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The influence of food supply on foraging behaviour in a desert spider

Abstract We tested the alternative hypotheses that foraging effort will increase (energy maximizer model) or decrease (due to increased costs or risks) when food supply increased, using a Namib desert burrowing spider, *Seothyra henscheli* (Eresidae), which feeds mainly on ants. The web of *S. henscheli* has a simple geometrical configuration, comprising a horizontal mat on the sand surface, with a variable number of lobes lined with sticky silk. The sticky silk is renewed daily after being covered by wind-blown sand. In a field experiment, we supplemented the spiders' natural prey with one ant on each day that spiders had active webs and determined the response to an increase in prey. We compared the foraging activity and web geometry of prey-supplemented spiders to non-supplemented controls. We compared the same parameters in food-deprived and supplemented spiders in captivity. The results support the "costs of foraging" hypothesis. Supplemented spiders reduced their foraging activity and web dimensions. They moulted at least once and grew rapidly, more than doubling their mass in 6 weeks. By contrast, food-deprived spiders increased foraging effort by enlarging the diameter of the capture web. We suggest that digestive constraints prevented supplemented spiders from fully utilizing the available prey. By reducing foraging activities on the surface, spiders in a prey-rich habitat can reduce the risk of predation. However, early maturation resulting from a higher growth rate provides no advantage to *S. henscheli* owing to the fact that the timing of mating and dispersal are fixed by climatic factors (wind and temperature). Instead, large female body size will increase fitness by increasing the investment in young during the period of extended maternal care.

Introduction

Organisms make foraging decisions based on the current distribution of resources, previous experience and the condition of the organism (Stephens and Krebs 1986). Much empirical and theoretical work has been devoted to the different kinds of responses of predators to changes in prey density (Abrams 1982). Increasing prey density may cause the predator to either increase or decrease its foraging effort, depending on how the change in food availability affects the benefits and costs of foraging, which, in turn, may depend upon the particular organism studied and on various constraints (e.g. Abrahams and Dill 1989). Mitchell et al. (1990) modelled the short-term responses of a predator to a decrease in available resources due to exploitative competition. Abrams (1991) examined some of the conditions under which a forager should change its foraging effort with increasing prey density. He showed that the predator's life history (semelparous or iteroparous), the time-scale of change in food abundance (short or long duration) and the cost of increasing foraging effort (risk of mortality or prey-handling costs) should all influence the predator's response. Surprisingly few field-conducted empirical studies of foraging effort in relation to increasing prey densities test the predictions of these models.

Web-building spiders have attracted considerable attention as subjects of foraging studies (reviewed by Riechert and Luczak 1982; Uetz 1988, 1991, 1992; see

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also Ward and Lubin 1992; Sherman 1994). As relatively sedentary foragers, they are unable to sample widely and foraging decisions are often based on encounter rates at the web site. For web-building spiders, foraging effort includes the construction and maintenance of a capture web as well as the active capture of prey trapped in the web. Some field studies indicate that spiders invest less in construction, maintenance or defence of webs in prey-rich habitats than in poor ones (Riechert 1981; Pasquet 1984; Higgins and Buskirk 1992; Pasquet et al. 1994; Sherman 1994). These results would follow if the costs of increased foraging activity exceed the marginal benefits of obtaining more food. For example, if web maintenance activities expose the spider to predators, then foraging effort should be reduced at higher prey densities. Conversely, at low prey densities, spiders might be expected to expend more effort in foraging and to take more risks in order to intercept more prey.

An alternative hypothesis is that spiders in good habitats should increase foraging effort relative to those in poor habitats. This is because spiders in good habitats can expect higher marginal rewards from increased foraging activity. Increased foraging effort will be favoured if the marginal costs of foraging increase less than the marginal benefits and to the extent that the spiders can use the additional energy to increase fitness. Ward and Lubin (1993) found that after correcting for body size, spiders in a prey-rich habitat had larger webs than those in a prey-poor habitat. This suggests that foraging effort increased where prey were more abundant beyond the simple increase due to allometric scaling of web and spider.

Features of web design such as web size and the density or length of capture elements may vary with the spider's perception of prey availability in the environment and are thus useful as measures of foraging effort (Ward and Lubin 1992; Rhisiart and Vollrath 1994; Sherman 1994). Spiders may vary independently the different components of the web. For example, orb-weavers can modify mesh size, orb diameter, density of radii and thread thickness (Witt and Baum 1960). While some web components may vary with prey availability, others may scale allometrically with spider size or may be constrained by space or other environmental factors (Eberhard 1990; Lubin et al. 1991, 1993; Rhisiart and Vollrath 1994). Few field studies to date allow us to separate the effects of changing prey densities on foraging effort from the effects of other environmental variables.

In the present study, we examine the relationship between food availability and foraging effort in a desert web-building spider, Seothyra henscheli Dippenaar 1991 (Eresidae), endemic to the sand dunes of the Namib Desert (Henschel and Lubin 1992). S. henscheli is a sit-and-wait predator that forages at the sand surface, using sticky cribellar silk to trap surface-active arthropods (Peters 1992). Physical features of the environment (e.g. wind and temperature) strongly influence foraging activity in this species (Lubin and Henschel 1990; Henschel and Lubin 1992). In a field experiment, we assessed changes in the spiders' foraging effort in response to supplemented prey as indicated by prey-capture activity and web dimensions. In the experiment, environmental conditions (with the exception of the feeding regime) were the same for all spiders, which allowed us to separate the effects of food and of other environmental factors.

Two alternative hypotheses predict opposite responses of S. henscheli to an increase in prey availability. Firstly, as energy maximizers, spiders in prey-rich sites will have a high expectation of obtaining prey and, therefore, should increase their foraging activity by being more active and by building larger capture webs than spiders in prey-poor sites. Alternatively, if the costs or constraints on foraging increase sharply with foraging effort, then spiders in prey-rich sites should decrease their foraging activity in comparison with individuals in poor sites. Risks of predation during foraging, or of interference from conspecifics, may represent such significant costs to foraging. Handling costs and rates of ingestion and assimilation of prey may ultimately constrain foraging and cause spiders to reduce their activity. A third possibility is that there will be no change in foraging effort in response to increasing prey because the spiders are satiated by naturally available prey. In the last mentioned case, experimental food-deprivation would provide a test of the two hypotheses.

We tested predictions derived from these hypotheses by supplementing prey to one group of spiders, depriving another, and comparing foraging effort and growth in prey-supplemented, non-supplemented and deprived individuals. Foraging effort was assessed by the proportion of time that spiders maintained active capture webs and by changes in web dimensions.

Materials and methods

Natural history

S. henscheli occurs in aggregations in the Namib dunes at densities of 2–50 individuals/m^2. Juveniles disperse in early summer (October) and mature by early winter (May–June) at a body length of 7–13 mm and mass of 58–239 mg ($n = 56$). The number of offspring ranges from 19 to 29 ($n = 3$ clutches).

The web of S. henscheli is characterized by a vertical tubular burrow and a horizontal silk mat on the sand surface (Fig. 1; Lubin and Henschel 1990; Peters 1992). The sticky, cribellar-silk capture lobes of the surface mat open onto depressions in the sand and trap arthropods which blunder into them. The 15-cm deep burrow serves as a thermal retreat from high surface temperatures during the day and enables the spider to forage throughout the day by shuttling between the hot surface web and the cool burrow (Lubin and Henschel 1990; Turner et al. 1993).

Wind limits spider activity by covering the capture lobes of the surface web with sand (Henschel and Lubin 1992). This typically occurred every summer afternoon. In the early evening when the wind abates, actively foraging spiders restore the trapability of the
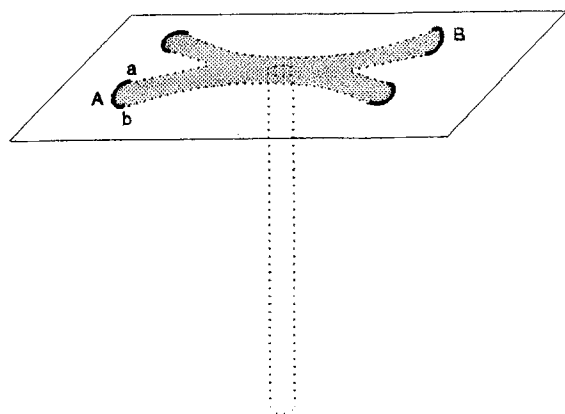
Fig. 1 The web and burrow of *Seothyra henscheli* showing four sticky capture lobes (thick arcs), sand-covered surface web (*shaded area*) and vertical burrow. Measurements were made of lobe diameter (a-b) and maximum web length (A-B)

web by flicking the sand away from the edges of the capture lobes and applying fresh cribellar silk. Spiders that had opened their webs by the morning inspection were designated as actively foraging spiders.

Methods

Field experiment

We carried out manipulations of prey on a population of *S. henscheli* inhabiting transverse dunes at Khommabes, 5 km NW of Gobabeb in Namibia (23°33'S, 14°49'E). In this area, the large, diurnal ant *Camponotus detritus* (Formicinae; mass: mean ± SE 24.4 ± 1.7 mg, range 11–62 mg) formed a major part of the diet of *S. henscheli*. We chose medium to large spiders for the experiment (body length > 5 mm, mass > 6 mg) because smaller spiders might have difficulty handling the large ants.

We marked the locations of 153 webs in c. 200 by 50 m² of dune. The spiders were assigned randomly to one of three groups. Group SUP (supplemented) received prey from us, up to one *C. detritus* ant daily, in addition to their natural prey. Groups NON (not supplemented) and UNM (unmanipulated) both received no additional prey, but were allowed to forage naturally. The experiment was carried out over a period of 42 days between 4 January and 16 February 1989.

Before the start of the experiment, the webs of SUP and NON spiders were measured and then excavated to remove the spiders. Excavating the burrows allowed us to measure burrow depth and to analyse prey remains taken from the burrow. We measured and weighed the spiders in the laboratory, and released them at the capture sites. The spiders immediately excavated new burrows within a few centimetres of the release point (Henschel and Lubin 1992). Excavation imposed an initial energetic handicap on these spiders by forcing them to construct new webs. SUP and NON spiders thus entered the experiment in a similar state and any changes in web dimensions or foraging activity between them should reflect differences due to the effects of the different treatments (prey supplementation versus no supplementation).

UNM spiders were removed without damaging the web and burrow by enticing them to strike at a prey stimulus and capturing them at the edge of the surface web. The spiders were measured in situ and were returned immediately to their own webs without further manipulation. They could not be weighed because weighing entailed removal to the laboratory, after which it is not possible to return them to their burrows. The UNM group was a control for

SUP and NON groups, enabling us to determine the effect of replacement of the web and burrow on the response variables measured.

All webs were checked daily, and SUP spiders that were active (i.e. had exposed, sticky capture lobes) were given one ant each; the ant was dropped onto the sticky threads and the spider's response was noted.

Variables measured throughout the experiment were (1) activity, (2) the response to prey (SUP only), i.e. whether or not the spider attacked the ant, (3) the number and maximum diameter of active lobes on the capture web and (4) the length of the surface web. After 6 weeks we excavated all burrows, including UNM, weighed and measured the spiders and collected the prey remains. We assessed changes in spider condition and prey capture success under the different treatments from (5) changes in total body length and mass of spiders, and (6) the amount of prey remains accumulated in the burrow during the experiment (SUP and NON). We identified prey items and categorized them into *C. detritus*, other ants and other taxa. Prey size estimates were based on average measurements of a sample of live insects of the same prey taxa.

The energy maximization hypothesis (see above) predicts that all response variables should have higher values for SUP than for NON and UNM, reflecting greater foraging activity in SUP. The alternative hypothesis predicts that response variables 1-4 will have lower values for SUP than for NON and UNM.

Laboratory experiment

It was impossible to deprive spiders in the field of prey because any barrier constructed would create a barrier to sand flow, resulting in either formation of sand mounds or scouring of the web. To circumvent this problem, we conducted another experiment in an outside enclosure at Gobabeb. Twenty spiders constructed new webs in buckets (diameter and depth 15 cm), which were placed into the ground in a location that was exposed to normal sunlight, but was sheltered from strong winds. Wandering insects were excluded by covering the buckets with thin cloth veils. Ten spiders (group SUP) were fed daily with one *C. detritus* ant each and ten were deprived of prey altogether (group DEP). The experiment was continued for 7 weeks.

Statistical tests

Analysis of variance (ANOVA) was used to compare treatment means for most variables measuring foraging activity, spider growth, and web dimensions. Non-parametric tests were used where necessary. When a variable was shown to scale to spider size, analysis of covariance (ANCOVA) was performed, with body size (length or mass) as a covariate.

Our hypotheses allow a priori comparisons between SUP and NON and UNM (supplemented spiders versus controls) and between NON and UNM (manipulated versus unmanipulated controls). These follow the procedure outlined by Sokal and Rohlf (1981).

Results

Field experiment

Foraging activity

Supplemented spiders (SUP) reduced foraging effort in comparison to the non-supplemented (NON) and unmanipulated (UNM) spiders. Of SUP, 43% were

active for 30 days or less (half the duration of the experiment) in comparison with 8% and 14% for NON and UNM, respectively (Fig. 2; NON versus SUP, $\chi^2 = 48.8$; UNM versus SUP, $\chi^2 = 49.8$, $df = 1$, $P < 0.001$).

The reduction in foraging activity of SUP spiders in comparison with the two control groups (NON and UNM) was due to more bouts of inactivity and, in particular, a greater number of long bouts of inactivity. Almost 98% of the supplemented spiders had at least one long bout of inactivity which lasted ≥ 7 days (median = 10 days, $n = 41$ spiders), in comparison with 32% and 27% for UNM ($n = 38$) and NON ($n = 44$) spiders, respectively (spiders which were inactive at the end of the experiment were not included in this analysis). Even after removing the long bouts of inactivity, SUP spiders were inactive for a total of 19 days and UNM and NON spiders for 7 and 4 days, respectively (medians for each group; Kruskal-Wallis statistic = 55.95, $P < 0.001$, $df = 2$).

The number of spiders active on any day was remarkably constant over the 6 week period for NON and UNM (mean number of spiders, CV = 41.8, 5% and 37.3, 9%, respectively), but varied considerably for SUP (mean, CV = 24.3, 39%; Fig. 3). Over the first 2 weeks, the number of active foragers of SUP declined to 16% of the population. The numbers rose slowly over the next 2–3 weeks, but never reached the original level and remained well below the levels of activity of NON and UNM spiders. Another low-activity period occurred at 6 weeks (18% of the population active). The dip in activity of all groups on day 28 was probably due to strong winds during the previous night. NON spiders had the highest level of activity throughout the experiment.

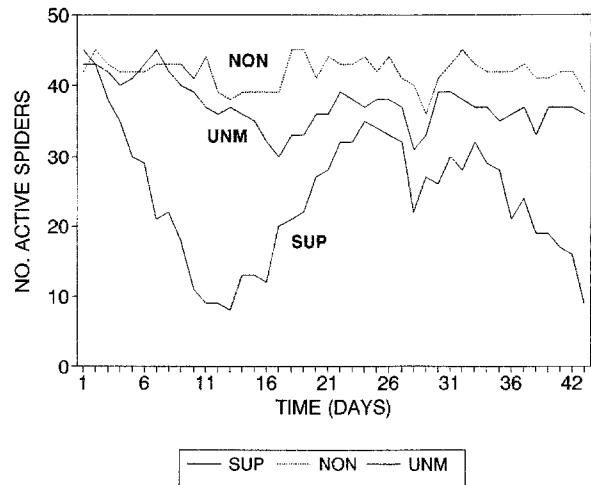The modal number of active capture lobes was never greater than two for SUP spiders, whereas NON spi-

Fig. 3 Number of spiders with active capture webs over the duration of the field experiment (*SUP* supplemented, *NON* non-supplemented, *UNM* unmanipulated)

ders had three and four capture lobes on 28% and UNM on 44% of the days. The difference in distribution of modal capture lobe numbers was significant ($\chi^2 = 32.16$, $df = 6$). The number of days on which spiders had webs with more than a single active lobe also reflected the differences in foraging effort: for SUP 18 ± 1.1 days (mean $\pm$ SE), whereas for NON and UNM 33 ± 1.4 and 31 ± 1.6 days, respectively (ANOVA, $F_{2,145} = 33.89$, $P < 0.001$).

SUP spiders attacked one ant every 2.4 days on average. Actual captures were probably lower, because not all ants that were attacked were subsequently captured and consumed. Based on prey remains found in the excavated burrows at the end of the study, SUP each ate at least one *C. detritus* every 14 days, compared to one eaten by NON every 38 days (Table 1). *C. detritus* constituted 92% and 61% of the prey biomass of SUP and NON, while other smaller ants constituted 1% and 3%, respectively. SUP consumed a significantly higher mass of food than NON (mean $\pm$ SE: 1.8 ± 0.3 versus 1.1 ± 0.2 mg day^{-1}, respectively; $t = 2.48$, $df = 85$, $P < 0.02$). These consumption rates are underestimates, because spiders did not retain all prey remains in the burrow.

Survival and growth

More NON spiders disappeared (20.4%) before the end of the 6-week experiment than did SUP (14.3%) and UNM spiders (12.0%), although the differences between the three treaments were not significant.

Supplemented spiders grew more than did non-supplemented ones. At the end of the experiment, SUP spiders had significantly greater mass and body length (Fig. 4a, b). While SUP spiders gained an average of $2.08 \pm 0.09\%$ mass day^{-1}, NON gained only $0.66 \pm 0.07\%$ mass $\cdot$ day^{-1}. SUP spiders were not only larger

Fig. 2 Frequency distribution of spider activity (no. of days with active capture webs) in the field experiment. Unmanipulated (*UNM*), $n = 49$; supplemented (*SUP*), $n = 49$; non-supplemented (*NON*), $n = 50$
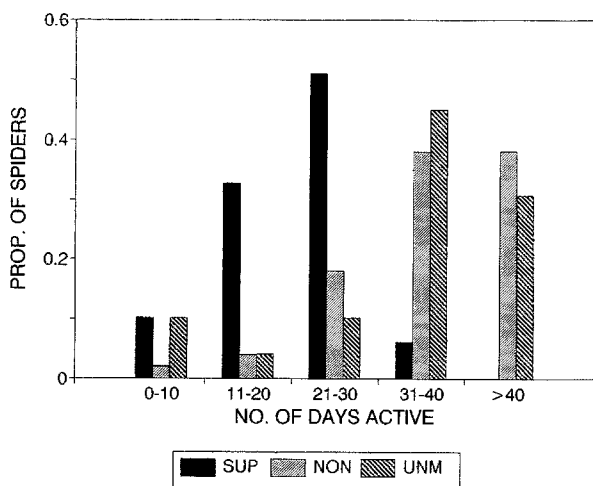
Table 1 Mean ± SE (percentages) of the number of prey items (head capsules or entire exoskeletons) from excavated burrows of *Seothyra henscheli* at the end of the experiment [*UNM* unmanipulated spiders (*n* = 36), *SUP* supplemented spiders (*n* = 42), *NON* non-supplemented spiders (*n* = 45)]

Group	*Camponotus detritus*	Other ants	Other taxa	Total
UNM prey (%)	2.5 ± 0.3 (33)	3.7 ± 1.1 (49)	1.2 ± 0.2 (16)	7.5 ± 1.2
SUP prey (%)	2.9 ± 0.5 (78)	0.4 ± 0.1 (11)	0.4 ± 0.1 (11)	3.7 ± 0.5
NON prey (%)	1.1 ± 0.2 (34)	0.9 ± 0.2 (28)	1.2 ± 0.5 (38)	3.2 ± 0.5
t: SUP vs NON	$P < 0.001$	$P < 0.05$	$P < 0.1$	n.s.

and heavier than the other groups, they were also heavier for their size, i.e. in better condition (ANCOVA on final body mass, with final body length as covariate, $P < 0.001$).

SUP spiders moulted more often than either NON or UNM. Based on the exuviae found in the excavated nests at the end of the experiment, 57% of SUP moulted at least once and 6% moulted twice (*n* = 49), while only 32% of NON (*n* = 50) moulted once, and none twice ($\chi^2 = 11.36$, $df = 4$, $P < 0.025$). Two SUP spiders reached maturity and six (14.6%, *n* = 41) were subadults at the end of the experiment. All UNM spiders remaining at the end of the experiment (*n* = 36) were juveniles, and only two NON spiders (4.8%, *N* = 42) were subadults.

Another indication of differences in growth comes from the long bouts of inactivity. For SUP and NON treatments, there was a significant association between the presence of exuviae in the nest and the occurrence of bouts of inactivity lasting longer than one week

($\chi^2 = 9.45$, $P < 0.005$, $df = 1$). We surmise that periods of inactivity of 1 week or more are associated with moults. Using this criterion, SUP spiders required fewer days to reach the first moult (median = 8 days) than did UNM (11.5 days) or NON spiders (17.5 days; Kruskal-Wallis statistic = 9.09, *n* = 64, *P* = 0.01).

For SUP, final body mass and mass increment (final mass minus initial mass) were strongly positively correlated with the number of ants attacked ($r = 0.85$ and $r = 0.93$, respectively, *n* = 42, $P < 0.001$) and with the number of days with active capture webs ($r = 0.82$ and $r = 0.91$, respectively, *n* = 42, $P < 0.001$). Mass increment was linear over a range of final body masses of 70–250 mg. In a multiple regression of final body mass on initial body mass, the number of ants attacked and number of days active, only the first two were significant, explaining 92% of the variation in final body mass. Body length and length increment of SUP spiders showed the same pattern in relation to foraging activity as body mass.

Fig. 4 a–d Initial (I) and final (*F*) measurements of parameters in the field experiment: **a** body mass, **b** body length, **c** web length, and **d** capture-lobe diameter (*SUP* supplemented, *NON* non-supplemented, *UNM* unmanipulated)
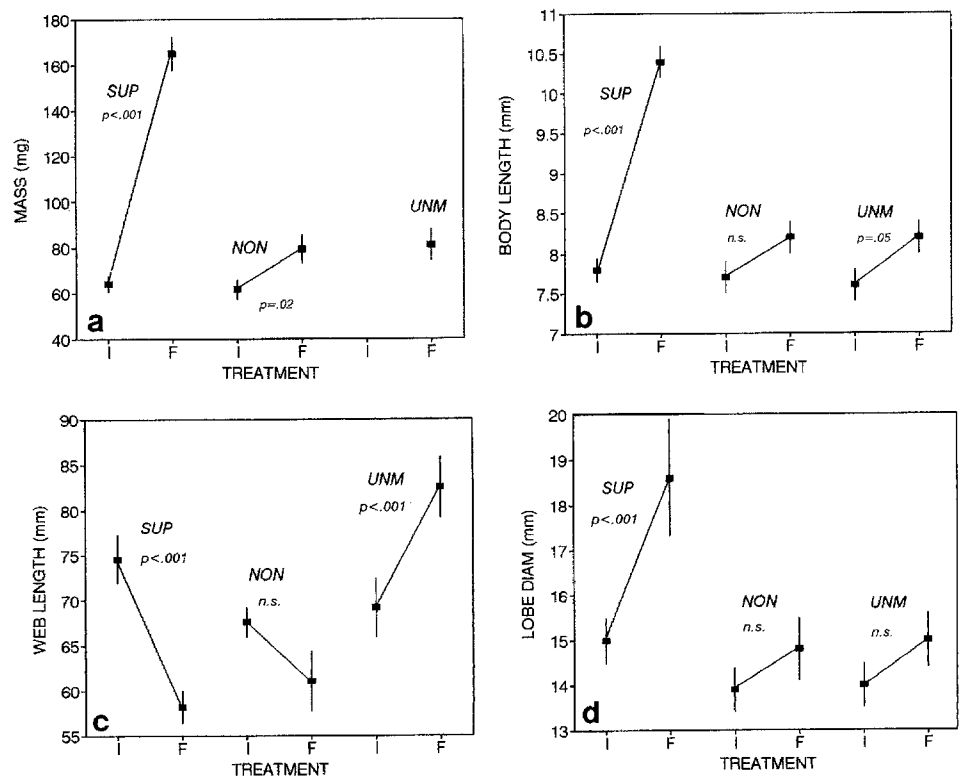
There was no significant relationship between the number of days active and body mass of UNM. In this group, most spiders were active every day (Fig. 2). NON had a weak negative relationship between final mass and number of days active ($r = -0.37$, $F_{1,43} = 6.8$, $P = 0.013$) which was not evident when mass increment was used instead of final mass.

Web geometry

The length of the surface web was only weakly correlated with body length ($r = 0.27$, $n = 138$ measurements of original webs, before the start of the experiment). Web length increased throughout the experiment for all spiders, but most rapidly for SUP and NON which had to construct new webs at the start of the experiment. Surface-web length of NON increased steadily over the first 4 weeks (at 11% per week), whereas the increase was more erratic in SUP (32% increase in the 1st week). Final web length did not differ between SUP and NON (Fig. 4c; $t = -1.16$, $P > 0.1$). At the end of the experiment, the average web length for both SUP and NON was still significantly smaller than that of UNM (ANOVA, $F_{2,134} = 31.03$, $P < 0.001$).

We compared measurements of web length in the final webs and the original, pre-manipulation webs (Fig. 4c). SUP had significantly smaller webs at the end of the experiment, UNM had significantly larger webs, and final webs of NON did not differ in length from original webs. Thus, SUP had a relatively smaller increase in web size with time than either NON or UNM.

The diameter of the capture lobe was positively correlated with spider body length ($r = 0.36$, $n = 135$ pre-manipulation webs and initial spider size measurements). At the end of the experiment, SUP had

Fig. 5 Proportion of ants attacked by supplemented spiders in the laboratory experiment in relation to the number of active capture lobes ($n = 470$ web-days)
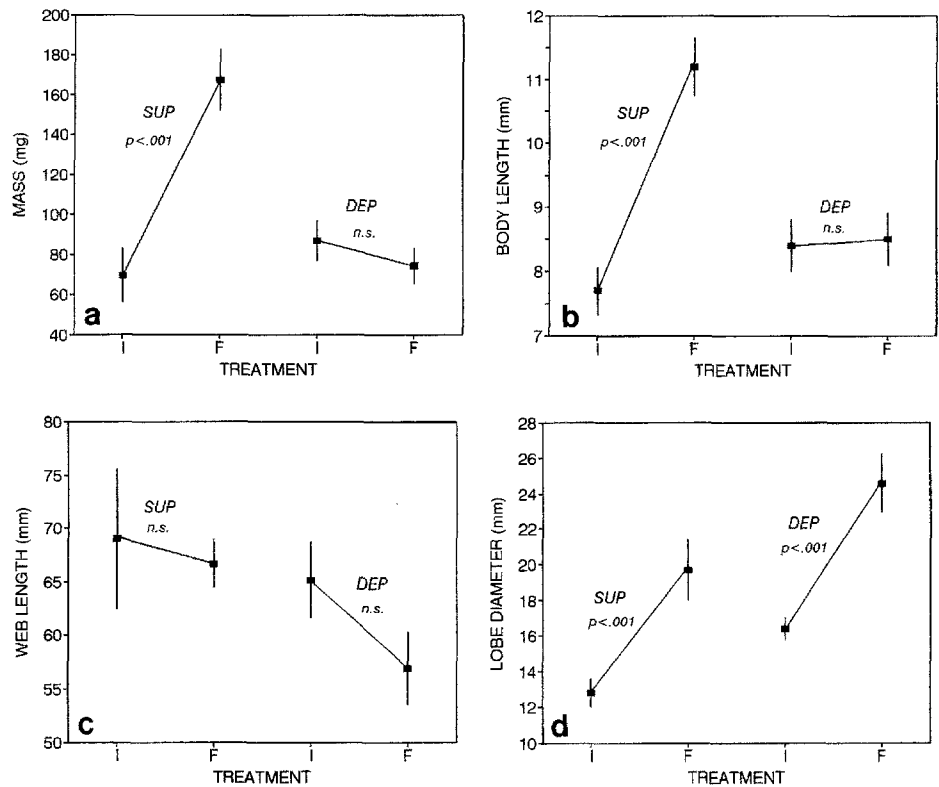

significantly larger capture lobe diameters than either NON or UNM (ANOVA, $F_{2,79} = 3.497$, $P = 0.035$), but this difference disappeared when spider size was taken into account (ANCOVA, covariate: body length, $P > 0.1$). Thus, capture lobe size reflects the changes in spider size due to the different feeding regimes. Comparing measurements of original (pre-manipulation) webs and final webs (Fig. 4d) reinforces this conclusion. There was a significant increase in capture lobe diameter in SUP only.

Laboratory experiments

Foraging activity

As in the field experiment, foraging activity was depressed in SUP. Prey-deprived spiders (DEP) were active on all 48 days, while SUP were active on 65.7% of the days. DEP also had significantly more capture lobes active than SUP (Wilcoxon, $z = 29.01$, $n = 490$ web-days for each group, $P < 0.001$).

SUP attacked an ant on 1 out of every 1.9 days on average. Spiders with active capture lobes attacked ants on 79.9% of the feeding trials, and individuals with a greater number of active capture lobes were more likely to attack (Fig. 5).

Growth

All 20 spiders survived the 7 week period of the experiment. SUP spiders grew significantly more than DEP. This is reflected in differences in body mass (mean ± SE: SUP = 167.3 ± 15.6 mg, DEP = 74.2 ± 9.1 mg; $P < 0.001$) and body length (SUP = 11.2 ± 0.37 mm, DEP = 8.5 ± 0.41 mm; $P < 0.001$). Body mass and length increased significantly in SUP over the duration of the experiment, but not in DEP (Fig 6a,b). On average, SUP gained 1.84 ± 0.20% mass day^{-1}, while DEP lost 0.33 ± 0.08% mass day^{-1}. All ten SUP moulted at least once, whereas only one DEP moulted during the study. There was a weak positive correlation between the increment in mass of SUP and the number of ants attacked ($r_s = 0.49$, $n = 10$, $P = 0.056$).

Web geometry

At the end of the experiment, SUP had significantly larger webs than DEP ($F_{1,18} = 5.78$, $P = 0.03$). Web length increased for all spiders over the duration of the study. With the exception of the 1st week, however, SUP always had larger webs than DEP. For both groups, final web length did not differ significantly from the original, pre-manipulation measurements, in spite of SUP having increased significantly in body size (Fig. 6c).
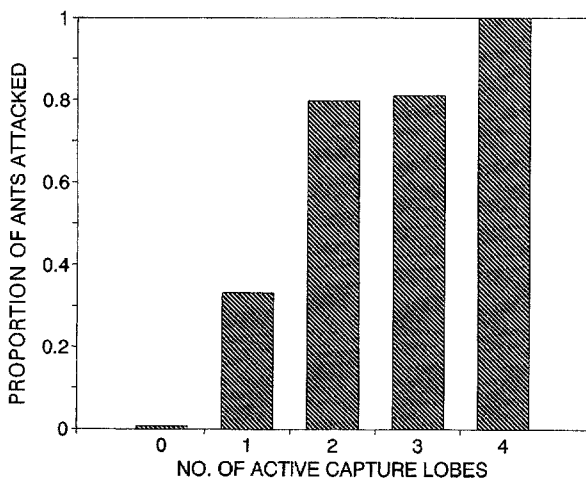
Fig. 6a–d Initial (*I*) and final (*F*) measurements of parameters in the laboratory experiment: **a** body mass, **b** body length, **c** web length, and **d** capture-lobe diameter (*SUP* supplemented, *DEP* deprived of food)

The diameter of the capture lobe also increased with time for all spiders. Final lobe diameter was significantly greater than initial diameter for both DEP and SUP spiders (Fig. 6d). Initial lobe diameter was significantly greater in DEP spiders than in SUP (ANCOVA, covariate = body length, $P = 0.008$), although there was no significant difference in initial body size between the two treatments. Final lobe diameters corrected for body size did not differ significantly between DEP and SUP (ANCOVA, $P > 0.1$), nor did they differ when initial lobe diameter was used as a covariate (ANCOVA, $P > 0.1$).

Discussion

The hypotheses

The results of these experiments support the hypothesis that foraging imposes a cost. The alternative hypotheses (energy maximization and natural satiation) are not supported. The "costs of foraging" hypothesis predicted that animals in a good habitat would reduce their foraging effort, thereby reducing the costs or risks associated with foraging. When prey availability was increased, *S. henscheli* reduced foraging activity by not maintaining an active capture web, whereas the control spiders (NON and UNM) renewed their webs nearly daily and had relatively larger surface webs. In captivity, food-deprived spiders increased their foraging effort by significantly widening the capture lobes.

Increasing lobe diameter by 1 mm increases the length of sticky capture silk by 1.5 mm (Henschel and Lubin 1992).

After only a few prey items, supplemented spiders ceased to forage and there was a rapid decline in the number of active spiders over a period of 12 days. The reduction in foraging activity in food-supplemented spiders was due to (1) long breaks in activity of more than one week and (2) short pauses of 1–2 days. Long pauses may occur before a moult. All of the supplemented spiders increased in body size (prosoma width) indicating at least one moult. In another eresid, *Stegodyphus lineatus*, moulting occurs during a single night, but well-fed spiders may close their nest tube and cease to forage for prey for a week or more before moulting (personal observation). This suggests that cessation of activity long before a moult is a foraging decision rather than a physiological requirement of the moulting process.

The short pauses in activity may occur because time is required to digest the prey or to renew the digestive enzymes before resuming foraging (Riechert and Harp 1987). Alternatively, spiders may stop foraging because, when satiated, the costs of foraging outweigh the expected marginal benefits. While these explanations are not necessarily mutually exclusive, the former suggests the operation of a digestive constraint, the latter a decision based on relative benefits and costs.

What are the costs of foraging for *Seothyra henscheli*, and does reduced activity in this instance indicate a

digestive constraint or a trade-off between additional food and foraging costs? For web spiders, foraging effort is expressed mainly as web renewal or repair. Web maintenance entails recurrent costs for *S. henscheli* (Lubin and Henschel 1990; Henschel and Lubin 1992). The webs are built on sand surfaces that are regularly shifted by wind. Consequently, a spider is faced daily, and sometimes twice a day, with the decision whether to renew the trap by removing the sand and renewing the sticky edges of the capture lobes. Removal of sand from the capture web is accomplished in a few seconds by flicking the sand away from the edges of the capture lobes (personal observation), but the production of cribellate silk may be energetically costly both in the production of silk and in the duration of spinning activity (Lubin 1986).

Predation risk is likely to be an important cost of foraging in this species. Predators may detect the spiders while they are active in web renewal or prey capture, or they may use the web itself as a cue. *Palpimanus* sp. (Palpimanidae), a spider that specializes on other spiders, was observed to attack *S. henscheli* by perching on the edge of the surface mat and plucking the threads to attract the host to the surface. *Palpimanus* sp. was found in burrows of *S. henscheli* (with remains of the host) on eight occasions (Henschel and Lubin 1992). Other predators of *S. henscheli* include gerbils, birds, lizards and other spiders (Henschel and Lubin 1992).

Two indirect lines of evidence suggest that digestive constraints may influence web-renewal decisions. First, a physiological growth constraint is suggested by the comparison of growth in the field and laboratory experiments. Webs in the laboratory were protected from wind and did not require daily renewal. In spite of the additional renewal costs for field supplemented spiders, the rates of mass gain and the final sizes of SUP spiders in the field and laboratory were similar (Figs. 4a, 6a). This supports the idea that food-supplemented spiders in both experiments were growing at the maximal rate and had reached a ceiling in the rate of resource utilization.

Second, in the field experiments, each supplemented spider could have received one large ant every day on which it had a web. However, the spiders actually attacked supplemented ants on only 42% of the days. Assuming that spiders could ingest 50% of each c. 24 mg ant carcass (see Henschel 1994), the potential maximum benefit from ants that spiders attacked was equivalent to 4.4% of a spider's average body mass per day, a potential that spiders apparently did not realize. SUP spiders daily gained 1.8% and 2.15% of body mass in the laboratory and field experiments, respectively. If the daily loss of 0.33% mass by food-deprived laboratory spiders represents metabolic costs, then the actual average daily consumption by SUP spiders was equivalent to 2.2–2.4% of their mass, which is only half the maximum potential supplement. Thus, the spiders

apparently captured more than they consumed, indicating that the ability to utilize additional captured prey rather than foraging costs limited hunting activity in *S. henscheli*.

Consequences of foraging success

Life-history theory suggests that rapid growth increases the chances of survival to maturity, allows early maturation and reproduction, and consequently rapid generation turnover (Stearns 1992). The cost of rapid growth and maturation may be a lower adult body size and consequently lower fecundity (fecundity is generally correlated with adult body size in spiders: Wise 1979, 1993; Vollrath 1987), implying a trade-off between early maturation and fecundity. Does this apply in the case of *S. henscheli*? For *S. henscheli*, more prey may indeed reduce mortality during growth owing to reduced activity on the surface, which will decrease both the exposure to surface-active predators and the likelihood of desiccation. However, given abundant prey, *S. henscheli* not only grew faster and matured earlier, but also had larger absolute mass and larger mass/size than non-supplemented spiders. Thus, when an increase in food results in a change in the growth trajectory, there need not be a trade-off between adult size and time to maturity.

A large body size may be the most important factor determining the number of surviving offspring in *S. henscheli*. *S. henscheli* females guard the cocoon, feed the young, and in the end are eaten by the young (behaviours shared with other eresids; Seibt and Wickler 1987; Schneider 1992). A larger female body mass (as a consequence of living in a rich habitat) may mean both more eggs (Ward and Lubin 1992; J. Schneider and Y. Lubin, to be published) and larger offspring size at dispersal. In *Stegodyphus lineatus*, an eresid spider with a similar life history, an increase of 1 mg body mass for a juvenile female at dispersal corresponded to ten more eggs when the female attained adulthood. This represents up to a 20% increase in fecundity (J. Schneider, to be published). Thus, for *Seothyra henscheli*, being able to acquire more prey will have large direct effects on female fecundity and indirect effects on the survival and the ultimate fecundity of the offspring.

Unlike larger body size, early maturation should not increase fitness in *S. henscheli*. *S. henscheli* is generally annual and semelparous. The timing of the breeding season appears to be regulated by the physical environment (Henschel and Lubin 1992). First, there is a short season (May–July) when cool sand temperatures allow the aposematically-coloured males to move on the surface during the day in search for females. Second, the spiderlings must disperse in early summer (October–November), before sand temperatures become too high for the young spiders to dig burrows

deep enough to escape the surface heat (Lubin and Henschel 1990). Thus, earlier maturation owing to a super-abundant food supply cannot result in earlier reproduction and shorter generation times. In our field experiment, SUP females that matured in February, a full 2 months early, would have to wait for males till May. For a small proportion of *S. henscheli* females that overwinter as subadults or juveniles and reproduce the following year (6–14% at one site; Henschel and Lubin 1992), additional food might ensure reproduction in the 1st year.

The normal consumption rate of non-supplemented (NON) spiders was equivalent to 1.0% of their body mass per day during the 42 day study (average mass gain plus calculated metabolic cost). This is low for a c. 100 mg spider (Edgar 1969, 1970; Humphreys 1975), but comparable to another Namib Desert dune spider, the 1700 mg *Leucorchestris arenicola* that consumes the equivalent of 0.7% body mass per day (Henschel 1994). The low consumption rate for spiders from this hyper-arid region may be due to a low biomass of prey, about two orders of magnitude less than in semi-arid regions (Louw and Seely 1982). However, given the opportunity, *S. henscheli* could more than double its normal intake of food. Likewise, Anderson (1974) found that wolf spiders (Lycosidae) could double their normal food intake in the field when supplemented.

Food-deprived spiders increased their foraging effort by increasing the trapping area of the web, but did not relocate their burrows. Other web-building species were shown to relocate their webs when hungry (e.g. Gillespie 1981; Olive 1982). Web relocation may be a limited option for *S. henscheli* owing to the high cost of constructing a new burrow and web and to the risk of predation during dispersal (Vollrath 1985; Henschel and Lubin 1992). In addition, large spatial and temporal variation in prey is expected to decrease the value of changing foraging site (Janetos 1982). The lack of predictable changes in the abundance of ants at any given web-site may mean that *S. henscheli* cannot expect to improve its access to prey by relocating to a new web site (Lubin et al. 1993). Settling in a prey-poor environment may explain the 81–87% mortality of *S. henscheli* during the interval between dispersal of the young and reproduction (unpublished data from 1988 and 1989).

We conclude that natural populations of *S. henscheli* are food-limited. When food is abundant, spiders can rapidly increase in mass, which allows them to reduce activity, perhaps increase their survival in the long-term and have more and better-fed offspring. Conversely, in a low-prey environment, hungry spiders increase foraging effort, but apparently do not relocate their webs. A certain flexibility of growth, allowing maturation to occur after 2 years rather than after 1 year (personal observation), may be a way to survive long-term shortages of prey. We suggest that poor quality habitats will have a higher proportion of spiders that mature only in their 2nd year. The influence of habitat quality on population dynamics and on variation in life-history traits is currently being examined.

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