

# The adaptive value of gluttony: predators mediate the life history trade-offs of satiation threshold

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Lycosidae;  
optimal foraging theory;  
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## Abstract

Animals vary greatly in their tendency to consume large meals. Yet, whether or how meal size influences fitness in wild populations is infrequently considered. Using a predator exclusion, mark–recapture experiment, we estimated selection on the amount of food accepted during an *ad libitum* feeding bout (hereafter termed ‘satiation threshold’) in the wolf spider *Schizocosa ocreata*. Individually marked, size-matched females of known satiation threshold were assigned to predator exclusion and predator inclusion treatments and tracked for a 40-day period. We also estimated the narrow-sense heritability of satiation threshold using dam-on-female-offspring regression. In the absence of predation, high satiation threshold was positively associated with larger and faster egg case production. However, these selective advantages were lost when predators were present. We estimated the heritability of satiation threshold to be 0.56. Taken together, our results suggest that satiation threshold can respond to selection and begets a life history trade-off in this system: high satiation threshold individuals tend to produce larger egg cases but also suffer increased susceptibility to predation.

## Introduction

Optimal foraging theory posits that foraging organisms will behave in such a way as to maximize their energy intake per unit time. Optimal foraging studies commonly consider an organism’s diet breadth (MacArthur & Pianka, 1966; Perry & Pianka, 1997), time spent among resource patches (Pyke, 1984; Brown *et al.*, 1994), foraging mode (Pianka, 1966; Huey & Pianka, 1981; Perry *et al.*, 1990) and capture tactics (Foelix, 1996). Rarely, however, do investigations consider the amount of food organisms will consume during foraging bouts (hereafter ‘satiation threshold’) and the potential fitness consequences of these decisions (Garland & Arnold, 1983; Huey *et al.*, 1984; Ford & Shuttlesworth, 1986; Andreadis & Burghardt, 2005; Pruitt, 2010). The paucity of field data on satiation threshold is not surprising, given

that evolutionary ecology has classically emphasized the importance of *limited* resources. However, resources commonly vary both spatially and temporally, and where/when resources are abundant, the role of overly exploitative behaviour may be important in determining fitness.

Large meals confer a number of costs and benefits. If, for instance, resource availability is variable, individuals with high satiation thresholds might be more likely to survive resource-limited periods (e.g. hibernation: Hellgren, 1998; Buck & Barnes, 1999). Such individuals may reach larger sizes or, by mere virtue of a short-term mass increase, appear more attractive to their prospective mates (e.g. *Humans*: Barber, 1995; *Birds*: Searcy & Yasukawa, 1995; *Spiders*: Riechert & Singer, 1995). Individuals with high fat stores may also be more resistant or resilient to/from disease (Pollack *et al.*, 1985). However, large meal sizes put physiological and mechanical strains on animals (Ford & Shuttlesworth, 1986; Woods, 1991; Finke & Litzinger, 1992); gorged individuals frequently experience reduced performance after meals (e.g. running speed, endurance; see Irschick *et al.*, 2008

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for a review on performance traits), and many authors suggest this may make them more susceptible to predation (Garland & Arnold, 1983; Huey *et al.*, 1984; Pough & Andrews, 1985; Ford & Shuttlesworth, 1986; Herzog & Bailey, 1987; Martin, 1996). In artificial scenarios, excessively high satiation thresholds can even generate persistent maladaptive body conditions, e.g. obesity in humans (Prentice & Jebb, 1995; Egger & Swinburn, 1997; Stunkard *et al.*, 1998). Taken together, contemporary satiation thresholds likely reflect the selective trade-off of increased risk of predation versus the uncertainty of future food availability. Thematically, this trade-off is not unlike those of classical foraging theory [e.g. the marginal value theorem (Charnov, 1976), giving up time (Stephens & Krebs, 1986), giving up density (Brown, 1988)] and could be formalized with similar models.

Animals vary tremendously in their tendency to consume large meals (i.e. their satiation threshold) (Myer & Kowell, 1971; reviewed in Collier & Rovee-Collier, 1981; Branch *et al.*, 2002; Pruitt, 2010). At one extreme, some animals consume small frequent meals throughout their diel activity pattern. For example, chickens engage in 30–40 small, discrete meals per day, which, in total, sum to only a small fraction of the chicken's body mass (Collier & Rovee-Collier, 1981). At the other extreme, many taxa are adapted for taking large, infrequent meals. For instance, some snakes eat only every few months (Myer & Kowell, 1971) but can consume prey items in excess of 150% of their body mass (Branch *et al.*, 2002). Humans fall intermediately along this continuum, consuming between two and five meals per day; daily consumption rarely exceeds 3% of humans' body mass (Collier & Rovee-Collier, 1981).

Despite inter-disciplinary interest in animals' satiation threshold, the adaptive significance of such feeding behaviour in wild populations remains largely unexplored.

In this study, we experimentally investigate the adaptive value of satiation threshold in a wild population of the wolf spider *Schizocosa ocreata* (Araneae, Lycosidae). Spiders are an excellent taxon for investigating the adaptive significance of satiation thresholds because they exhibit a suite of adaptations for a feast-or-famine existence (e.g. extensible abdomen, external digestion, polyphagy (Riechert & Harp, 1987)) and because individuals vary tremendously in both the number of consecutive prey items they attack and the amount of those prey they consume during singular foraging bouts (Riechert & Maupin, 1998; Maupin & Riechert, 2001; Pruitt *et al.*, 2008; Pruitt & Riechert, 2009). In the present study, we investigate (i) whether variation in satiation thresholds influences individual fitness, (ii) whether the fitness consequences of satiation thresholds change in the absence of predators, (iii) whether females' satiation thresholds influence their rate of egg case production and (iv) whether satiation threshold exhibits a significant heritability (i.e. additive genetic variation).

## Materials and methods

### Study system

*Schizocosa ocreata* is a polyphagic wolf spider common throughout the eastern United States. Wolf spiders, family Lycosidae, are a cursorial non-web-building family, which wander in low vegetation and leaf litter in search of prey. Family Lycosidae is noteworthy in exhibiting parental care: post-parturition, females carry their eggs in spherical silk structures attached to their abdomen via their spinnerets. After hatching, spiderlings climb their mother's legs and reside on her abdomen for their early development (Foelix, 1996; Ubick *et al.*, 2005).

### Collection, maintenance and breeding

Immature spiders ( $n = 514$ ) were collected from a temperate deciduous forest site in east Tennessee in March 2009. Spiders were brought back to laboratory, housed individually in clear plastic cups (473 mL) and maintained under natural lighting conditions between 21.1 and 23 °C. Spiders were fed a maintenance diet of two 2-week-old crickets twice weekly (hereafter, the 'adult maintenance diet'). Containers were misted with water once each week, and a moist paper towel was provided for drinking. Individuals were checked daily for moults, and mature individuals were identified for breeding. Females' probability of mating decreases with age (Norton & Uetz, 2005); therefore, all individuals were mated within 3 days of maturation. No individual was mated more than once in our study. One day after a routine feeding, in preparation for mating the following day, females were fed an *ad libitum* meal of 2-week-old crickets (see 'Assessment of Female Satiation Threshold' below). This *ad libitum* meal reduces the probability of females cannibalizing their males.

For mating, females' containers were placed in the centre of a large rectangular arena, and the lids to their containers were removed. Two minutes before male's entry, two artificial leaves were taped to the side of each female's container to allow males an escape route. A randomly selected male was then coaxed into the females' containers using an open-tipped syringe (after Riechert, 1978; Pruitt & Husak, 2010). The pairs were then given 24 h to court and mate; males were removed after this time.

Spiderlings produced from our matings were collected as they dropped from their mother's abdomen and housed individually in 59-mL plastic cups. Spiderlings ( $N = 1194$  spiderlings;  $N = 217$  broods) were maintained in these enclosures, misted every other day with water and fed a maintenance diet of three termite workers, three times weekly. Upon reaching their fourth instar, spiderlings were switched to larger enclosures (473 mL) and transitioned to the adult maintenance diet.

Individuals were checked daily for maturity; mature individuals were mated following the protocol described earlier, and their satiation threshold was assessed (see 'Assessment of Female Satiation Threshold'). Three days after mating, two of our lab-reared females were randomly selected from each brood for use in our selection experiment.

### Assessment of female satiation threshold

We assessed the satiation threshold of female spiders after the protocol of Pruitt (2010). Satiation threshold has a repeatability of  $r = 0.56$  for *S. ocreata* (Pruitt, 2010).

Female satiation threshold was assessed 1 day after a routine feeding by offering females size-matched prey items (25% of test female mass  $\pm 3\%$ ) at 10-min intervals until two consecutive prey items were rejected (i.e. detected and ignored). *Schizocosa ocreata* do not use webbing to detect, capture or cache food; therefore, the ten-minute interval was extended if the spider required more time to detect or subdue their prey (e.g. it was actively feeding on one prey item and incapable of subduing another). After two consecutive prey items were rejected, the rejected prey items were removed and the spiders were allowed 24 h to finish feeding. Individuals were weighed two hours prior to their satiation threshold trials and were reweighed after their 24-h feeding period. Satiation threshold was measured as an individual's percentage increase in mass following a gluttonous feeding trial.

### Assessment of selection

To determine the degree to which females' satiation threshold influences fitness, we performed a mark-recapture study at our deciduous forest site in east Tennessee (after Jayne & Bennett, 1990; Calsbeek & Irschick, 2007; Pruitt, 2010). The study site is characterized by shallow leaf litter and mesophytic deciduous trees; poison ivy (*Rhus radicans*) dominates the understory vegetation. Twelve  $1.5 \times 1.5$  m quadrats were haphazardly selected at our site and bordered with aluminium siding. Siding extended 10 cm into the ground and 30 cm above. Poison ivy was trimmed back on either side of the siding to prevent spiders from entering or leaving the enclosures. Each quadrat was sampled by carefully hand-sifting through the leaf litter. Searches were performed for two hours, every other day for 14 days (seven research periods). We counted and removed the resident *S. ocreata* in each plot. We deemed all of the *S. ocreata* to be removed from a plot after two consecutive search periods yielded no new individuals. Other large spiders and predatory insects ( $> 15$  mm) were removed and housed in laboratory for the duration of our seven search periods. In half of our plots ( $n = 6$ ), we returned these large, predatory spiders and insects, and for the other six plots, we released the predatory

arthropods in an adjacent woodlot (hereafter, 'predator exclusion treatment'). Avian predation is thought to be a major selective force for *S. ocreata* (Lohrey *et al.*, 2009); thus, we placed two layers of large-grade ( $4 \times 3$  cm) mist nets over the aluminium siding of our predator exclusion plots.

We placed a number of individually marked, size-matched ( $\pm 2\%$  body mass), lab-reared female *S. ocreata* in each plot equal to the number of resident *S. ocreata* removed during our seven initial surveys to mimic naturalistic densities. Females were marked by painting their cephalothorax with a unique sequence of colours using fast-drying modelling paint (after Riechert *et al.*, 2001; Pruitt, 2010). We checked these plots every other day for the next 40 days and noted (i) females bearing egg cases and (ii) the mass of these egg cases. Egg cases were massed using a portable electronic balance (VWR Portable Electronic Balance). At the end of this 40-day period, each plot was searched by hand until all ground cover was removed. Females not recovered at the end of this experiment were presumed dead.

### Statistical methods

None of the variables analysed violated the assumptions of normality or homogeneity of variance. Before assessing selection on satiation threshold, we tested for differences in mean satiation threshold and starting mass between treatments using Student's *t*-tests.

We estimated selection gradients using females' egg case mass\*survival (1, 0) as our composite estimate of individual fitness. Female egg case mass is highly correlated with the number and quality of offspring produced (reviewed in Foelix, 1996). We used general linear models to quantify linear ( $\beta$ ) and nonlinear ( $\gamma$ ) forms of selection (i.e. the change in relative fitness per change of one standard deviation of the trait mean) (Lande & Arnold, 1983; Kingsolver *et al.*, 2001; Calsbeek & Irschick, 2007). However, when testing the effect of satiation threshold on survival specifically, we used logistic regression to compute significance values, after Janzen & Stern (1998). First, individuals' mass and satiation thresholds were entered into the model as linear terms, and then quadratic and interaction terms were added to test for stabilizing or disruptive selection. We present the single best model of selection based on Akaike's Information Criterion (AIC) model selection criterion here (Akaike, 1987), but we provide the AIC scores for all possible combinations of the quadratic polynomial online (see Tables S1 and S2). To determine whether selection on satiation threshold and starting mass differed among treatments, we used an ANCOVA with fitness as our response variable, treatment (predator inclusion or exclusion) as a main effect and plot nested within treatment as main effects, and satiation threshold and starting mass as covariates. A significant interaction term between treatment and a covariate indicates

selection on the covariate differs between treatments (i.e. the magnitude or direction of the relationship), and a significant interaction term between plot and a covariate indicates selection on satiation threshold differs among plots within treatments.

The heritability of satiation threshold was assessed using linear, dam-on-offspring regression. We used the mean of two randomly selected female offspring from each brood ( $n = 205$ ) as the response variable in this analysis. Heritability was estimated as two times the slope of the regression line (after Fernandez & Miller, 1985; Boake, 1994). All statistical procedures were performed using Statistical Analysis Software 9.1 (SAS, 100 Sas Campus Dr, NC, USA).

## Results

Because similar individuals were assigned to each treatment (predator inclusion or exclusion), there were no significant differences in individuals' satiation threshold ( $T = 1.43$ , d.f. = 410,  $P = 0.15$ ) or starting mass

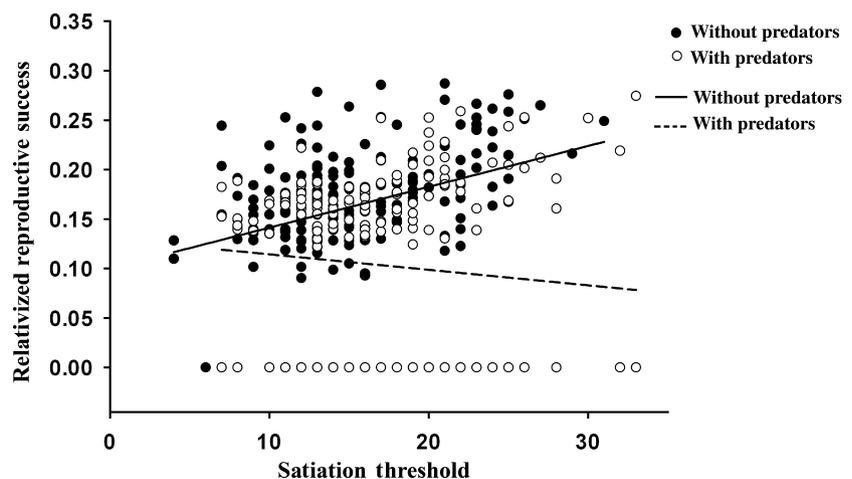
( $T = 0.10$ , d.f. = 410,  $P = 0.92$ ) among treatments. As in previous experiments, individuals' satiation threshold was highly correlated with the number of prey they attacked ( $r = 0.67$ , d.f. = 409,  $P < 0.001$ ), and we failed to show a relationship between satiation threshold and body length in our lab-reared population ( $r = 0.08$ , d.f. = 409,  $P = 0.11$ ). No significant effects were detected for treatment ( $F_{1,388} = 0.02$ ,  $P = 0.88$ ), plot within treatment ( $F_{1,10} = 0.07$ ,  $P = 0.97$ ), satiation threshold ( $F_{1,388} = 1.80$ ,  $P = 0.18$ ), plot\*satiation threshold ( $F_{1,10} = 0.51$ ,  $P = 0.88$ ), mass ( $F_{1,388} = 0.03$ ,  $P = 0.86$ ), plot\*mass ( $F_{1,10} = 1.40$ ,  $P = 0.19$ ) or treatment\*mass ( $F_{1,388} = 0.99$ ,  $P = 0.32$ ). The interaction term satiation threshold\*treatment ( $F_{1,388} = 13.68$ ,  $P < 0.001$ ) was the only significant effect in our ANCOVA. Selection on satiation threshold therefore differed among treatments but not among plots within treatments; thus, for the remainder of our selection analyses, we combine plots within treatments but analyse each treatment independently.

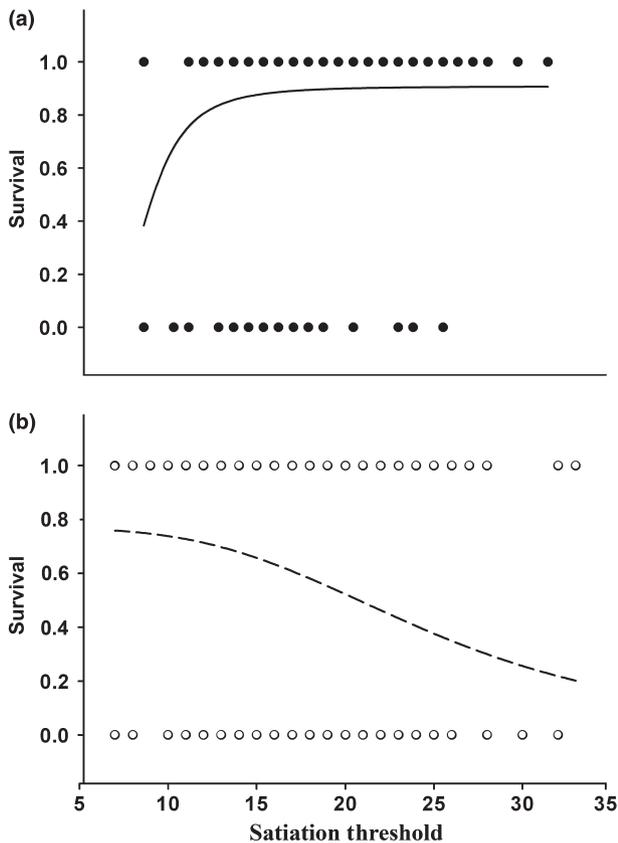
For both our predator inclusion and predator exclusion treatments, the best model contained satiation threshold and no other terms. Model comparisons using AIC never supported the inclusion of individuals' starting mass, or quadratic and interaction terms. These terms never had significant  $P$ -values (all were  $P > 0.09$ ), and including them never improved AIC scores (see Tables S1 and S2). In our predator exclusion treatment, we detected a positive linear relationship between satiation threshold and fitness (Table 1, Fig. 1) and no significant logistic relationship between survival and satiation threshold ( $\chi^2_1 = 0.29$ ,  $P = 0.59$ , Fig. 2). In contrast, in our predator inclusion treatment, we failed to detect a significant relationship between satiation threshold and fitness in our predator inclusion treatment (Table 1, Fig. 1). However, we detected a negative logistic relationship between survival and satiation threshold in our predator inclusion treatment ( $\chi^2_1 = 15.34$ ,  $P = 0.001$ , Fig. 2). Irrespective of treatment, we detected a negative linear relationship

**Table 1** Models describing selection gradients operating on satiation threshold. Fitness was estimated as female egg case mass\*survival. When predators were excluded, there was a significant positive relationship between fitness and satiation threshold, but no fitness gradient was significant in the presence of predators. See text for more information on the analysis.

Model	d.f.	Parameter	$\beta$	SE	$F$	$P$ -value	AIC
Predator exclusion							
$y = \beta_1x + \alpha$	206	Satiation threshold	0.139	0.025	30.575	< 0.001	162.54
		Intercept	-0.008	0.025			
Predator inclusion							
$y = \beta_1x + \alpha$	204	Satiation threshold	-0.084	0.061	1.909	0.169	528.52
		Intercept	-0.005	0.060			

**Fig. 1** Selection gradients on satiation threshold in the predator exclusion (solid line) and predator inclusion (dashed line) treatments as estimated by the linear regression between individuals' satiation threshold (change in mass/initial female body mass) and egg case mass(grams)\*survival. The data presented here are untransformed.





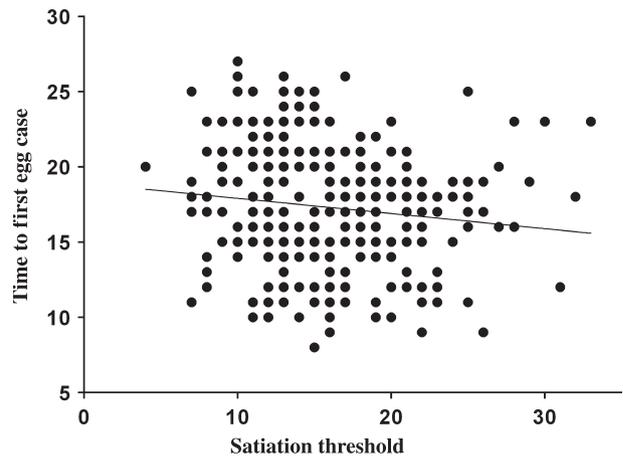
**Fig. 2** Logistic regressions between survival and satiation threshold (change in mass/initial female body mass) in the predator exclusion (a) and predator (b) inclusion treatments.

between the day we first observed females' egg cases and their satiation threshold ( $F_{1,191} = 5.24$ ,  $P = 0.022$ , Fig. 3).

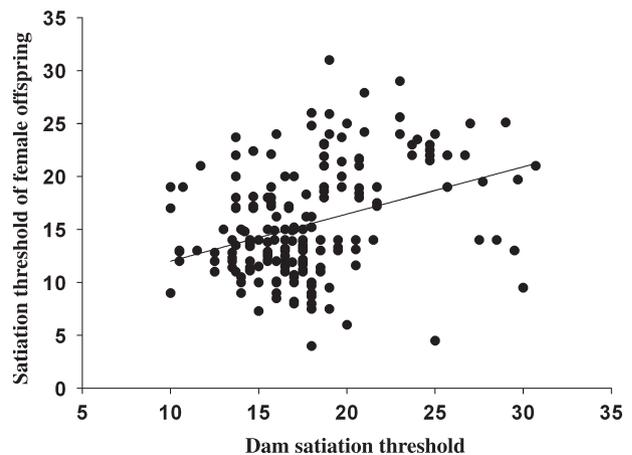
Our assessment of heritability detected a positive linear relationship between the satiation threshold of dams and their female offspring ( $F_{1,204} = 26.31$ ,  $P < 0.001$ ,  $\beta = 0.28$ ,  $SE = 1.71$ ,  $h^2 = 0.56$ , Fig. 4).

## Discussion

Although several authors have suggested an adaptive cost to the taking of large meals (Garland & Arnold, 1983; Huey *et al.*, 1984; Pough & Andrews, 1985; Ford & Shuttlesworth, 1986; Herzog & Bailey, 1987; Andreadis & Burghardt, 2005; Pruitt, 2010), direct assessments of selection in wild populations are lacking. Our data suggest that satiation threshold generates one or more life history trade-offs in the wolf spider *S. ocreata*. Increased satiation threshold is positively associated with faster egg case production and larger egg cases; however, gluttonous individuals also experience a greater susceptibility to predation. Taken together, our data suggest that although there is an associated fecundity–survival trade-off, in the presence of predators, individuals exhibiting



**Fig. 3** Linear regression between individuals' satiation threshold (change in mass/initial female body mass) and the time until their first egg case was produced. High satiation threshold females tend to produce egg cases sooner ( $F_{1,191} = 95.2$ ,  $P = 0.022$ ,  $R^2 = 0.04$ ).



**Fig. 4** Linear regression between the satiation threshold of dams and the satiation thresholds of their female offspring. Heritability of satiation threshold was significant ( $P < 0.001$ ) and estimated at 0.56.

varying degrees of satiation threshold have similar expected fitness (Table 1, Fig. 1).

In order for satiation threshold to respond to selection, it must exhibit a significant heritability. The results of our breeding study suggest satiation threshold exhibits a significant heritability ( $h^2 = 0.56$ ). Although our breeding study does not fully control for indirect genetic effects (e.g. maternal effects), there is now empirical and theoretical evidence suggesting that indirect genetic effects can drive the evolution of traits, which may themselves lack a genetic influence (Wolf *et al.*, 1998; Hunt & Simmons, 2002). Thus, by either direct or indirect genetic effects, gluttonous feeding tendencies

are transmitted across generations and therefore can respond to selection.

In the absence of predators, gluttonous individuals experience two benefits: they produce (i) larger egg cases (ii) at a faster rate. It seems intuitive that higher satiation threshold individuals should produce larger egg cases, because they have more resources available for reproduction. Furthermore, they also enjoy the benefit of rapid egg case production (Fig. 3) and therefore need not persist as long as lower threshold individuals to reproduce. Thus, faster egg case production can, to some extent, ameliorate the survival costs of gluttonous behaviour.

When predators are present, increased susceptibility to predation attenuates the advantages of satiation threshold. Several previous studies have linked gluttonous foraging behaviour with impaired locomotor performance (Taylor *et al.*, 1980; Garland & Arnold, 1983; Huey *et al.*, 1984; Pough & Andrews, 1985; Ford & Shuttlesworth, 1986; Herzog & Bailey, 1987; Martin, 1996) and suggest that selection to maintain locomotor performance might set an upper limit to the amount individuals consume during feeding bouts. For instance, in the garter snake *Thamnophis marcianus*, large meals were associated with reduced speed and endurance, and some individuals even regurgitate prey after experiencing a predator threat (Ford & Shuttlesworth, 1986). In a related study on spiders, Pruitt (2010) demonstrated a negative association between gluttonous foraging and burst speed and that burst speed was positively associated with survival in two wolf spiders, *Hogna helluo* and *S. ocreata*. Consistent with this performance-driven hypothesis, we found a direct negative logistic relationship between survival and satiation threshold in the predator inclusion treatment. Gluttonous individuals may be more susceptible to predation owing to their reduced locomotor performance, increased visibility to predators or an increased activity pattern (e.g. spending more time searching for food).

Taken together, satiation threshold can be viewed as a high-risk life history strategy: highly gluttonous individuals either produce large egg cases quickly or die without ever reproducing. Alternatively, gluttonous individuals might persist as variants in the population that could achieve higher fitness levels during periods of high resource available and lower predation risk, for example during outbreaks of prey populations when spider predators are also targeting the more populous prey.

## Conclusions

For *S. ocreata*, the fitness consequences of satiation threshold change with intensity of predation. When predators are absent, gluttonous individuals are favoured, producing larger egg cases and at a faster rate. However, when predators are present, gluttonous individuals

experience increased susceptibility to predation and thereby lose their selective advantages. We conjecture spatial and temporal heterogeneity in predation pressure and resource availability may have a hand in maintaining variation in satiation threshold in *S. ocreata*. For instance, the presence of cover objects, understory foliage type and leaf litter depth may affect intensity of predation across microhabitats. Future investigations will target the interaction between microhabitat and selection on satiation threshold and whether avian or arthropod predators impose the greater selective force.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Table S1** The best ten models with 1–5 variables predicting individuals' fitness in the predator *exclusion* treatment using AIC model selection criteria. Satiation threshold (ST).

**Table S2** The best ten models with 1–5 variables predicting individuals' fitness in the predator *inclusion* treatment using AIC model selection criteria. Satiation threshold (ST).

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