

The relationship between offspring size and performance in the wolf spider *Hogna helluo* (Araneae: Lycosidae)

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ABSTRACT

Life-history theory predicts a trade-off between number of offspring and investment (size) per offspring. An important component of this trade-off is how offspring size influences performance and survival. In this study, we examined the relationships between maternal size, offspring size and clutch size, as well as the relationship between offspring size and performance, in the wolf spider, *Hogna helluo*. Offspring dispersing from field-collected female *Hogna helluo* with egg sacs were counted and their carapace width was measured. The relationships between feeding performance (number of prey captured), starvation tolerance and offspring size were examined to determine if offspring size was correlated with offspring performance. Clutch size increased with female size, but there was little evidence for a trade-off between offspring size and number. Starvation tolerance and feeding performance were positively related to offspring size. Our results show that offspring performance increases with offspring size and are consistent with the hypothesis that parental fitness is maximized by producing as many offspring as possible given constraints on a minimum viable offspring size.

Keywords: life history, optimality, resource allocation, size–number trade-off.

INTRODUCTION

Numerous theoretical and empirical studies have examined the relationships between offspring size and number (e.g. Lack, 1947; Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992; Sinervo and Doughty, 1996; Sinervo *et al.*, 2000). Assuming a limited energy supply, reproductive effort should be divided in some fashion between offspring size and number, resulting in a size–number trade-off (Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992; Carriere and Roff, 1995). This optimal division of resources should result in an equilibrium clutch size at which the increase in fitness accruing from producing larger (and,

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therefore, more viable) offspring is offset by the decrease in fitness from producing fewer offspring (Lloyd, 1987). This type of strategy is predicted to maximize parental fitness (Roff, 1992; Stearns, 1992).

A critical aspect of optimal clutch or egg size models is the positive relationship between offspring size and performance traits. Many factors, including growth rate, escape ability and feeding capacity, may influence survival and fitness and may be correlated with offspring size (Sinervo, 1990; Roff, 1992). In terrestrial species that are food-limited, hatchling size may have important effects on the ability of offspring to survive initial periods without food and influence their ability to capture prey. In the spider *Agelena limbata* (Araneae: Agelenidae), for example, offspring size is correlated with survival without food (Tanaka, 1995) and smaller individuals appear to be more vulnerable to parasitism and predation (Tanaka, 1992). Since spiders are frequently food-limited and often exhibit cannibalism (Wise, 1993), size at hatching may have important fitness consequences.

In spiders, clutch size increases with female size both intraspecifically and interspecifically (Peterson, 1950; Kessler, 1971; Fritz and Morris, 1985; Killebrew and Ford, 1985; Vollrath, 1987; Morse, 1988; Uetz, 1992; Simpson, 1993, 1995; Marshall and Gittleman, 1994; Buddle, 2000). Although clutch size and female size are generally positively correlated, variation in food intake can also influence the number of eggs laid by a female (Kessler, 1971; Wise, 1975, 1979; Spence *et al.*, 1996). The relationship between clutch size and offspring size in spiders is not as clear. This can vary between studies, between species and within species between years (e.g. Simpson, 1993, 1995; Marshall and Gittleman, 1994). Variation between species could be explained by differences between species in their allocation of resources to reproduction (Roff, 1992). However, differences occurring within a species between seasons suggests that environmental heterogeneity may influence the optimal reproductive strategy of a given species at a given time and place. In fact, theoretical models predict that variation in the amount of resources available for reproduction can result in no relationship or a positive relationship between offspring size and number, rather than an inverse relationship (Venable, 1992). In addition, the extent to which offspring size is fixed or variable among populations of spiders is equivocal (Marshall and Gittleman, 1994).

An important factor that has not been examined in many spider species is the relationship between offspring size and performance traits that may be related to offspring fitness. This is important when evaluating the fecundity advantage of producing small offspring versus the survival advantage of producing fewer, larger offspring (Sinervo, 1990; Roff, 1992; Tanaka, 1995). To address these questions, we examined the relationships between maternal size, offspring size and clutch size to determine if there is a trade-off between offspring size and number. In addition, to test the hypothesis that offspring size is related to offspring performance, we determined if offspring size influenced the survival and feeding success of spiderlings in the wolf spider *Hogna helluo* (Walckenaer 1837).

MATERIALS AND METHODS

Hogna helluo is a large wolf spider that is widely distributed across the eastern United States and southern Canada and is found in a variety of habitats, including littoral zones and agricultural fields (Kaston, 1981; Dondale and Redner, 1990; Marshall and Rypstra, 1999). As adults, *H. helluo* are generally sedentary with females sometimes building retreats (Walker *et al.*, 1999a,b).

A behavioural characteristic of wolf spiders that makes them ideal organisms for these sorts of studies is that females carry the egg case until hatching and then carry the newly hatched offspring for 1–2 weeks, at which time they disperse from the mother (Stratton, 1985; Dondale and Redner, 1990). During this time the offspring do not feed (Dondale and Redner, 1990). In addition, *H. helluo* have quite a large clutch size relative to other wolf spiders and exhibit significant variation in offspring size (S.E. Walker, S.D. Marshall and A.L. Rypstra, unpublished data; Marshall and Gittleman, 1994).

Hogna helluo were collected from Miami University's Ecology Research Center, Butler County, Ohio in the summer of 1996. Individuals with eggs were taken to the laboratory and maintained at 25°C and 70% relative humidity until the offspring dispersed ($n = 19$ females). The females were maintained in 1.4 litre plastic containers with 7–10 cm moist peat moss. It was easy to determine when spiderlings started to disperse, since they moved off of the female's abdomen and went to the top of these containers. In most cases, spiderling dispersal occurred over a 1 week period, with most spiderlings dispersing in the first few days. We waited until approximately 95% of the clutch had dispersed and then randomly sampled spiderlings ($n = 13$ –25 depending on the clutch) from each clutch. In addition, most spiderlings in a clutch dispersed very rapidly and it was quite difficult to determine the order in which they dispersed. The carapace width of these individuals was measured using a dissecting microscope equipped with an ocular micrometer (± 0.01 mm). After dispersal, the total number of offspring were counted and maternal size was measured as the female's carapace width.

Relationships between clutch size, mean offspring size and female size were examined using multiple regression and simple linear correlations (Neter *et al.*, 1990; Sokal and Rohlf, 1995). Mean offspring size was determined as the mean carapace width of a sample of individuals within a clutch ($n = 13$ –25 spiderlings per clutch, $n = 17$ females). In addition, we tested for a trade-off between clutch size and offspring size using multiple regression on log-transformed values (Neter *et al.*, 1990). The model took the form:

$$\log(\text{clutch size}) = \beta_0 + \beta_1 \times \log(\text{offspring size}) + \beta_2 \times \log(\text{female size}) \quad (1)$$

where β_0 was the intercept, β_1 relates $\log(\text{offspring size})$ to $\log(\text{clutch size})$ while holding female size constant, and β_2 relates $\log(\text{female size})$ to $\log(\text{clutch size})$ while holding $\log(\text{offspring size})$ constant. To establish if there was significant variation in offspring size between females, we used a one-way random effects analysis of variance (Littell *et al.*, 1996). We also calculated an intraclass correlation coefficient as a measure of similarity among individuals within families relative to the differences between families (Sokal and Rohlf, 1995). We obtained confidence intervals for the intraclass correlation coefficient using the jackknife method (Sokal and Rohlf, 1995).

As a measure of the importance of offspring size, we evaluated the relationship between survival and offspring body size (carapace width). In the laboratory, we have not observed mortality of individuals while they are being carried by the female. Since we were interested in a surrogate measure of spiderling survival, we measured the starvation tolerance of individuals after dispersal. To do this, we randomly sampled 82 individuals from four different clutches 2 days after the beginning of dispersal. Day zero of the experiment was when we removed spiderlings from the maternal container. On day zero, we measured the carapace width of the spiderlings using the same methods as above. Food was not provided to the spiders; however, water was available *ad libitum*. Spiderlings were maintained in 100 ml round deli cups. We recorded the time in days that the spiderlings lived.

As an additional measure of the importance of body size, we examined the relationship between the functional response of hatchling *H. helluo* and body size using a two-factor design, which included mother and prey density. Twenty hatchlings were randomly selected from five different females within 2 days of the beginning of dispersal and then five individuals from each clutch were assigned to one of four different prey densities (1, 2, 4 or 8 vestigial winged fruit flies, *Drosophila melanogaster*). All spiders were measured before the experiment using a dissecting scope with an ocular micrometer. Spiderlings were maintained in 100 ml round plastic cups with 1–2 cm of moist peat moss substrate. Twenty-four hours after the introduction of prey, we counted the number of fruit flies remaining.

A mixed model analysis of covariance was used to examine the relationship between starvation time and offspring body size while accounting for the fact that individual clutches are not independent (Littell *et al.*, 1996). We treated family as a random effect and estimated the relationship between offspring survival time and offspring size (carapace width). Since classic optimality models assume a non-linear relationship between offspring fitness and offspring size (e.g. Roff, 1992), we fit a model that initially included quadratic terms to account for any non-linearity in the data. If these terms were not significant at $P < 0.05$, they were removed and the model fitted again without them. Offspring survival and size were both natural log-transformed before analysis.

There are three basic types of functional response (Juliano, 1993). A type I response is defined by a linear increase in the number of prey killed as prey density increases and is generally considered unrealistic, since it suggests predators are not limited by handling time or never reach satiation (Gotelli, 1995). A type II response is characterized by an increasing number of prey killed that approaches an asymptote hyperbolically. A type III functional response is characterized by a sigmoid shaped curve relating the number of prey killed to prey density. These different types of curve can be differentiated by examining the relationship between the proportion of prey killed and prey density (Juliano, 1993). There is no relationship between the proportion of prey killed and prey density in a type I response; there is a negative relationship between the proportion of prey killed and prey density in a type II response; and a type III response is characterized by an initially increasing relationship between the proportion of prey killed and prey density (Juliano, 1993).

Since logistic regression is the appropriate method to determine the type of functional response (Juliano, 1993), we modelled the proportion of prey killed using a generalized linear mixed model with binomial error distribution and a logit link (Littell *et al.*, 1996). This enabled us to determine if the functional response was type II, in which case the proportion of prey killed would decrease as prey density increased, or if it was type III, in which case the proportion of prey killed would increase with prey density (Juliano, 1993). Mixed models were fit using the Mixed procedure (survival data) or the glimmix macro (functional response data) (Littell *et al.*, 1996). Likelihood ratio tests were constructed to test for random effects (family) and degrees of freedom for all analyses were determined using Satterthwaite's approximation (Littell *et al.*, 1996). All statistical analyses were performed using SAS v. 6.12.

RESULTS

Female carapace width and clutch size were measured on 19 individuals and offspring size (carapace width) was measured on 411 spiderlings from 17 different clutches (Table 1). In many spider species, female size was positively correlated with clutch size ($r = 0.608$,

Table 1. Clutch size, offspring size and female size

Trait	<i>n</i>	Mean \pm standard deviation (minimum, maximum)	Coefficient of variation (standard error ^a)
Female size (mm)	19	6.3 \pm 0.649 (5.33, 7.42)	0.102 (0.070)
Offspring size (mm)	17	0.88 \pm 0.047 (0.81, 0.965)	0.054 (0.009)
Clutch size	19	186.1 \pm 85.19 (88, 411)	0.458 (0.074)

Note: Offspring size and female size are measured as carapace width. Offspring size is presented as the mean of the mean offspring size of each clutch.

^a Calculated from Sokal and Rohlf (1995: 138).

$P = 0.0047$) (Fig. 1). However, there was no significant relationship between female size and offspring size ($r = -0.095$, $P = 0.7221$) or between offspring size and clutch size ($r = -0.118$, $P = 0.6527$). Multiple regression analysis indicated a positive relationship between clutch size and female size while holding offspring size constant (Table 2). However, clutch size was not significantly related to offspring size while holding female size constant (Table 2). Note that we had relatively little power to detect a relationship for this particular test (*post-hoc* power analysis, power = 0.058). We did find that there was significant variation between clutches in offspring size (likelihood ratio test, $\chi^2 = 299.7$, $P < 0.0001$). However, siblings were much more similar to each other than to unrelated individuals (intraclass correlation coefficient = 0.60, 95% confidence interval 0.4902–0.7168).

Offspring size was significantly correlated with both of our measures of performance. There was no significant effect of family on survival ($\chi^2 = 2.4$, $P = 0.060$), but it was significantly related to offspring body size (slope = 3.03 ± 0.94 , $t = 3.23$, d.f. = 20.7, $P = 0.0040$). There was no significant effect of family on the proportion of prey killed ($\chi^2 = 0.6$, d.f. = 1, $P = 0.2193$). The proportion of prey killed decreased with prey density (slope = -0.1369 ± 0.039 , $t = -3.43$, d.f. = 93.6, $P = 0.0009$) and increased with offspring size (slope = 5.0981 ± 2.0 , $t = 2.54$, d.f. = 74.3, $P = 0.0130$). Since the proportion of prey killed decreased with prey density, we have evidence indicating a type II functional response for these spiderlings. No quadratic terms were significant in any analysis ($t < 1.25$, $P > 0.25$).

DISCUSSION

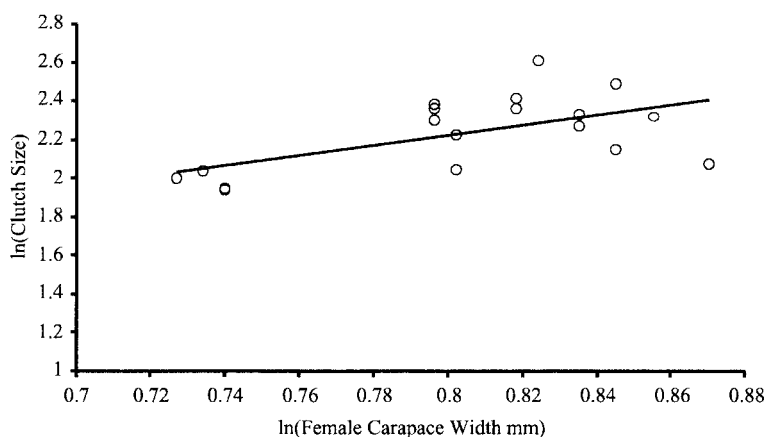
Although it has been suggested that variation in clutch size is a primary target of selection in spiders (Marshall and Gittleman, 1994), few studies have examined the importance of offspring size in spiders. As we might have expected from results of previous studies (Simpson, 1993, 1995; Marshall and Gittleman, 1994; Buddle, 2000), we found evidence for a positive correlation between female size and clutch size in *Hogna helluo*. Although we found evidence of a trade-off between offspring size and number, it was not statistically significant. In addition, offspring survival and feeding success were positively correlated with offspring size.

Clutch size exhibited a great deal of variation, while there was relatively little variation in offspring size in this species (range 0.7–1.0 mm, coefficient of variation = 5.4%; Table 1). In

Table 2. Results of multiple regression analysis of clutch size against offspring size and female size

Parameter	Coefficient (standard error)	<i>t</i>	<i>P</i>
Intercept	-0.010 (0.702)	-0.15	0.9886
ln(Female size)	2.769 (0.882)	2.769	0.0073
ln(Offspring size)	-0.491 (1.75)	-0.491	0.7831

Note: All data were log-transformed before analysis to meet assumptions of linear regression. Standard errors of parameter estimates are given in parentheses following the parameter estimate.

**Fig. 1.** Relationship between the natural log of clutch size and the natural log of female size in the wolf spider *Hogna helluo*. The line represents the best fit from ordinary least squares linear regression.

fact, clutch size varied approximately eight times more than offspring size (coefficient of variation = 45.8%; Table 1), indicating much greater variability in the amount of resources invested in a clutch than in allocation of resources to individual offspring. Variability in clutch size can be explained by several factors. In many species, clutch size is related to female feeding history and body size (Wise, 1993; Marshall and Gittleman, 1994; Simpson, 1995; Spence *et al.*, 1996). In *H. helluo*, the large variation in clutch size observed could be a result of variation in food intake between individual females. Thus it is likely that adult size may set a limit on the number of eggs in terms of space when environmental conditions are good (see Spence *et al.*, 1996); however, under conditions of food limitation or high variation in food resource availability, larger females may not necessarily have a reproductive advantage over smaller females.

Little variation in offspring size could be the result of many factors. Marshall and Gittleman (1994) have suggested that spiders maximize clutch size with constraints on a minimum viable offspring size. Our results are consistent with this hypothesis; however, we have no data on minimum viable offspring size. In addition, when clutch size is fairly large and offspring survival is low, there is weak selection for the optimal offspring size and

maximizing the total number of offspring produced maximizes parental fitness (Forbes, 1991). It is probable that *H. helluo* spiderlings have low survival in the field, since there are adult *H. helluo* as well as other invertebrate predators (e.g. other wolf spiders and predatory arthropods) that might consume them (Marshall and Rypstra, 1999).

Although many studies have tried to show a trade-off between offspring size and number in spiders, their results are equivocal (e.g. Simpson, 1993, 1995; Marshall and Gittleman, 1994; this study). This could potentially be because there is no trade-off between offspring size and number or because it is very difficult to detect. Our results suggest a trade-off (negative coefficient relating offspring size to offspring number), but the result was not statistically significant and we had relatively little power to detect this relationship (*post-hoc* power analysis, power = 0.058). In addition, variation in resource availability can mask a correlation between, or result in positive or neutral correlations between, offspring size and number (Van Noordwijk and de Jong, 1986; Venable, 1992; Christians, 2000; Glazier, 2000).

We detected significant family effects on offspring size. Since our experimental design had groups of full siblings, we cannot distinguish between genetic or maternal effects. Jakob and Dingle (1990) also found family effects (significant differences between clutches) when examining growth parameters (size, number of instars to maturity, etc.) in the pholcid spider, *Holocnemus pluchei*. Given that maternal effects have been noted in other species of arthropods (e.g. Fox and Mousseau, 1998), it is likely that similar factors may influence offspring size and behaviour in spiders, thus warranting further investigation.

Larger offspring survived periods of poor food availability better than smaller offspring, as Tanaka (1995) also showed. Our results also show that hatchling *H. helluo* exhibit a type II functional response that appears to be typical of spiders (Wise, 1993; Walker and Rypstra, 2001, 2002). However, in addition to demonstrating a type II functional response, we showed that larger offspring kill more prey across all prey densities than smaller offspring. Thus, the functional response of *H. helluo* spiderlings can be viewed as a type II functional response in which the number of prey killed increases with prey density and also increases with offspring size. The effects of hatchling size on survival and functional response indicate that larger spiderlings have a two-fold advantage: they can acquire more food and also have more time to acquire it. Also, since density-dependent cannibalism may play a role in population regulation in wolf spiders (Wagner and Wise, 1996), larger individuals may have an advantage in interactions with other spiderlings (see Samu *et al.*, 1999). Since many species of spider are considered food-limited (Wise, 1993) and large size may be beneficial in interactions with prey and other spiders, large offspring size would appear to be advantageous in terms of survival and foraging. Indeed, we found that the effect of offspring size on starvation tolerance is quite noticeable. Offspring size ranged from approximately 0.7 to 1.0 mm. Based on the regression model, this would indicate that, in terms of survival, females producing the largest offspring in this study would survive approximately twice as long (6 vs 11 days) as the smallest offspring. Under laboratory conditions without predators, this indicates that larger spiderlings have a survival advantage over smaller spiderlings. Although the positive relationship between spiderling body size, resistance to starvation and predatory ability seems obvious, it would be harder to imagine an advantage for spiderlings to be small under field conditions. It was much harder to evaluate the advantage larger offspring may have over smaller offspring in terms of feeding, since this may be confounded by larger spiderlings not becoming satiated as quickly as smaller spiderlings.

Regardless, based on the range of offspring sizes observed and the generalized linear model parameters, the largest spiderlings would probably kill almost twice as many fruit flies as the smallest spiderlings. Whether this is due to size constraints on consumption or size being a good indicator of the prey capture ability of the spiderlings, it would presumably translate into an advantage for larger offspring in terms of energy acquisition and perhaps growth.

Marshall and Gittleman (1994) proposed that spiders maximize clutch size with constraints on a minimum viable offspring size. This hypothesis is consistent with our results. *Hogna helluo* females potentially have as large a clutch as possible with very little variation in offspring size. In addition, our results are also consistent with theoretical treatments of size–number trade-offs, either when resources or resource allocation vary (Van Noordwijk and de Jong, 1986; Venable, 1992; Christians, 2000; Glazier, 2000) or when offspring survival is variable (Forbes, 1991). We did note significant variation between families in offspring size and positive effects of offspring size on offspring performance. However, at this time it is unclear which factors determine spiderling size. Given that we found strong evidence of fitness-associated consequences for spiderling body size, the lack of any apparent size–number trade-off remains enigmatic.

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