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The effect of previous foraging success on web-building behaviour in the sheet-web spider, *Frontinellina* cf. *frutetorum* (Araneae Linyphiidae)

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We examined the influence of previous foraging success on foraging effort in the sheet web spider *Frontinellina* cf. *frutetorum* (Linyphiidae). Foraging effort was estimated via the spider's investment in web construction as indicated by web size. We manipulated previous foraging success by providing spiders with supplementary prey items for 2 days and subsequently removed the webs. Fed spiders were in a better condition than control spiders. However, in contrast to previous studies, supplemented spiders did not reduce their foraging effort. On the contrary, control spiders built smaller webs after web removal, while fed spiders did not reduce the size of their webs. Moreover, we found a positive relationship between spider body condition and web size. We suggest that high energetic demands of web construction as well as web longevity in sheet weavers results in a web-management strategy in which further investment in web size is a positive function of foraging success.

KEY WORDS: state-dependent decisions, food supplementation, foraging effort, sheet-web, body condition, web-building spiders.

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INTRODUCTION

Foraging effort can be viewed as a compromise between the energetic needs of the individual and the costs and risks associated with foraging activity (LIMA & 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 & KACELNIK 1991, PASQUET et al. 1999). In web-building spiders, foraging costs associated with the capture web include the energy required to construct and maintain the web, such as silk production and the costs of activity (TANAKA 1989, UETZ 1992), as well as the risks associated with being exposed while active on the web (RIECHERT & HEDRICK 1990, BLACKLEDGE et al. 2003). The benefit from building a web is derived from prey caught in it. Web size may be considered as a measure of foraging effort, reflecting a trade off between these various costs and benefits (LUBIN & HENSCHEL 1996, VENNER et al. 2000).

Web building behaviour may depend on the body condition of the individual (LUBIN & HENSCHEL 1996), its energetic needs for maintenance, growth and reproduction (HIGGINS 1990) and environmental factors such as prey availability (PASQUET et al. 1994). Several studies of foraging spiders showed that well-fed spiders invest less in web construction (HIGGINS & BUSKIRK 1992, SHERMAN 1994, HIGGINS 1995, LUBIN & HENSCHEL 1996, PASQUET et al. 1999, VENNER et al. 2000). This has been attributed to greater marginal value of prey capture for hungry spiders, which may drive them to build a bigger web than well-fed spiders. However, if the marginal cost of web building is very large, a hungry spider may be reluctant or unable to invest in a larger web, while a well-fed spider will still be able to benefit from building a larger web as a future investment.

We studied the influence of previous foraging success on the foraging effort of the sheet-weaving spider *Frontinellina* cf. *frutetorum*. Sheet weavers such as linyphiids build relatively dense webs that are renewed infrequently, and they do not recycle the web silk (JANETOS 1982, TANAKA 1989). We manipulated the foraging success of the spiders by providing them with supplementary prey items. Foraging effort was estimated by the spider's investment in the web, measured as web size. Our goal was to determine if previous foraging success affects web-building decisions in a spider that does not renew its web daily and has potentially high costs of web building.

METHODS

The study was conducted between 28.IV.2003 and 1.V.2003 in Mt Meron Nature Reserve, upper Galilee, Israel (32°N, 35°E). The climate in the area is Mediterranean, with dry summers and cool, wet winters. Average annual precipitation is 900 mm, January and July average temperatures are 14 °C and 25 °C, respectively (MARKUS 1994). The vegetation is species-rich Mediterranean Oak maquis (*Quercus calliprinos-Pistacia palestina* association) dominated by low evergreen trees. Open spaces between the trees are covered by low vegetation, dominated by spiny shrubs of *Sarcopoterium spinosum* (WAIZEL 1984).

We studied *Frontinellina* cf. *frutetorum* (Linyphiidae), a small spider, 3-6 mm in size and distributed in mesic habitats in central and northern parts of Israel (AMITAI 1987). Specimens were deposited in the National Collection of Arachnids at the Hebrew University of Jerusalem. The spiders build a saucer or bowl-shaped web on bushes or low branches of trees and adults are found from late spring to autumn. Webs of *F. frutetorum* were commonly found in open spaces. All webs that were used in this study were found on *S. spinosum* bushes.

We divided the spiders randomly into two treatment groups: control (n = 27, on which no manipulation was done) and supplementary feeding (n = 27, in which spiders were provided with food items). Spiders in the feeding treatment were provided with two first-instar grasshoppers (*Schistocerca gregaria*) on the first day of the supplementary feeding and two juvenile house crickets (*Acheta domestica*) on the second day. Not all prey items were caught in the web; therefore at the end of the second day we added another cricket to those spiders that did not succeed in capturing previous supplementary prey. Supplemented prey items were larger than natural prey items found in the webs.

After the 2 days of supplementary feeding, we measured leg length (tibia and patella of the first leg) and dorsal-ventral depth of the abdomen in all spiders using digital calipers (precision: ± 0.02 mm). The length of the leg does not change between molts, while the size of the abdomen changes according to body condition. Body condition was calculated as the residuals of abdomen depth regressed against leg length. We did not measure body condition before treatment since the capture severely damages the webs and stresses the animals, which could cause them to abandon their webs. But since spiders were randomly assigned to treatments we assumed that any difference found between the treatment groups would be the result of the feeding manipulation. We marked all spiders individually with coloured dots on the abdomen, using water-based paint. We then removed all the webs. On the next day we searched for the webs of the colour-marked spiders.

Webs were measured three times during the study. We measured the length and width of the sheet-web to a precision of ± 0.5 cm, using a ruler. Web size was calculated as an ellipse using the formula: web size = (web length/2) * (web width/2) * π. The measurements were taken as follows:

1. the first day prior to the first feeding event (*pre-treatment web size*);
2. the third day, after the end of the feeding treatments and before the removal of the webs (*post-treatment web size*);
3. the fourth day, after locating the colour-marked spiders that rebuilt their webs at or near the location of their old webs (*rebuilt web size*).

We used t-test to compare body condition between the treatment groups. We used ANCOVA to compare pre-treatment, post-treatment and rebuilt web size between the treatment groups, with leg length and previous web size as a covariate. For pre-treatment web size, we used only leg length as a covariate, as this was the first measurement of web size. Additionally, we compared webs before and after the treatment and post-treatment to rebuilt webs by means of paired t-tests, for each group separately. Regression analysis was used to examine the relationship between body condition and web size.

RESULTS

Most of the webs were of adult females (n = 31); some were of juveniles (n = 14) and only few of adult males (n = 9). Since only a few males (n = 4) and juveniles (n = 3) built a new web after web removal, we analysed the female data only.

Eight out of 15 females from the control group and nine out of 16 from the feeding treatment group stayed in the same location throughout the experiment and rebuilt a new web. There was no significant difference between these groups in the proportion of spiders that stayed (Chi square, $\chi_1^2 = 0.027$, $P = 0.870$).

The body condition of fed spiders was significantly higher than that of control spiders (Fig. 1, t-test, $t = -4.320$, $P < 0.001$, n = 31).

We found no significant difference between control and fed spiders in the size of pre-treatment, post-treatment and rebuilt webs (ANCOVA, $F_{1,28} = 0.101$, $P = 0.753$;

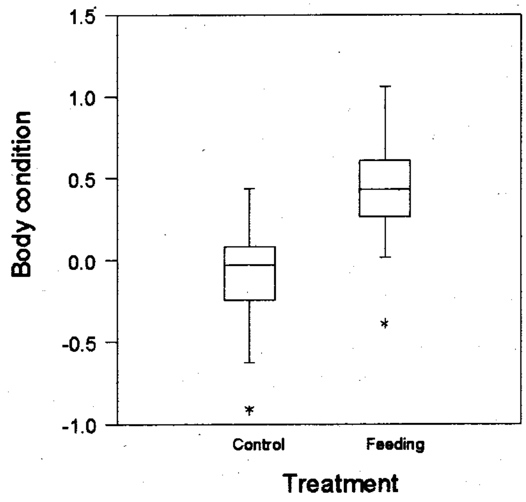

Fig. 1. — The body condition of females in the treatment groups. Control group, n = 15; Supplementary feeding group, n = 16. The body condition of fed spiders is significantly higher than that of control spiders (t-test, t = – 4.320, $P < 0.001$). The data are presented as box plots showing: medians (horizontal line), upper and lower quartiles (boxes) and range of the points that fall between the boundaries of 1.5 * the difference between the upper and the lower quartiles (whiskers). Asterisks are outliers that fall outside these boundaries.

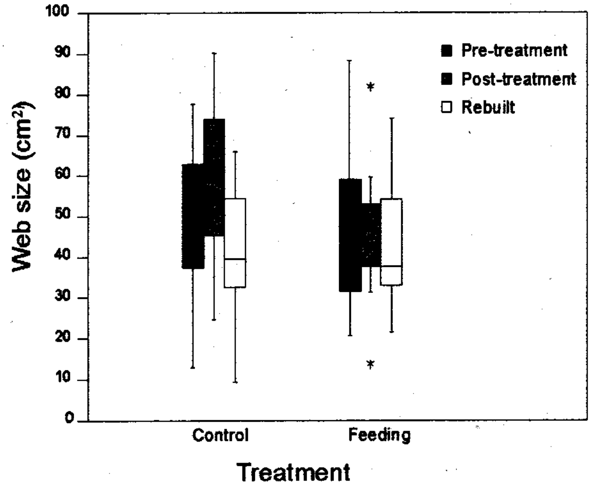

Fig. 2. — The size of pre-treatment, post-treatment and rebuilt webs in the different treatments (only spiders that rebuilt). Rebuilt webs are significantly smaller than post-treatment webs in control spiders (paired t-test, t = 4.435, $P = 0.003$, n = 8), but not in fed spiders (paired t-test, t = 0.960, $P = 0.365$, n = 9). The data are presented as box plots (see Fig. 1).

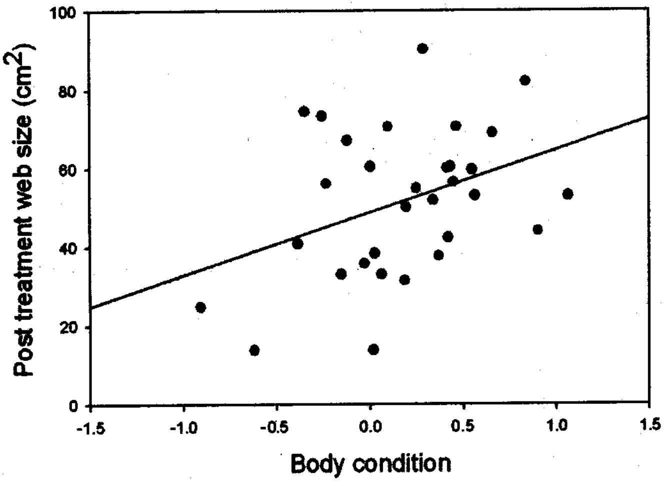

Fig. 3. — Regression analysis of post-treatment web size versus body condition (residuals of abdomen depth regressed against leg length) of adult females (control and fed groups combined, n = 31, $R^2 = 0.108$, $F_{1,29} = 4.630$, $P = 0.04$). See text for details.

$F_{1,27} = 0.017$, $P = 0.898$ and $F_{1,13} = 2.105$, $P = 0.171$ respectively). Leg length (covariate) did not influence web size in any of the stages of the experiment, but there was a significant influence of pre-treatment on post-treatment web size ($F_{1,27} = 11.505$, $P = 0.002$) and of post-treatment on rebuilt web size ($F_{1,13} = 17.240$, $P = 0.001$).

In paired comparisons of web size within each treatment group, there was no significant difference between pre-treatment and post-treatment for the control spiders (paired t-test, t = – 1.123, $P = 0.281$, n = 15) or the fed spiders (paired t-test, t = 0.928, $P = 0.368$, n = 16). Rebuilt webs, however, were significantly smaller than post-treatment web size in control spiders (paired t-test, t = 4.435, $P = 0.003$, n = 8), but not in fed spiders (paired t-test, t = 0.960, $P = 0.365$, n = 9) (Fig. 2).

Pooling data from both groups, we found a significant positive relationship between body condition and post-treatment web size (Fig. 3, $R^2 = 0.108$, $F_{1,29} = 4.630$, $P = 0.04$).

DISCUSSION

The disappearance of spiders during the experiment may have been due to predation, web relocation or both. Sheet weavers do not often relocate their webs (Janetos 1982). In this case the spiders may have relocated more often due to our disturbance. Spiders that were supplemented with prey disappeared with the same frequency as the unfed control spiders. Several studies have shown that spiders relocate less frequently when food is abundant (Vollrath 1985, Hodge 1987). Other studies have shown a random pattern of relocation with regard to food availability (Vollrath & Houston 1986, Kareiva et al. 1989), or even more frequent relocation when food is abundant (CARACO & GILLESPIE 1986, WARD & LUBIN 1993). In our case it seems that spiders disappeared regardless of previous foraging success (see also review by UETZ 1992).

Spiders that were provided with prey for even a short period of two days were in better body condition than the unsupplemented, control spiders. However, fed spiders did not reduce their foraging effort. On the contrary, we showed that the reduction in web size was smaller for the well-fed spiders than for control spiders. Moreover, we found a positive relationship between spider body condition and web size. These data are in contrast to the results of other studies where well-fed spiders reduced their foraging effort by reducing their web size. Several studies were done on orb-web spiders (HIGGINS & BUSKIRK 1992, PASQUET et al. 1994, SHERMAN 1994, HIGGINS 1995, VENNER et al. 2000). Orb weavers usually renew their webs daily, eat and recycle the silk (TANAKA 1989, FOELIX 1996). A similar trend was found in eresid spiders (LUBIN & HENSCHEL 1996, PASQUET et al. 1999), which also construct renewable sticky webs, although in the latter case the sticky silk is not necessarily renewed daily.

There are several factors that may account for the differences between our data and these previous studies. First is the longevity of *F. frutetorum* webs. Since sheet weavers do not renew their webs frequently, the size of the web does not directly reflect the current state of the spider. Instead, web size may reflect the sum of experiences over a period of time, as well as investment in the future, taking into account the expected longevity of the current web. Secondly, the high energetic cost of building a sheet web may prevent a spider in poor body condition from investing in a large web. Well-fed spiders, however, might build larger webs as a future investment. In contrast, for an orb weaver, the cost of building a web is relatively low (JANETOS 1982, TANAKA 1989) and this may allow an orb web spider to invest in a larger web in spite of being in poor condition. BLACKLEDGE & WENZEL (2001) found no difference in the total area of silk added to webs by well-fed spiders compared to poorly fed spiders of *Dictynidae voucripes* (Dictynidae). These spiders build tangle webs, which like webs of linyphiids are constructed over many days and require high energetic investment. Thirdly, linyphiids lack a refuge or retreat, unlike nest-building spiders such as eresids. The linyphiid sheet-web itself functions as a refuge as well as for catching prey (BLACKLEDGE et al. 2003). A larger sheet web may increase the ability of the spider to avoid predators. As a consequence, a well-fed spider may be stimulated to build a bigger web although the marginal value of web building, in terms of food, may be relatively low. Finally, it is possible that supplementary feeding over a longer period of time with repeated measurements of rebuilt webs would have resulted eventually in a reduction in the investment of the well-fed spiders in their webs. SHERMAN (1994) studied changes in web size after prey consumption in the orb-weaving spider, *Lariniodes cornutus*. He showed that spiders maintained a relatively large web area for the first web built after consumption of prey, while the area of successive webs continued to drop. Sheet weavers do not renew their webs daily but they might enlarge the web by adding silk. Thus, well-fed spiders may have added less silk than control spiders in the following days after the experiment. However, this is an unlikely explanation for the larger webs of the food-supplemented individuals, because a positive relationship was found between body condition and web size prior to the removal of the webs. It seems that, in this species, spiders in better condition do build bigger webs.

What determines the size of the sheet web in *F.* cf. *frutetorum*? The positive relationship between the size of the post-treatment web and the size of the rebuilt web, but not between leg length and the size of the rebuilt web suggests that variation in web size among individuals is affected by the cumulative foraging experience of the spider. Therefore recent foraging success may allow the spider to adjust its web size but it does not replace the cumulative effect of past foraging experience. This may be especially true in sheet weavers whose webs are not renewed frequently.

In conclusion, we found that well-fed spiders did not reduce their foraging effort, measured as the size of the capture web. Moreover, we found a positive relationship between body condition of the spiders and the size of the web. We suggest that high energetic demands of web construction as well as web longevity in sheet weavers results in a web-management strategy in which further investment in web size is a positive function of foraging success.

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