predict the individual and population-level impacts of perceived predation and competition. I hypothesize that:

1) Perceived predation risk and perceived competition induce distinct stress responses.
2) Predation risk outweighs perceived competition as a factor, so the combined treatment will be similar in direction to that of predation risk alone.

My predictions, based on Preissor and Bolnick's (2005) meta-analysis, are in Table 1. *Predation*: Due to the energetic costs of anti-predator responses, I predicted that crickets exposed to perceived predation risk will exhibit reduced size, reduced food intake, and faster growth rates (as rapid moults result in smaller size). Based on a previous study, I predicted that predation risk would increase escape behaviour, leading to shorter times to exit a container as part of a behavioural assay (Leung 2016.). Greater energetic investment into anti-predator responses could also divert resources from reproduction, resulting in decreased fecundity.

Competition: I predicted that crickets exposed to perceived competition risk would delay growth to reach larger sizes and invest more into reproduction, as measured by mass of reproductive organs and number of eggs (Bretman et al. 2011, Kasumovic et al. 2011). As competitive responses may decrease foraging behaviour, I predicted that food consumption would decrease (Halliday & Morris 2013).

I also theorized that the combined treatment would have similar effects as the predation treatment, as the consequences of failing to avoid predation are more detrimental than failing to avoid competition (death brings future fitness to zero). This has been demonstrated in mammals where the threat of predation outweighs competition, though that study involved interspecific rather than intraspecific competition (Abramsky 1998).

MATERIALS & METHODS

Fall field crickets were reared under conditions of perceived predation and perceived competition and monitored for impacts on growth, behaviour, and fecundity. I used 180 juvenile fall field crickets of approximately equal male:female ratio, split evenly in four randomly-assigned treatments: control, predation, competition, and combined predation+competition groups (Table 2). There were no significant differences in initial cricket mass ($F_{3,176}$=0.993, p=0.397) or size ($F_{3,176}$=0.146, p=0.934) amongst treatments. Similar to Kasumovic et al.'s study (2011), treatments began during the 4th instar and continued until all crickets moulted into adults (approximately 1-2 months).

Cricket Housing

Crickets were housed individually in transparent 6 oz. plastic cups with air holes and egg cartons for shelter, similar to established methods (Des Marteaux & Sinclair 2016). This physical but not acoustic isolation prevents mating and cannibalism, while still allowing each individual to be exposed to treatment cues. Cricket cups in each treatment group were placed in acoustically-isolated rooms in a 58.7 cm x 38 cm x 30.3 cm rectangular plastic tank and kept at 25±1°C, 70-80% humidity, and a 12h:12:h light cycle (7:00am-7:00pm). Within each tank, cups were placed in three layers and separated with two mesh dividers (Appendix A). To ensure equal exposure to cues, layers were shifted down and individual cups rotated daily in a double Latin-square design (Appendix B) (pers.comm. Ashael Raveh).

Crickets were given *ad libitum* food (Martin Mills' Little Friends™ Original Rabbit Food) and water. Crickets were monitored daily and their backs were marked with a spot of liquid white-out to track moults. I recorded date of moults, beginning and end body mass (using Acculab analytical balance), femur and pronotum length at each moult (Appendix C), and food consumption throughout the experiment.

Treatment Cues (Table 3)

We exposed crickets to visual, chemical, and auditory cues for predation and competition. Cues were presented for four days at a time, with auditory cues alternating four days off and the start date for visual /chemical cues randomized weekly (Appendix D), to prevent habituation.

Visual cues: For perceived predation risk, three live female orbweaver spiders (*Larinioides spp.,* Araneae: Araneidae) were allowed to roam inside each tank, separated by mesh dividers to prevent cannibalism (following Bateman & Fleming 2006 and Leung 2016). For perceived competition risk, three adult fall field crickets were used, with sexes randomized due to limited availability of adults. The control for these cues were pipe cleaner circles of similar size and colour, taped onto the tank sides in locations the crickets and spiders were seen to frequent.

Chemical cues: Crickets are sensitive to chemical and scent cues of predators and conspecifics (Storm & Lima 2008). To simulate these cues, 5.5cm^2 filter papers circles were placed under orbweaver spiders (for predation) and adult fall field crickets of randomized sex (for competition) for 24 hours. The filter papers were cut into eighths and placed into individual cricket cups. Though concentration of scents may vary, this method for chemical cues has been successfully used in previous studies (Leung 2016, Kortet & Hedrick 2004). The combined treatment received one of each filter paper eighth (spider and cricket), while the control received a clean one.

Auditory cues: MP3 playbacks of recorded calls provided auditory cues, similar to previous studies using crickets by Kasumovic et al. (2011) and Leung (2016). Calls were randomized to come from one to four speakers (65dB, 20 cm away from tanks) at any given time.

Predation risk was simulated using recordings of native diurnal insectivorous predators obtained from the Borror Laboratory of Bioacoustics (Ohio State University, Columbus, Ohio). Predator calls used were of American Crow (*Corvus brachyrhynchos*), American Kestrel (*Falco sparverius*), Northern Flicker (*Colaptes auratus*), Brown-headed Cowbird (*Molothrus ater*), and Northern Cardinal (*Cardinalis cardinalis*). Predator recordings were played in the mornings (7:00am – 9:00am) and evenings (7:00pm – 9:00pm), to avoid overlap with competition playbacks (Appendix E). Competition was manipulated using adult male fall field cricket calls obtained from the Macauley Library (Cornell University, Ithaca, New York). Playbacks were presented during dark hours from 9:00pm to 7:00pm, representing the crickets' peak activity periods. During the day (9:00am – 5:00pm), we used playbacks of a lower rate (half the amount of cricket calls) to reflect naturally lower activity during daylight hours.

In order to control for sound, each predator and competition playlist had a corresponding pure tone counterpart that matched in pitch and frequency (Appendix F). This ensured crickets were responding to the information in recordings, rather than just the presence of sound. All playback editing was done using Audacity software (version 2.1.1, July 2015, http://www.audacityteam.org).

Behavioural Assay

We used a behavioural assay to determine if crickets raised under perceived predation or competition conditions have differing behavioural responses, following established methods (Hedrick & Kortet 2006, Kortet & Hedrick 2004). Cricket antipredator behaviour was measured as the time to exit from a vial into a novel environment. Ten days after moulting into adulthood, crickets were placed in a clear plastic vial wrapped with black paper and lowered into an opaque walled arena lined with paper towel (Appendix G). After a card blocking the vial's opening was removed, the trial was timed until the cricket's entire head exited the container or when ten minutes elapsed. The trials were filmed in a dim room (reflecting crickets' nocturnal nature) using a Sony Handyman DR-SR65 digital camera on a tripod, and videos were analyzed frame-by-frame using VirtualDub software (version 1.10.4, http://www.virtualdub.org).

Fecundity Measures

Adult crickets were weighed and frozen immediately after behavioural assays to halt development of reproductive organs at ten days past the adult moult. Crickets were thawed and dissected to assess reproductive investment. For males, gonads (which hold sperm) and accessory glands (which contain secretions that aid preservation, protection, and transfer of sperm) were removed, dried, and weighed (Bailey et al. 2010, Garcia-Gonzalez & Simmons 2010). In females, ovaries were removed, dried, and weighed, and the number of mature and immature eggs were counted. As the cuticles of mature eggs do not stain, mature eggs were identified by staining ovaries with carmine red, following established protocol (Humason 1972, McNeil & Delisle 1989). I dried organs in a 50°C oven until they reached a constant mass, which took two days on average. Abdominal fat was collected by scraping the remaining contents of the body cavity and centrifuging the entire abdomen at 15,000 rpm for two minutes. The fat that floated to the top was then pipetted out, dried as above, and weighed.

Statistical Analyses

I analyzed growth, behaviour, and fecundity measures using two-factor ANOVA (for sex and treatment), one-way ANOVA (for sex-specific measures), and Kruskal Wallis tests (for non-normal data). IBM SPSS software (version 23, https://www.ibm.com/analytics/us/en/technology/spss/) was used to conduct the statistical tests.

RESULTS

My results show that perceived predation and competition do affect growth, behaviour, and fecundity (see Table 4 for summary).

Growth Results

Perceived competition negatively affected growth, with crickets reaching smaller sizes when reared under competition risk. Overall, perceived competition led to decreased femur growth for both sexes, smaller males, and slow-developing females. Femur growth was defined as the difference in femur length at the adult moult compared to femur length at the experiment start date. The main effect of treatment was statistically significant for femur growth ($F_{3,132}$=4.149, p=0.008), as was sex ($F_{1,132}$=33.485, p=4.96×10^{-8}) with females having greater growth, while the interaction was not significant ($F_{3,132}$=1.518, p=0.213) (Figure 1a). Post-hoc Tukey's HSD tests showed that crickets in the competition and combined treatments had significantly less femur growth compared to the control and predator groups.

Males in the competition treatment showed significantly shorter adult pronotum lengths ($F_{3,63}$=3.765, p=0.015) and adult femur lengths ($F_{3,63}$=4.367, p=0.007) compared to the control

(Figure 1b). Females delayed development under perceived competition, taking a significantly longer time to reach their adult moult (calculated as number of days between the first moult and adult moult) than the control (x^2_3=9.684, p=0.021) (Figure 1c). There were no significant differences between treatments for pronotum growth, average femur/pronotum growth, adult body mass, or change in mass from experiment start to end (all p-values > 0.05).

Perceived competition also reduced food intake. Crickets in the competition and combined treatment consumed a significantly smaller total mass of food compared to the control group (Treatment: $F_{3,133}$=0.128, p=0.018, Sex: $F_{1,133}$=135.965, p<0.0001), Interaction: $F_{3,133}$=1.816, p=0.147) (Figure 2). Even when accounting for the differing time periods during which the crickets ate (from experiment start date to behavioural assay date), the same pattern holds. The average daily mass eaten was significantly lower than both the control and predator groups (Treatment: $F_{3,132}$=5.854, p=0.0009, Sex: $F_{1,132}$=246.72, p<0.0001, Interaction: $F_{3,132}$=0.949, p=0.419).

Behaviour Results

The behavioural assays showed that predation cues did have an impact on cricket behaviour, but effects varied by sex (Figure 3). Though not statistically significant (x^2_3=6.727, p=0.081), there was a clear trend in the time to exit from a vial in females. Females in the predation and combined treatments exited the vial faster than crickets that were not exposed to any predation cues. In contrast, males showed no patterns but took longer to exit from the vial than females across all treatments. When sex is excluded, a Kruskal Wallis test found no significance overall in the times to emerge from the vial by treatment (x^2_3=3.79, p=0.285).

Fecundity Results

Female: Females in the control group had the highest fecundity. The control group had significantly heavier ovaries compared to the predation, competition, and combined treatments

($F_{3,70}$=7.482, p=0.0002) (Figure 4a). Females in the control group also had a significantly greater number of mature eggs ($F_{3,70}$=9.494, p<0.0001) and total eggs ($F_{3,70}$=9.312, p<0.0001) compared to the three other groups (Figure 4b). Interestingly, the control and competition treatments had significantly lighter eggs (calculated as ovary dry mass/total number of eggs) compared to the predation treatment, which had the heaviest average mass per egg ($F_{3,70}$=6.404, p=0.001) (Figure 4c). There were no significant patterns for the number of immature eggs or the mass of abdominal fat (all p-values > 0.05).

Male: In males, perceived predation and competition also led to reduced reproductive organ masses, except the combined treatment did not experience this reduction. The control and combined treatments had significantly heavier accessory glands compared to the predation and competition treatments ($F_{3,63}$=6.987, p=0.0004) (Figure 5a). The total mass of reproductive organs (gonads and accessory gland) followed the same pattern and was significant by treatment ($F_{3,63}$=3.390 p=0.023), though a Tukey's HSD post-hoc test showed no significance in pairwise patterns (Figure 5b). There were no significant patterns for gonad mass or abdominal fat mass across treatments (all p-values > 0.05).

Across both sexes, the control group had the greatest fecundity, as measured by reproductive organ mass. Both predation and competition treatments reduced fecundity.

DISCUSSION

Indirect cues for predation and competition do impact the growth, behaviour, and fecundity of fall field crickets, though patterns vary by the effect measured and by sex. In addition, perceived predation effects dominate in influencing behaviour, while perceived competition is the major influencer for other measures of growth, development, and fecundity.

Growth

Being raised in an environment of high perceived competition impacts growth and development. Crickets of both sexes experienced decreased total femur growth and males also had decreased adult sizes (pronotum and femur lengths). This result is surprising given past studies demonstrate the advantages of large body size for crickets in high density environments (Simmons 1986, Hack 1997). This advantage is particularly evident in males, because body size is related to success in intrasexual conflicts, access to females, and offspring sired (Simmons 1986, Hack 1997). However, most studies manipulate actual density rather than perceived competition. In my experiment, the decreased growth and smaller adult sizes may be due to the costs of responding to competition. When males outnumber females (as in my experiment because playbacks consisted of male calls), male-male competition intensifies and crickets spend more time and effort competing for mates (Souroukis & Cade 1993). This means relatively less time is spent foraging and less energy is devoted to growth, hence explaining the smaller adult sizes (Halliday & Morris 2013). This is explanation is corroborated by the results for food intake, which did match my predictions. Crickets reared under perceived competition consumed less, allocating time to competitive responses rather than foraging behaviours.

Effects on development time were seen only in females, which took significantly longer to moult into adulthood. Since the playbacks simulated an environment with a high density of males, it is possible that there was no need for females to develop faster to ensure reproduction. With a perception that there are plentiful mates available to choose from, females are able to wait before moulting into adults. Delaying maturity allows crickets more time to grow and develop, which benefits fecundity of females in particular (Rohde 2015). This pattern of delayed maturity is also found in other invertebrates, with a study on mustard beetles (*Phaedon cochleariae*) finding that larvae raised under high densities develop more slowly than isolated larvae (Muller et al, 2016). The combined treatment for females did not show the same delayed maturity effect; this aligns with my prediction that perceived predation effects outweigh competition effects, because of the mortality risk of failing to avoid predators (Abramsky 1998). The predation cues in the combined treatment may have induced faster development in females so that they could reproduce before being eaten.

Behaviour

As expected, perceived predation – and not competition – affected cricket behaviour, since the assay is designed for anti-predator behaviour. Females exposed to predation cues showed a trend in emerging from the vial earlier, indicating that the skittish behaviour is an anti-predator response. This matches the findings of a previous study on fall field crickets, indicating that scared crickets tend to flee or escape faster and therefore exit quickly from the vial (Leung 2016). However, my results for females showed a trend but no statistical significance, which may be due to the level of predation cues. The previous study used both diurnal and nocturnal predator sounds playing day and night to create a more ‘dangerous’ environment, while I was only able to use diurnal predators due to the logistics of adding cricket sounds for competition risk at night. Interestingly, a different study by Hedrick found that crickets under predation risk took longer to exit from a tube (Hedrick 2000). This opposite response may be because crickets exhibited hiding behaviour rather than fleeing, or because the close-ended opaque vial used was perceived as unsafe. Future studies could consider identifying multiple different behaviours and using differently shaped (i.e. open ended) vials.

Unlike previous studies, I found no pattern for males, which exited the vial later than the females across all treatments. This may be attributed to the lower level of predation cues as explained previously; perhaps males only exhibit increased anti-predator responses if the ‘danger’ level exceeds a certain threshold (that is higher than females’). It may be advantageous for males to behave riskily, as boldness helps crickets outcompete rivals to gain access to mates (Alexander 1961). In the trade-off between attracting mates with conspicuous behaviour and attracting predators, perhaps males can improve their reproductive success by taking risks. In contrast, females exhibit greater caution, though they also face a trade-off between searching for higher quality males and being more visible predators (Hedrick & Dill 2000).

Fecundity

Fecundity was suppressed by perceived predation and competition risk in both sexes.

Females: In females, all groups exposed to predation and competition cues had less mature and total eggs and lighter ovary mass, with no differences between the predation, competition, or combined treatments. This suggests that both perceived predation and competition act as stressors that impose fecundity costs, perhaps due to more resources being allocated to anti-predator and competitive behaviours than to reproductive organs.

Unexpectedly, average egg mass was the only metric that did not follow this pattern – the predation treatment had significantly heavier eggs. This result may be attributed to the trade-off between offspring quantity and quality, with heavier eggs leading to improved viability but fewer offspring, due to the greater resources needed to produce larger eggs (Stahlschmidt 2013). It is possible that under predation risk, higher quality offspring are better equipped to survive in a dangerous world, so resources are dedicated to heavier eggs; however, this would need to be studied in further detail.

Males: For males, accessory gland and total reproductive organ mass were lower under perceived predation and competition. Reproductive organ mass quantifies lifetime reproductive investment and accessory gland mass positively influences embryo survival (Garcia-Gonzalez & Simmons 2010), leading to the conclusion that both perceived predation and competition degrade fecundity. This was unexpected, as I predicted that crickets under competition risk would invest more into reproduction. As with females, this result may be due to the costs of being alert to predators and rivals, so less energy is devoted to reproduction. A study on mustard beetles found that reproductive success was lower for individuals raised in high densities, so a similar effect is possible with perceived competition (Muller et al 2016). Additionally, studies on house crickets (*Acheta domesticus*) found that males can adjust the number and viability of sperm based on competition levels (Worthington et al 2013), so it is possible that males did invest in reproduction under the competition treatment, but sperm was not measured.

Finally, the combined treatment did not experience the same decrease in reproductive investment; males that were exposed to both predation and competition cues had similar reproductive organ masses as the control group. This warrants further investigation, but may be due to the combination treatment creating such a risky environment that it is advantageous for crickets to put everything into reproduction and die young, since they are likely to be eaten or be outcompeted anyway.

CONCLUSION

Perceived predation and perceived competition both have significant impacts on fall field crickets in different ways. For growth, competition risk leads to less food consumed, decreased femur growth, smaller males, and slow-developing females. For behaviour, predation risk causes skittish females to exit from a vial faster. And finally, for fecundity, both competition and predation risk have costs that reduce reproductive success. My findings confirm that the perception of risk is enough to change growth, behaviour, and fecundity. These changes do not just affect individual fitness; altered development and fecundity could lead to population-level effects that impact communities or ecosystems. The results of my study can help expand our understanding of perceived predation and competition in insects. This also opens up possibilities for future using different indirect cues, additional metrics, natural settings, or even different species. Measuring the impacts of predation and competition risk can improve our knowledge of individual and population effects, and garner insights on how perceptions of risk can impact organisms.

FIGURES

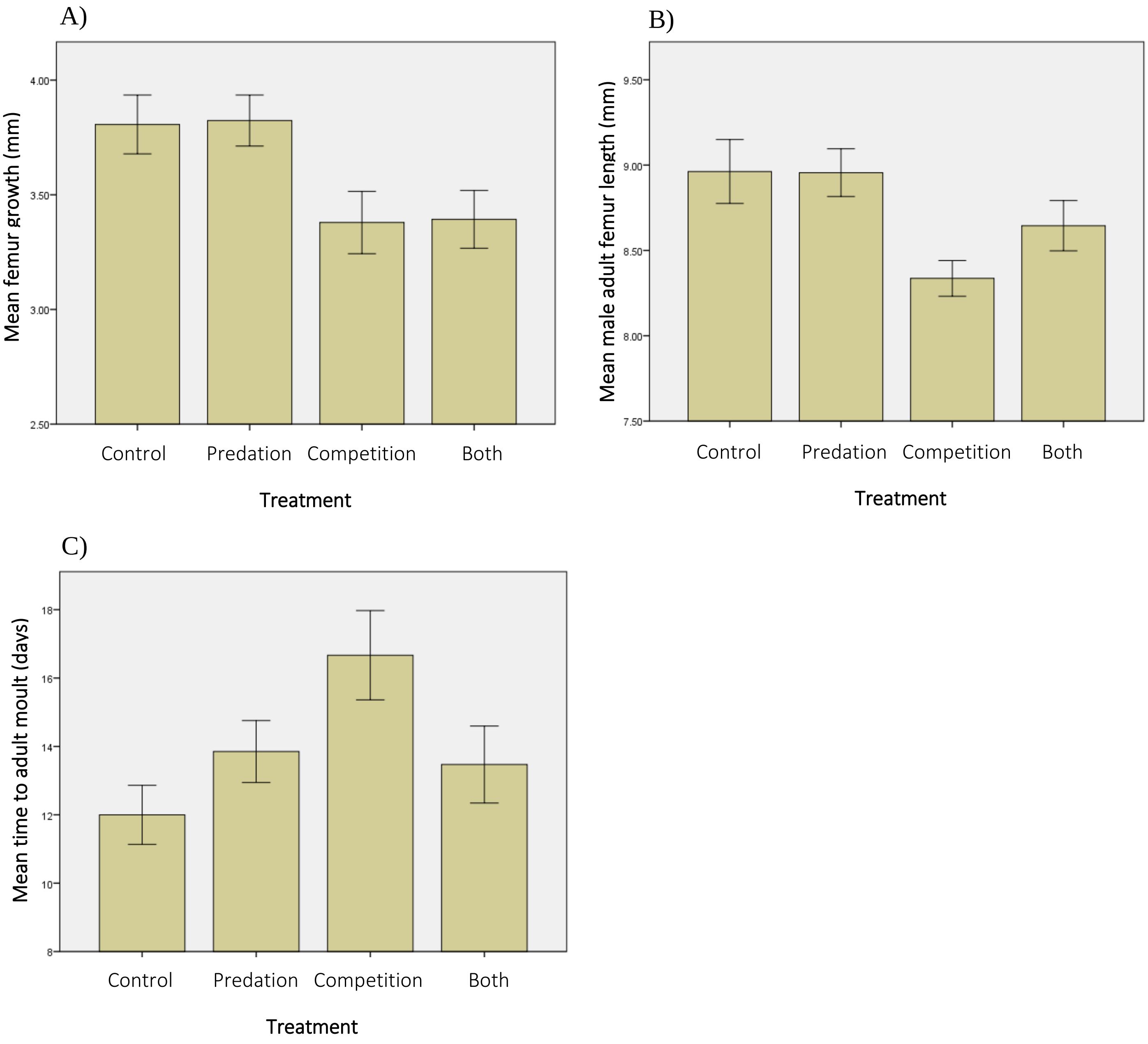


Figure 1. Graphs of growth measures. A) Mean femur growth (mm) from experiment start to adult moult, by treatment. B) Mean adult femur length (mm) for males, by treatment. C) Mean time to adult (days) from first moult to adult moult, by treatment.

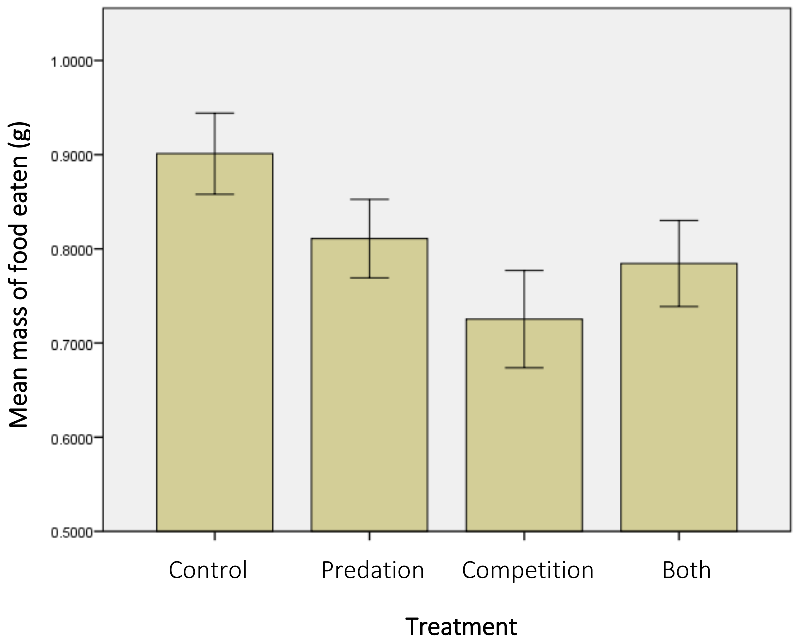


Figure 2. Graph of mean mass of food eaten (g) from start to end of experiment, by treatment

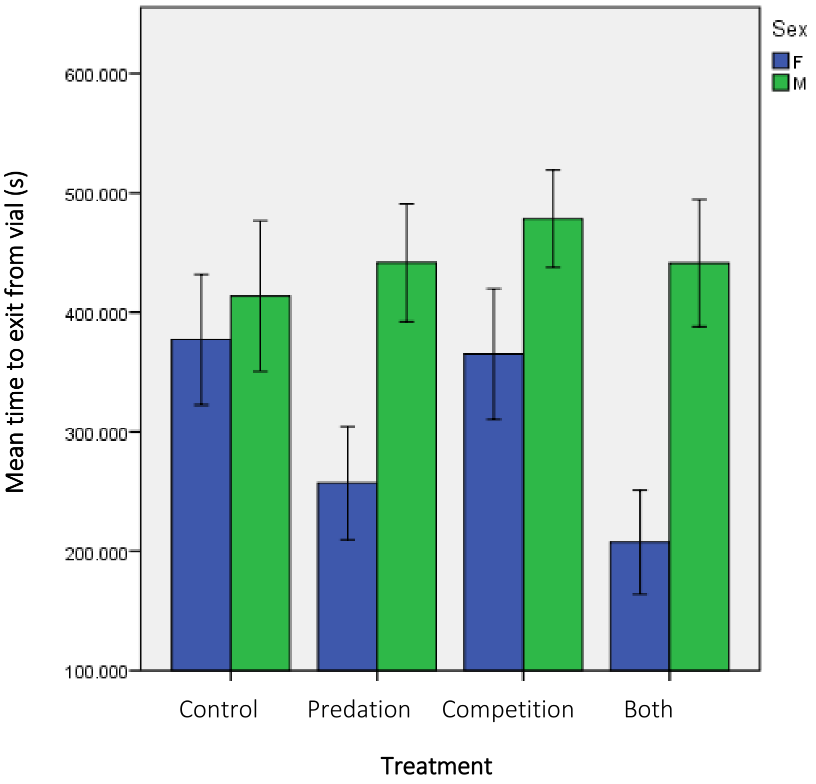


Figure 3. Graph of mean time to exit from vial (s) in behavioural assays, by treatment and sex

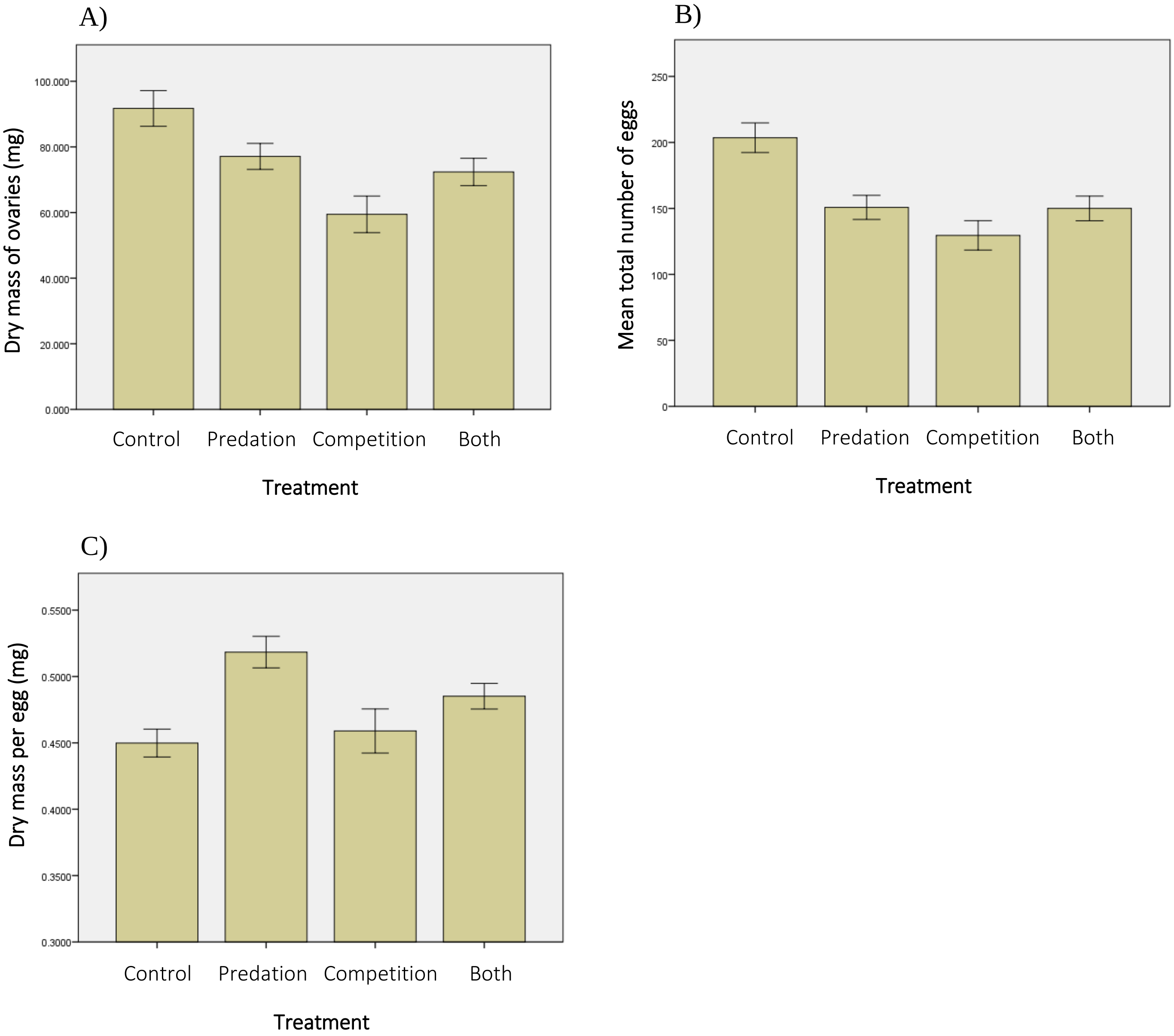


Figure 4. Graphs of female fecundity measures. A) Mean dry mass of ovaries (mg), by treatment. B) Mean total number of eggs for females, by treatment. C) Dry mass per egg (mg), by treatment.

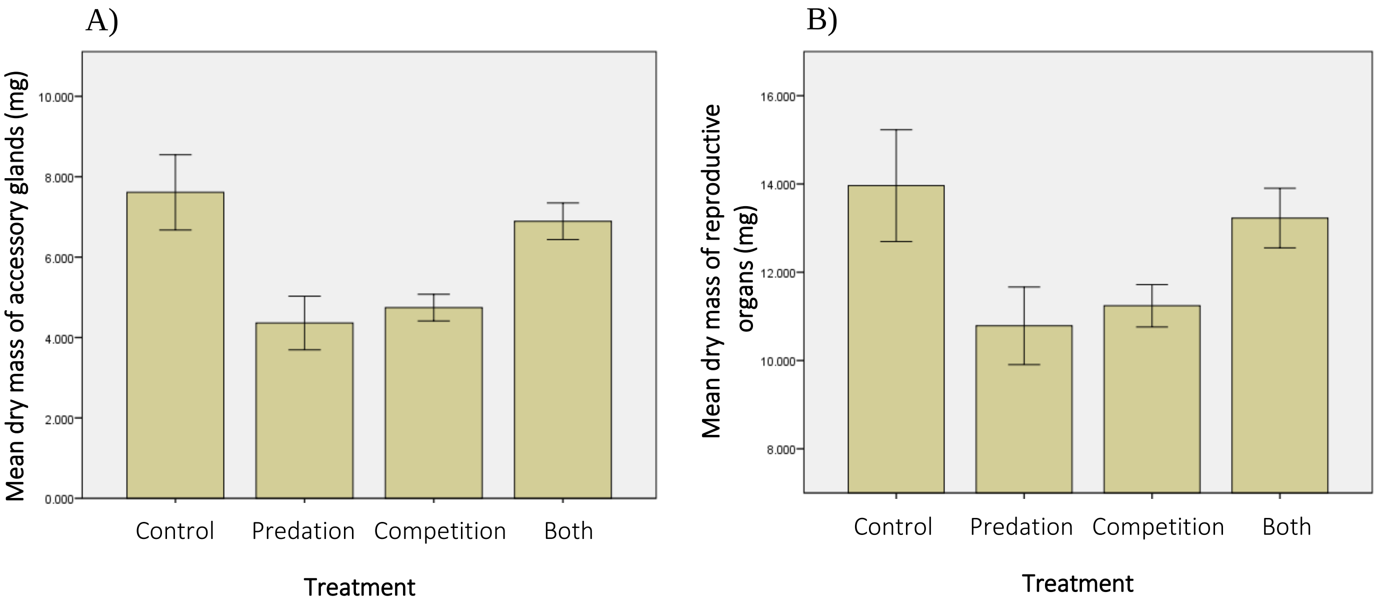


Figure 5. Graphs of male fecundity measures. A) Mean dry mass (mg) of accessory glands for males, by treatment. B) Mean dry mass (mg) of total reproductive organs (gonads + accessory gland) for males, by treatment.

TABLES

Table 1. Predicted behavioural and physiological changes due to perceived predation, perceived competition, and a combination of predation+competition risk, as compared with control group

Parameter affected	**As measured by**	**High predation risk**	**High competition** (density)	**Combined** (high predation and competition)
Growth	Body mass and femur/pronotum length	**Decrease**	**Increase**	**Decrease**
	Development time (days to adult moult)	**Increase**	**Decrease**	**Increase**
	Food consumption (mass)	**Decrease**	**Decrease**	**Decrease**
Behaviour	Time to emerge from vial	**Decrease**	**No change**	**No change**
Fecundity	Ovary mass, number of eggs, mass/egg (females)	**Decrease**	**Increase**	**Decrease**
	Mass of gonads and accessory glands (males)	**Decrease**	**Increase**	**Decrease**

Table 2. Levels of perceived predation risk and perceived competition for four treatments

	Control	**Predation Treatment**	**Competition Treatment**	**Combined Treatment** *(Competition + Predation)*
Perceived Predation Risk	**LOW**	**HIGH**	**LOW**	**HIGH**
Perceived Competition (Conspecific Density)	**LOW**	**LOW**	**HIGH**	**HIGH**

Table 3. Visual, chemical, and auditory cues used to manipulate perceived predation and perceived competition

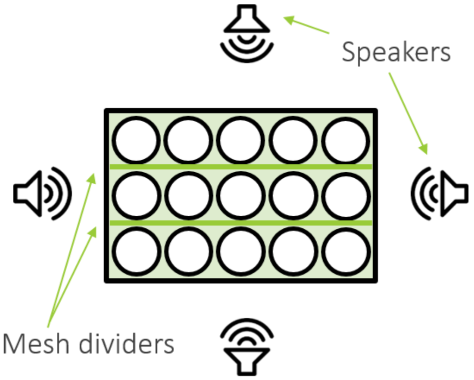
Modality	**Perceived Predation Cues**	**Perceived Competition Cues**
Visual	**Live female orbweaver spiders** inside plastic tanks (3/tank, separated by mesh to prevent cannibalism)	**Live adult fall field crickets** (randomized sex) inside plastic tanks (3/tank, separated by mesh to prevent cannibalism)
	Control: pipe cleaners of similar size, shape, and colour taped to sides of tank (3/tank)	
Chemical	**Filter papers placed under orbweaver spiders** 24 hours prior; cut into eighths and inserted into cups	**Filter papers placed under adult fall field crickets** (randomized sex) 24 hours prior; cut into eighths and inserted into cup
	Control: plain filter papers cut into eights and inserted into each cricket cup	
Auditory	**Playlist of diurnal predator calls**, randomized to come from any of 4 speakers	**Playlist of adult male fall field cricket calls**, randomized to come from any of 4 speakers
	Control: pure tones matching in pitch and frequency, randomized to come from any speaker	

Table 4. Summary of statistically significant results (unless noted otherwise) for growth, behaviour, and fecundity by treatment

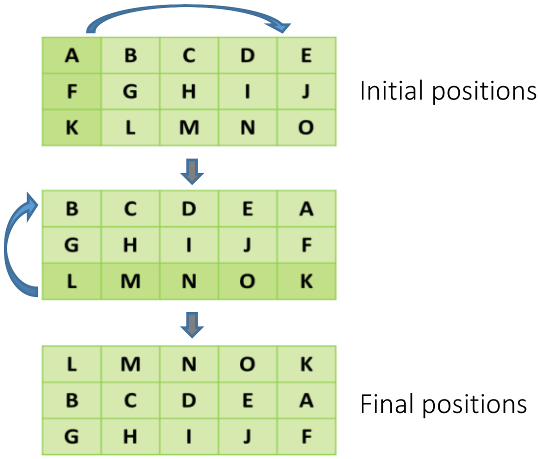
Measure	**Predation Treatment**	**Competition Treatment**	**Combined Treatment** *(predation+competition)*
GROWTH			
Femur growth	▬ *No change*	⬇ *Decrease*	⬇ *Decrease*
Males only: **Adult femur & pronotum length**	▬ *No change*	⬇ *Decrease*	⬇ *Decrease*
Females only: **Development time** (days from 1st to adult moult)	▬ *No change*	⬆ *Increase*	▬ *No change*
Mass Eaten (total & daily average)	▬ *No change*	⬇ *Decrease*	⬇ *Decrease*
BEHAVIOUR			
Females only: **Time to Emerge from Tube** *(*Trend, not statistically significant)*	⬇ *Decrease*	▬ *No change*	⬇ *Decrease*
FECUNDITY			
Females: **Ovary mass** (wet & dry)	⬇ *Decrease*	⬇ *Decrease*	⬇ *Decrease*
Females: **Number of mature eggs & total eggs**	⬇ *Decrease*	⬇ *Decrease*	⬇ *Decrease*
Females: **Average mass per egg** (dry mass)	⬆ *Increase*	▬ *No change*	▬ *No change*
Males: **Accessory gland and total reproductive organs mass**	⬇ *Decrease*	⬇ *Decrease*	⬇ *Decrease*

APPENDIX

A. Overhead view of experimental setup



B. Double Latin square pattern for rotating cricket cups



Initial positions

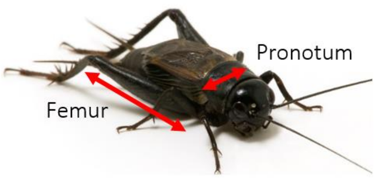
A	B	C	D	E
F	G	H	I	J
K	L	M	N	O

B	C	D	E	A
G	H	I	J	F
L	M	N	O	K

Final positions

L	M	N	O	K
B	C	D	E	A
G	H	I	J	F

C. Photo of fall field cricket indicating femur (hind leg) and pronotum (back)



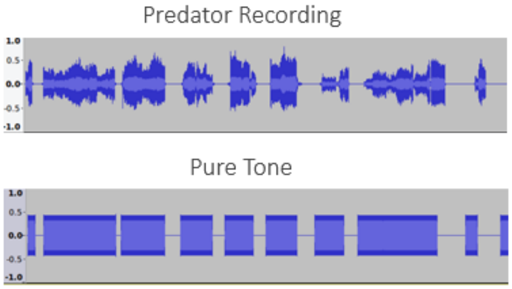
D. Schedule indicating timing of chemical, visual, and auditory cue exposure.

Date	Chemical Cues	Visual Cues	Auditory Cues
05-Nov			
06-Nov			
07-Nov			Sounds on
08-Nov	*Filter paper*		Sounds on
09-Nov	Insert cues	Insert live animals	Sounds on
10-Nov	Cues in	Animal in	Sounds on
11-Nov	Cues in	Animal in	
12-Nov	Remove cues	Remove animals	
13-Nov			
14-Nov			
15-Nov			Sounds on
16-Nov	*Filter paper*		Sounds on
17-Nov	Insert cues	Insert live animals	Sounds on
18-Nov	Cues in	Animal in	Sounds on
19-Nov	Cues in	Animal in	
20-Nov	Remove cues	Remove animals	
21-Nov			
22-Nov			
23-Nov	*Filter paper*		Sounds on
24-Nov	Insert cues	Insert live animals	Sounds on
25-Nov	Cues in	Animal in	Sounds on
26-Nov	Cues in	Animal in	Sounds on
27-Nov	Remove cues	Remove animals	
28-Nov	*Filter paper*		
29-Nov	Insert cues	Insert live animals	
30-Nov	Cues in	Animal in	
01-Dec	Cues in	Animal in	Sounds on
02-Dec	Remove cues	Remove animals	Sounds on
03-Dec			Sounds on
04-Dec			Sounds on
05-Dec			
06-Dec			
07-Dec	*Filter paper*		
08-Dec	Insert cues	Insert live animals	
09-Dec	Cues in	Animal in	Sounds on
10-Dec	Cues in	Animal in	Sounds on
11-Dec	Remove cues	Remove animals	Sounds on
12-Dec	*Filter paper*		Sounds on
13-Dec	Insert cues	Insert live animals	
14-Dec	Cues in	Animal in	
15-Dec	Cues in	Animal in	
16-Dec	Remove cues	Remove animals	

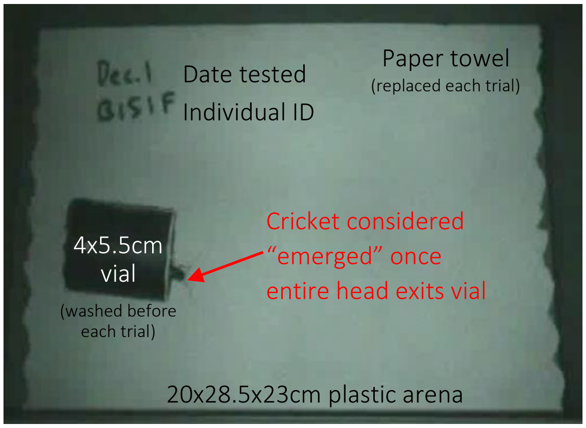
E. Schedule for auditory cues, indicating timing of recordings for each treatment

Treatment	**Morning** **7:00am-9:00am**	**Day** **9:00am-5:00pm**	**Evening** **5:00pm-7:00pm**	**Night** **7:00pm-7:00am**
Control	Pure tones (predator)	Pure tones (cricket) at ½ rate	Pure tones (predator)	Pure tones (cricket)
Predation	Predator sounds 	Pure tones (cricket) at ½ rate	Predator sounds 	Pure tones (cricket)
Competition	Pure tones (predator)	Cricket sounds at ½ rate 	Pure tones (predator)	Cricket sounds 
Combined (predation + competition)	Predator sounds 	Cricket sounds at ½ rate 	Predator sounds 	Cricket sounds 

F. Predator playback clip with pure tone equivalent (matching pitch & frequency)



G. Still of recorded video showing setup for behavioural assay



REFERENCES

Abramsky, Z., Rosenweig, M.L., and Subach, A. (1998) Do gerbils care more about competition or predation? *Oikos* 83, 75-84

Adamo, S.A., Kovalko, I. and Mosher, B. (2013) The behavioural effects of predator-induced stress responses in the cricket (*Gryllus texensis*): the upside of the stress response. *J. Exp. Biol.* 216, 4608–4614

Alexander, R.D. (1961) Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour* 17, 130–223

Bailey, N.W., Gray, B. and Zuk, M. (2010) Acoustic experience shapes alternative mating tactics and reproductive investment in male field crickets. *Curr. Biol.* 20, 845-849

Bateman, P.W. and Fleming, P.A. (2006) Sex, intimidation and severed limbs: the effect of simulated predator attack and limb autotomy on calling and emergence behaviour in the field cricket *Gryllus bimaculatus*. *Behav. Ecol. Sociobiol.* 59, 674–681

Bolnick, D.I and Preisser, E.L. (2005) Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology* 86, 2771-2779

Bretman, A., Westmancoat, J.D., Gage, M.J.G., and Chapman, T. (2011) Males use multiple, redundant cues to detect mating rivals. *Curr. Biol.* 21, 617–622

Bucher, R., Binz, H., Menzel, F. and Entling, M.H. (2014) Spider cues stimulate feeding, weight gain, and survival of crickets. *Eco. Entomology* 39, 1-7

Des Marteaux, L. and Sinclair, B.J. (2016) Ion and water balance in *Gryllus* crickets during the first twelve hours of cold exposure. *J. Insect Physiol.* 89, 19-27

Dill, L.M., Hedrick, A.V. and Fraser, A. (1999) Male mating strategies under predation risk: do females call the shots? *Behav. Ecol.* 10, 452–461

Garcia-Gonzalez, F. and Simmons, L.W. (2010) Male-induced costs of mating for females compensated by offspring viability benefits in an insect. *J. Evol. Biol.* 23, 2066-2075

Gray, B. and Simmons, L.W. (2013) Acoustic cues alter perceived sperm competition risk in the field cricket *Teleogryllus oceanicus*. *Behav. Ecol.* 24, 982–986

Hack, M.A. (1997) Assessment strategies in the contests of male crickets, *Acheta domesticus*. *Anim. Behav.* 53, 733–747

Halliday, W.D. and Morris, D.W. (2013) Safety from predators or competitors? Interference competition leads to apparent predation risk. *J. Mammal.* 94, 1380-1392.

Hawlena, D., Kress, H., Dufresne, E.R. and Schmitz, O.J. (2011) Grasshoppers alter jumping biomechanics to enhance escape performance under chronic risk of spider predation. *Funct. Ecol.* 25, 279-288

Hedrick, A.V. (1986) Female preferences for male calling bout duration in a field cricket. *Behav. Ecol. Sociobiol.* 19, 73–77

Hedrick, A.V. (2000) Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc. R. Soc. Lond. B* 267, 671-675

Hedrick, A.V. and Dill, L.M. (1993) Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* 46, 193–196

Hermann, S.L. and Thaler, J.S. (2014) Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia* 176, 669-676

Humason, G.L. (1972) Animal Tissue Techniques. Freeman WH and Company, San Francisco, p. 498

Hunt, J. *et al.* (2004) High-quality male field crickets invest heavily in sexual display but die young. *Nature* 432, 1024–1027

Iba, M., Nagao, T. and Urano, A. (1995) Effects of population density on growth, behavior and levels of biogenic amines in the cricket, *Gryllus bimaculatus. Zool. Sci.* 12, 695-702

Kasumovic, M.M., Hall, M.D., Try, H. and Brooks, R.C. (2011) The importance of listening: juvenile allocation shifts in response to acoustic cues of the social environment. *J. Evol. Biol.* 24, 1325–1334

Kortet, R. and Hedrick, A. (2004) Detection of the spider predator, *Hololena nedra* by naïve juvenile field crickets (Gryllus integer) using indirect cues. *Behaviour* 141, 1189-1196

Kortet, R. and Hedrick, A. (2007) A behavioural syndrome in the field cricket Gryllus integer: intrasexual aggression is correlated with activity in a novel environment. *Biol. J. Linn. Soc.* 91, 475–482

Leung, V. (2016) It's a scary world out there: effects of predation risk on fall field crickets (*Gryllus* pennsylvanicus). Honour's Thesis. University of Western Ontario

McNeil, J.N. and Delisle, J. (1989) Host plant pollen influences calling behavior and ovarian development of the sunflower moth, *Homoeosoma electellum*. *Oecologia* 80, 201-205

Müller, T., Küll, C.L. and Müller, C. (2016) Effects of larval versus adult density conditions on reproduction and behavior of a leaf beetle. *Behav. Ecol. Sociobiol.* 70, 2081

Pérez-Tris, J., Diaz, J.A., Telleria, J.L. (2004) Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? *Anim. Behav.* 67, 511–521

Persons, M.H., Walker, S.E., Rypstra, A.L., Marshall, S.D. (2001) Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). *Anim. Behav.* 61, 43–51

Preisser, E.L. and Bolnick, D.I. (2008) The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE* 3, 2465

Preisser, E.L., Bolnick, D.I., and Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86, 501–509

Rodríguez-Muñoz, R., Bretman, A., and Tregenza, T. (2011) Guarding males protect females from predation in a wild insect. *Curr. Biol.* 21, 1716–1719

Rohde, K., Dreher, E., and Hochkirch, A. (2015) Sex-specific phenotypic plasticity in response to the trade-off between developmental time and body size supports the dimorphic niche hypothesis. *Biol. J. Linn. Soc.* 115, 48-57

Saleh, N.W., Larson, E.L. and Harrison, R.G. (2014) Reproductive success and body size in the cricket *Gryllus firmus*. *J Insect Behav* 27, 346.

Shonfield, J., Taylor, R.W., Boutin, S., Humphries, M.M., and McAddam, A.G. (2012) Territorial defense behavior in red squirrels is influenced by local density. *Behaviour* 149, 369–390

Sih, A. (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* 210, 1041–1043

Simmons, L.W. (1986) Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus*. *Anim. Behav.* 34, 567–579

Simmons, L.W. (1988) Male size, mating potential and lifetime reproductive success in the field cricket, *Gryllus bimaculatus*. *Anim. Behav.* 36, 372–379

Souroukis, K. and Cade, W.H. (1993) Reproductive competition and selection on male traits at varying sex ratios in the field cricket, *Gryllus pennsylvanicus. Behaviour* 126, 45-62

Stahlschmidt, Z.R., Rollinson, N. Acker, M. and Adamo, S. (2013) Are all eggs created equal? Food availability and the fitness trade-off between reproduction and immunity. *Funct. Ecol.* 27, 800-806

Storm, J.J. and Lima, S.L. (2008) Predator-naïve fall field crickets respond to the chemical cues of wolf spiders. *Can. J. Zool.* 86, 1259–1263

Worthington, A.M., Gress, B.E., Neyer, A.A., and Kelly, C.D. (2013) Do male crickets strategically adjust the number and viability of their sperm under sperm competition? *Anim. Behav.* 86, 55-60

Zanette, L.Y., White, A.F., Allen, M.C., Clinchy, M. (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334, 1398–1401