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Multiple feeding in wolf spiders: the effect of starvation on handling time, ingestion rate, and intercatch intervals in *Lycosa lapidosa* (Araneae : Lycosidae)

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Abstract

Multiple prey capture, the behaviour of a predator attacking prey whilst handling a previously caught item, occurs in a variety of spiders that do not build webs. The effects of recent feeding history on the frequency of multiple prey attacks, handling time, ingestion rate, and intercatch intervals were examined experimentally in the wolf spider *Lycosa lapidosa* McKay. Juvenile spiders were subjected to two different feeding regimes (starvation for 14 and 28 days) and then provided with two different prey types (blowflies, *Lucilia cuprina*, and crickets, *Acheta domestica*). These two starvation levels or prey types had little effect on the frequency (75%) of multiple prey attacks. Spiders ingested approximately half the weight of any captured prey, regardless of how many prey items they attacked. At the same time, the handling time per prey item decreased with an increasing number of prey attacked. This indicates a more efficient ingestion rate when more prey are consumed. While the attacking time for the first prey was the same for all treatments, the first intercatch interval was longer for spiders that were starved longer. Chronically starved *L. lapidosa* appear to secure a previously caught item rather than optimise their capture rate by attacking further available prey.

Introduction

Traditional, optimal foraging models assume that searching for prey and handling prey are mutually exclusive (Charnov 1976; Pyke *et al.* 1977; Stephens and Krebs 1986). Single feeders are predicted to abandon prey when the rate of extraction from that prey item has fallen to the long-term average rate of gain from the environment (e.g. Charnov 1976). More recently, McNair (1983), Lucas and Grafen (1985) and Juliano (1989) proposed models for the functional response of predators that attack more than one prey item at a time. Such multiple feeders are predicted to abandon a prey item after the rate of extraction has fallen below the long-term average of the environment, therefore increasing their rate of net energy intake above that of other predators that feed on single prey items (McNair 1983). Handling times for the first prey in a 'handling queue' are predicted to be shorter than for the second item, and intercatch intervals between two prey items should decline with increasing queue size (Juliano 1989). Multiple prey capture has been reported in salamander larvae (Sih and Petranka 1988), heteropterans (Cook and Cockrell 1978; Bailey 1985; Cloarec 1991) and a variety of cursorial spiders (Haynes and Sisjovek 1966; Williams 1979), including wolf spiders (Nakamura 1977; Samu and Bíró 1993). These studies mainly focus on the effects of varying prey densities on prey-capture behaviour (i.e. the functional response), particularly handling time and intercatch intervals. Cloarec (1991) and Samu and Bíró (1993) found that handling time was longer for the first prey than for following prey items, thus contradicting the predictions derived from Juliano's (1989) model. No studies have examined the effects of the recent feeding history (i.e. the satiation level) on the foraging behaviour of multiple feeders.

Shortage of prey appears to be a major selective factor in the evolution of foraging strategies of spiders because they can endure long periods of starvation. Spiders typically display an energy-efficient sit-and-wait foraging strategy and are able to lower their basal metabolic rate (Greenstone and Bennett 1980; Riechert and Harp 1987; Wise 1993). The highly flexible

abdomen of most spiders allows them to ingest large amounts of prey (Anderson 1974), and some spiders feed on more than one prey item at a time (e.g. Williams 1979; Samu and Bíró 1993). Most studies that have investigated the effects of a varying food supply concentrate on the energetic investment of foraging spiders, such as changes in their foraging site (e.g. Janetos 1982; Provencher and Riechert 1991; Bradley 1993), or, in the case of web-building spiders, adjustments to the architecture of the web (e.g. Sherman 1994; Lubin and Henschel 1996; Herberstein *et al.* 2000). Only a few studies have examined the effect of different hunger levels on the attack behaviour of spiders (e.g. Bridge and Wootton 1998; Herberstein *et al.* 2000). Here, we investigate whether the level of starvation affects the frequency of multiple prey captures, the amount of prey digested and the handling time per prey item in *Lycosa lapidosa* McKay 1974. In particular, we analyse the intervals between subsequent catches for spiders subjected to different levels of starvation.

Lycosa lapidosa is a large (total length up to 22 mm) nocturnal wolf spider that lives on gravel banks in flood plains of south-eastern Australia (McKay 1974; Framenau 1998). It is typically vagrant; only females caring for their brood, and hibernating spiders remain in self-made, silk-lined excavations underneath rocks. *Lycosa lapidosa* has a biannual life cycle with individuals reaching maturity in about 16 months. Adults reproduce in spring, two years after hatching (Framenau 1998).

Materials and Methods

We collected 40 juvenile *L. lapidosa* from the gravel banks of the Avon River in central Gippsland (eastern Victoria) in February 1998. Spiders were housed separately in clear plastic containers (80 mm × 80 mm × 40 mm) under natural light conditions and room temperature (20–22°C). A cotton-plugged vial provided a constant supply of water. Spiders were fed two blowflies (*Lucilia cuprina*) twice a week for 6–8 weeks prior to the experiment.

We randomly assigned spiders to one of four treatments that comprised two levels of food deprivation (either 14 or 28 days) and two kinds of prey (blowflies, *L. cuprina*: mean weight ± s.e. 0.022g ± 0.003 g, $n = 70$; juvenile crickets, *Acheta domestica*: 0.024 g ± 0.008g, $n = 70$). All spiders were fed both blowflies and crickets *ad libitum* for two days before the onset of food deprivation in order to attain similar nutritional status.

Feeding experiments were conducted in the spider's familiar housing. The water vials were removed to avoid the obstruction of the spider's attacking behaviour. Each spider was initially supplied with four prey items simultaneously. Observations started when the prey items were inserted. One additional prey item was added after all four items were captured, and after every subsequent attack. Observations ceased 30 min after a spider stopped handling prey and did not attack a newly introduced prey item. We recorded the time when each prey item was captured. It was not possible to determine the handling time for a single prey item in multiple prey captures because wolf spiders combine all prey into a single, large ball of food. Therefore, the average handling time for one item was estimated by dividing the time from the capture of the first item until all remains were dropped by the total number of prey items handled. Prey remains may lose weight during feeding due to desiccation (Pollard 1988), so the spiders were weighed before and after feeding to obtain measures of weight gain from ingested material.

All statistical analyses were performed using SYSTAT 7.0.1 (Wilkinson 1997). Data that were not normally distributed were log-transformed.

Results

Eight of the 40 tested spiders did not attack any prey and data for these spiders were excluded from the analysis. All spiders were of a similar size before starvation, with an average weight of 0.436 ± 0.053 g (mean ± s.e., $n = 32$); there was no significant difference in the weight of the spiders between the four treatment groups (ANOVA, $F_{3,28} = 1.08$, $P = 0.38$). All spiders lost weight after periods of food deprivation of 14 or 28 days (mean weight loss ± s.e. 10.9% ± 3.8%, $n = 32$). However, there was no difference in the weight loss of spiders between the two different starvation levels (mean weight loss ± s.e. for 14 days 0.044 ± 0.016 g, for 28 days 0.051 ± 0.02 g; paired $t = -1.05$, d.f. = 30, $P = 0.30$).
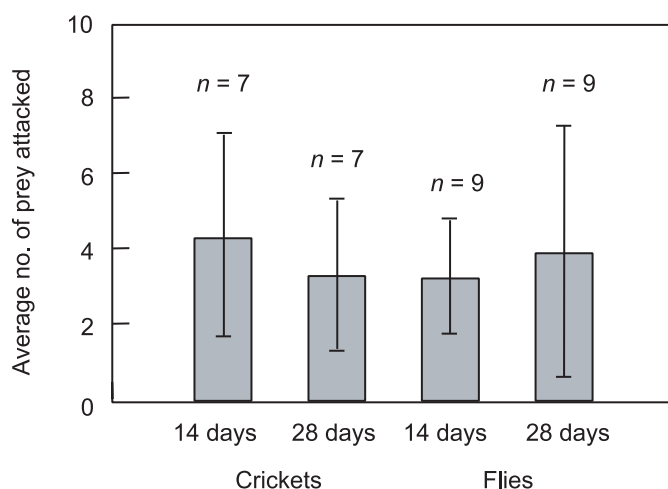
Fig. 1. The average number of prey attacked by the spiders in the four treatment groups (starvation level 14 or 28 days; prey type crickets or flies). Error bars represent ± 1 s.e.

Two different types of prey-capture behaviour could be distinguished: single and multiple prey attack. Of 32 spiders, 8 (25%) handled only one prey item at any time and were designated 'single feeders'. In these cases, spiders either attacked one item only, or they abandoned previously caught prey before attacking a second item. Therefore, 'single' feeders might have attacked more than one prey item. The remaining 24 spiders (75%) attacked a prey item while handling previously caught prey and were designated 'multiple feeders'. There was no significant difference in the frequency of multiple attacks between spiders of the different starvation levels (14 days: 13 multiple feeders; 28 days: 11 multiple feeders; $\chi^2 = 0.67$, d.f. = 1, $P = 0.41$) or prey types (flies: 14 multiple feeders, crickets: 10 multiple feeders; $\chi^2 = 0.17$, d.f. = 1, $P = 0.68$).

The average number of prey attacked by a spider was 3.75 ± 2.3 items (mean ± s.e., $n = 32$) and was not influenced by either starvation level or prey type (two-way ANOVA, starvation level: $F_{1,28} = 0.17$, $P = 0.68$; prey type: $F_{1,28} = 0.05$, $P = 0.82$; interaction: $F_{1,28} = 0.88$, $P = 0.36$; Fig. 1). The maximum number of prey items that a spider handled simultaneously was 12.

All spiders ingested an average of 0.009 ± 0.004 g (mean ± s.e., $n = 32$) per attacked prey, about half the weight of any captured item. There was no evidence that the level of starvation (two-way ANOVA, $F_{1,29} = 0.49$, $P = 0.45$) or the total number of prey obtained ($F_{1,29} = 0.36$, $P = 0.55$) had an influence on the amount ingested per prey. However, the handling time per prey item decreased with an increasing number of prey captures (two-way ANOVA, $F_{1,29} = 15.53$, $P < 0.001$; Fig. 2) indicating a more efficient ingestion rate in spiders with an increasing number of prey. The level of starvation did not show a significant influence on the average handling time per prey item ($F_{1,29} = 3.38$, $P = 0.08$; Fig. 2).

On average, multiple feeders showed a significantly lower handling time per prey item (mean ± s.e. = 59.3 ± 21.4 min, $n = 24$) than single feeders (103.4 ± 30.2 min, $n = 8$) (paired $t = 4.56$, d.f. = 30, $P < 0.001$). Consequently, the ingestion rate was higher for multiple feeders (mean ± s.e. = 0.183 ± 0.09 mg min^{-1}, $n = 24$) than for single feeders (0.103 ± 0.062 mg min^{-1}, $n = 8$) (paired $t = -2.41$, d.f. = 30, $P = 0.02$), even if single feeders attacked more than one prey item.

In all four treatment groups spiders attacked the first prey item within 1–5 min, with no statistically significant difference between the treatments (two-way ANOVA, starvation level:
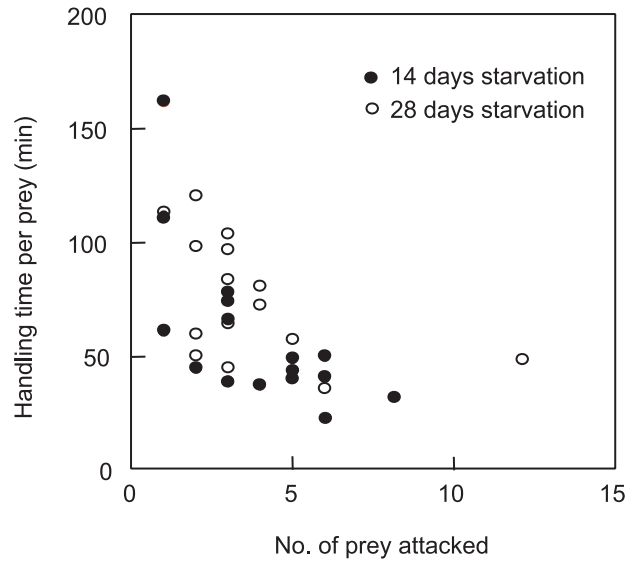
Fig. 2. The handling time per prey item as a function of the total number of prey attacked by a spider. The handling time decreased with an increasing number of prey captures per spider (●, starvation 14 days: $R^2 = 0.47$, $P = 0.04$, $n = 16$; ○, starvation 28 days: $R^2 = 0.28$, $P = 0.004$, $n = 16$).
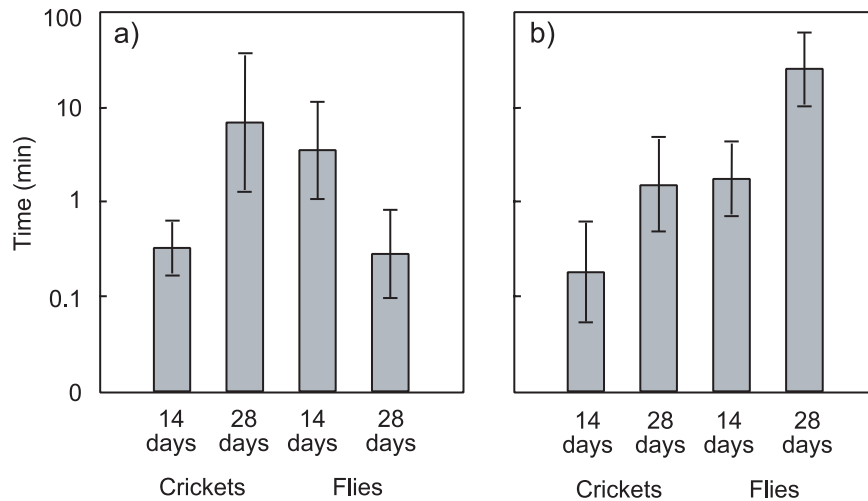

Fig. 3. Time to first catch (*a*) and first intercatch interval (*b*) for the four treatment groups (starvation level 14 or 28 days; prey type crickets or flies). The longer intercatch interval for flies was most likely caused by differences in the behaviour of flies and crickets: crickets stayed on the bottom of the feeding boxes whereas flies additionally used the walls and the lid, thereby decreasing their effective density. Error bars represent ± 1 s.e.

$F_{1,25} = 0.05$, $P = 0.83$; prey type: $F_{1,25} < 0.001$, $P = 0.98$; interaction: $F_{1,25} = 5.15$, $P = 0.03$; Fig. 3*a*). However, the time from the first to the second attack was significantly longer for longer-starved spiders (two-way ANOVA, $F_{1,25} = 6.57$, $P = 0.02$) and longer for flies than for crickets ($F_{1,25} = 7.44$, $P = 0.01$) with no significant interaction between both factors ($F_{1,25} = 0.09$, $P = 0.76$; Fig. 3*b*).

Discussion

Although spiders have a highly flexible abdomen, gut capacity and the amount of prey already ingested seems to be the major factor limiting their food intake (Nakamura 1977, 1987). In *L. lapidosa*, the total number of prey attacked and the amount ingested per prey item was not influenced by our experimental manipulation of starvation levels. Following a 14-day starvation period, spiders no longer lost weight, indicating an empty gut. Consequently, spiders of both starvation treatments (14 or 28 days) had a similar available gut volume and could therefore accommodate a similar volume of prey.

Lycosa lapidosa appears to ingest the same amount per prey item regardless of the total number of prey attacked. This differs from the lycosid *Pardosa hortensis*, which consumed a similar amount of the first 70% of all attacked prey, but then significantly decreased the food intake per prey item (Samu 1993). *L. lapidosa* decreased the average handling time per prey item with an increasing number of prey. Multiple prey capture therefore appears to optimise the ingestion rate of *L. lapidosa*. A similar pattern was found for *P. hortensis* which, due to a smaller body size, had a lower overall ingestion rate than *L. lapidosa* (Samu 1993; Samu and Bíró 1993). In arthropods with extra-oral digestion, a shorter handling time with increasing prey numbers can be observed in both multiple and single feeders that subsequently consume more than one item (Giller 1980; Bailey 1985; Cloarec 1991). The reasons for this shorter handling time for subsequent prey items are poorly understood. The higher efficiency in prey consumption for later prey items is not consistent with the fact that extra-orally digesting predators invest much more of their enzyme resource in the first prey item than in subsequent catches (Cohen 1995). It is also not consistent with McNair's (1983) optimal foraging model for multiple prey captures, which predicts an increase in handling time for later prey items.

There was no evidence that the frequency of multiple prey attacks (75% in *L. lapidosa*) differed between spiders of the two starvation levels. Overall, this frequency is higher than that for *P. hortensis*, which increased the ratio between multiple and single feeding with increasing prey-encounter rates (Samu and Bíró 1993). In *P. hortensis*, the frequency of single feeding was approximately 10 times higher than multiple feeding (Samu and Bíró 1993). The shorter starvation period of only 3 days in *P. hortensis* (compared with 14 or 28 days for *L. lapidosa*) may explain why multiple feeding was more prevalent in our study.

Spiders can constantly assess their nutritional status, which is not only reflected by the contents of their gut but also by their metabolic rate (Riechert and Harp 1987). In *Lycosa lenta* the metabolic rate decreased until after the potential gut-clearing period, i.e. the 14–30th day (Anderson 1974). Furthermore, spiders gradually metabolise digestive enzymes during starvation, which limits the ingestion of food (Cohen 1995). Both of these factors may show an effect on the attack behaviour of *L. lapidosa* and explain differences in the first intercatch interval between the two starvation levels. Food limitation should increase the pressure to maximise the rate of net energy uptake (Sih and Petranka 1988). Thus, longer-starved animals should take prey in shorter intervals and maximise energy uptake (Juliano 1989). Our observations are not consistent with this model because longer-starved *L. lapidosa* are more reluctant to attack a second prey item. *L. lapidosa* appears to concentrate on securing the first prey item rather than attacking a second one.

The foraging behaviour of *L. lapidosa* is not consistent with the current optimal foraging models for multiple feeders, which are based on the optimisation of energy intake (McNair 1983; Juliano 1989). Studies of other non-web-building spiders show similar inconsistencies (e.g. Herberstein *et al.* 1998; Brigde and Wootton 1998). Perhaps other factors, such as the

physiological condition of a starved animal, have a greater influence on the foraging behaviour than a long-term energy gain.

Acknowledgments

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