

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

Shelby R. Lyon, Charlotte A. Sjulín, Kirsten M. Sullivan, John P. DeLong*

School of Biological Sciences, University of Nebraska - Lincoln, Lincoln, NE 68588, USA

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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:

$$f_{pc} = \frac{aR}{1 + ahR} \quad (1)$$

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

* Corresponding author.

E-mail address: jpdelong@unl.edu (J.P. DeLong).

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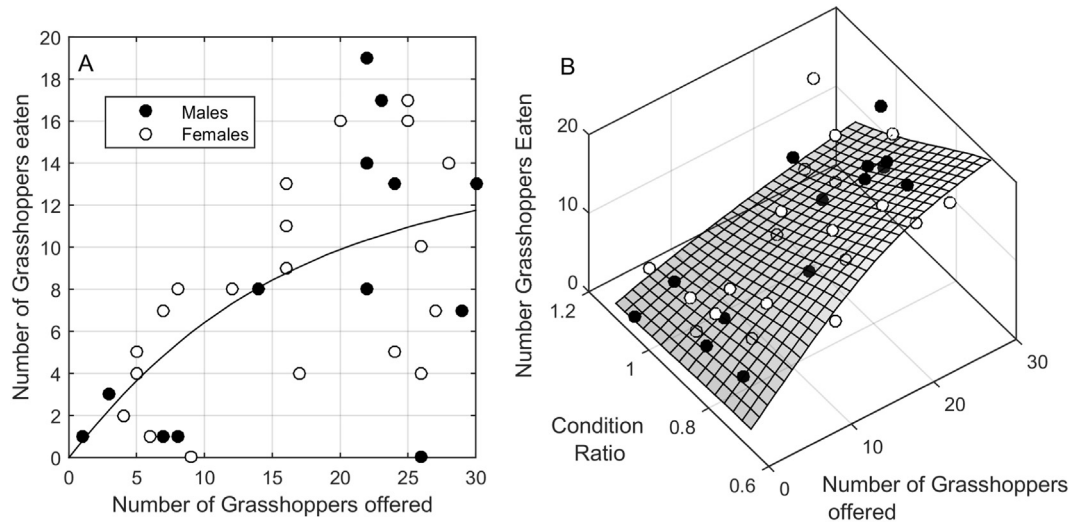


Fig. 1. Functional response for *Hogna baltimoriana* foraging on grasshoppers. A. Standard type-II functional response for both sexes combined. B. Type-II functional response with the space clearance rate (functional response parameter a) dependent on the condition ratio of the individual foragers (Eq. (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):

$$N_e = N_0 - \frac{W(ahN_0e^{-a(t-hN_0)})}{ah}, \quad (2)$$

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_0M^θ 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_0M^θ 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

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