Condition-dependent foraging in the wolf spider *Hogna baltimoriana*

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ABSTRACT

Spiders are major predators of terrestrial arthropods, so understanding the underlying drivers of spider foraging is crucial for understanding how energy and nutrients pass through terrestrial food webs. We tested predictions made by allometric and optimal foraging theory using the wolf spider *Hogna baltimoriana* and grasshopper prey as a model (Caelifera). Allometric foraging theory predicts that functional response parameters will be dependent on body size, whereas optimal foraging theory asserts the importance of energetic state in determining foraging behaviors. We found that space clearance rate (type II functional response parameter a) was negatively related to the ratio of abdomen width to carapace width (a measure of energetic state) but not to body mass or carapace width. Thus, a key factor in determining the strength of foraging interactions in spiders may be recent energy intake that determines the current body condition of foragers.

Consumer-resource interactions facilitate the movement of energy through food webs (McCann, 2011; Pimm et al., 1991). These interactions also determine the energy available for fitness-enhancing activities of the forager, so traits or behaviors that influence foraging may alter individual-level fitness and food web function (Gibert et al., 2015). Understanding how variation in traits and individual physiological state influences foraging is therefore crucial for understanding the structure and dynamics of food webs (Bolnick et al., 2011; Gibert and Brassil, 2014).

Foraging interactions are often quantified using the functional response, or the relationship between prey density and foraging rate (Holling, 1959). The typical form of this relationship is the type II, or saturating, functional response:

$$f_{pc} = \frac{aR}{1 + ahR} \tag{1}$$

where a is the space clearance rate (i.e., the space cleared of prey by the predator per unit time) and h is the handling time, or the time needed to process prey and return to foraging. The parameters of Eq. (1) vary across both predator and prey taxa (DeLong and Vasseur, 2012; Kalinoski and DeLong, 2016; Rall et al., 2011, 2012; Thompson, 1975) and with defensive and offensive traits of prey and predator, respectively (Hammill et al., 2010; Kalinoski and DeLong, 2016; Kopp and Tollrian, 2003).

The parameters of Eq. (1) also may show consistent variation across predator and/or prey body size (DeLong et al., 2015; DeLong and Vasseur, 2012; Rall et al., 2012; Riede et al., 2011; Thompson, 1975). Body size is often related to space clearance rate and handling time through power-law (allometric) relationships due to the effects of size on searching velocity, detectability, and morphology (Aljetlawi et al., 2004; McGill and Mittelbach, 2006; Pawar et al., 2012). This is due to the fact that space clearance rate is the outcome of spatial interactions and foraging decisions, often modeled as $a = A_d \sqrt{V_r^2 + V_c^2}$, where A_d is the area of detection, V_r is the prey velocity, and V_c is the consumer velocity (Aljetlawi et al., 2004; DeLong and Vasseur, 2013; Pawar et al., 2012). Since velocity scales with body size of the forager, space clearance rate should also scale with body size, regardless of whether the variation in size is within or across species. Thus, one view on variation in functional response parameters focuses on the physical effects of predator and prey traits on predator-prey encounters and the biomechanical aspects of foraging.

An alternative view is provided by optimal foraging theory, where variation in functional response parameters is driven by individual differences in feeding history, nutrient content of prey, and energetic expenditures required to obtain prey (Charnov, 1976). Thus, while allometric foraging theory would predict that body size (mass or structural size) would play a strong role controlling variation in foraging, optimal foraging theory would predict that energetic state (some metric of recent foraging success) would play a strong role in controlling variation in foraging rates among individuals. Despite having different theoretical underpinnings, it is also possible that body size and energetic state interact to influence functional response (Mittelbach, 1981). Body size may influence handling times (DeLong et al., 2015; Rall et al., 2012), for example, and thus the expected energy gain of a prey item. Similarly, hunger may influence area of detection by
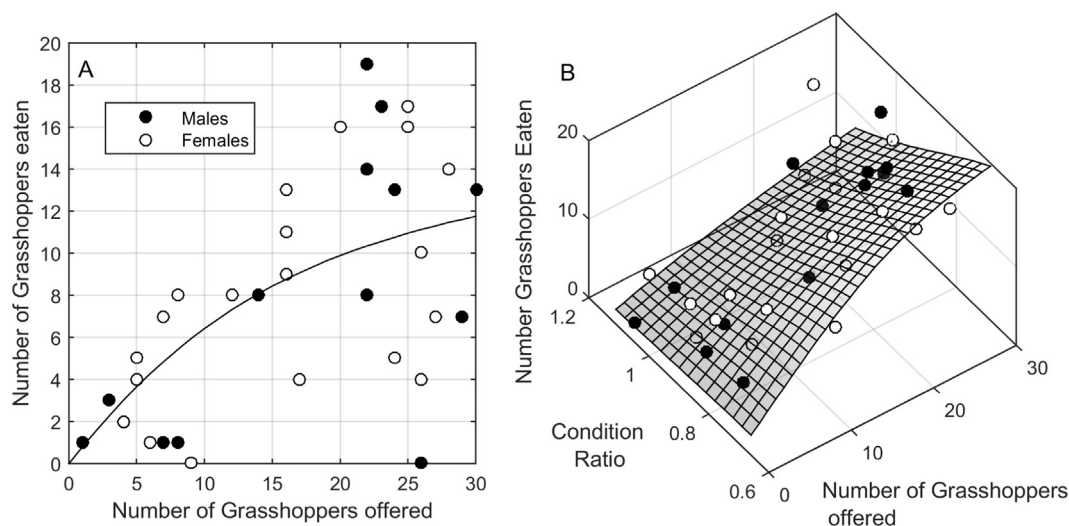
Fig. 1. Functional response for *Hogna baltimoriana* foraging on grasshoppers. A. Standard type-II functional response for both sexes combined. B. Type-II functional response with the space clearance rate (functional response parameter *a*) dependent on the condition ratio of the individual foragers (Eq. (2) in text).

influencing the distances over which foraging attempts are made or the probability of those attempts. Thus, a third hypothesis is that body condition and body size are related and interact to influence the functional response.

We conducted foraging trials with the wolf spider *Hogna baltimoriana* consuming small grasshoppers (Caelifera). Globally, spiders consume 400–800 million metric tons of insect prey per year, transferring huge amounts of energy to higher trophic levels in terrestrial ecosystems (Nyffeler and Birkhofer, 2017). Given this, understanding how energy and nutrients pass through terrestrial food webs depends on understanding what determines variation in spider foraging. Wolf spiders show evidence of size-based foraging (Vucic-Pestic et al., 2010) as well as foraging responses to nutritional state (Schmidt et al., 2012; Walker et al., 1999). We evaluated the effects of both body size (body mass and structural size) and energetic state (body condition ratio) on the functional response, endeavoring to determine whether foraging mechanics or individual energetic state, or their interaction, is relatively more important in driving variation in this food-web interaction.

We collected spiders at night by spotlighting in grassy areas around Cedar Point Biological Station, along the south shore of Lake Ogallala, Nebraska, USA, over two consecutive nights. Spiders weighed 0.22 ± 0.12 (SD) g ($N = 34$). We collected grasshoppers of different species by sweep-netting these same areas during the day. Grasshoppers weighed, on average, 20 mg and were chosen to minimize size differences among individuals. We determined the sex of spiders by the presence/absence of an epigynum. It is possible that immature females were sometimes mistaken for males if the epigynum was partial or not highly visible; however, at the time of collection many female *H. baltimoriana* were observed with egg sacs or carrying spiderlings. Thus, we expect that errors in gender assignment were minimal. We weighed spiders and measured the widths of their carapace and abdomens, using the ratio of the abdomen width to the carapace width as an index of body condition (energetic state). This condition index was tightly correlated with the residuals from a regression of carapace width on abdomen width ($r = 0.99$, $p < 0.001$), and thus the ratio is a good proxy for body condition. We use the ratio rather than the residual in our analysis because we cannot use negative numbers in the power-law functional form we analyze (see below).

We conducted foraging trials at night in circular plastic arenas (25 cm diameter, 9 cm depth, with lids), with sides painted to limit visual disturbance. We filled the bottom of the arenas with a thin layer of locally-collected, sifted sand to create a natural substrate. We first added grasshoppers to the arenas and then added spiders, with

individual spiders randomly assigned to different densities of prey. We released spiders in arenas at 21:00 h and removed them at 7:30 the following morning, when we counted remaining living grasshoppers. Each spider was used in only one foraging trial, and all spiders were released at the end of the experiment, precluding the recapture and reuse of individual spiders.

We did not replenish consumed prey during the experiment, and therefore we fit the Roger's random predator equation to our data (Bolker, 2011; Rogers, 1972):

$$N_e = N_0 - \frac{W\left(ahN_0 e^{-a(t - hN_0)}\right)}{ah}, \tag{2}$$

where N_e is the number of prey eaten after time t (10.5 h), N_0 is the number of prey offered (between 1 and 30 grasshoppers), and W is the Lambert W function. To incorporate body size and body condition into Eq. (2), we substituted power functions in place of a or h. For example, to make handling time in Eq. (2) respond to body size or condition, we substituted $h_0 M^\theta$ for h, where M is alternatively body mass, carapace width, or condition ratio, θ is a scaling exponent, and h_0 is the value of h when $M = 1$. Likewise, we substituted $a_0 M^\theta$ for a to assess the effects of body mass, carapace width, and condition ratio on space clearance rate. We conducted fits using ordinary non-linear least squares regression in Matlab. To determine which effects were best supported by the data, we ranked models using Akaike's Information Criterion corrected for small sample sizes (AICc). We initially fit all the models for male and female spiders separately, as functional responses in wolf spiders can differ by sex (Walker and Rypstra, 2001), but we found there was no difference between genders and so combined the two groups for the analysis presented here.

We found that the functional response of *H. baltimoriana* on small grasshoppers (Eq. (2)) was a standard type II ($a = 77.78$ cm² per pred per h, 95% confidence intervals [Cis]: −37.18 to 192.73; $h = 0.63$ h, CIs: 0.047 to 1.21; $R^2 = 0.40$; Fig. 1A). The scatter in this relationship was considerable, and we found that including body condition, but not body mass or carapace width, improved precision on parameter estimates and increased the explained variance (Table 1). AICc ranks indicated that a model where the space clearance rate was dependent on body condition was the best model ($a = 38.82$ cm² per pred per h, CIs: 11.65 to 66.0; $h = 0.43$ h, CIs: 0.025 to 0.83; $\theta = -4.95$, CIs: −8.58 to −1.32; $R^2 = 0.65$; Table 1, Fig. 1B). The effect of condition ratio on space clearance rate was negative, meaning that the lower their energetic state, the more grasshoppers the spiders killed. Finally, body mass and body condition were not correlated ($r = 0.30$, $p = 0.09$) and

Table 1
Model rankings for the effects of body mass, carapace width, and condition ratio (abdomen width divided by carapace width) on functional response parameters a (space clearance rate) and h (handling time) (Eq. (1)). Both sexes combined. Rankings indicate that the best model is one in which the space clearance rate of the spiders depends negatively on spider body condition.

Model type	AIC	ΔAIC
a ~ condition ratio	90.75	0.00
h ~ condition ratio	92.77	− 2.02
Size independent	106.67	− 15.93
a ~ carapace	108.32	− 17.58
a ~ mass	109.11	− 18.37
h ~ carapace	109.25	− 18.51
h ~ mass	109.25	− 18.51

thus acted independently to influence foraging.

We tested alternative predictions about how variation in consumption rates of wolf spiders foraging on grasshoppers might arise. Allometric theory suggests that foraging rates depend primarily on the body size of the spiders. In contrast, optimal foraging theory emphasizes the role of energetic state on foraging decisions. Finally, if body size and body condition are correlated, we might expect the two variables to interact in their effect on the functional response. Our data supports the prediction from optimal foraging theory because the space clearance rate was negatively related to condition ratio, which is an index of current energetic state. Furthermore, our data also indicate that energetic state influenced the functional response independent of size, as condition ratio was not correlated with body size. One of the potential mechanisms for this effect is that spiders with lower condition ratios moved around the arenas more, leading to higher rates of predator-prey encounters and thus greater foraging rates. For example, in an experiment with *H. helluo*, starved spiders moved more frequently than their fed counterparts, which presumably is related to increased searching in the starved spiders (Walker et al., 1999). Alternatively, spiders could have foraged more aggressively, making more foraging attempts or choosing to attack even when the likelihood of success is low (Petersen et al., 2010).

Although larger foragers cover more ground and therefore can encounter and capture prey at higher rates (Calder, 1996; McGill and Mittelbach, 2006), we did not find a size effect on foraging in *H. baltimoriana*. In fact, AICc ranks suggested that the models without any size effects were better supported than any of the body size-based models (Table 1). It is possible that size variation in our spiders was relatively small, preventing detection of a size effect. Alternatively, due to the fixed size of our arenas, the size-based variation in movement may have been suppressed. Nonetheless, because size-dependent foraging is widely observed in spiders and many other taxa (DeLong et al., 2015; Thompson, 1975; Vucic-Pestic et al., 2010), further work on the size-dependence of foraging in wolf spiders is merited. However, because energetic state contributes to variation in body size, comparing body size and energetic state effects in different systems may help resolve questions about the role of body size on functional responses.

One potential implication of our results is that spiders with lower condition ratios may be moving more to increase encounter rates with prey (Walker et al., 1999). This increased movement can be risky, however, as it may lead to greater risk of detection by predators that can consume *H. baltimoriana*. Spiders are at risk of predation from other spiders, including their own species (Rypstra and Samu, 2005). Thus, body condition may influence the foraging interaction between a predator and its prey as well as the likelihood that a predator may be exposed to other predators, including cannibals or other intra-guild predators (Heithaus et al., 2007).

Foraging interactions determine the flow of energy through food webs. What sets the rate of foraging is thus crucial to understanding energetic fluxes within ecosystems. Although across species, body size seems to play an important role in setting foraging rates (DeLong et al.,

2015; Pawar et al., 2012; Rall et al., 2012), our results suggest within species, energetic state may be more crucial in some cases. Because spiders are abundant predators that consume a large amount of insect prey worldwide (Nyffeler and Birkhofer, 2017), understanding the factors that drive variation in their foraging interactions is important for understanding energy flow in most terrestrial ecosystems.

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