



Are males more scared of predators? Differential change in metabolic rate between males and females under predation risk



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HIGHLIGHTS

- Little is known about the energetic impact of non-consumptive effects of predation.
- We measured change in prey's metabolic rate when presented with predatory cues.
- Prey's resting metabolic rate increased when a predatory cue was present.
- Males showed a greater increase in resting metabolic rate than females.

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ABSTRACT

The non-consumptive effects of predation contribute to reduce preys' fitness. In this way, predation imposes a cost to animals, not only through direct consumption, but also as an energetic cost. One way used to estimate this cost in the past has been to measure the production of CO₂ to estimate the change in metabolic rate because of predation. It has been proposed that this change is mediated by the insect stress neurohormone octopamine. Here we study the change in metabolic rate of the black field cricket (*Teleogryllus commodus*), and how the production of CO₂ varies when a chemical cue from a sympatric predator is added. We hypothesised that after the addition of a predatory cue, the metabolic rate will increase. Moreover, since the pressure of predation is stronger on females, we propose that females will have a greater increase in the CO₂ produce as consequence of the added cues from the predator. Our results confirmed our first hypothesis, showing an almost two-fold increase in CO₂ when the predatory cue was added. However, males were the ones that showed a greater increase, in opposition to our second hypothesis. We put these results in the context of the escape theory and, in particular, the "landscape of fear" hypothesis. Also, because the timing between the increase of metabolic rate we measure here and the release of octopamine reported in previous studies do not match, we reject the idea that octopamine causes the increase in metabolism.

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1. Introduction

The risk of predation imposes various costs on animals, such as increased cost of reproduction [39,41,54], costs associated with using different habitats [9,19,40,46], reduction of foraging rates [1,8,32,33,39], loss of body mass [47] and reduced growth rates [8,21,22,48]. Moreover, the risk of predation can produce significant changes in the physiology of animals, affecting stress hormone levels [25,26], and even resulting in oxidative damage [30].

Using an elegant experimental design, Abrahams and Dill [1] demonstrated that an equivalency exists between energy expenditure by prey and predatory risk: the risk of predation can be expressed as an

energetic cost for the prey, which can be estimated by measuring the prey's standard metabolic rate. Standard metabolic rate is defined as the lowest level of metabolism of an inactive ectotherm animal, in a post-absorptive state [13], and represents the energetic cost for body maintenance. Evidence suggests that predation affects metabolism in two different ways simultaneously. Standard metabolic rate of prey shows plastic response to the presence of predators (effect at the individual level) and, at the same time, predation selects for high standard metabolic rates (effect at the micro-evolutionary level, [34,35]), which in turn may lead to populations of animals showing increasing metabolic rates.

Abrahams and Dill's [1] idea of equivalence between predatory risk and metabolism remained largely untested until recent evidence indicated that metabolic rate increases immediately after a predator is detected [42,52]. However, under constant risk, animals showed a lower standard metabolic rate than animals not exposed to predators [6,23].

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We have a reasonably solid understanding of the effects of predation risk on prey's metabolic rates in aquatic species, such as fish [4,5,24,28,43], and limited examples from other aquatic taxa, such as amphibians [6] and molluscs [42,49]. Surprisingly, arthropods have received scarce attention (crustaceans: [8], insects: [34,35]).

Predation risk and hence the indirect costs of predation may differ between the sexes because of the differences in life-history between males and females. For example, male-biased risk of predation may arise because males are usually searching for or attracting mates [41], as is the case of the parasitoid fly *Ormia ochracea* [14]. On the other hand, other predators may target larger individuals, which in the case of insects are typically females [18,31,54].

Based on the established knowledge base, predation is likely to have significant, yet sex specific metabolic costs for prey and our overall aim is to quantify these costs in a model species for which the direct cost of predation has already been established [36]. Here, we test the prediction that the standard metabolic rate of the Black field cricket (*Teleogryllus commodus*) will increase in the presence of chemical cues from a sympatric predator, the Eastern water skink (*Eulamprus quoyii*), as part of the stress response. This represents a measure of the indirect cost of predation. Moreover, we expect adult female crickets to have a greater increase in metabolic rate in the presence of predator cues, because of their higher cost of reproduction - females expend more energy for egg production [29], and because of their increased risk of been preyed upon [18,50,53].

2. Materials and methods

2.1. Study species

To study the effect of predator cues on metabolic rate, we used the black field cricket (*Teleogryllus commodus*), a model species used to study different aspects of behaviour and physiology [55]. Of further advantage is that the escape behaviour and sensory system are well characterized for this species [15,17,20,36]. Crickets used in the experiments were adults of the 8th and 9th generation of a laboratory-reared population. They were kept in 12:12 light cycle, with *ad libitum* water and food (Friskies senior ®).

2.2. Metabolic rate measurements

Open-system respirometry (LI-COR Li-6400 respirometer, LiCor, Lincoln, NE, USA) was used to measure the CO₂ following the methods described in Krams et al. [34,35]. A single cricket was placed in a cylindrical chamber, 6 cm length × 3 cm diameter. This size of the chamber restricted the movement of the crickets, preventing any confounding effect of CO₂ production through physical activity. The chamber was connected to a gas analyser that compares the air from a standard sample and the air from the metabolic chamber. The respirometer was set to take a measurement every 5 s, with a precision of 1 μmol CO₂/mol.

Experiments were conducted between October 2013 and February 2014. Measurements were taken between 11 am and 4 pm, which corresponds to the period of inactivity for this species. Temperature ranged between 18.9 and 29.3 °C (mean ± SD = 23.4 ± 3.8 °C). Since temperature is known to affect metabolic rate, both males and females were randomly exposed to every range of higher and lower temperatures to prevent any bias in the metabolic rate measured because of

temperature. Before experiments were conducted, crickets were weighed to the nearest 0.001 g (Meter Toledo analytic balance).

2.3. Experimental manipulation

Two metabolic chambers were prepared. One (the 'predator chamber') contained a square piece of paper (2 × 2 cm approx.) with fresh faeces from an Eastern water skink (*Eulamprus quoyii*), a sympatric predator of *T. commodus*. Chemical signals present in the faeces of predators (*i.e.* kairomones) have been shown to evoke anti-predator responses [7, 16]. A second chamber (the 'control chamber') also contained a square of paper of the same dimensions as before, but clean or impregnated with a non-predatory control. During all the measurements, the chambers were covered with a grey piece of fabric to keep the cricket from visual disturbances.

In a first set of experiments, a single cricket was introduced in the 'control chamber', and was allowed to habituate for 10 min. After this period was over, the cricket's production of CO₂ was recorded every 5 s, for a period of 10 min. Then, the cricket was gently moved to the 'predator chamber', which was plugged into the respirometer. Once again, the CO₂ produced by the cricket was recorded every 5 s, for a period of 10 min. 66 crickets were used in this experiment, 43 females and 23 males.

The experiments were always conducted in the same order: first the 'control' and then the 'predator treatment'. We did not randomize the order in which treatments were applied, because the focus was to test the effect of a chemical cue on a cricket that was first unaware of the presence of a predator and subsequently detected a chemical cues from a predator. This could mislead our interpretation of the results, since any change detected may be due to habituation to the experimental setup rather than a response to the treatment. To test for this possibility, two set of experimental controls were performed. First, to control for the possible effect of habituation to the experimental setup, a second set of experiments was conducted, but this time the 'predator treatment' was replaced by a second control (*i.e.* another piece of clean paper). Fifty nine crickets were used in this experiment, 31 females, 16 males and two juveniles in the final instar. This allowed us to observe any changes in metabolic rate due to the extended duration in the experimental chamber.

Second, it is possible that any change in cricket's respiration may be due to the detection of a novel odour. To control for this, a third set of experiments was conducted using 31 crickets, where the predator cue was replaced with a solution of five drops of 100% pure eucalyptus oil on 0.5 ml of water.

2.4. Data analyses

The respirometer measured the concentration of CO₂ in μmol. We transformed this to ml by assuming that 1 mol of gas occupies 22.4 l. Additionally, since metabolism is affected by the mass of the individuals [44], the concentration of CO₂ measured was divided by the mass of each individual. This value was transformed to volume of CO₂ produced per day per gram (ml × g⁻¹ × day⁻¹). Likewise, as temperature affects the metabolic rate of animals [44], we included it as a covariate in our analyses.

To analyse the differences between the CO₂ produced under the different combinations of sex and treatment, we used a generalized linear

Table 1

Summary of interactions included in the first five hypothesised models. Based in the ΔAICc and Akaike weight criteria, only the first model has enough evidence, which only provides support for the interaction between sex and the predation treatment.

Model	Int	Sex × Tem	Sex × Tre	Tem × Tre	Sex × Tem × Tre	Loglike	AICc	ΔAICc	Akaike weight
1	2.61	No	Yes	No	No	9616.4	−19,208.7	0	0.98
2	2.37	Yes	Yes	No	No	9612.3	−19,200.7	8.06	0.017

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