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## Original Research Article

# Responses of a salticidae's metabolism to the risk of predation

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### ABSTRACT

In addition to eating their victims, predators also change their characteristics (e.g. physiology and behaviour). In a laboratory context, this study investigated how prey's metabolic rate, as determined by CO<sub>2</sub> release, alters in response to the presence of a predator. The study subject was the salticidae (jumping spider) *Irura mandarina*. As visual signals, *Bactocera dorsalis*, two species of oriental fruit flies, *Plexippus paykulli* and *Ptocasius strupifer*, and two species of jumping spiders were used. *Pl. paykulli* was employed as a predator cue since it is larger than *irura mandarina*. As reference controls, *Pt. strupifer* and *B. dorsalis*, two species that are smaller than *irura mandarina*, were utilised. *Irura mandarina*'s reaction to *Pl. paykulli* was dynamic, with CO<sub>2</sub> release first rising in response to the predator's detection and then falling to a low level. When *irura mandarina* spotted the other species, no comparable responses were seen. The findings reveal that *irura mandarina*'s dynamic expressions of metabolism contain rich information about how it perceives the environment and that it responds to visual cues of predation threat by swiftly modifying its metabolic rate.

## 1. Introduction

As predation risk is perceived, prey exhibit a variety of behaviours, morphologies, and life-history features [1-3]. The dynamics of populations, communities, and ecosystems are significantly impacted by these modifications in prey features, which are recognised as nonconsumptive effects of predators [4-6]. For instance, stress brought on by the possibility of predation (measured by the level of the stress hormone glucocorticoids) lowers the fertility and modifies the population cycle of snowshoe hares [7, 8]. When grasshoppers are under stress from predators, their body's elemental makeup changes, slowing the breakdown of plant litter in the ecosystem [9].

A thorough understanding of how prey perceive predators in their habitat is crucial for examining the non-consumptive effects of predators in ecological processes [10, 11]. Prey, for instance, may come into contact with predators in isolated, acute episodes, and they may use this encounter to alter how they perceive the environment (e.g. predator density). Yet, little is understood about how perception actually works, and models make naive assumptions about how information is updated [12, 13]. Moreover, it is challenging to evaluate predictions for internal perception, although predictions for behavioural responses (such as vigilance behaviour) may be easily checked. This is true even when a model predicts an animal's internal perception and the related behavioural actions.

Individuals' metabolic rates are dynamic variables that are affected by a variety of circumstances. For instance, individuals may display a greater metabolic rate in the presence of predators in fish [14, 15] and insects [16–18]. Depending on the type of predators, prey may display a particular metabolic response [19, 20]. As a result, changes in metabolic response can reveal how individuals perceive particular predator cues differently. These findings imply that

metabolic rate can serve as a valuable proxy for examining how organisms perceive their environment. The long-term (i.e., longer than a day) average metabolic response has, however, been the focus of previous studies that examined the relationship between metabolic rate and predation risk, and little is known about how the metabolic rate of prey dynamically responds to predation threat.

This study investigated the relationship between predation danger and the metabolic rate of the jumping spider, *irura mandarina*. Jumping spiders have highly evolved visual systems and primarily identify items based on visual cues (body form) [21–23]. They are omnivorous generalists that eat a variety of prey, including other spiders [24]. Jumping spiders adjust their behaviour (becoming attentive) when they visually identify large jumping spiders (possible predators), which affects population and community dynamics. It is also known that leaping spiders' metabolic rates fluctuate quickly [25, 26], which is significant if metabolic rate were to track potentially changing perception quickly (e.g. sudden encounter with a predator). Due to these characteristics, jumping spiders provide suitable study subjects for investigations on the physiological response to predator risk.

The metabolic reactions of prey to predators are qualitatively variable, according to earlier research [27–29]. For instance, when threatened, the swamp rabbit *Sylvilagus aquaticus* may freeze and slow its heartbeat, a condition known as fear bradycardia. In contrast, the grasshopper, *Melanopus femurrubrum*, experiences threat under the stress paradigm and boosts its metabolic rate to increase survival. Moreover, depending on the temporal scale, such as acute versus chronic exposure to predator cues, the metabolic response of prey may vary [30]. The metabolic response of *irura mandarina* was thus examined for two different time scale foci: (1) 3 min after an encounter representing an immediate response and (2) 30 min



after an encounter representing the subsequent response, in order to fully account for the two hypotheses (fear bradycardia and the stress paradigm).

## 2 Materials and methods

### 2.1 Study animals

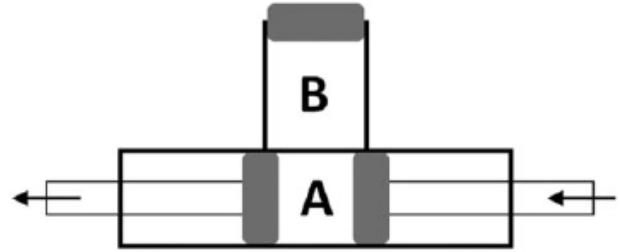
The study's subject was the jumping spider *irura mandarina*. *Irura mandarina* is a global species that exhibits sexual dimorphism [31]. They are typically seen in Indian forests and are present all year round. Three visual signals were tested: the adult Oriental fruit fly, *Bactrocera dorsalis*; a large species of jumping spider, *Plexippus paykulli* (Araneae: Salticidae); and a small species of jumping spider, *Ptocasius strupifer* (Araneae: Salticidae) (Diptera: Tephritidae). Due to their different sizes, *Pl. paykulli* and *Pt. strupifer* function as *irura mandarina*'s respective prey and predator (the predations were readily observed in the laboratory).

The size difference between *Pl. paykulli* and *Pt. strupifer* may have an impact on the metabolic responses (e.g. high metabolic response to large organisms regardless of they are predators or not). The response to *B. dorsalis* was also evaluated to make sure that size was not the main determinant of the outcome. Although *B. dorsalis* is larger than *irura mandarina* in terms of body length, it is not a predator. Differential reactions to *Pl. paykulli* and *B. dorsalis* suggest that elements besides the size of the visual signal also have an impact on metabolic rate. The average ( $\pm$ sd) body masses of *irura mandarina*, *Pl. paykulli* and *Pt. strupifer* used in the study were  $0.034 \pm 0.007$  g,  $0.099 \pm 0.016$  g,  $0.011 \pm 0.004$  g and  $0.013 \pm 0.001$  g, respectively ( $n = 12$  for all).

### 2.2 CO<sub>2</sub> output measurement

Using a flow-through device, the metabolic rate of *irura mandarina* was calculated as the rate of CO<sub>2</sub> emission. The animal chamber consisted of a clear plastic tube with an inner diameter of 13 mm that was closed at both ends at a distance of 5 mm (Figure 1). As mobility impacts metabolic rate, the limited area was employed to deter animal movement. The movement of the subjects was a complicating element because the aim of this study was to investigate how perception affects metabolic rate. As a visual signal, an animal was kept in another clear tube. The cue chamber's inner diameter was 12 mm. The subject and the visual cue were separated by the transparent wall of the subject room and could see one another because one side of the tube was attached to the animal chamber's wall. A plug secured the other end of the cue chamber. To allow a cue animal to move around the chamber during a trial, the arena for a visual cue was 2 cm long.

A flow controller C100L and an air pump UN-40PT were used to pump air through the system at a rate of  $50 \text{ mL min}^{-1}$ . Before entering the animal compartment, the air was forced through a container containing soda lime to remove CO<sub>2</sub>. Using a gas analyzer LI-7000, which also assessed the CO<sub>2</sub> concentration in the air before and after it passed through the animal chamber, the rate of CO<sub>2</sub> emission was monitored every second. The LI7000 software on a computer connected to the gas analyzer was used to record the CO<sub>2</sub> concentration in ppm. The CO<sub>2</sub> output was determined by comparing the levels of CO<sub>2</sub> in the air before and after it had passed through the animal chamber. All measurements were changed to the standard unit of  $\text{mol min}^{-1} \text{g}^{-1}$  based on the weight of each individual.



**Figure 1:** Transparent tubes were used to build the experimental chambers. *Irura mandarina* was put in the compartment marked A, while visual cues were put in the compartment marked B. The direction of the air flow is shown by the arrows. Grey things can be moved and positioned differently. The figure has not been scaled.

### 2.3 Experiment

The experiment was carried out in a 28°C temperature-controlled space. *Irura mandarina* received enough prey to last for 24 hours. Given that hunger affects metabolic rate [32], the *irura mandarina* was then fasted for 1 day before testing to standardise their satiation condition. *Irura mandarina* was exposed to the three cues (*Pl. paykulli*, *Pt. strupifer*, and *B. dorsalis*) in order (see below for details about the sequence order). *Irura mandarina* was kept in the animal chamber linked to the flow-through system for at least one hour prior to the introduction of the first visual signal, which was long enough for its metabolic rate to settle. In the cue chamber during this time of acclimatisation, no animal was present. The three visual signals were then presented in order (cue 1, break, cue 2, break, cue 3). Each cue was displayed for one hour, and each break—the time between taking down one cue and putting up the next—was also one hour. During the hours of 9:00 and 16:00, when jumping spiders are active in the wild, every experimental trial was carried out. Every conceivable sequence was employed to account for a potential order effect [for example, metabolism related to nutrition absorption [33] and memory from prior encounter experience] [34] due to the repeated-measure design (each subject receiving the three cues in sequence). The three visual signals made it possible to order things in six different ways. Two repetitions of each ordering were carried out (i.e. 12 spiders in total were tested). Only one trial was conducted on each individual. The experimental environment was maintained constant, with the exception of removing and reintroducing visual signals, to minimise disruption because jumping spiders are sensitive to visual stimuli. A video camera was used to record *irura mandarina*'s movements, and it was determined that *irura mandarina* mainly remained stationary and did not move in a way that could have influenced the results.

### 2.4 Analysis

Analysis was done on both the immediate and delayed responses to the cues. The average metabolic rate measured over a 1-min period 3 minutes after the initial cue was presented served as a proxy for the immediate response to a stimulus. To account for the order effect, only the initial response to each replication's cue was examined for the analysis of the immediate response. Because the immediate metabolic response was swift, a brief time of only one minute was chosen (see Results). The baseline metabolic rate was the rate at the conclusion of the acclimatisation phase (5 minutes prior to the introduction of the first stimulus). By using a

paired t-test, the impact of each cue on metabolic rate was evaluated (i.e. a paired sample is the difference between the response to a cue and the baseline response).

The average metabolic rate for a recording period of 30 minutes, taken 30 minutes following the introduction of a cue, served as a proxy for the subsequent response. The data were analysed using a generalised linear mixed model with Gaussian error structure and a random intercept parameter to account for non-independence due to the repeated-measures design; CO<sub>2</sub> emission was the response variable and the visual cues were described by a factorial explanatory variable [35].

### 3 Results

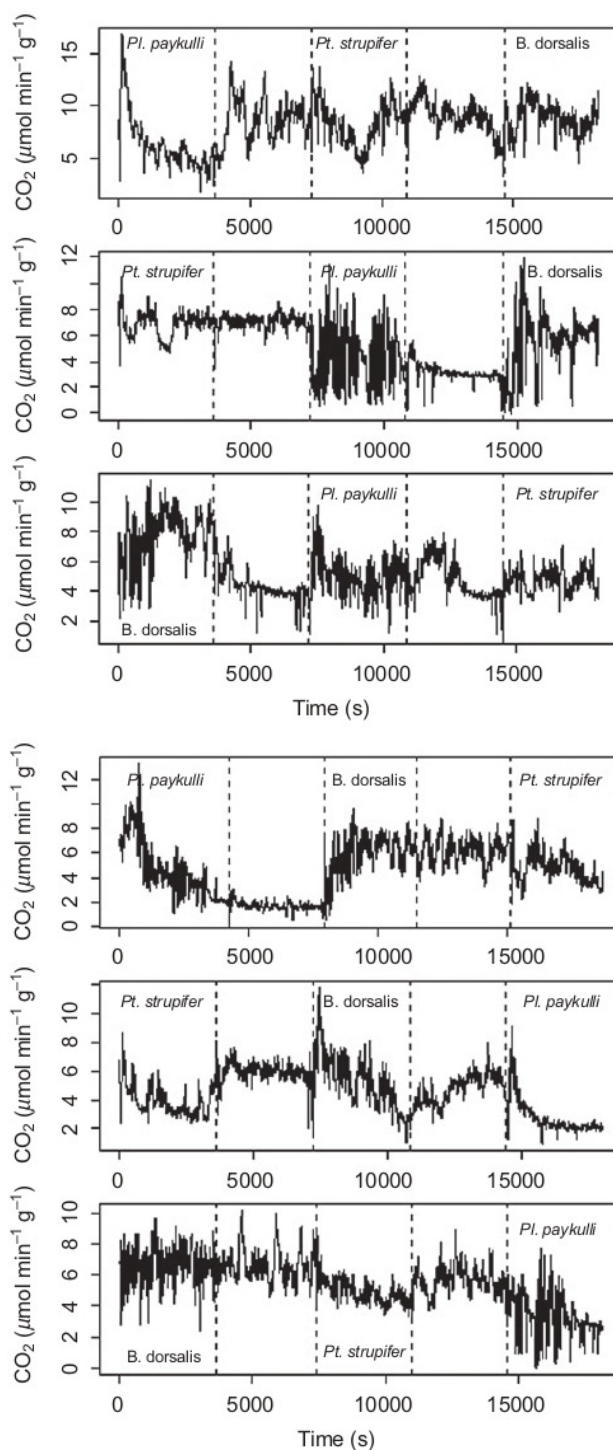
Rapid changes occurred in *irura mandarina*'s metabolic response (Fig. 2). When *irura mandarina* discovered *Pl. paykulli*, it immediately doubled its metabolic rate. ( $2.90 \pm 1.37 \text{ mol min}^{-1} \text{ g}^{-1}$ , mean  $\pm$  sd; paired t-test;  $t = 4.2493$ , d.f. = 3,  $P = 0.0239$ ) and decreased the metabolic rate in response to *B. dorsalis* ( $-1.75 \pm 0.78 \text{ mol min}^{-1} \text{ g}^{-1}$ ; paired t-test;  $t = -4.5058$ , d.f. = 3,  $P = 0.0204$ ; Fig. 3). *Pt. strupifer* did not affect the immediate metabolic response (paired t-test;  $t = -1.2073$ , d.f. = 3,  $P = 0.314$ ).

When *Pl. paykulli* was presented, the metabolic rate for the subsequent response was at its lowest (Fig. 4). The mean ( $\pm$ sd) metabolic rates (in  $\text{mol min}^{-1} \text{ g}^{-1}$ ) were  $0.512 \pm 0.11$  (baseline),  $0.236 \pm 0.08$  (*Pl. paykulli*),  $0.359 \pm 0.08$  (*Pt. strupifer*) and  $0.43 \pm 0.12$  (*B. dorsalis*). The model's potential pairwise comparisons were all statistically distinct from one another (Tukey multiple comparison,  $P < 0.05$  for all comparisons).

### 4 Discussion

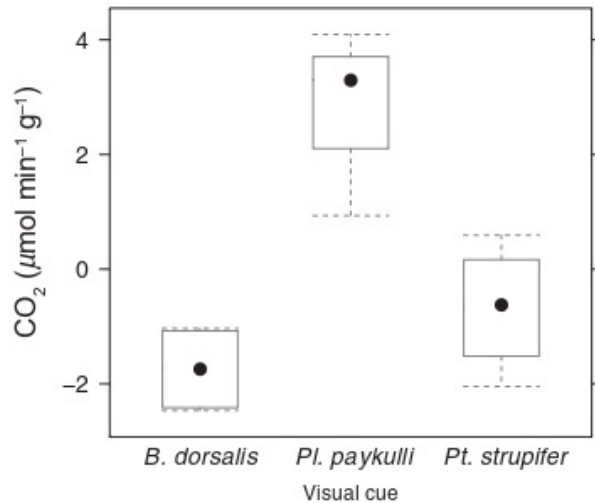
When *irura mandarina*, a jumping spider, noticed *Pl. paykulli*, a predator, it released CO<sub>2</sub> in a dynamic manner. In particular, when *irura mandarina* was repeatedly exposed to the predator, the metabolic rate first increased following the discovery of *Pl. paykulli* and later declined. This suggests that the metabolic rate contains information about the perception state of *irura mandarina* that cannot be conveyed by externally observable movement. These changes were quick (e.g. within seconds) and were noticed without any physical movement of *irura mandarina*. Knowing how predation danger (along with other factors) and metabolic rate interact may help us better understand how people react to their surroundings.

Both theories were congruent in a time-dependent manner when compared to the physiological stress paradigm and fear bradycardia, which is also referred to as a "fight-or-flight" reaction. The metabolic rate of *irura mandarina* first increased, which is consistent with the physiological stress paradigm. This reaction might have happened because prey could have escaped more successfully due to the increased metabolic rate [36, 37]. The resulting decreased metabolic rate is consistent with bradycardia from fear. In fish, fear bradycardia was followed by a quick increase in metabolism to make up for any accumulated oxygen debt, but our study did not record such an elevated metabolic rate. Instead, in some instances, the decreased metabolic rate persisted for a considerable amount of time even after the predator cue was eliminated (Fig. 2).

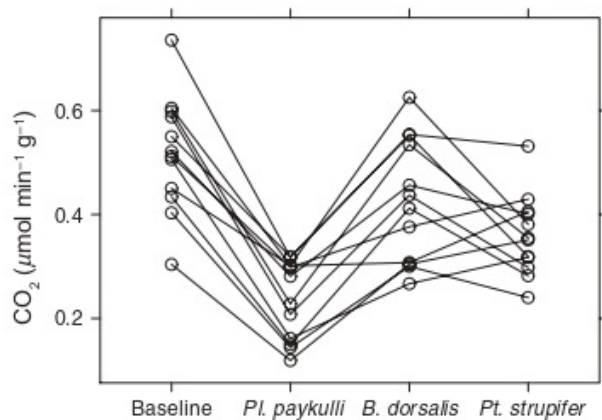


**Figure 2:** An illustration of the CO<sub>2</sub> release in real time by *irura mandarina*. Breaks are depicted by the times when there is no indicator (no cue was presented). Predator, prey, and controller, respectively, are *Plexippus paykulli*, *Ptocasius strupifer*, and *Bactrosera dorsalis*.





**Figure 3:** Before (baseline) and after the inclusion of a visual signal, there was a change in CO<sub>2</sub> emission. An increase in CO<sub>2</sub> emission following the introduction of a visual signal is shown by a positive number. *Plexippus paykulli*, *Ptocasius strupifer*, and *Bactrosera dorsalis* are, respectively, predator, prey, and control.



**Figure 4:** Under various visual cues, *irura mandarina* releases CO<sub>2</sub> on average. Lines link the data from the same individuals together. Predator, prey, and controller, respectively, are *Plexippus paykulli*, *Ptocasius strupifer*, and *Bactrosera dorsalis*.

The experimental setup could be responsible for the metabolic rate decrease. The predator cue was constantly present in this study's confined chamber, which may have aided the response that causes fear bradycardia. *Irura mandarina* was also discouraged from moving around in there. The option to fight (e.g., escape) was thus eliminated from the experimental design for the fight-or-flight response. So, a prey individual's physical state may determine whether it increases or decreases its metabolic rate in response to a predation danger (e.g. the possibility of escape). Contrary to this study's findings, other research that looked at the long-term impact of predation risk discovered that predation risk raises the metabolic rate of prey (see Introduction). In this study, the response would have been qualitatively different if *irura mandarina* had been given more freedom to move around as opposed to being confined in the tiny enclosure, albeit it would be challenging to distinguish between the effects of perception

and physical movement. Prey and predator encounters can occur in a variety of ecological circumstances, and while this study focused on a particular context, the same can be said of all other investigations. As a result, careful evaluation of the findings among studies is required.

The result is not the consequence of an order effect because the predator cue led to the lowest metabolic rate across all replications. It does not imply that there is no order impact, though. For instance, *irura mandarina* frequently maintained a low metabolic rate even after the predator cue was eliminated. To put it another way, *Pl. paykulli* seemed to have a significant impact on *irura mandarina*'s metabolic rate even after it was removed (Fig. 2), whereas equivalent effects of *Pt. strupifer* and *B. dorsalis* were not noticed. This could be as a result of the potent fitness-based selective force of predation. Because of the cue that was previously presented, the metabolic rate was very variable in the absence of any visual cue, perhaps causing an order effect. Further study on the order effect will be crucial to understanding how people update their view as they sequentially learn new information.

Understanding how prey perceive threat in their environment is crucial for research on the non-consumptive effects of predators. The study's quick metabolic rate dynamics imply that metabolic responses can be used in conjunction with behavioural observations to analyse how animals update their knowledge and transform perception into behavioural choices. Moreover, metabolic rate affects a number of life history features, which are crucial factors in, for instance, population dynamics [38]. Understanding a range of ecological processes can be aided by understanding the dynamic metabolic response to predators and other creatures.

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