



## Differential effects of predator cues versus activation of fight-or-flight behaviour on reproduction in the cricket *Gryllus texensis*



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How prey animals determine predation risk remains uncertain. We propose that one signal of high predation risk is repeated activation of fight-or-flight behaviour. We activated escape runs in the cricket *Gryllus texensis* by blowing air on the cerci. Escape runs were induced for 5 min, three times per day, three times per week for 4 weeks. Repeated fight-or-flight behaviour led to a loss in mass and decreased life span, suggesting a decline in somatic maintenance. However, there was an increase in egg laying, which we interpret as terminal reproductive investment. Stress responses remained robust. Octopamine (OA), a stress neurohormone in insects, increased in concentration in the haemolymph after running, and the magnitude of the increase was the same even after repeated activation (i.e. there was no habituation of the response). There was also no increase in basal OA haemolymph levels. In a second experiment, crickets were exposed to a mantid (predator, *Tenodera sinensis*), a walking stick (nonpredator, *Carausius morosus*), or an empty container. None of the crickets exhibited fight-or-flight behaviour. However, mantid-exposed crickets decreased egg laying. There was no decrease in life span or mass. There was no change in basal levels of OA, or in the magnitude of the OA increase after running. These results are consistent with the hypothesis that repeated fight-or-flight behaviour induces reproductive responses that would be adaptive for a shortened life span. These responses differ from those produced by predator cues alone. Even short-lived animals, such as crickets, appear to alter reproduction depending on the relative predation risk and their residual reproductive potential.

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Predators are a major selective force on prey (Lima & Dill, 1990). As a result, prey have evolved a range of antipredator responses (Clinchy, Sheriff, & Zanette, 2013; Hawlena & Schmitz, 2010; Lima & Bednekoff, 1999). These include not only fight-or-flight behaviours, but also changes in reproduction (Harris & Carr, 2016; Zanette, Clinchy, & Suraci, 2014). These reproductive changes are thought to maximize an animal's fitness for the current conditions (e.g. due to trade-offs between reproduction and other systems vital for survival in a predator-rich environment, Boonstra, 2013). Typically, predator stress decreases reproduction (Harris & Carr, 2016; Zanette et al., 2014), and, therefore, this response should be expressed only when necessary. How animals determine predation risk remains an open question (Harris & Carr, 2016).

Predator risk is not an all-or-none phenomenon. Predators can make repeated attack attempts on prey, inducing multiple bouts of fight-or-flight behaviour, or they can merely be chronically present

in the environment. Prey are sensitive to the relative level of predation risk (Lima & Bednekoff, 1999). Typically, prey responses to predators increase in magnitude as the intensity of the predator/prey interaction increases (Harris & Carr, 2016). For instance, increased predator proximity produces greater declines in reproduction (e.g. Thomson, Tomas, Forsman, Broggi, & Monkkonen, 2010). Sensory cues given off by predators can alert prey to their presence, but activation of fight-or-flight behaviour, with the concomitant activation of the classic stress response (Harris & Carr, 2016), may be the most reliable signal of life-threatening levels of predator threat. To what extent stress responses are involved in determining and/or mediating the relative level of risk remains uncertain (Harris & Carr, 2016).

Predator cues that result in fight-or-flight behaviour produce different responses in prey compared with those that do not. For example, while exposure to predator cues produces a modest increase in metabolic rate in crickets (ca. 20%, Lagos & Herberstein, 2017), fighting between two male crickets increases metabolic rate by 400%, depending on the duration of the fight (Hack, 1997). In vertebrates, the magnitude of the increase in stress hormone levels is higher during fight-or-flight behaviour (e.g. escaping from a

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predator attack) than after exposure to predator cues (e.g. handling stress, Pakkala, Norris, & Newman, 2013). Live predators are more effective at activating the mammalian stress response than are predator cues without the predator present (Harris & Carr, 2016; Monclus, Palomares, Tablado, Martinez-Fonturbel, & Palme, 2009). In some animals, predator cues alone do not elicit any stress hormone response, especially if the cues are chronically present in the environment (Harris & Carr, 2016). In insects too, sensory cues alone produce less of a stress hormone increase than does activation of fight-or-flight behaviour, at least in the context of aggressive behaviour (Adamo, Linn, & Hoy, 1995). These endocrinological differences could signal predation risk to the reproductive system.

A recent review of the vertebrate literature found that stress hormones (e.g. glucocorticoids) often have complex effects on reproduction, especially when predator stress is chronic (Harris & Carr, 2016). The interactions among predator stress, stress hormone release and reproductive success is difficult to study in vertebrates because of their complicated stress response systems (Harris & Carr, 2016), and the complexities introduced by the existence of parental care and multiple breeding seasons. Moreover, there are serious methodological issues regarding the measurement of glucocorticoid stress hormones (e.g. Breuner, Delehanty, & Boonstra, 2013; Dickens & Romero, 2013; Johnstone, Reina, & Lill, 2012). Examining interactions among predator stress, stress hormone release and reproductive success in insects may provide more definitive results. Insects have a more straightforward fight-or-flight response system (Adamo, 2012; Orchard, Ramirez, & Lange, 1993; Roeder, 2005). The major stress hormone (i.e. neurohormone), octopamine (OA), is a biogenic amine (Roeder, 2005) and is relatively easy to measure. OA enhances the ability of crickets to escape predation (Adamo, Kovalko, & Mosher, 2013) and is involved in antipredator behaviour in other insects (Jones et al., 2011; Nishi, Sasaki, & Miyatake, 2010), demonstrating a link between this stress hormone and antipredator behaviour. As in vertebrates, predators can have long-lasting effects on insect prey (e.g. Krams et al., 2016), including on their reproduction (Xiong et al., 2015). Most insect species have a single breeding season and no parental care, allowing more direct interpretations of the effects of predator exposure on reproduction. In this study, we use the cricket *Gryllus texensis* to test whether predator cue exposure, with or without repeated fight-or-flight behaviour, affects OA haemolymph concentrations and reproductive investment.

Crickets are near the bottom of the food chain and are often exposed to predator cues (Hedrick & Kortet, 2006), which may explain why predator cues alone do not induce fight-or-flight behaviour (Storm & Lima, 2008). Nevertheless, predator cues affect metabolic rate in beetles (*Tenebrio molitor*) (Krams et al., 2013), and crickets alter metabolic rate in response to startle, although the strength of this response varies across individuals (Krams et al., 2017). We predicted that frequent activation of fight-or-flight behaviour would signal high predation risk to female crickets and lead to an increase in their reproduction (i.e. terminal reproductive investment, Clutton-Brock, 1984). Crickets have a single breeding season (Murray & Cade, 1995) and no parental care (Walker & Masaki, 1989). Females contain mature eggs stored in their lateral oviducts, allowing them to increase egg laying without an increase in egg production (Shoemaker & Adamo, 2007). Therefore, under high predation risk, we predicted that female crickets would increase oviposition in order to increase the likelihood of laying all of the mature eggs in their lateral oviducts prior to death. Female crickets exhibit such terminal reproductive investment when faced with a life-threatening attack from pathogens (Adamo, 1999; Shoemaker, Parsons, & Adamo, 2006). We further predicted that to increase egg laying, and fuel fight-or-flight behaviour, females would reduce other investments, resulting in

a decline in somatic maintenance (e.g. Janssens & Stoks, 2013; Janssens et al., 2014) and a decrease in mass and life span, consistent with work on other insects (e.g. McCauley, Rowe, & Fortin, 2011). We also expected that the production of new eggs would decline, as frequent attacks suggest that the female's life span would be too short to be able to mature and lay them. In addition, when predator attacks are frequent, robust stress responses are necessary if the animal is to survive long enough to benefit from terminal reproductive investment. We expected that fight-or-flight behaviour would increase OA concentration, as has been found previously in this species (Adamo & Baker, 2011; Adamo et al., 1995), even after chronic exposure to predator attacks. Any long-term negative effects of repeatedly activating the stress response (Romero, Dickens, & Cyr, 2009) are unlikely to reduce fitness under these conditions because the animal's life span will probably be short. Therefore, when predation risk is high, females should be selected to have both robust stress responses and increased reproduction.

We predicted that under conditions of moderate predator risk (i.e. exposure to predator cues without attack), crickets would reduce risky behaviours, such as egg laying and foraging, as seen in other animals (Zanette et al., 2014). This strategy would allow crickets to extend their reproductive life span, possibly until a time when predator risk may be lower. Increased predation risk has been shown to depress egg laying in crickets (Stahlschmidt, Rollinson, Acker, & Adamo, 2013, 2014). We also predicted that some aspects of somatic maintenance would increase in order to maintain reproductive life span, despite the likely costs of heightened vigilance (e.g. Janssens & Stoks, 2014; Slos & Stoks, 2008). For example, predator stress can induce an upregulation of heat shock proteins (Slos & Stoks, 2008); these proteins help buffer cells against damage, such as those produced by the increased metabolic rate initiated by predator cues (Slos & Stoks, 2008). Therefore, we predicted that crickets exposed to predator cues would have a normal life span but would decline in mass because of reduced feeding and/or the costs of increased antipredator behaviour (Adamo & Baker, 2011). We also expected that crickets under moderate predator risk would maintain robust stress responses to help maintain reproductive life span but not exhibit the high levels of haemolymph OA concentration observed during fight-or-flight behaviour, which we suggest is a potent internal signal of high predation risk in crickets.

## METHODS

Long-winged crickets (*G. texensis*) were maintained at  $25 \pm 2^\circ\text{C}$  on a 12:12 h light:dark cycle and provided with dried cat food pellets and water ad libitum. All studies were approved by the University Committee on Laboratory Animals (of Dalhousie University) (I-11-025) and are in accordance with the Canadian Council of Animal Care.

Chemicals were obtained from Sigma Chemical Co. (St Louis, MO, U.S.A.) unless otherwise noted.

### *Does Repeated Escape Running Reduce Life Span and Increase Reproduction?*

Female crickets were isolated into clear containers (17 × 15 cm and 9.5 cm high) at the moult to adulthood and were provided with shelter as well as food and water ad libitum. Crickets were assorted to groups so that there was no significant difference in the initial body mass across groups. At 7 days of age, a male was placed in each container overnight to allow for mating. Females were given a different male each night for a total of 3 nights. This procedure allows females to store enough sperm for a lifetime (Shoemaker

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