Previous foraging success influences web building in the spider *Stegodyphus lineatus* (Eresidae)

Alain Pasquet,[a] Raymond Leborgne,[a] and Yael Lubin[b]

[a]Laboratoire de Biologie et Physiologie du Comportement, URA CNRS n°1293, UHP Nancy 1, B.P. 239, 54506 Vandoeuvre les Nancy Cedex, France, and [b]Mitrani Center for Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University, Sede Boker Campus, 84993 Israel

Stegodyphus lineatus (Eresidae) is a desert spider that builds an aerial capture web on bushes in the Negev desert in southern Israel. Web building for spiders is costly in energy, time, and risk of predation. Spiders should trade-off these costs with the benefits in terms of prey capture. We tested the hypothesis that the previous foraging success of the spider influences the effort invested in foraging. Specifically, we asked whether an increase in food intake causes spiders to reduce web renewal activity and web size. Alternatively, time constraints on foraging and development, resulting from a short growing season, could induce spiders to continue foraging even when supplemented with prey. The cost of web building was measured as time and mass loss. To build an average size web (about 150 cm²), we calculated that a spider requires 6 h and that spiders lose 3%–7% of their weight. In field experiments, spiders responded differently to food supplementation in 2 different years. In 1994, they improved their condition compared to individuals whose webs were removed to reduce foraging opportunities and compared to control spiders. In 1995, spiders tested earlier in the season than the previous year did not improve their condition in response to prey supplementation. Nonetheless, in both years, food-supplemented spiders built significantly smaller webs than food-deprived and control spiders. This result was confirmed in a laboratory experiment where prey intake was controlled. We conclude that for *S. lineatus* immediate foraging risks outweigh the potential time constraints on foraging. *Key words:* Eresidae, food supplementation, optimal foraging, spiders, *Stegodyphus lineatus,* web building. *[Behav Ecol 10:115–121 (1999)]*

Foraging effort can be viewed as a compromise between the energetic needs of the individual for maintenance, growth, and reproduction and the costs or risks associated with foraging activity (Lima and Dill, 1990). The benefits of foraging are frequently traded off against costs, which may vary in accordance with the condition or "state" of the forager (Krebs and Kacelnik, 1991). These foraging trade-offs provide a fertile field for investigating decision-making processes in animals and, in particular, the ways that conflicts are resolved between competing requirements over different time scales—for example, over the time scale of a foraging bout versus the time scale of the forager's life span.

For web-building spiders, foraging costs associated with the capture web include the energy required to construct and maintain the web (silk production and costs of activity) and the risks associated with being exposed while active on the web (Lubin, 1973; Uetz, 1992). The benefit from building a web is derived from prey caught in the web. The presence of an effective capture web determines the spider's energy budget in the short term. Thus, the decision to build a web is a foraging decision, which, in the context of optimal foraging theory, should be sensitive to the expected ratio of benefits to costs summed over the duration of the web (Higgins, 1990; Higgins and Buskirk, 1992; Riechert and Luczak, 1982). The web-building process is repeated at intervals during the spider's lifetime, and the number of webs built during the lifetime varies among species. In some species new webs are constructed daily, while in others both the frequency and the extent of web renewal are more variable (Eberhard, 1986; Lu-bin, 1986; Tanaka, 1989). Because web-building is costly, each web-building decision can have important consequences for the spider's lifetime success.

The benefit and the cost to a spider of building and maintaining a web are influenced by three main factors: (1) the spider's energetic needs for maintenance and reproduction, which will vary with its developmental stage—for example, during moulting or egg maturation (Higgins, 1995; Vollrath, 1987), (2) abiotic and biotic environmental conditions (e.g., wind: Eberhard, 1971; Henschel and Lubin, 1992; prey availability: Pasquet et al., 1994; competition with other individuals: Leborgne and Pasquet, 1987; Ward and Lubin, 1992), and (3) the individual's immediate condition or internal state (Lubin and Henschel, 1996; Witt et al., 1968). Condition is a function of the spider's previous foraging success (i.e., the ratio of benefits to costs obtained from previous webs). Decisions regarding web construction may be strongly influenced by condition: the marginal value of prey capture, and thus of web renewal, is greater for a hungry spider than for a well-fed individual, but the marginal cost of web renewal may also be greater. Will an individual in poor condition be more likely to accept the costs of web renewal? Will a spider in good condition show a more conservative strategy?

Some studies of foraging in spiders showed that well-fed spiders reduced their investment in web construction (Higgins, 1990; Lubin and Henschel, 1996; Sherman, 1994). Food-supplemented female orb-weaving spiders (*Larinioides cornutus,* Araneidae) switched from foraging to reproduction (Sherman, 1994), whereas in a desert spider (*Seothyra henscheli,* Eresidae), well-fed individuals avoided the risks of predation and desiccation by remaining in their burrows (Lubin and Henschel, 1996). In both instances, foraging appeared to be traded off against other activities (reproduction or protection), and the outcome of the trade-off was influenced by the individual's condition.

Do other activities always take precedence over foraging when an individual is well-fed, or are there situations in which foraging activity will be maintained in spite of decreased marginal benefits to the individual? The benefits of continued foraging should be greater if there is a time constraint on growth. For example, if the food resource or other conditions essential for development are present only during a limited time period, continuous foraging will allow maximal utilization of these resources. We predict this to occur in species that have an annual life cycle and a short "growing season," limited, for example, by the timing of insect activity, as might be the case in strongly seasonal habitats.

In the present study, we examined the influence of previous foraging success on the decision to build a web in a desert spider, *Stegodyphus lineatus* (Eresidae). The capture web of *S. lineatus* is orblike in structure, with sticky, cribellate-silk lines connecting nonsticky lines that radiate out from a tubular silk retreat (Henschel et al., 1992; Ward and Lubin, 1993). The web captures mainly flying insects that strike the surface, become entangled in the sticky silk, and are pulled into the nest by the spider. *Stegodyphus lineatus* does not renew its web daily, and frequently renews only a part of the surface, or enlarges the web by adding cribellate silk to existing nonsticky threads (Pasquet et al., personal observations). When the web is renewed, the old silk is discarded, and this energy investment is lost to the spider.

In the Negev desert, the life cycle of *S. lineatus* is generally annual, and most of the growth to maturity occurs during 2–3 months in the spring (March–May), when flying insects are most abundant (Schneider, 1995, 1996; Ward and Lubin, 1993). The energetic demands are greatest during this period of growth to maturation. Spiders that do not reach maturity during the spring have a low probability of surviving to reproduce the following year. Thus, in *S. lineatus,* the limited duration of high prey availability may be expected to select for foraging behavior that will maximize prey capture opportunities independent of body condition.

We used an experimental approach on natural populations in the field and on spiders in captivity to ask whether the spider's feeding state affects its decision to renew the web. Food availability was manipulated to create one group of well-fed individuals and another of food-deprived spiders, while unmanipulated spiders provided a control for changes in behavior that might result from other environmental factors. The energetic cost of web building was measured in terms of the loss of body mass after the construction of a new web and the time to produce a capture web. The decision to rebuild a web was assessed by the number of new webs constructed in each group and their sizes; body condition was assessed at the beginning and end of the experiment. We predicted that spiders foraging in a condition-dependent manner should reduce web building when well fed; alternatively, if long-term growth constraints influence foraging decisions, spiders should maintain active webs even when they are well fed.

METHODS

The study was conducted during March and April of 1994 and 1995 in the Negev desert in southern Israel. The study sites were in two wadis (dry stream beds) separated by approximately 5 km. The wadis are grazed intensively by sheep, goats, and camels, and the vegetation is sparse, consisting mainly of dwarf shrubs (*Artemisia herba-alba, Zygophyllum dumosum, Hammada scoparia*), spiny or aromatic annuals (*Centaurea* spp.), and scattered, small trees (*Thymelea hirsuta, Retama retaem*). The spider builds a silken tubelike nest (retreat), incorporating plant material and prey remains and attached to branches of shrubs. Nests frequently occur in the tops of the shrubs, but they may also be at ground level (Henschel et al., 1992) and are often aggregated (Lubin et al., 1998). At the beginning of March, most spiders were subadult or juvenile and by the end of April some had already reached adult stage.

Web and spider parameters

The web of *S. lineatus* is composed of one or more (two to four) two-dimensional surfaces: the general form is a rectangle or a triangle with the nest tube at one end (Ward and Lubin, 1993). To obtain an estimate of web area, we measured the length and width of a rectangular surface and the height and base of a triangular surface: web size was calculated as the sum of the areas of the different surfaces. In some cases the spider had no capture web, but had spun some cribellate threads around the entrance of the nest tube. Such threads could occasionally trap insect prey; however, in most instances its function appears to be protection against predators or ants. We did not regard these cribellate threads as foraging webs, and they were not included in the web measurements.

Spider size was determined by the total length of the body including the abdomen and cephalothorax (LGTH) and by the width of the cephalothorax (CTW). For spiders, the first measure is correlated with the amount of food ingested, and the second is a measure of the stage of development (Lubin et al., 1991; Vollrath, 1988). In *S. lineatus,* total body length is positively correlated with body mass (Ward and Lubin, 1993). The residuals of regressions of LGTH or mass on CTW provide a measure of body condition independent of size (Jakob et al., 1996; Ward and Lubin 1993).

In 1994, 171 spiders were measured and individually marked in two wadis (wadi 1: 114, wadi 2: 57), and in 1995 we marked and measured 137 spiders. The spiders in the 1994 population were significantly larger than in 1995, both in cephalothorax width (CTW) and in total length (LGTH) (mean ± SD, CTW 1994: 3.03 ± 0.76 mm; CTW 1995: 2.65 ± 0.63 mm, Mann-Whitney $U = 15.013$, $n = 308$, $p < .001$; LGTH 1994: 11.1 ± 2.46 mm; LGTH 1995: 10.1 ± 1.97 mm, $U = 14.533$, $n = 308$, $p < .001$). This difference was due to the fact that observations were begun earlier in the season in 1995.

In both years, there was a significant positive correlation between web area and spider size (see also Ward and Lubin, 1992): larger spiders built larger webs (Pearson correlation of log-transformed web area with LGTH, 1994: $r = .338$, $n = 106$, $p < .001$; 1995: $r = .275$, $n = 81$, $p = .013$).

Cost of web building

Duration of web building
The cost of an activity can be assessed as the relative amount of time spent in the activity. Web-building time was studied under standardized conditions (temperature 22°C, humidity 50%) in the C.N.R.S. laboratory at the University of Nancy. The spiders were brought from the Negev and were kept in boxes (16 × 9 × 8 cm) where they were fed twice a week with cricket nymphs. For the observations of web building, the spiders were transferred with their nests to larger cages (50 × 50 × 10 cm), and each nest was tied to a wire mesh in the center of the cage. The spiders were active at night, so observations of building behavior were made in the dark with a red light. Web building can be divided into two stages: first, construction of radii and nonsticky silk supporting-lines and second, construction of the sticky, cribellate silk. In the laboratory, the spiders built complete webs over a period of several days and web sizes differed from one spider to another.

We defined the speed of building the radii as the mean speed (mm/s) for seven bouts of different lengths and the

speed of laying cribellate silk of known length as equal to the mean of four bouts. As webs were of different sizes, we standardized these results by focusing in each web on a surface of 12 cm^2 (an area equal to the smallest web built in the laboratory). The total length of radii and cribellate silk was measured in this area, and we obtained the total mean length of the radii and cribellate silk for this determined surface. By multiplying this length by the average speed, we obtained the time required for *S. lineatu*s to build 12 cm^2 of web.

Loss of body mass

The cost of web construction was assessed by weighing spiders before and after web building to obtain the mass lost after constructing a web (Henschel and Lubin, 1992). The spiders for this experiment were collected in the Municipal Zoo of Beer Sheva (50 km north of Sede Boker) and removed together with their nest tubes. The nests were attached to chicken-wire fences (about 12 m long and 2 m high) which were inside a screened insectary (14 × 6 × 3 m) in Sede Boker. The spiders build webs readily on the wire mesh (Schneider and Lubin, 1996), and the enclosure prevented entrance of prey, parasites, or predators.

Before installation on the fence, we weighed and measured each spider. After 24 h, the spiders were removed and weighed again. Some had built a functional web, while others constructed only nonsticky radii or no silk at all. Functional webs were measured, and we compared the difference in mass lost between spiders with or without a functional web. To obtain an estimate of body mass loss under resting conditions (i.e., no construction activity), another group of spiders was acclimated to the fence for 2–4 weeks and allowed to build webs; we weighed the spiders on 2 consecutive days and noted whether they had built new webs.

Influence of previous feeding on web building

Field experiments

To study the influence of the spider's condition on its web-building decisions, we used the following experimental design: on the first day, all the spiders found were measured (total length and cephalothorax width) and marked for individual recognition with a dot of acrylic paint. We measured web size (see above) and removed all of the webs (removing silk attachments to branches, radii, and sticky spiral threads). The following day, we measured the new webs that were constructed overnight and for the following experiment we used only those spiders that had built new webs, with the rationale that these individuals would be in a similar initial state. Spiders were assigned randomly to three groups: one group which was not manipulated (control group), another in which we removed the web (web-removal group), and a third in which we removed the web after feeding the spiders with prey (prey-supplemented group). Removing the web in the morning reduced the time available for foraging, as spiders could renew the web only during the following night and foraging occurs both during the day and night. We used flour beetles (*Tenebrio molitor*) of about 100 mg as prey, which are a relatively large meal for these spiders. This procedure was repeated every other day over the next 8 days (i.e., four web-removal and feeding manipulations). Each day we noted the presence of the spider and web and measured web size. During daily monitoring of nests, we noted if spiders had moulted, moved to a new site, or if there were males, predators, or ants in the nest or on the web. On the final day of the experiment (day 9) we monitored spider presence and web size and then removed the spiders from their nests and measured their body size.

The same experimental procedure was repeated in each of the two study sites in 1994. In 1995, only one wadi was used for the experiment. In both years, we used only adult and subadult females and eliminated from the data analysis any individuals that moulted during the experiment or that disappeared or moved to a new web-site.

Laboratory experiment

A similar experiment on spiders in captivity (cages 50 × 50 × 20 cm) was conducted in April 1994. In this experiment, we were able to control prey intake and to determine the relationship between prey mass and spider condition. Spiders collected in the field were assigned to one of three groups after they built their first web: in the first group, spiders received three or four prey (houseflies) over 4 days, in the second group, they received one prey over the 4 days, and in the third group they received no prey at all. The presence of a web was noted each day, and after 4 days we weighed and measured the spiders. We did not measure web size as this was constrained by the size of the cage.

RESULTS

Cost of web building

The speed of radii construction was 20 times that of the speed of constructing cribellate lines (mean ± SD, radii: 3.10 ± 0.33 mm/s, cribellate lines: 0.15 ± 0.02 mm/s, $n = 8$). The length of radii and of cribellate silk in a surface of 12 cm^2 was highly variable among spiders (length of radii: 279 ± 28 mm, $n = 14$ and cribellate silk length: 205 ± 13 mm, $n = 14$). For such a surface, there was no correlation between spider body mass and the length of the radii ($r^2 = .02$, $n = 14$, $p = .61$) nor between mass and the length of the cribellate silk ($r^2 = .02$, $n = 14$, $p = .60$). The average time calculated to build a complete surface of 12 cm^2 was 1770 s ($n = 8$, SD = 292 s). There was no significant correlation between the time spent to construct this surface and the mass of the spider ($r^2 = .09$, $n = 8$, $p = .47$). From the above calculations, the time necessary for building a web of 150 cm^2, the average size of the web found in the field, is about 6 h.

The energetic cost of web building was assessed by measuring weight loss after web construction. We compared the residuals of a regression of the difference between the initial and final body mass against initial mass (log-transformed measurements) for spiders that had constructed a web overnight and those that did not build a web. Individuals that built a web lost significantly more mass than those without a web ($t = -3.26$, df = 57, $p < .002$). Spiders that constructed a web lost on average 8% (range: 1%–17%) of their body mass, whereas those that did not build a capture web lost 5% (range: 0%–9.5%). All of these spiders may have had some exploratory and spinning activity while attaching their nests to the fence. Spiders that had been acclimated to the fence and already had functional webs lost on average 0.72% (−5.5%–3.5%, $n = 20$) of their body mass overnight. Thus, on average, 3%–7% of body mass was lost during web-building activity. The average web size constructed during this period was 101 cm^2 (SE = 16, $n = 24$), which is smaller than an average-size web in the field (150 cm^2). Thus, the mass loss calculated above is a conservative estimate of the cost of web building.

Frequency of web building in natural populations

Over the experimental period of 9 days, the median number of days a functional web was present for the control spiders was 6.5 in 1994 (range 2–9) and 7 in 1995 (range 3–9). The median number of new webs per spider over this period was
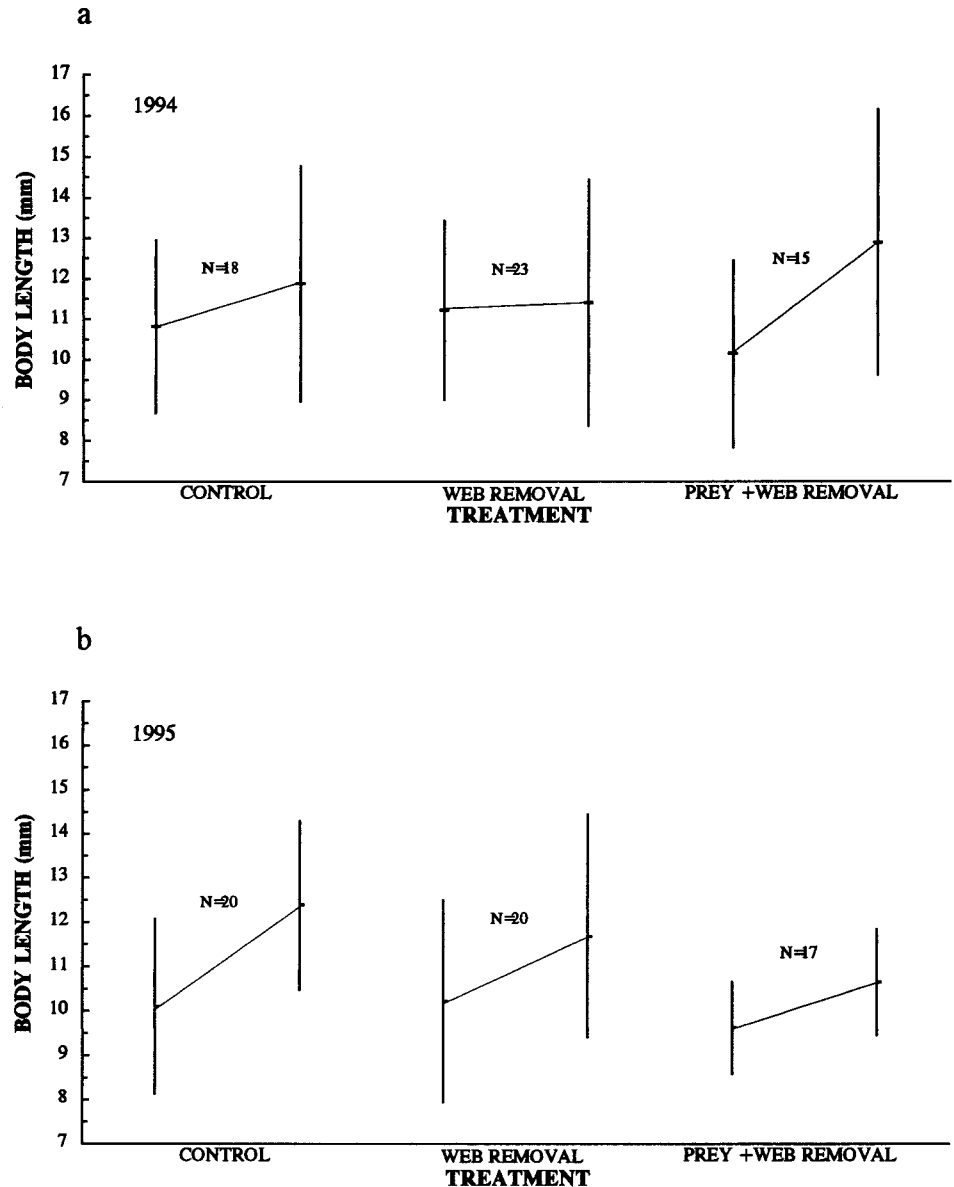
Figure 1
Mean body size (total length, mm, ±1 SD) of spiders at the beginning and end of the field experiment in each of the three groups in (a) 1994 and (b) 1995.

1 in 1994 (0–2) and 0 in 1995 (0–3). These figures underestimate the frequency of web renewal because they do not take into account partial web renewal. Web destruction or damage occurred naturally due to prey-capture, wind, and livestock.

Using the spiders in the control group, we determined the percentage of spiders in the population that had webs over the period of the experiment. This varied from 50% (in wadi 2 in 1994) to 86% (in 1995) (see Figure 2). For each wadi, there was no significant difference among days in the percentage of spiders with webs (1994 wadi 1, $G = 2.91$, df = 7, ns; wadi 2, $G = 2.98$, df = 7, ns; 1995, $G = 5.28$, df = 7, ns). Neither was there significant variation in the total number of web-days in the three control groups (wadis 1 and 2 in 1994 and wadi 2 in 1995). Thus, any variation observed in the occurrence of new webs in the treatment groups could be attributed to the manipulations.

Influence of body size and condition on foraging decisions

Changes in spider size and condition
We determined the changes that occurred in spider size and condition over the period of the field experiment. The spiders

were measured before the experiment began and at the end of the experiment on day 9. Total body length (LGTH) and body condition (residuals of LGTH on cephalothorax width, CTW) were compared among the three treatment groups at the end of the experiment. All size measurements were log transformed.

Final body length was analyzed by ANCOVA, with the initial body length (measured before the start of the experiment) as the covariate and the experimental treatment and year (1994 and 1995) as factors. The experimental treatment had an effect on final body length ($F_{2,106} = 2.913$, $p = .059$), and there was no significant difference between the years ($F_{1,106} = 0.575$, $p = .45$). However, there was a significant interaction between year and experimental treatment ($F_{2,106} = 6.312$, $p = .003$), which indicates that the pattern of change in spider size differed in the 2 years (Figure 1). Indeed, in 1994, prey-supplemented spiders (fed group) increased in body size significantly more than those whose webs were removed and not given supplementary prey (web-removal group; Bonferroni adjusted pairwise comparison, $p = .013$). In 1995, however, the fed spiders were significantly smaller in body size than the
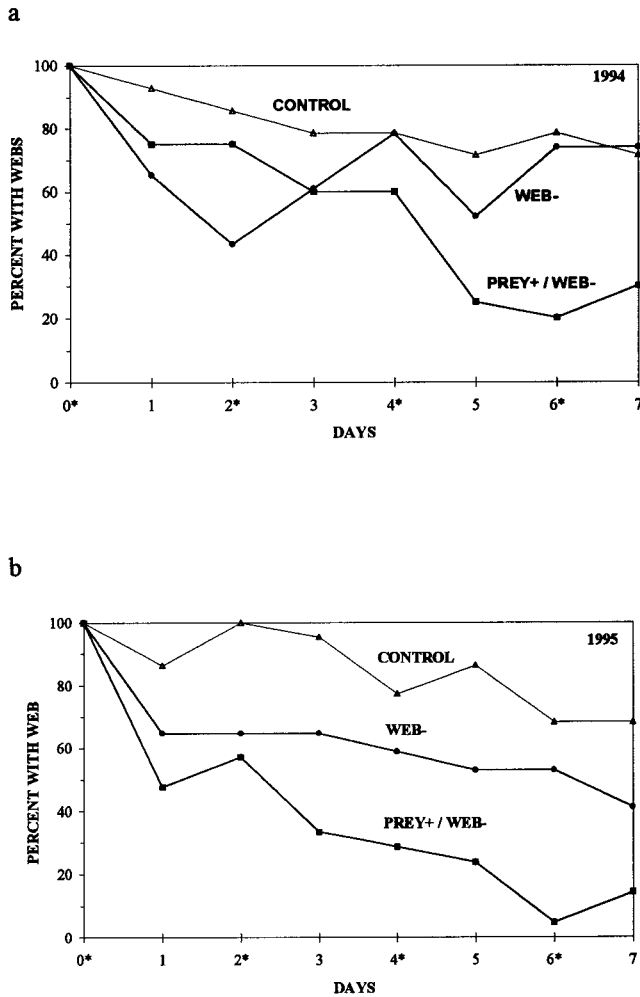
a

b

Figure 2
Percentage of spiders with webs over the duration of the field experiment in (a) 1994 (both sites combined) and (b) 1995 in each of the three groups: control, web removal (web−) and supplemented spiders (prey+/web−). *The webs were removed on days 0, 2, 4, and 6.

control spiders at the end of the experiment (pairwise comparison, $p = .015$), though not different from the web-removal group ($p > .1$). Initial body size did not differ among spiders assigned to the different treatments (ANOVA, $F_{2,107} = 1.184$, $p = .31$), but there was a weak effect of year ($F_{1,107} = 2.975$, $p = .087$).

Body condition (as indicated by the residuals of LGTH on CTW) showed the same pattern as body length (above). There was a significant interaction between year and treatment group (ANOVA, $F_{2,107} = 8.02$, $p = .001$), indicating that the body condition of spiders in the three treatment groups responded differently in the 2 years of the experiment. In 1994, only the fed group had a positive condition index (positive residuals), whereas in 1995, the condition index of the fed group was negative. Thus, spiders that were supplemented with prey in the first year (1994) showed greater growth and were in better condition at the end of the experiment than spiders in the other treatment groups, while in the second year (1995) feeding did not result in greater growth.

Influence on web building
In both years, the number of spiders with webs decreased with time in the prey-supplemented group (Figure 2). In the con-

Table 1
Web-building responses of spiders in the field experiment

Treatment	With webs (%)	Total	G (df = 2)
Year 1, Wadi 1			3.135, ns
Control	55.5	9	
Web removal	69.2	13	
Fed	33.3	12	
Year 1, Wadi 2			9.667 ($p < .01$)
Control	100	5	
Web removal	80	10	
Fed	25	8	
Year 2			13.257 ($p = .001$)
Control	68.2	22	
Web removal	41.2	17	
Fed	14.3	21	

The percentage of spiders with new webs at the end of the experiment is shown for each year and site separately.

trol and web-removal groups, the number of webs was variable, but with no general trend over the duration of the experiment.

At the end of the experiment, 22% of the fed spiders had webs (data combined from the 2 years), in comparison with 69.4% of control spiders and 60% of the web-removal group. Fewer fed spiders had webs in all three samples (year 1: wadis 1 and 2, year 2: wadi 2). The three treatments differed significantly in two of the three samples (Table 1), and the combined probabilities of the three separate tests (Sokal and Rohlf, 1981) show a significant difference between the three groups ($\chi^2 = 22.46$, df = 6, $p < .001$).

The total number of days with a web (web-days) for prey-supplemented spiders was less than for web-removed individuals that did not receive prey (mean ± SD number of web-days, supplemented: 4.62 ± 2.44, $n = 43$, web removal: 6.26 ± 2.12, $n = 34$). The difference was significant in the second-year sample (ANOVA, $F_{1,34} = 3.075$, $p < .001$), and combining the probabilities of the three tests yielded a significant difference overall ($\chi^2 = 15.22$, df = 6, $p < .025$).

Influence on web size
To reduce the effect of daily variations in web size, we used the average web area for each individual over the last 4 days of the experiment as a measure of the spider's response to each treatment. The average web size was compared among the three treatments. Web area measurements were log-transformed to normalize the data.

There was a significant effect of the experimental treatments on web size (ANOVA, $F_{2,79} = 3.851$, $p = .025$), as well as a significant difference in web size between the years (ANOVA, $F_{1,79} = 11.08$, $p = .001$), but no interaction between year and treatment ($p > .1$). Webs of the fed spiders were significantly smaller than those of the control spiders (Bonferroni adjusted pairwise comparison, $p = .022$), and this pattern was consistent in both years (Figure 3).

Laboratory experiment
We tested the web-building response in the laboratory on two occasions, with 13 and 15 spiders, respectively. The results were homogeneous, so we combined the data. Thus, 9 spiders were fed 3–4 prey, 10 spiders were given 1 prey, and 10 were given no prey over 4 days.

The results of the experiments in the laboratory confirmed those of the field experiment (Table 2). Fewer new webs were spun by well-fed spiders (three prey) than by spiders given
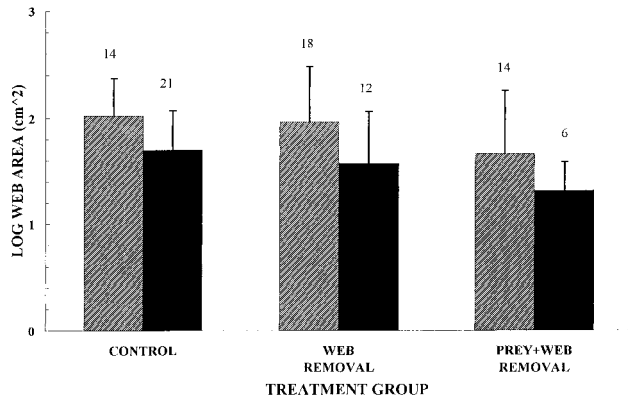
Figure 3
Mean size of webs (± 1 SD) during days 4–8 of the field experiment (log-transformed web area, cm^2) of spiders in each of the three groups in 1994 (hatched bars, both sites combined) and 1995 (solid bars).

less food (one prey; Fisher's Exact test, $p = .070$) or none at all during the experiment (Fisher's Exact test, $p = .015$); there was no difference between the latter two groups (Fisher's Exact test, $p = .582$).

DISCUSSION

Our results show that spiders reduce their foraging effort following successful foraging. Spiders supplemented with food decreased the size of the web, and many of them stopped building altogether. The behavior of spiders whose webs were removed but did not receive supplementary feeding did not differ from the controls that were not prevented from foraging. Thus, the response of prey-supplemented spiders was not due to web removal, but rather to the addition of prey.

All of the spiders increased in size and condition over the course of the field experiment, but there were differences in the response to feeding in the 2 years of the experiment. In 1994, the fed spiders were significantly larger and in better condition than the web-removal and control spiders at the end of the experiment, but this was not the case in 1995. The different growth responses of spiders in the 2 years may be related to the timing of the experiments. The second-year experiment was conducted early in the season, when spiders were smaller (see Methods) and perhaps were constrained by the amount of additional food they could consume. Although fed spiders were in significantly better condition only in one year, in both years they reduced both web size and the frequency of web renewal. This suggests that the proximate cue for web renewal is not body condition, but perhaps the presence or absence of prey. This idea is supported by other studies showing that insect activity (potential prey) can induce web building and web relocation (Pasquet et al., 1994; Riechert, 1985).

In the field experiment, spiders whose webs were removed in the morning lost the opportunity to forage until the web could be renewed in the evening. Repeated web removals meant that these spiders could not forage during at least 4 days out of the 8-day experiment. This repeated disturbance did not cause spiders to desert their web sites, unlike some more mobile species (Leclerc, 1991). However, the loss of foraging time represented an extra cost for these spiders, and we anticipated both greater loss of condition and increased foraging effort than in the control or fed spiders (see Lubin and Henschel, 1996). Nonetheless, web-removal spiders did not differ in condition from the controls, nor did they differ

Table 2
Web-building responses of spiders under different feeding regimes in the laboratory experiment

Percentage of spiders	No prey	1 prey	3 prey
With web ($n = 17$)	47.1	41.2	11.8
Without web ($n = 11$)	9.1	27.3	63.6

The percentage of spiders with new webs at the end of the experiment (after removing all webs the previous day); $\chi^2 = 8.94$, df $= 2$, $p < .05$.

in their tendency to renew the web. We conclude that food supplementation over the relatively short period of the experiment could have a significant effect on body condition and behavior, but food deprivation over the same time period had little effect. The lack of effect of food deprivation is perhaps no surprise, given that spiders are known to tolerate long periods of fasting (reviewed by Nakamura, 1987).

We proposed that a time constraint on growth could increase the value of foraging relative to other activities. In the case of *S. lineatus*, we predicted that the spiders would maintain an active capture web even when well fed. This prediction was based on the assumptions that (1) *S. lineatus* has a short growing season, (2) spiders that fail to mature in one season will have low expected fitness, (3) maintaining a web increases the likelihood of capturing prey, and (4) increased prey capture translates into greater reproductive success (Schneider and Lubin, 1977; Ward and Lubin, 1993). Our results were contrary to the predicted outcome: the spiders reduced web building when supplemented with prey. If we accept the basic assumptions, one must then ask if we neglected to take into account some aspect of the biology of *S. lineatus*, or if the hypothesis itself is not supported here.

A reduction in foraging effort in well-fed individuals has also been documented in other organisms (e.g., scorpions: Skutelsky, 1996). This behavior can be attributed to satiation or other digestive constraints or the existence of a large cost to maintaining foraging activity, which decreases the marginal benefit of foraging. Proximate causes, such as satiation or digestive constraints, are inadequate explanations for the reduction of web building because a spider with a functional web can capture prey and store it for later consumption. However, for *S. lineatus*, we showed that web construction carries a large cost in terms of time (approximately 6 h to build a complete web) and energy expenditure during web building (as indicated by up to 10% loss of body mass per web). Web construction in *S. lineatus* is time consuming because of the slowness of laying down the sticky, cribellate threads (see also Eberhard, 1988; Lubin, 1986). Aside from the direct energetic cost, web-building activity exposes the spider to potential nocturnal predators. During the day, prey capture activity on the web can be risky because of predators such as birds, lizards, mantids, and wasps. These risks are similar for individuals in any state, but spiders in good condition have less to gain from renewing a web than individuals in poor condition.

There are also indirect risks associated with having a web: it may attract predators to the nest. If an insect is trapped in the web or captured and not consumed by the spider, it can attract ants (Henschel, 1998; Schneider, 1995, 1996; Schneider and Lubin, 1997) as well as visually hunting predators. The ants are not a direct threat to the spider (except when moulting), but they often attack in large numbers, forcing the spider to vacate its nest and sit exposed on the web or supporting threads. Our preliminary observations suggest that ant attacks are frequent and that once ants discover a nest with prey, this nest becomes a repeated target. Ants may be a

threat particularly when several prey items are present in the nest or web and when the prey insects are large and feeding duration is long (personal observations; Schneider, personal communication).

Our conclusion that *S. lineatus* modifies web-building behavior in response to a short-term change in prey availability agrees with other studies of web-building spiders that showed an influence of previous foraging success on web-building decisions (Lubin and Henschel, 1996; Sherman, 1994). We had proposed that a growth constraint over the spider's lifetime would change the benefit-to-cost ratio of foraging in a risky environment by increasing the value of continued foraging. This was not the case, but whether physiological constraints or direct and indirect risks of predation are responsible for lower foraging effort following feeding remains to be investigated.

REFERENCES

Eberhard WG, 1971. The ecology of the web of *Uloborus diversus* (Araneae: Uloboridae). Oecologia 6:328–342.

Eberhard WG, 1986. Effects of orb-web geometry on prey interception and retention. In: Spiders: webs, behavior, and evolution (Shear WS, ed). Stanford, California: Stanford University Press; 70–100.

Eberhard WG, 1988. Combing and sticky silk attachment behavior by cribellate spiders and its taxonomic implications. J Arachnol 7:247–251.

Henschel JR, 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae: Eresidae). J Arachnol 26:61–63.

Henschel JR, Lubin Y, 1992. Environmental factors affecting the web and activity of a psammophilous spider in the Namib desert. J Arid Environ 22:173–189.

Henschel JR, Ward D, Lubin Y, 1992. The importance of thermal factors for nest-site selection, web construction and behaviour of *Stegodyphus lineatus* (Araneae: Eresidae) in the Negev desert. J Therm Biol 17:97–106.

Higgins LE, 1990. Variation in foraging investment during the intermolt and before egg laying in the spider *Nephila clavipes*. J Insect Behav 3:773–783.

Higgins LE, 1995. Direct evidence for trade-offs between foraging and growth in a juvenile spider. J Arachnol 23:37–43.

Higgins LE, Buskirk RE, 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Anim Behav 44:485–499.

Jakob EM, Marshall SD, Vetz GW, 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Krebs JR, Kacelnik A, 1991. Decision making. In: Behavioural ecology, 3rd ed. (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific; 105–136.

Leborgne R, Pasquet A, 1987. Influence of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). Behav Ecol Sociobiol 20:203–208.

Leclerc J, 1991. Optimal foraging strategy of the sheet-web spider *Lepthyphantes flavipes* under perturbation. Ecology 72:1267–1272.

Lima SL, Dill LM, 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640.

Lubin Y, 1986. Web building and prey capture in the Uloboridae. In: Spiders: webs, behavior, and evolution (Shear WS, ed). Stanford, California: Stanford University Press; 132–171.

Lubin Y, Hennicke J, Schneider J, 1998. Settling decisions of dispersing *Stegodyphus lineatus* (Eresidae) young. Israel J Zool 44:217–226.

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

Lubin Y, Kotzman M, Ellner S, 1991. Ontogenetic and seasonal changes in webs and websites of a desert spider. J Arachnol 19:40–48.

Lubin YD, 1973. Web structure and function: the non-adhesive orb-web of *Cyrtophora moluccensis* (Doleschall) (Araneae: Araneidae). Form Funct 6:337–358.

Nakamura K, 1987. Hunger and starvation. In: Ecophysiology of spiders (Nentwig W, ed). Heidelberg: Springer-Verlag; 287–295.

Pasquet A, Ridwan A, Leborgne R, 1994. Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. Anim Behav 47:477–480.

Riechert SE, 1985. Decisions in multiple goal contexts: habitat selection of the spider *Agelenopsis aperta* (Gertsch). Z Tierpsychol 70:53–69.

Riechert SE, Luczak J, 1982. Spider foraging: behavioral responses to prey. In: Spider communication: mechanisms and ecological significance (Witt PN, Rovner JS, eds). Princeton, New Jersey: Princeton University Press; 353–385.

Schneider JM, 1995. Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insect Soc 42:237–248.

Schneider JM, 1996. Differential mortality and relative maternal investment in different life stages in *Stegodyphus lineatus* (Araneae, Eresidae). J Arachnol 24:148–154.

Schneider JM, Lubin Y, 1997. Does high adult mortality explain semelparity in the spider *Stegodyphus lineatus* (Eresidae)? Oikos 79:92–100.

Sherman PM, 1994. The orb-web: an energetic and behavioural estimator of a spiders dynamic foraging and reproductive strategies. Anim Behav 48:19–34.

Skutelsky O, 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. Anim Behav 52:49–57.

Sokal RR, Rohlf FJ, 1981. Biometry. New York: W.H. Freeman.

Tanaka K, 1989. Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. Oecologia 81:459–464.

Uetz GW, 1992. Foraging strategies of spiders. Trends Ecol Evol 7:155–159.

Vollrath F, 1987. Growth, foraging and reproductive success. In: Ecophysiology of spiders (Nentwig W, ed). Heidelberg: Springer-Verlag; 357–370.

Vollrath F, 1988. Spider growth as an indicator of habitat quality. Bull Br Arachnol Soc 7:217–219.

Ward D, Lubin Y, 1992. Temporal and spatial segregation of web-building in a community of orb-weaving spiders. J Arachnol 20:73–87.

Ward D, Lubin Y, 1993. Habitat selection and the life history of a desert spider *Stegodyphus lineatus* (Eresidae). J Anim Ecol 62:353–363.

Witt PN, Reed CF, Peakall DB, 1968. A spider's web. New York: Springer-Verlag.