



Dealing with your past: experience of failed predation suppresses caterpillar feeding behaviour



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Many animals face a trade-off between choosing to forage and avoiding predation. This trade-off may be optimized if animals assess short-term changes in predation risk and match their investment in costly antipredator behaviours to the current level of risk. Although there is growing evidence that insects are sensitive to predation risk, using a range of cues in their assessments, little is known about how variation in these cues influences responses. We used simulated nonlethal predator attacks, a direct physical cue of predation risk, to investigate how the frequency and location of attacks influence the feeding behaviour of gumleaf skeletonizer caterpillars, *Uraba lugens*. We found that a caterpillar's immediate behavioural response depended upon where on the body it was attacked. Caterpillars attacked on the abdomen were more likely to walk away or rear their head, whereas caterpillars attacked on the head were more likely to move their head sideways or regurgitate. Changes to subsequent feeding behaviour were influenced more by the frequency of attack. Caterpillars experiencing a high frequency of attack were less likely to start feeding within 3 h behavioural trials compared with caterpillars experiencing an attack of low frequency. Of those that did feed, attacked caterpillars significantly reduced their rate of ingestion and total consumption. The changes to feeding behaviour displayed by attacked caterpillars are consistent with reducing future risk of predation and demonstrate an ability to have nuanced responses to predation risk, shaped by the type of nonlethal attack experienced. Such sensitivity is important if animals are to respond effectively to predation risk.

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The process of acquiring food is essential for survival but often puts an animal at increased risk of predation (Bednekoff, 2007; Brown & Kotler, 2007). Animals can decrease predation risk by altering aspects of their feeding behaviour, such as when, where, how much, how often and on what they feed (Bednekoff, 2007; Lima & Dill, 1990). However, behaviours aimed at decreasing predation risk often come at the cost of decreased nutrient acquisition (Bednekoff, 2007; Brown & Kotler, 2004; Brown & Kotler, 2007). This conflict between nutrient acquisition and avoidance of predation is one of the most fundamental and pervasive trade-offs in ecology (Bednekoff, 2007; Brown & Kotler, 2007; Lima & Dill, 1990). While not responding appropriately to predators can be lethal, the consequences of unnecessary or excessive response can also be detrimental. Therefore, the trade-off between nutrient acquisition and avoidance of predation will be optimized when animals are capable of assessing short-term changes in predation risk and matching their investment in

antipredator behaviour to the prevailing conditions (Kats & Dill, 1998; Lima & Dill, 1990).

Being able to assess changes in predation risk requires the use of cues that convey information about the probability of future attack (Lima & Steury, 2005). These cues may be direct (i.e. related to the presence of or produced by the actual predator, such as experience of an attack (e.g. Jones & Dornhaus, 2011) or exposure to a predator's by-products (e.g. Kirmani, Banks, & McArthur, 2010)) or indirect (i.e. correlated with the chance of an encounter, such as habitat complexity; e.g. Obermaier, Heisswolf, Poethke, Randlkofer, & Meiners, 2008); and may be in the form of visual, chemical, physical and/or auditory stimuli (Castellanos & Barbosa, 2006; Dicke & Grostal, 2001; Kats & Dill, 1998; Lima & Steury, 2005). Two decades ago, the extent to which herbivorous insects were able to base their behavioural decisions on assessments of the level of predation risk was largely unknown (Montllor & Bernays, 1993). However, there is now a growing body of evidence that insects can be sensitive to predation risk (e.g. Griffin & Thaler, 2006; Hlivko & Rypstra, 2003; Rypstra & Buddle, 2013; Thaler & Griffin, 2008), and are capable of using a range of physical (e.g. Castellanos & Barbosa, 2006; Castellanos, Barbosa, Zuria, Tammaru, & Christman, 2011; Jones & Dornhaus, 2011), chemical (e.g. Dicke & Grostal, 2001)

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and auditory (e.g. Fournier, Dawson, Mikhail, & Yack, 2013; Jacobs, Ratcliffe, & Fullard, 2008) cues to make their assessments. This evidence also shows that the consequences of insect herbivore responses to predation risk can extend beyond the individual to influence populations and even ecosystem structure and function (e.g. Hawlena, Strickland, Bradford, & Schmitz, 2012; Schmitz, Beckerman, & O'Brien, 1997; Schmitz et al., 2008), and that these nonconsumptive or nonlethal predator effects can be equal to or even greater than the lethal effects of predators (Preisser, Bolnick, & Benard, 2005; Thaler & Griffin, 2008).

Despite the importance of insect herbivore responses to predation risk, little is known about how variation in the cues that insects use to assess risk influences the type and extent of responses (Castellanos & Barbosa, 2006; Lima & Steury, 2005). Using the gumleaf skeletonizer, *Uraba lugens* Walker (Lepidoptera: Nolidae) as a model species, we aimed to investigate how caterpillars respond to variation in a direct physical cue of predation risk, experience of nonlethal predator attacks. *Uraba lugens* is native to Australia and has a wide distribution throughout the country (Campbell, 1962). The larvae feed predominantly on myrtaceous tree species including a variety of *Eucalyptus* and *Angophora* species (Berndt & Allen, 2010). Feeding occurs gregariously during the first five instars, with larvae skeletonizing leaves, whereas older larvae disperse to feed individually, consuming almost the entire leaf (Cobbinah, 1978). Larvae are subject to intense parasitism and predation in the field (Allen, 1990b; Berndt & Allen, 2010; Farr, 2002). They are attacked by a wide range of parasitic wasps and flies (Allen, 1990b; Berndt & Allen, 2010; Farr, 2002), while known invertebrate predators include jumping spiders, various predatory bugs and lacewings (Berndt & Allen, 2010). Larvae grow to about 20–25 mm in length and are well defended with urticating hairs which are thought to protect them from predation by birds (Allen, 1990b). The larvae are also known to rear their heads and thrash about in the presence of their parasitoids, a behaviour that can greatly increase their chance of escaping parasitism (Allen, 1990a).

We simulated nonlethal predator attacks to investigate how caterpillars respond when attacked on different parts of the body and at different frequencies. We predicted that caterpillars would perceive attacks on different parts of the body and of different frequency as varying in their danger or severity, since an individual's capacity to fight back or escape a predator attack could be affected by where on the body and how frequently it gets attacked. Indeed, different parts of the body often differ in their vulnerability and a common morphological defence seen across taxa is to deflect attacks away from these parts of the body. For example many larval (Hossie & Sherratt, 2012) and adult Lepidoptera (Ruxton, Sherratt, & Speed, 2004) possess fake eyespots which are thought to function as an antipredator defence, such as by disguising the location of the actual head. We therefore hypothesized that in response to attack, caterpillars would modify their behaviour in ways consistent with increasing chances of escape (e.g. head rearing and walking away) and reducing future predation risk (e.g. decreasing foraging). More specifically, we hypothesized that the type and extent of response would vary according to the location and frequency of attack, such that caterpillars would respond more strongly when the perceived risk was greater.

METHODS

Collection Details

We collected groups of early instar *U. lugens* at Middle Head in Sydney Harbour National Park (151°15'E, 33°49'S) in August 2012 and January 2013. Field collections were made under National Parks

and Wildlife Services N.S.W. Scientific Licence number SL100838. The caterpillars were housed in plastic tubs and supplied regularly with fresh local foliage (*Angophora floribunda* (Sm.) Sweet). The caterpillars used in the behavioural trials were in the 7th–10th instar, when all were feeding solitarily. After the study, caterpillars were reared through to adulthood to attempt establishment of a laboratory colony.

Behavioural Trials

We investigated the short-term behavioural responses of *U. lugens* caterpillars to simulated nonlethal predator attack in 3 h behavioural trials. Caterpillars were fasted for at least 3 h before a trial to standardize motivation for feeding. They were then transferred to separate leaf units, which consisted of two fresh *A. floribunda* leaves in a small vial of water. The stem to which the leaves were attached was placed through a hole in the lid of the vial which was then sealed using a small amount of reusable putty (Blu Tack, Bostik Australia Pty. Ltd.) to prevent caterpillars from entering the vial and drowning. We used a soft paintbrush when transferring the caterpillars to minimize disturbance, and left them to settle on the leaf unit for at least 5 min before imposing predator attack treatments. Since arthropods are the main predators of *U. lugens* caterpillars (Allen, 1990b; Berndt & Allen, 2010), we simulated attack from predatory arthropods by lightly pinching caterpillars using soft forceps (rounded blunt tip 3 mm, 0.41 mm gauge thick; Australian Entomological Supplies Pty. Ltd.). This technique has often been used to mimic the mandible bite of an arthropod or the peck from an insectivorous bird (e.g. Bowers, 2003; Brown, Boettner, & Yack, 2007; Bura, Rohwer, Martin, & Yack, 2011; Cornell, Stamp, & Bowers, 1987; Grant, 2006; Jones & Dornhaus, 2011). Caterpillars were randomly allocated to one of five attack treatments: control (undisturbed), low head (two pinches applied to head), high head (six pinches applied to head), low abdomen (two pinches applied to abdomen) or high abdomen (six pinches applied to abdomen). To standardize the pressure applied to the caterpillars as much as possible, all pinches were applied by a single experimenter and each pinch was made to last 1 s, with 5 s between successive pinches. The same experimenter then recorded the caterpillar's immediate response to attack, including whether it walked away, dropped from the leaf, stopped feeding, reared or moved its head, regurgitated or curled up its body (see [Supplementary material](#) for a video demonstrating how simulated attacks were applied and for examples of immediate responses). These behaviours were not mutually exclusive and individual caterpillars often displayed multiple responses. The behaviours were scored once for each individual even if they occurred multiple times. The experimenter then watched the caterpillars for 3 h. If an individual was feeding at the end of the 3 h, it was allowed to complete that feeding bout. For the purpose of our study, a feeding bout was considered to have ended if the caterpillar had not fed for at least 5 min. During the trial, the timing of feeding bouts was recorded using a stopwatch. This allowed us to calculate the time taken to start feeding following treatment application, the duration of the first feeding bout, the average bout duration, the total number of feeding bouts started, the duration of the interval between bouts and the total time spent feeding (as a percentage of trial duration). The number of areas of feeding damage on the leaves was also recorded.

We weighed each caterpillar before and after the trial and recorded head capsule width using a dissecting microscope fitted with an eyepiece graticule. For at least 48 h after a trial, the caterpillars were kept separately in vials without food so that all frass produced as a result of feeding during the trial could be collected, dried and weighed. We also recorded whether a caterpillar

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