The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae)

SEAN E. WALKER*, SAMUEL D. MARSHALL*, ANN L. RYPSTRA† & DOUGLAS H. TAYLOR*

*Department of Zoology, Miami University, Oxford
†Department of Zoology, Miami University, Hamilton

We compared the influence of recent feeding history on locomotory behaviour in two species of wolf spiders, *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz, in the laboratory. Both species are cursorial hunters. We maintained the spiders in the laboratory on satiation and stringent feeding regimes and measured their locomotory activity levels for 1 h using a digital activity recording device. We subjected *H. helluo* to either ad libitum feeding for 14 days or no food for 14 days. We subjected *P. milvina* to ad libitum feeding or fasting treatments for 7 and 14 days. We found that *H. helluo* showed a shift in locomotory activity depending on feeding regime, whereas *P. milvina* did not. Food-limited *H. helluo* travelled further than satiated *H. helluo*, and did so by moving more frequently. *Pardosa milvina* was in general much more active than *H. helluo*. We propose that *P. milvina* is an active forager compared with the sit-and-wait strategy of *H. helluo*. This difference in foraging strategy is correlated with differences in body size and habitat use.

© 1999 The Association for the Study of Animal Behaviour

The foraging process is made up of locating, subduing (or otherwise preparing), and ingesting a subset of the potential food items in the environment. The degree of satiety (or hunger) an animal experiences at a given time may have a profound influence on any of these steps in the foraging process. For instance, hungry animals may be more willing to risk predation while foraging than satiated animals (Dill & Fraser 1984; Gilliam & Fraser 1987; Godin & Sproul 1988), may alter movement patterns and prey selection criteria (de Ruiter et al. 1989; Wallin & Ekbom 1994), or even change social spacing patterns which may influence access to food (Gill & Wolf 1975; Cangialosi & Uetz 1987).

Body size has been found to correlate with a wide range of physiological, ecological and behavioural traits (Peters 1983; Reiss 1989) and research to date has suggested that body size is tied to foraging strategy in both spiders (Enders 1976) and reptiles (Vitt & Congdon 1978; Huey & Pianka 1981; Vitt & Price 1982). These comparative studies have presented evidence that more active foragers are more likely to be small-bodied than sit-and-wait

foragers. Mechanisms to explain this include the relatively greater energetic cost of movement for larger taxa (Peters 1983) and the observation that larger animals are more conspicuous and so may be under greater predation risk while moving (Huey & Pianka 1981).

Spiders are obligate predators which employ an array of sensory modalities and behaviours in foraging. Despite their diverse adaptations for detecting and capturing prey, data suggest that spiders under natural conditions are hungry (Anderson 1970, 1974; Nakamura 1987; Wise 1993). While spiders are relatively resistant to starvation (Anderson 1970, 1974; Nakamura 1987), reproductive success is closely tied to foraging success (Uetz 1992; Wise 1993). Therefore, it is assumed that spiders are food limited. To date, studies of the influence of hunger on foraging in spiders have focused on spiders that build webs, and it has been amply demonstrated that foraging success can influence site residence time (Turnbull 1964; Gillespie 1981; Olive 1982; Janetos 1982a, b, 1986; Uetz 1992; Bradley 1993; McNett & Rypstra 1997) as well as foraging effort (Lubin & Henschel 1996). Janetos (1986) found that site investment is correlated with the latency to change foraging site in spiders. He found that web-building spiders that build webs that they cannot ingest (e.g. the family Linyphiidae) relocate sites less often than those that are able to recycle silk by eating their webs each day (orbweavers in the families Araneidae and

Correspondence: S. E. Walker, Department of Zoology, Miami University, Oxford, OH 45056, U.S.A. (email: walkers2@muohio.edu). S. D. Marshall is now at Hiram College, James H. Barrow Field Station, Department of Biology, Hiram OH 44234, U.S.A. A. L. Rypstra is at the Department of Zoology, Miami University, 1601 Peck Boulevard, Hamilton, OH 45011, U.S.A.

Tetragnathidae), suggesting that site investment influences relocation rate, with higher site investment being correlated with longer site residence times.

Much less work has been conducted on the effects of hunger on foraging behaviour of spiders that do not use a web to capture prey. Most wolf spiders are vagile ambush predators, which are thought of as sit-and-wait predators (Ford 1978; Stratton 1985). It has been suggested that movement levels of wolf spiders should decrease with declining food levels (see reviews in Riechert & Luczak 1982; Nakamura 1987). Yet the marginal value theorem suggests that abundant prey should result in higher residence times at a particular location (Charnov 1976). Numerous studies of web-building spiders support the contention that these spiders are much less likely to relocate when prey capture is high (Turnbull 1964; Gillespie 1981; Olive 1982; Janetos 1986; Uetz 1992; Bradley 1993; McNett & Rypstra 1997). Additionally, there are several studies of wolf spiders that suggest at least some species respond to recent prey capture in a similar manner. For instance, Ford (1978) found that the presence of prey increased site residence time in the wolf spider *Pardosa amentata* (Clerck). Wagner & Wise (1997) similarly found that the presence of prey increased patch residence time in the wolf spider *Schizocosa ocreata* (Hentz). Also, sensory information from prey alone is enough to increase patch residence time in *S. ocreata* (Persons & Uetz 1996). However, Anderson (1974) found no relationship between hunger and the frequency with which the wolf spider *Lycosa lenta* Hentz emerges from its burrow to forage at night.

We compared the effects of hunger level on locomotory behaviour in two species of wolf spider, *Hogna helluo* (Walckenaer) and *Pardosa milvina* Hentz (hereafter referred to as *Hogna* and *Pardosa*). These species co-occur in early successional habitats and agroecosystems in the eastern and central U.S.A. where they forage on or near the soil surface for invertebrate prey. *Hogna* and *Pardosa* offer an interesting contrast because they differ in both adult body size and degree of site investment. An adult *Hogna* is approximately 10 times the mass of an adult *Pardosa*, and also facultatively constructs burrows from which it forages (Dondale & Redner 1990; Walker et al., in press). In contrast, *Pardosa* is active and locally abundant on the soil surface during daylight hours and never builds a retreat (Montgomery 1903; Kaston 1981). Because *Hogna* and *Pardosa* are related (i.e. members of the same family, Lycosidae) and are syntopic, they present a chance to compare behavioural responses to hunger levels in two species that differ in size and site investment but use the same microhabitats in similar ways. We hypothesized that *Hogna* and *Pardosa* differ in their behavioural response to food deprivation. Because *Hogna* is large and invests energy in the construction of a retreat from which it forages, the cost of relocation is higher than it is for *Pardosa*. As a result, we predicted that *Hogna* would be more likely to disperse or relocate when hungry. On the other hand, because *Pardosa* has little or no measurable site investment, its dispersal pattern should be less dependent on hunger. In fact, given that high levels of activity can potentially enhance encounter rates with prey (e.g. Norberg 1977; Huey & Pianka 1981; De Vita 1982; Helfman 1990; Kreiter & Wise 1997), we might expect *Pardosa* to change foraging sites frequently at all hunger levels. We tested for these differential effects of hunger on the locomotory behaviour of *Hogna* and *Pardosa* in the laboratory using a video-based, motion-recording system.

METHODS

General Protocols

In 1994 and 1995 we collected *Hogna* and *Pardosa* from Miami University's Ecology Research Center (approximately 5 km north east of Oxford in Butler County, Ohio). We used juvenile *Hogna* ($\bar{X} \pm$ SE carapace width=3.6 ± 0.6 mm, N=42) reared from eggs laid by wild-caught females, and adult female *Pardosa* (2.2 ± 0.2 mm, N=72), which were collected as subadults in the field and raised to maturity in the laboratory. We used wild-caught *Pardosa* as we have been unable to culture them in the laboratory. We only used immatures and adult females because adult male spiders spend much of their time seeking females rather than foraging. In contrast, immatures of both sexes are under selection to maximize food intake in order to maximize adult body size, and adult females, to maximize egg production (Uetz 1992). Therefore we assumed that sexual maturity should not influence the foraging strategies used by female *Pardosa*. We held the spiders in an environmental chamber on a 12:12 h light:dark cycle at approximately 25°C and 70% relative humidity. We fed the spiders a mixed diet of mealworms, *Tenebrio molitor*, crickets, *Acheta domestica*, and vestigial-winged fruit flies, *Drosophila melanogaster*, twice weekly prior to the beginning of the experiment. Spiders were maintained in 100-ml plastic cups with 1.0–1.5 cm of moist peat moss substrate.

Measurement and Analysis of Locomotory Behaviour

We measured the carapace width of each spider to 0.1 mm using a dissecting microscope with an ocular micrometer at 12 × magnification and weighed them to the nearest 0.1 mg using an electronic balance. We then randomly assigned the spiders to one of two treatment groups: High fed and Low fed. The High-fed group received sufficient numbers of prey (either vestigial-winged fruit flies or mealworms) three times weekly during the treatment period to ensure a constant supply of food in the rearing container. The Low-fed group received no food for the treatment period. All spiders were given water ad libitum. *Hogna* (N=21 per treatment) were maintained in either treatment group for 14 days, whereas *Pardosa* were maintained in either treatment group for either 7 days (N=24 per treatment) or 14 days (N=9 per treatment). We elected to add a shorter food deprivation treatment for *Pardosa* due to mortality we attributed to starvation in the 14-day group. Following the treatment period, we again measured mass and carapace width.

Locomotory activity of the spiders was assayed on the last day of the treatment period. Because *Hogna* is primarily nocturnal and *Pardosa* diurnal, we measured locomotory activity of *Hogna* between 2000 and 0000 hours and *Pardosa* between 1000 and 1700 hours. These time periods overlap with the periods of activity we have observed in the field. We made activity measurements in an environmental chamber at 25°C and 70% relative humidity. When we assayed locomotory activity of *Hogna*, the room was illuminated with an infrared lamp to permit use of a infrared-sensitive video camera. We assumed that, as in most other spiders ([Foelix 1996](#)), *Hogna* would be unable to perceive light at this wavelength, and would behave as if they were in the dark. We measured locomotory activity by placing a single spider into a plastic arena measuring $13 \times 13 \times 4$ cm with white paper secured in the bottom of the container. Two of these arenas were used simultaneously so we could pair the spiders within species, one from each feeding regime. In this way we could control for the possible effects of small changes in temperature and humidity on spider behaviour. To eliminate any bias from the position of the arenas, we alternated the treatment groups from one side to the other between trials. Each spider was allowed at least 1 h to acclimate to the arena prior to data collection. The paper was changed and the arenas washed with soap and rinsed with distilled water between trials to eliminate the possibility of intraspecific cues influencing activity.

In each trial we monitored locomotory activity for 1 h. We measured distance travelled (cm) and speed (cm/s) using a Panasonic infrared camera and an automated video-based, digital-data collection system (Videomex-V, Columbus Instruments, Columbus, Ohio). The Videomex-V converts a video image to a field of black and white pixels and continuously tracks an object moving against a contrasting field, in this case a dark spider against white paper. We set the Videomex to output distance travelled and speed at 3-min intervals for 1 h. This system is very sensitive and can quantify even slight changes in location ([Farr et al. 1994](#)). We set it to track spiders in increments approximately equal to their body length (1 cm).

We calculated total distance travelled by summing the distance travelled over all 3-min intervals ($N=20$) during the hour. We defined frequency of movement as the number of monitoring periods out of the total of 20 during which an animal moved. We calculated average speed as the mean of all speed measurements for each individual, excluding 3-min intervals during which the animal did not move. We calculated maximum speed as the fastest speed recorded for any of the 20 3-min intervals during the hour of data collection.

Analysis of Locomotory Behaviour

We used the Wilcoxon rank-sum test to compare the total distance travelled and the frequency of movement between High-fed and Low-fed *Hogna* because these variables could not be transformed to meet the assumptions of parametric statistics. We compared maximum and average speeds of High-fed and Low-fed *Hogna* using

analysis of variance (ANOVA) on log-transformed data. We examined differences in total distance travelled, average speed and maximum speed of *Pardosa* using a two-factor (time and feeding regime) ANOVA on transformed data. To meet the assumptions of ANOVA, average and maximum speed were log transformed and total distance travelled was square-root transformed. We compared the frequency of movement for each feeding regime and time combination using a Kruskal–Wallis nonparametric ANOVA.

Analysis of Weight Gain

We examined changes in weight in response to treatment for *Hogna* using a one-way analysis of covariance (ANCOVA), with initial mass as the covariate, feeding regime as the independent variable and final mass as the dependent variable. We examined changes in weight for *Pardosa* dependent on feeding regime and time spent in the feeding regime using a two-way ANCOVA with initial mass as the covariate and final mass as the dependent variable. To examine the differences between species in response to feeding regimes we used a two-way ANCOVA, with initial mass as the covariate and final mass as the dependent variable. To meet the assumptions of ANCOVA, all mass data were natural log transformed prior to analysis. We made comparisons between treatments using a Bonferroni procedure on ANCOVA adjusted means ([Neter et al. 1990](#)). Thus, weight change is defined as the ANCOVA adjusted mean of final mass.

RESULTS

Locomotory Behaviour

Feeding regime significantly affected total distance travelled (Wilcoxon rank-sum test: $Z=-3.13$, $N=21$, $P=0.0017$; [Fig. 1a](#)), frequency of movement (Wilcoxon rank-sum test: $Z=-3.35$, $N=21$, $P=0.0009$; [Fig. 1b](#)) and maximum speed (ANOVA: $F_{1,32}=5.70$, $P=0.0232$; [Fig. 1c](#)) in *Hogna*. High-fed *Hogna* did not move as far, as frequently, or as fast as Low-fed *Hogna*. However, there was no shift in average speed in *Hogna* (ANOVA: $F_{1,32}=2.86$, $P=0.1008$; [Fig. 1c](#)). There was no significant interaction between time (7 versus 14 days of treatment) and feeding regime in *Pardosa* for total distance travelled ($F_{1,61}=2.22$, $P=0.1414$), average speed ($F_{1,61}=0.83$, $P=0.3646$), or maximum speed ($F_{1,61}=2.43$, $P=0.1239$). There was also no significant effect of feeding regime or time for total distance travelled (ANOVA: $F_{2,62}=1.88$, $P=0.1611$; [Fig. 2a](#)), average speed (ANOVA: $F_{2,62}=2.35$, $P=0.1035$; [Fig. 2c](#)), or maximum speed (ANOVA: $F_{2,62}=1.61$, $P=0.2073$; [Fig. 2c](#)). There was also no significant effect of feeding regime or time on frequency of movement (Kruskal–Wallis test: $\chi_3^2=1.8321$, $P=0.6080$; [Fig. 2b](#)).

Weight Gain

High-fed animals of both species were generally heavier relative to their initial mass following treatment ([Fig. 3a](#),
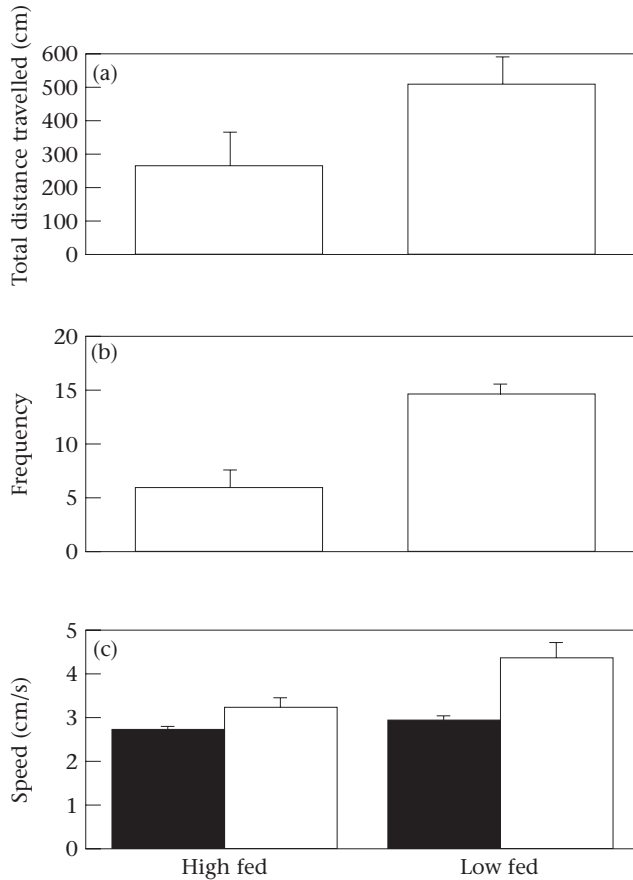
Figure 1. Mean +SE activity level for *Hogna* during the 1-h sampling period. (a) Total distance travelled, (b) frequency of bouts of activity of *Hogna*, and (c) average (■) and maximum (□) speed of travel.

Figure 2. Mean +SE activity level for *Pardosa* during the 1-h sampling period. (a) Total distance travelled, (b) frequency of bouts of activity of *Pardosa*, and (c) average (■) and maximum (□) speed of travel.

b, c). The two-way ANCOVA examining weight change in *Pardosa* indicated that changes in weight were more pronounced in the animals treated for 14 days relative to animals treated for 7 days (significant time∗feeding regime interaction: $F_{1,65}=8.55$, $P=0.0048$; Fig. 3a). High-fed *Hogna* gained more weight than Low-fed *Hogna* ($F_{1,39}=77.55$ $P<0.0001$; Fig. 3b). *Hogna* and *Pardosa* responded differently when maintained for 14 days on either feeding regime (species∗feeding regime interaction: $F_{1,59}=6.60$, $P=0.0129$; Fig. 3c). Low-fed subjects of both species tended to lose similar amounts of weight after 14 days (*Hogna* versus *Pardosa*: $t_{28}=1.606$, $P=0.1193$), but High-fed *Hogna* gained significantly more weight than High-fed *Pardosa* (*Hogna* versus *Pardosa*: $t_{28}=3.867$, $P=0.0006$).

DISCUSSION

Our data show that, overall, *Pardosa* is more active than *Hogna*, and does not change its locomotory behaviour under different feeding regimes as does *Hogna*. Low-fed *Hogna* moved further than High-fed *Hogna* and did so by moving more often, rather than faster. *Pardosa,* on the other hand, was relatively active regardless of feeding regime, reflecting what we hypothesized to be an active-
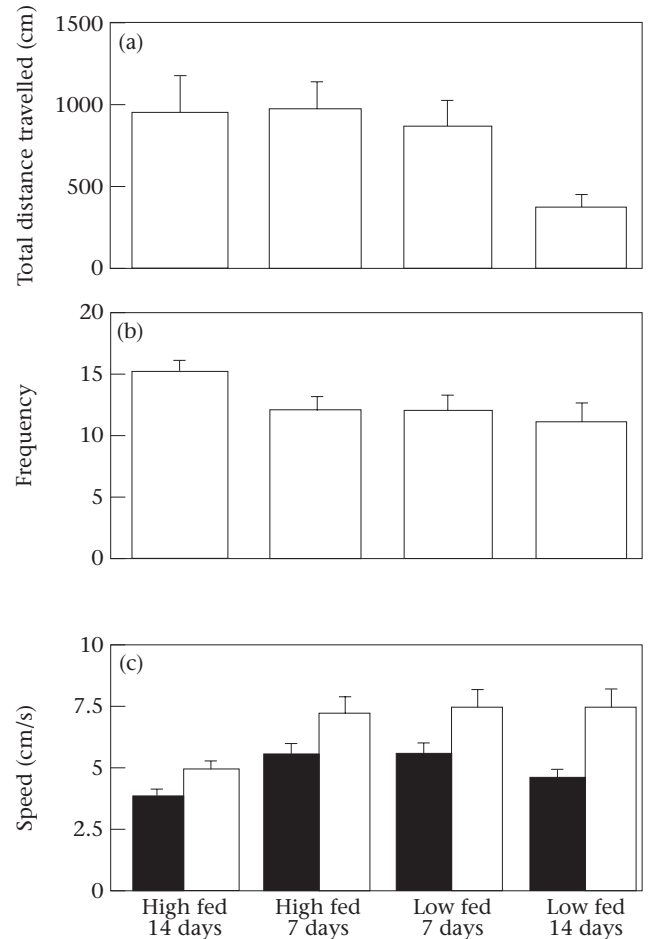
foraging strategy. We also found that *Pardosa* cannot accumulate nutritional stores to the same degree as *Hogna*, nor is *Pardosa* as tolerant of starvation as *Hogna*.

While these spiders were tested under artificial conditions, we have strong evidence that there is an influence of hunger level on movement in *Hogna* but not in *Pardosa*. The body conditions resulting from our feeding regimes differed significantly between treatments, which is evidence that we successfully manipulated nutritional status. If we can use this morphological indicator of nutritional status as a mirror of an internal state (hunger), then the Low-fed animals were hungrier than the High-fed animals.

Pardosa showed generally higher levels of activity, and thus may attempt to maintain a constant level of activity to achieve some minimal level of prey intake, because increased activity can increase prey encounter rate (Norberg 1977; Huey & Pianka 1981; De Vita 1982; Helfman 1990). In contrast, *Hogna* given food ad libitum showed a large decrease in activity level. Thus, *Hogna* conserve their energy and expend it only as needed to maintain food intake rates. *Hogna* has been observed to build silk-lined burrows (Dondale & Redner 1990; Walker
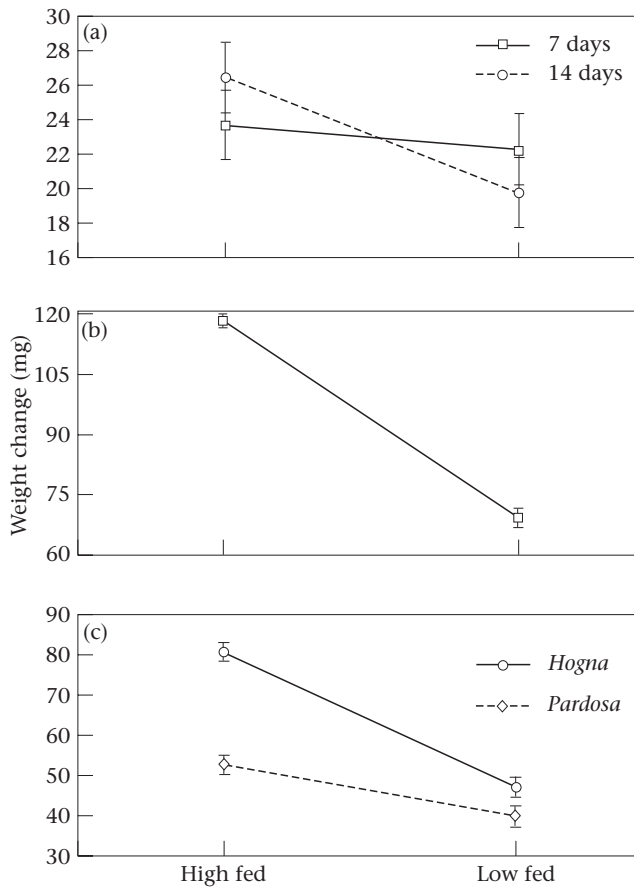
Figure 3. Mean ±2 SE weight change (defined as the ANCOVA-adjusted mean of final mass) for (a) *Pardosa*, (b) *Hogna* and (c) *Pardosa* and *Hogna* in the 14-day treatment period.

et al., in press), but this kind of site investment is lacking in *Pardosa*. Because *Hogna* will make a site investment in a burrow, this raises the cost of site abandonment. For *Hogna*, higher hunger levels will correspond to lower prey availability; therefore, increased activity could be related to the search for a more suitable patch. Thus, the behavioural responses we recorded in the laboratory are likely a reflection of evolved, adaptive, foraging strategies expressed in the field.

One generally accepted dichotomy in foraging strategies is the 'sit-and-wait' versus 'active' foraging behaviour of predators. Different authors have used different criteria for categorizing predators along this continuum. Pianka (1966) and Schoener (1969) stressed the energetics of food acquisition behaviour, with each strategy defined by allocation of energy to food finding versus other activities. Riechert & Luczak (1982) defined the two strategies ethologically, and proposed that only predators that search out sessile prey could be said to be truly active foragers. Janetos (1982a), on the other hand, defined the categories as more of a patch choice decision based on the likelihood that an animal will change foraging sites between meals. He took the view that sit-and-wait foragers typically invest energy in a foraging site and should only relocate under conditions in which the increase of food intake resulting from the change of site will more

than compensate the animal for the cost of the move. If the term 'active' is restricted to those foragers that search the landscape for immobile food items (e.g. eggs or seeds), then few predators would qualify. If the timing of the foraging-site change is the criteria, then the category becomes more inclusive. We suggest that if these terms are to have general utility, then we should use the latter criteria as formulated by Janetos (1982a).

Spiders in general have repeatedly been characterized as sit-and-wait predators that can exploit periods of prey abundance and then store this energy, allowing them to tolerate food deprivation over a long period (Anderson 1970; Riechert & Luczak 1982; Nakamura 1987). Ford (1978) examined the locomotory behaviour of a British wolf spider, *Pardosa amentata*. He found that *P. amentata* relocated often (approximately 13 times in 6 h at 15°C) but was actually in motion for only 0.32% of the day. He concluded that *P. amentata* was a sit-and-wait predator, rather than an active hunter, despite its high site-abandonment rate (compared with web-building spiders, which relocate once a day at most; Janetos 1986). The fact that the sit-and-wait versus active forager dichotomy really represents a continuum of foraging styles makes Ford's (1978) conclusion (from intensive investigation of a single species) difficult to interpret. It is much more straightforward to place animals along this continuum when considered relative to other species that use similar resources in a similar manner. Our comparative data for *Pardosa* and *Hogna* enables us to state definitively that *Pardosa* is more active than *Hogna* and that hunger has a larger effect on the movement patterns of *Hogna* than it does on those of *Pardosa*. These conclusions invite further investigations that clarify the differences in which these two co-occurring species use their environment and perhaps further our understanding of the mechanisms that enable them to coexist.

These data indicate that the contrasting foraging strategies that *Pardosa* and *Hogna* display may be correlated with their contrasting body sizes and site-investment strategies. Although other factors may be involved, the species-specific responses to manipulation of hunger level support the hypothesis that behavioural flexibility can be constrained by differences in physiology and morphology. Further comparative studies of these two species may provide some new insights into the kinds of selective factors influencing foraging behaviour.

References

Anderson, J. F. 1970. Metabolic rates of spiders. *Comparative Biochemistry and Physiology*, **33**, 51–72.

Anderson, J. F. 1974. Responses to starvation in the spiders *Lycosa lenta* (Hentz) and *Filistata hibernalis* (Hentz). *Ecology*, **55**, 41–57.

Bradley, R. A. 1993. The influence of prey availablity and habitat on activity paterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). *Journal of Arachnology*, **21**, 91–106.

Cangialosi, K. R. & Uetz, G. W. 1987. Spacing in colonial spiders: effects of environment and experience. *Ethology*, **76**, 236–246.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.

De Vita, J., Kelly, D. & Payne, S. 1982. Arthropod encounter rate: a null model based on random motion. *American Naturalist*, **119**, 499–510.

Dill, L. M. & Fraser, A. H. G. 1984. Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology*, **16**, 65–71.

Dondale, C. D. & Redner, J. H. 1990. *The Insects and Arachnids of Canada. Part 17.* Ottawa: Biosystematics Research Institute.

Enders, F. 1976. Clutch size related to hunting manner of spider species. *Annals of the Entomological Society of America*, **69**, 991–999.

Farr, A. J., Chabot, C. C. & Taylor, D. H. 1995. Behavioural avoidance of fluoranthene by fathead minnows (*Pimephales promelas*). *Neurotoxicology and Teratology*, **17**, 265–271.

Foelix, R. 1996. *Biology of Spiders.* 2nd edn. Oxford: Oxford University Press.

Ford, M. 1978. Locomotory behaviour and the predation strategy of the wolf spider *Pardosa amentata* (Clerck) (Lycosidae). *Animal Behaviour*, **26**, 3331–3335.

Gill, F. & Wolf, L. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology*, **56**, 333–345.

Gillespie, R. G. 1981. The quest for prey by the web-building spider *Amaurobius similis* (Blackwell). *Animal Behaviour*, **35**, 675–681.

Gilliam, J. F. & Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**, 1856–1862.

Godin, J.-G. J. & Sproul, C. D. 1988. Risk taking in parasitized sticklebacks under threat of predation: effects of energetic need and food availability. *Canadian Journal of Zoology*, **66**, 2360–2367.

Helfman, G. S. 1990. Mode selection and mode switching in foraging animals. In: *Advances in The Study of Animal Behaviour.* Vol. 19 (Ed. by P. J. B. Slater, J. S. Rosenblatt & C. Beer), pp. 249–290. San Diego: Academic Press.

Huey, R. B. & Pianka, E. R. 1981. Ecological consequences of foraging mode. *Ecology*, **62**, 991–999.

Janetos, A. 1982a. Active foragers vs. sit-and-wait predators: a simple model. *Journal of Theoretical Biology*, **95**, 381–385.

Janetos, A. 1982b. Foraging tactics of two guilds of web-spinning spiders. *Behavioral Ecology and Sociobiology*, **10**, 19–27.

Janetos, A. 1986. Web-site selection: are we asking the right questions? In: *Webs, Spiders and Evolution* (Ed. by W. Shear), pp. 9–22. Stanford: Stanford University Press.

Kaston, B. 1981. *Spiders of Connecticut.* Hartford: Connecticut Geological and Natural History Survey.

Kreiter, N. & Wise, D. H. 1997. Age-related changes in movement patterns in the fishing spider *Dolomedes triton* (Araneae, Pisauridae). *Journal of Arachnology*, **24**, 24–33.

Lubin, Y. & Henschel, J. 1996. The influence of food supply on foraging behavior in a desert spider. *Oecologia*, **105**, 64–73.

McNett, B. J. & Rypstra, A. L. 1997. Effects of prey supplementation of survival and web site tenacity of *Argiope trifasciata* (Araneae:Araneidae): a field experiment. *Journal of Arachnology*, **25**, 352–360.

Montgomery, T. 1903. Studies on the habits of spiders, particularly those of the mating period. *Proceedings of the Philadelphia Academy of Sciences*, **55**, 59–149.

Nakamura, K. 1987. Hunger and starvation. In: *Ecophysiology of Spiders* (Ed. by W. Nentwig), pp. 287–295. Berlin: Springer-Verlag.

Neter, J., Wasserman, W. & Kutner, M. H. 1990. *Applied Linear Statistical Models.* 3rd edn. Burr Ridge, Illinois: Irwin.

Norberg, R. A. 1977. An ecological theory of foraging time and energetics and choice of optimal food searching method. *Journal of Animal Ecology*, **46**, 511–529.

Olive, C. W. 1982. Behavioral response of a sit-and-wait predator to spatial variation in foraging gain. *Ecology*, **63**, 912–920.

Persons, M. H. & Uetz, G. W. 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*, **51**, 1285–1293.

Peters, R. 1983. *The Ecological Implications of Body Size.* Cambridge: Cambridge University Press.

Pianka, E. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology*, **47**, 1055–1059.

Reiss, M. 1989. *The Allometry of Growth and Reproduction.* Cambridge: Cambridge University Press.

Riechert, S. E. & Luczak, J. 1982. Spider foraging: behavioural responses to prey. In: *Spider Communication: Mechanisms and Ecological Significance* (Ed. by P. N. Witt & J. S. Rovner), pp. 353–385. Princeton, New Jersey: Princeton University Press.

de Ruiter, P. C., van Stralen, M. R., van Eeuwijk, F. A., Slob, W., Bedaux, J. J. M. & Ernsting, G. 1989. Effects of hunger and prey traces on the search activity of the predatory beetle *Notiophilus biguttatus*. *Entomologica Experimentia et Applicata*, **51**, 87–95.

Schoener, T. 1969. Models of optimal size for solitary predators. *American Naturalist*, **103**, 277–309.

Stratton, G. E. 1985. Behavioural studies of wolf spiders: a review of recent research. *Revue Arachnologique*, **6**, 57–70.

Turnbull, A. L. 1964. The search for prey by a web-building spiders *Achaearanea tepidariorum* (C. L. Koch) (Araneae, Theridiidae). *Canadian Entomologist*, **96**, 568–579.

Uetz, G. W. 1992. Foraging strategies of spiders. *Trends in Ecology and Evolution*, **7**, 155–159.

Vitt, L. J. & Congdon, J. D. 1978. Body shape, reproductive effort and relative clutch mass in lizards: resolution of a paradox. *American Naturalist*, **112**, 595–608.

Vitt, L. J. & Price, H. J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica*, **38**, 237–255.

Wagner, J. D. & Wise, D. H. 1997. Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider *Schizocosa*. *Oecologia*, **109**, 474–482.

Walker, S. E., Marshall, S. D. & Rypstra, A. L. In press. The effect of feeding history on retreat construction in the wolf spider *Hogna helluo* (Araneae, Lycosidae). *Journal of Arachnology*.

Wallin, H. & Ekbom, B. 1994. Influence of hunger level and prey densities on movement patterns in three species of *Pterostichus* beetles. (Coleoptera: Carabidae). *Environmental Entomology*, **23**, 1171–1181.

Wise, D. H. 1993. *Spiders in Ecological Webs.* Cambridge: Cambridge University Press.