

# Effects of predation risk and plant resistance on *Manduca sexta* caterpillar feeding behaviour and physiology

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**Abstract.** 1. Because predation risk typically alters how prey forage for food, interactions between predation risk and food availability are commonly found. Less is known about how host plant quality and predation risk interact to affect prey behaviour and physiology.

2. Using the caterpillar, *Manduca sexta*, and its predator, *Podisus maculiventris*, the effects of predation risk and host plant quality on caterpillar feeding, growth, assimilation efficiency, and resting metabolic rate were tested.

3. Overall, caterpillars on low-resistance tomato plants (*jasmonate-insensitive*) gained 14% more mass than caterpillars on high-resistance plants (wild-type tomato). On low-resistance plants, the presence of predators caused caterpillars to eat 32% less, but they gained the same mass as unthreatened caterpillars (i.e. a 19% increase in assimilation efficiency). In addition, caterpillars showed a 17% increase in resting metabolic rate in the presence of predators. On high-resistance plants, predation risk caused a decrease in feeding, but did not alter assimilation efficiency or resting metabolic rate.

4. The reduction in physiological responses to predation risk on high- versus low-resistance plants demonstrates a tradeoff between the ability to respond to predation risk and the ability to grow, especially on well-defended plants.

**Key words.** Host plant quality, jasmonate pathway, *Manduca sexta*, non-consumptive effects, *Podisus maculiventris*, *Solanum lycopersicum*, trait-mediated effects.

## Introduction

Herbivore abundance, location, and behaviour have been shown to be affected by interactions between predation and host plant quality (Boethel & Eikenbary, 1986). Prey seeking to avoid predators, for example, may choose to feed on less palatable plants (Hawlena & Perez-Mellado, 2009; Christianson & Creel, 2010), and, once there, move less to avoid detection by predators. The concentrated damage that results may induce especially strong plant defence responses (Rodríguez-Saona & Thaler, 2005). Because feeding

can also increase exposure to predators (Bernays, 1997), many organisms alter their feeding behaviour (Bernays & Woods, 2000) and eat less in the presence of predators; this may exacerbate the consequences of reduced food quality. Recent reports in the literature suggest that predation risk can greatly influence multiple components of prey behaviour and physiology (Boeing *et al.*, 2006; Cressler *et al.*, 2010). To predict the effect of predation and poor host plant quality on prey performance, we must understand the prey's behavioural and physiological responses to both of these stresses simultaneously.

Plant quality has the potential to influence physiological processes such as growth rate and resting metabolic rate. Diet quality, availability and predictability have been shown to influence the basal metabolic rate of animals (Cruz-Neto & Bozinovic, 2004; Castaneda *et al.*, 2010). While food limitation can reduce resting metabolic rate (Roark & Bjorndal, 2009; but

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see Hulbert *et al.*, 2004), feeding on poor-quality diets low in protein tends to increase metabolic rate (Calabrese & Stoffola, 1974; Karowe & Martin, 1989; Urrejola *et al.*, 2011)

There has recently been increased interest in exploring how predators alter prey physiology (Preisser, 2009; Sheriff *et al.*, 2009). Predator-induced stress and the need for increased vigilance may alter prey metabolism (Hawlana & Schmitz, 2010b). While risk-induced increases in metabolic rates have been repeatedly noted in vertebrate taxa (Chabot *et al.*, 1996), there are only three studies on invertebrates (Beckerman *et al.*, 2007; Slos & Stoks, 2008; Hawlana & Schmitz, 2010a). In addition, a common response to predation risk is a reduction in consumption because feeding frequently increases the probability of being eaten (Bernays, 1997; Slos & Stoks, 2008). As a consequence, predation risk may indirectly reduce metabolic rate via reduced feeding, although the effects of reduced consumption *per se* are variable (Roark & Bjorndal, 2009). Thus, the effect of predation risk on metabolic rate will not be consistent across different species of prey, predators and environmental conditions.

Digestive processes are known to be plastic in response to diet quality, often with higher efficiency on higher-quality diets (Yang & Joern, 1994b). Predator exposure can also change digestive processes by reducing assimilation efficiency, presumably because stress reduces the energy available for growth (Hawlana & Schmitz, 2010b). More surprisingly, recent evidence shows that predation risk can also increase food assimilation efficiency (McPeck, 2004; Hawlana *et al.*, 2011; Thaler *et al.*, 2012).

While interactions between plant quality and predation risk are likely to be common, few studies have investigated their interactive effects on herbivore physiology and feeding behaviour. The 'fight or flight' predation stress model predicts that prey physiological responses to predation risk will be induced regardless of the environment (Cannon, 1915). In particular, this predation stress model predicts that markers of physiological stress such as metabolic rate will increase rapidly in response to predator exposure, regardless of the environment. Nonetheless, there is growing evidence of a strong impact of environmental conditions on the costs and benefits of prey responses to predation risk (Sheriff *et al.*, 2012). Thus, it is an open question as to how varied an animal's response to predation risk should be.

In this study, we measured the independent and combined effects of host plant resistance and predation risk on metabolic rate, consumption, assimilation efficiency, and growth of *Manduca sexta* L. caterpillars. Our previous work showed that *M. sexta* can compensate for decreases in feeding caused by exposure to predators by increasing assimilation efficiency and developmental rate in the first days following predator exposure (Thaler *et al.*, 2012). The current study builds on these results by testing whether prey responses to predators occur equally on high- and low-quality plants. In addition to measuring feeding and assimilation efficiency, we measured resting metabolic rate as a marker of the prey's rapid, generalised stress response. We manipulated plant quality using wild-type and mutant plants that vary in their level of expression of the jasmonate-inducible defence pathway.

These plants vary in their expression of anti-nutritive defences, such as proteinase inhibitors that interfere with the digestion of protein, and oxidative enzymes that can be toxic or anti-nutritive (Duffey & Felton, 1991; Kaplan & Thaler, 2010).

## Materials and methods

### *Plants and insects*

Plant resistance was manipulated using two tomato cultivars (*Solanum lycopersicum*) that differ in expression of the jasmonate pathway. The jasmonate pathway, one of the major hormonally mediated defence systems in plants, is typically induced by chewing damage and increases plant resistance to herbivores (Thaler, 1999). Castlemart is a wild-type cultivar that induces the jasmonate pathway after damage; the jasmonate-insensitive plants are mutants that do not perceive jasmonic acid and do not induce resistance following damage (Li *et al.*, 2004). The wild-type and jasmonate-insensitive plants have similar vegetative morphology and growth (Li *et al.*, 2004). Jasmonate-insensitive seeds were germinated from April to May 2011 in Petri dishes, screened with methyl jasmonate and transplanted in the greenhouse. Jasmonate-insensitive and wild-type seedlings were grown in 7.6-cm-high pots in the greenhouse (Sunshine Mix, Sun Gro Horticulture, Agawam, MA) until the four-leaf stage. Four trials of the experiment were conducted using the same methods except that in Trials 3 and 4 wild-type plants were sprayed with 0.5 mM jasmonic acid (Sigma, St. Louis, MO) to run-off, 2 days prior to use in experiments, to induce the jasmonate pathway and maximise the difference in resistance phenotype between the plant types. Individual plants were used only once and 13–15 replicates per treatment (three to four replicates per treatment per trial) were used.

Predaceous stink bugs (*Podisus maculiventris* Say) were obtained from a recently field-collected colony maintained in the laboratory in Ithaca, NY. Before use in experiments, the terminal segment of the beak was excised using a razor blade. This resulted in 'sham predators' that can hunt prey normally, but cannot kill them (Griffin & Thaler, 2006; Thaler & Griffin, 2008; Kaplan & Thaler, 2010). Stink bugs were maintained on a diet of meal worms and tomato leaves before use in experiments. A single adult stink bug per replicate was used in the predation risk treatments; individual stink bugs were used only once.

### *Experimental protocol*

Newly moulted third-instar *M. sexta* caterpillars were obtained from a laboratory colony (University of Arizona, Department of Neuroscience) reared on wheat germ-based artificial diet. Each caterpillar was selected for experiments within 1 day of moulting to the third instar and used only once. Caterpillars were weighed and left to rest individually for 20 min in tubes of 1-cm circumference (2 ml) loosely packed with cotton to limit movement. After resting metabolic rates (see later) were measured for each caterpillar, they were

transferred to plants in each of our four treatments: high resistance, no predator; high resistance, sham predator; low resistance, no predator; low resistance, sham predator. Spin polyester-mesh bags were placed around each plant to enclose the caterpillars and predators. After 24 h, caterpillars were removed from the plants, weighed, the resting metabolic rate was re-measured and the leaf area consumed was measured. Plants were photographed at the start of the experiment and the leaf area consumed after 24 h was calculated using an acetate grid and the plant photographs. Efficiency of conversion of ingested food was analysed using one-way ANCOVA testing the effects of predation risk on weight gain, with leaf consumed as a covariate and the interaction between predation treatment and leaf consumed as a factor (Raubenheimer & Simpson, 1992).

#### Measuring resting metabolic rates of caterpillars

The rate of CO<sub>2</sub> production ( $V_{CO_2}$ ) was measured using flow-through respirometry on individual caterpillars at rest. Caterpillars were placed in an environmental cabinet (PTC-1 Temperature Cabinet; Sable Systems International, Las Vegas, NV, U.S.A.) and temperature was maintained at 28 °C. Caterpillars were undisturbed for 20 min before metabolic rate data were collected. During this time, room air was pumped through two silica and one ascarite/drierite column to be scrubbed of water and CO<sub>2</sub>. This dry CO<sub>2</sub>-free air was then passed through a flow controller set at 50 ml min<sup>-1</sup> and into the respirometry chamber with the caterpillar. After this 20-min resting period, CO<sub>2</sub> release from the insect was measured using a Sable Systems FoxBox-C gas analyser;  $V_{CO_2}$  data were collected using Expedata data acquisition software (Sable Systems) controlling an eight-channel multiplexor. A total of four chambers were attached to the multiplexor: a baseline (no caterpillar) and three experimental (containing a caterpillar) chambers at a time. When a caterpillar was not being measured, its chamber was still perfused with CO<sub>2</sub>-free air at a rate equal to the regulated flow entering the measured chamber.

An experimental run lasted 21 min. During the first and last 3 min, measurements were taken from the empty chamber to provide a baseline used to correct for any drift during the experiment. During the 15-min period in the middle, 5 min of continuous data were sequentially collected from the three experimental chambers each containing a single caterpillar. Caterpillars were observed during the experiments for signs of activity and were not used if active.

Expedata analysis software was used to record and process measurements of  $V_{CO_2}$ . CO<sub>2</sub> levels were recorded as percentages. Data were zeroed using baseline values and these were converted to ml min<sup>-1</sup>. Data were exported into Excel and mass-specific metabolic rates ( $V_{CO_2}$  ml<sup>-1</sup> min<sup>-1</sup> g<sup>-1</sup>) were calculated.

#### Statistical analysis

Final mass, leaf consumption, and resting metabolic rate were analysed using three-way MANOVA. If the overall test was significant, the univariate main effects were examined

using three-way ANOVA with plant resistance level, predator treatment and trial as independent factors. Interactions between treatments and trial were removed from the model if they were not statistically significant. Because the two trials where wild-type plants were treated with jasmonic acid were not different from trials without the jasmonic acid treatment, all four trials were analysed together. Significant ANOVAs were followed by *posthoc* contrasts using the Benjamini–Hochberg adjustment and we considered significant contrasts for which  $P > \alpha/2$  (for the largest observed  $P$  value) to  $P > (\alpha/2)/m$  (for the smallest observed  $P$  value), where  $m$  is the number of comparisons. We used Pearson's correlations to assess the relationship between resting metabolic rate and assimilation efficiency and the relationship between resting metabolic rate and leaf consumption.

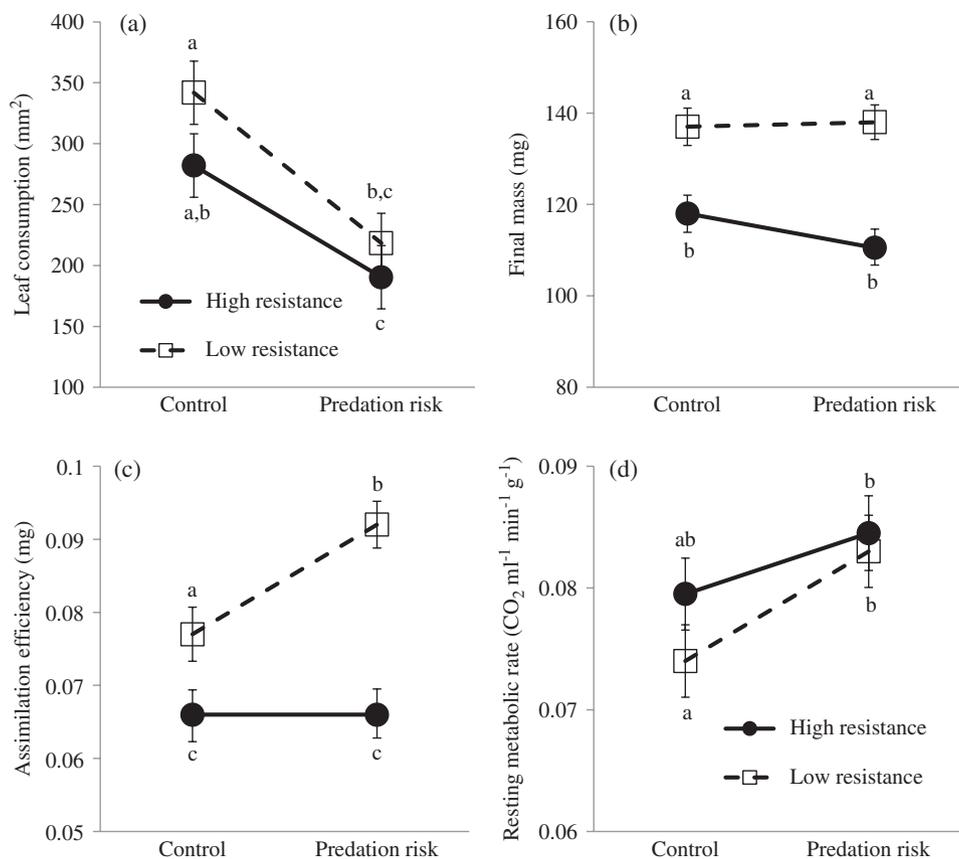
#### Results

A three-way MANOVA revealed significant main effects of plant resistance [Wilks'  $\lambda = 0.58$ ,  $F(3,42) = 8.11$ ,  $P < 0.01$ ] and predation [Wilks'  $\lambda = 0.68$ ,  $F(3,42) = 8.11$ ,  $P < 0.01$ ] on the three caterpillar response variables. Given the significance of the overall test, the univariate main effects were examined. High-resistance plants were of poorer quality for caterpillars in the absence of predation risk, with caterpillars eating the same amount but weighing 14% less and assimilating food 14% less efficiently (Fig. 1a–c) than on low-resistance plants. There was not an overall effect of plant resistance on resting metabolic rate, although in two out of four trials, resting metabolic rate was higher on high-resistance than on low-resistance plants (Table 1, plant type  $\times$  trial  $P = 0.007$ ).

Predation risk strongly affected the behaviour and physiology of caterpillars feeding on low-resistance plants (Table 1, Fig. 1). Caterpillars exposed to predation risk on low-resistance plants ate 36% less than (Fig. 1a), but weighed the same (Fig. 1b) as, control (i.e. no risk) caterpillars. This equal growth with less feeding was achieved by a 19% increase in assimilation efficiency (Fig. 1c). Additionally, caterpillars in the predation risk treatment had 12% higher resting metabolic rate than control caterpillars on low-resistance plants (Fig. 1d). There were no interactions between predation risk treatment and trial on any of the *M. sexta* responses.

Predation risk-induced changes in prey behaviour on high-resistance plants were not accompanied by the physiological changes found on low-resistance plants. As was found on low-resistance plants, caterpillars exposed to predation risk ate 32% less (Fig. 1a, Table 1). There was a marginally significant trend for a reduction in mass ( $P = 0.09$ , Fig. 1b). However, in contrast to our results from low-resistance plants, predation risk did not cause an increase in assimilation efficiency on high-resistance plants (Fig. 1, Table 1). Also in contrast to low-resistance plants, caterpillars in the predation risk treatment did not have different resting metabolic rate from that of control caterpillars on high-resistance plants (Fig. 1d).

To understand how these behavioural and physiological responses are related, we tested for correlations between responses at the level of individual caterpillars. While assimilation efficiency and resting metabolic rate both increased



**Fig. 1.** The effect of predation risk and host plant resistance on leaf consumption (a), final mass (b), assimilation efficiency (c), and resting metabolic rate (d) of *Manduca sexta* caterpillars. Bars indicate means  $\pm$  1 SE. Letters indicate significant differences following *post hoc* contrasts.

in the predation risk treatment on low-resistance plants (Fig. 1c,d), there was no relationship between the two for individual caterpillars on either type of plant (Table 2). This lack of relationship indicates that increased resting metabolic rate was not required for an individual to increase assimilation efficiency in the predation risk treatment. There was also no relationship between leaf consumption and resting metabolic rate on either type of plant in the predator treatment (Table 2), indicating that the behavioural response (reduced feeding) and the physiological response (increased resting metabolic rate) were independent.

Lowering food consumption and retaining food in the gut longer has the potential to increase assimilation efficiency. Therefore, the predator-induced reductions in feeding could be sufficient to cause the increase in assimilation efficiency found on the low-resistance plants. However, reductions in feeding did not increase assimilation efficiency on high-resistance plants. In addition, assimilation efficiency was higher in the predation risk treatment on low-resistance plants regardless of how much caterpillars ate (Table 1, see non-significant predator  $\times$  consumption interaction). If reduced consumption *per se* caused the increased assimilation efficiency, we would have expected that caterpillars that ate the least in the presence of the predator would have the highest assimilation efficiency.

## Discussion

*Manduca sexta* caterpillars exhibit rapid phenotypic plasticity in behavioural and physiological traits in response to predation risk. Caterpillars responded to predators by feeding less on both low- and high-resistance plants, but changes in physiological processes were different on the two plant types. Not surprisingly, final mass was lower on high-resistance plants than on low-resistance plants (Fig. 1b). This reduced mass occurred because assimilation efficiency was 19% lower on high-resistance than on low-resistance plants, and leaf consumption was marginally reduced. In the predation risk treatment on low-resistance plants, increases in assimilation efficiency allowed the caterpillars to maintain mass despite reduced feeding. By contrast, assimilation efficiency did not change and there was a trend towards reduced caterpillar mass in response to predation risk on high-resistance plants. Following the same pattern as assimilation efficiency, resting metabolic rate increased significantly in the predation risk treatment on low-resistance plants, but not on high-resistance plants. These results expand on previous work in this system (Kaplan & Thaler, 2010) where we reported that both the consumptive and non-consumptive effects of *P. maculiventris* on groups of *M. sexta* caterpillars were greater on low-resistance plants where predation rates were higher and feeding

**Table 1.** Factorial ANOVA for effects of predation risk and plant resistance on leaf area consumed (mm<sup>2</sup>), final mass (mg), assimilation efficiency (AE) (mg with consumption covariate) and resting metabolic rate (RMR) (CO<sub>2</sub> ml<sup>-1</sup> min<sup>-1</sup> g<sup>-1</sup>) for caterpillars after 24 h of predator exposure. Interactions between treatments are included only if they were statistically significant.

Factor	d.f.	F	P
<b>Leaf area consumed</b>			
Predator	1	18.48	≤ 0.0001
Plant type	1	3.07	0.086
Predator × plant	1	0.40	0.53
Trial	3	2.86	0.047
Error	47	–	–
<b>Final mass</b>			
Predator	1	0.65	0.42
Plant type	1	36.14	≤ 0.0001
Predator × plant	1	1.43	0.24
Trial	3	14.97	≤ 0.001
Initial mass	1	32.27	≤ 0.001
Error	46	–	–
<b>AE</b>			
Predator	1	3.22	0.079
Plant type	1	35.55	≤ 0.0001
Predator × plant	1	5.26	0.026
Trial	3	13.58	≤ 0.0001
Consumption	1	6.12	≤ 0.0001
Predator × consumption	1	0.61	0.44
Error	46	–	–
<b>RMR</b>			
Predator	1	7.11	0.011
Plant type	1	1.57	0.22
Predator × plant	1	0.57	0.45
Trial	3	3.00	0.040
Plant × trial	3	6.15	0.0014
Error	43	–	–

was most strongly reduced. The current study extends this result to show that physiological responses to predation risk are also stronger on low-resistance plants. Because jasmonate-inducible plant defences are commonly induced by chewing damage, herbivorous prey are likely to experience frequent tradeoffs in overcoming host plant defences and defending against predation.

Because caterpillar behavioural responses to predators were equal on low- and high-resistance plants, perceived predator risk appears equal on both plant types, and thus differences in physiological responses suggest a tradeoff between growing on a defended plant and responding to predation risk. Several factors could result in costs of feeding on high-resistance plants, which then limit responses to predation risk. First, on high-resistance plants, caterpillars may not have the resources to respond physiologically to predation risk, because caterpillars eat less, the food is of poorer nutritional quality (Yang & Joern, 1994a) and there may be costs of disarming plant defences (Cornell & Hawkins, 2003). Caterpillars in this study did grow 14% more slowly on the high-resistance plants in the absence of predation risk, showing that they are resource-limited compared with caterpillars on low-resistance

**Table 2.** Pearson's correlations between resting metabolic rate (RMR) and assimilation efficiency and between RMR and leaf consumption on low- and high-resistance plants in the predator and control treatments.

Treatment	RMR–assimilation efficiency correlation			RMR–consumption correlation		
	r	n	P	r	n	P
Low resistance, predator control	0.011	13	0.97	–0.67	13	0.012
Low resistance, predator	–0.38	13	0.20	–0.03	13	0.93
High resistance, predator control	0.41	13	0.17	–0.23	13	0.45
High resistance, predator	0.20	15	0.48	–0.30	15	0.27

plants. Secondly, the stress of being on a high-resistance plant may have elevated caterpillar metabolism to a ceiling, limiting further induction by predator stress. Because resting metabolic rate was not consistently higher on high-resistance plants, we do not have evidence for such a ceiling, but it is still a possibility. Thirdly, the ceiling for assimilation efficiency may be lower on high-resistance plants (Scott *et al.*, 2010) and therefore not inducible in response to predation risk. Our previous work (Thaler *et al.*, 2012) showed that one way in which caterpillars increased assimilation efficiency in the presence of predators was by increasing the percentage of nitrogen extracted from the food. Enzymes that interfere with protein digestion are an important component of jasmonate-based defences in tomato plants (Duffey & Felton, 1991) and digesting food more thoroughly may increase exposure to toxins.

General stress can divert resources from growth and therefore assimilation efficiency is predicted to decrease during predator exposure (Hawlena & Schmitz, 2010b). However, a growing number of studies of invertebrates find instead that assimilation efficiency increases during predator exposure (Hawlena *et al.*, 2011; McPeck 2004), an effect we previously found on tomato plants with intermediate levels of resistance (Thaler *et al.*, 2012). The increases in assimilation efficiency may benefit the prey in the short term by allowing them to maintain growth and reach a size refuge from predation as quickly as possible (Thaler *et al.*, 2012). Increases in assimilation efficiency may result from passive processes such as reduced movement and decreased energy expenditure in the presence of predators (Kaplan & Thaler, 2010) or active changes in gut physiology not yet investigated. While not addressed in this short-term study, even though body mass is maintained in the predation risk treatment on low-resistance plants, there may be costs in the long term that manifest themselves through changes in body composition, development, and physiology later in life (Steiner & Van Buskirk, 2009; Thaler *et al.*, 2012).

Prey can concurrently or independently deploy multiple responses to the presence of predators (Boeing *et al.*, 2006; Cressler *et al.*, 2010). Some of these traits are genetically

coupled, such as diel vertical migration and body size (Leibold & Tessier, 1991), while others, such as morphological and life-history responses, are not (Tollrian, 1995; De Meester & Pijanowska, 1996; Holopainen *et al.*, 1997). In this study we found that phenotypically plastic behavioural and physiological responses were decoupled. At the individual level, while feeding decreased and resting metabolic rate and assimilation efficiency increased in the presence of predators on low-resistance plants, these responses were not correlated (Table 2). In another study with *M. sexta*, the accelerated development found in the predation risk treatment was not correlated with changes in feeding behaviour or assimilation efficiency at the individual level (Thaler *et al.*, 2012). While it is possible that we failed to detect significant individual-level correlations within each treatment due to low statistical power, when we analysed the data with ANCOVAs to maintain the power (using resting metabolic rate or leaf consumption as covariates) we also failed to detect an effect of the covariates on dependent variables (analysis not shown).

The lack of individual-level correlations suggests that resting metabolic rate and assimilation efficiency increased as independent components of the general response to predation risk. Metabolic rate may increase as part of the prey's rapid response to acute stress and assimilation efficiency may increase as the prey compensates for decreased feeding. It is also possible that changes in caterpillar body composition during predation risk could increase resting metabolic rate (Speakman *et al.*, 2002). We previously found that caterpillars experiencing predation risk had higher lipid and glycogen content than caterpillars in the control treatment (Thaler *et al.*, 2012), but these tissues tend to have low mass-specific metabolic rates.

It is somewhat surprising that plant resistance itself did not affect caterpillar metabolic rate, as it did affect growth and consumption; however, in two of four trials, resting metabolic rate was higher on high-resistance plants. This trend is consistent with our prediction that feeding on high-resistance plants would increase caterpillar metabolism to fuel detoxification. However, while *M. sexta* does have specific inducible mechanisms for detoxifying plant allelochemicals such as alkaloids (Wink & Theile, 2002), incorporating alkaloids in the artificial diet did not increase caterpillar resting metabolic rate (Appel & Martin, 1992). Plant quality may also affect other attributes of caterpillars, such as movement patterns and food consumption, which may affect resting metabolic rate in divergent ways and obscure an overall effect. In a study on mice, food availability had a stronger effect on basal metabolic rate than food nutritional quality (Bozinovic *et al.*, 2007). This is consistent with our finding that the manipulation of predation risk, which reduced consumption more strongly than the manipulation of plant resistance, also had a stronger effect on resting metabolic rate than did feeding on a resistant plant. Given the dynamic nature of animal metabolism, it would be informative to compare the effects of predation risk and plant resistance on metabolic rates over longer periods of larval development.

In conclusion, our results demonstrate that prey responses to predation risk are influenced by resource quality. Both the

immediate physiological responses and compensatory mechanisms (but not consumption) in response to predation risk are reduced on high-resistance plants. This is consistent with prey responses to predation risk being shaped by costs and benefits which are variable depending on the environmental conditions (Creel, 2011; Sheriff *et al.*, 2012). Because plant resistance can so profoundly influence herbivorous prey condition, including behaviour, feeding physiology, and growth, it is not surprising that plant resistance also alters how prey resolve the foraging–safety tradeoff. We hypothesise that prey responses to predation will typically be suppressed on highly defended plants, but this remains to be tested in a wider number of systems (Dyer, 1995).

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