State-determinate foraging decisions and web architecture in the spider *Dictyna volucripes* (Araneae Dictynidae)

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Foraging behaviors result from dynamic trade-offs made by organisms, incorporating factors such as past foraging success, reproductive effort, and predation risk. But, decision-making by animals occurs with incomplete information about the environment. We examined the relationship of web architecture and foraging decisions in the tangle web-building spider *Dictyna volucripes* Keyserling, a common spider in North American fields. Tangle webs are constructed over many days, which increases the total material and energetic investment in webs compared to orb-webs that are rebuilt daily. This reduces the profitability of changing web sites for tangle web spiders, making decisions about allocation of resources to foraging within single patches critical. We studied how foraging success affected investment in webs for High Prey spiders, fed two *Drosophila* daily, and Low Prey spiders, fed half that amount, over a 9-day period. We found no difference in the total area of silk added to webs. Increase in web area was proportional to initial web size in High Prey spiders, all of which increased webs by approximately 50%, despite substantial variation in initial sizes of webs. But, some Low Prey spiders with small initial webs increased web size by 200-300% while others, with large initial webs, invested proportionately little silk in webs. We also compared the effects of web architecture on prey capture of High and Low Prey spiders, under standardized prey density. There was no difference between High and Low Prey spiders in the number of *Drosophila* captured. We found a significant positive correlation between sizes of webs and prey capture in High Prey spiders but not in Low Prey spiders. We present the hypothesis that web investment by *D. volucripes* may incorporate information about both previous foraging effort and foraging success.

KEY WORDS: foraging theory, silk, sit-and-wait predator, spider web, state-dependent decisions, trade-off.

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INTRODUCTION

Foraging decisions can be based upon many factors such as degree of satiation, availability of prey, risk of predation, and reproductive effort (STEPHENS & KREBS 1986). Allocation of resources becomes particularly important when animals are energetically stressed and are forced to make trade-offs that can have important fitness consequences (SIH 1980, PIANKA 1981, STEPHENS & KREBS 1986, MCNAMARA & HOUSTON 1987). However, organisms must make these decisions under perceptual constraints and with imperfect knowledge of their environment (REAL 1991, BEACHLY et al. 1995, NISHIMURA 1999). In particular, it may be difficult for animals to evaluate if poor foraging success is due to foraging in a poor quality patch, to foraging in a good quality patch that has high temporal variability, or to lack of sufficient foraging effort in an otherwise high quality patch. Thus, it is important to examine how organisms confront this uncertainty when allocating resources to foraging.

Spiders are dominant intermediate level predators in most terrestrial ecosystems (TURNBULL 1973, WISE 1993). And, web-building spiders are convenient models with which to study foraging decisions because spider webs are quantifiable measures of foraging effort. Often, hungry animals will invest more effort in foraging and take greater risks than satiated animals (LIMA & DILL 1990, SIH 1992, SKUTELSKY 1996). For example, satiated orb-weaving spiders are more likely to include defensive structures in webs, such as stabilimenta, that might reduce prey capture (BLACKLEDGE 1998, BLACKLEDGE & WENZEL 1999) or to reduce the length of foraging bouts (HIGGINS & BUSKIRK 1992, BRADLEY 1993). Satiated orb-weaving spiders are also less likely to make risky moves to new habitats (VOLLRATH 1985). Finally, hungrier orb-weaving spiders increase investments in foraging by building larger orb webs (HIGGINS & BUSKIRK 1992, PASQUET et al. 1994, SHERMAN 1994).

Unlike most spiders that build webs, orb-weaving spiders typically remove and rebuild webs each day, allowing these spiders to efficiently change foraging patches. Orb webs also have highly stereotyped architectures (EBERHARD 1986). Instead, most web-building spiders construct irregular tangle or sheet webs (EBERHARD 1990). Tangle webs are constructed over periods of many days, increasing the total material and energetic investment in a single web (FORD 1977, TANAKA 1989). This can reduce the profitability of changing sites for tangle web spiders (JANETOS 1982), making decisions about allocation of resources to foraging effort within a single patch critical. Yet, few researchers have examined how tangle- or sheet-weaving spiders manipulate foraging effort through changes in webs (e.g. LUBIN & HENSCHEL 1996, PASQUET et al. 1999). Our study examines how foraging success affects investment in web architecture and how architectural variation in webs affects prey capture in *Dictyna volucripes* Keyserling, a common tangle web-building spider in eastern North American fields.

METHODS

Adult female *D. volucripes* were collected from fields in Columbus and Marion, Ohio, USA in early June, 2 weeks prior to the experiment. Webs were commonly found on the tips of dead, dry plants (Fig. 1A). We collected spiders by removing all parts of the plants and webs, except for the 1-2 cm retreats, which contained the adult spiders, egg sacs, and young. We then placed individual retreats, containing spiders, on artificially constructed "trees" as web substrates. A total of 50 spiders, each on a separate tree, were allowed to rebuild their webs in the field for 2 weeks prior to the experiment. Twenty-five had established webs at the start of the experiment and we brought those trees into the Insectary at Ohio State University, Columbus, Ohio.

The trees. Much of the variation in architectures of dictynid webs is due to variation in the shapes of sticks, flower heads, and other dried plant materials upon which dictynids typi-cally build webs (Bond & Opell 1997). Therefore, we placed all of our spiders on standard-ized trees, constructed from 5 mm diameter, 80 cm long, wooden dowel rods and toothpicks (Fig. 1B). Four rows of toothpicks were glued to a dowel at 90° angles to one another. Each row consisted of four toothpicks, each 35 mm apart. In addition to controlling for the effect of substrate shape on web construction, this design confined spiders to build webs in two orthogonal planes, allowing us to characterize webs along "North" and "West" axes.

Web architecture. We brought spiders into the insectary at Ohio State University so that their prey capture could be controlled (15 June 1998). Temperature and sunlight were near outdoor levels and webs were sprayed with water each morning. We randomly assigned spi-ders to either a High Prey or Low Prey group. High Prey spiders were fed two *Drosophila melanogaster* each day for nine days while Low Prey spiders were fed two *D. melanogaster* on days one, five, and 9 (approximate dry weight = 200 μg/fly). All of the *D. melanogaster* were wingless and were placed directly into webs using a moist paintbrush.

We photographed webs along North and West axes on day one (prior to the initial feed-ing) and day ten of the experiment, allowing us to compare initial and final web architecture. We estimated web area by measuring the distance along each toothpick covered by cribellate capture threads and then summing the areas of the polygons thus outlined (Fig. 1B). Occa-sionally, spiders suspended a few lines of silk at the distal ends of toothpicks that did not
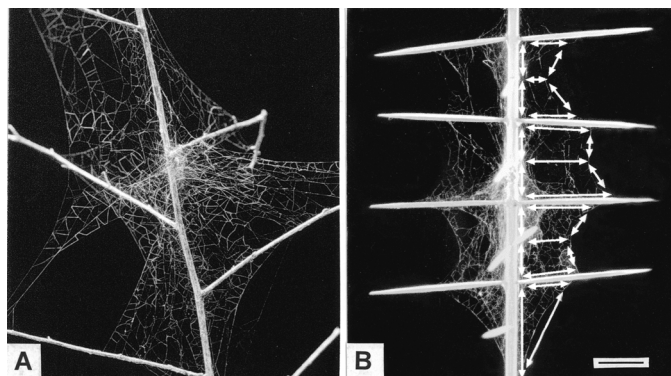

Fig. 1. — *Dictyna* spp. webs. A, natural web of *Dictyna* sp. from field site. B, web of *D. volucripes* on artificial tree. Arrows denote some of the polygons used to measure web area. Notice the simi-larity of both the web building substrate and the structure of the web to that of (A). Scale line = 20 mm.

connect to any capture thread, but we only measured webs to the most distal areas containing cribellate capture silk. We used an ANCOVA to compare the change in web area between High and Low Prey treatments, with initial web area as the covariate. Regressions were used to examine the relationship of initial web area to absolute and proportional (% of initial size) change in web area within each treatment.

Prey capture. We also examined the effect of web size on prey capture. After photographing webs on the final day of the Web Architecture experiment, we moved all of the trees into a $3 \times 4 \times 3$ m screened enclosure and arrayed them in a random order along the periphery. We then opened three cultures of winged *D. melanogaster* in the center of the room and monitored the prey capture of each spider every 15 min for 2 hr. Small diptera are common prey of dictynids (Jackson 1977). We used an ANCOVA, with final web area as the covariate, to compare the number of fruit flies captured between High and Low Prey treatments. Regressions were used to examine the effect of web size on prey capture within each treatment.

After the prey capture experiment, we collected spiders and retreats into 70% ethanol. We dried and weighed spiders to the nearest μg, using a Mettler UMT balance. We dissected retreats and counted the total number of winged *D. melanogaster* contained therein to verify our visual counts during the prey capture experiment. We also counted the total number of egg sacs in each retreat, though this included egg sacs produced prior to the start of the experiment.

Table 1.

Effect of foraging success on web architecture and subsequent prey capture for *D. volucripes* in High and Low Prey treatments.

	High prey (n = 11)	Low prey (n = 12)	P
Initial web size (cm^2)	91.3 ± 12.9	89.3 ± 15.0	NS[1]
Increase in web size (cm^2)	45.6 ± 9.8	58.4 ± 7.8	NS[2]
Total egg sacs in retreat	4.5 ± 0.4	4.7 ± 0.3	NS[1]
D. melanogaster captured	2.9 ± 0.7	1.9 ± 0.3	NS[2]
Final dry weight of spiders (μg)	1035 ± 95	944 ± 85	NS[1]

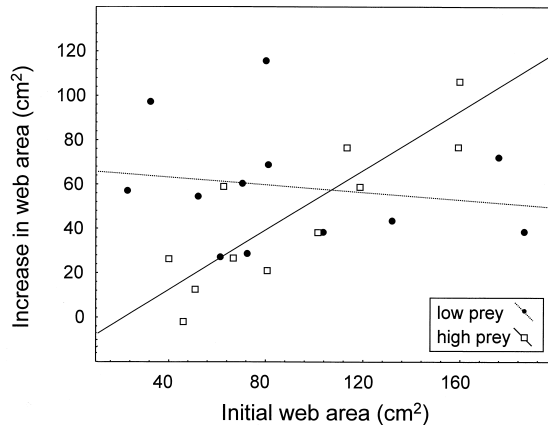[1] *P*-value from t-test. [2] *P*-value from ANCOVA.

Fig. 2. — Relationship between initial sizes of webs and absolute increases in size during the experiment. There was no difference between treatments in the total amount of silk added to webs (ANCOVA, $F_{1,20} = 1.18$, NS). Initial web size was significantly related to increase in web size for High Prey spiders ($R^2 = 0.727$, $F_{1,9} = 24.00$, $P < 0.001$) but not for Low Prey spiders ($R^2 = 0.036$, $F_{1,10} = 0.38$, NS).
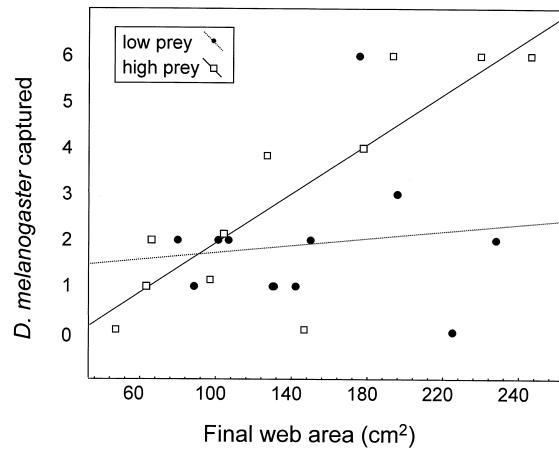
Fig. 3. — Relationship between sizes of webs and prey capture over 2 hr when all webs were placed within an enclosure containing *D. melanogaster*. There was no difference between treatments in the number of flies captured (ANCOVA, $F_{1,20}$ = 3.06, NS). Prey capture was related to web size in High Prey spiders (R^2 = 0.709, $F_{1,9}$ = 21.94, P < 0.005) but not in the Low Prey spiders (R^2 = 0.014, $F_{1,10}$ = 0.14, P < 0.717).

RESULTS

Web architecture. Size of webs did not differ between treatments at the start of the experiment (Table 1). In both treatments, webs increased in size during the experiment, and there was no difference between treatments in the magnitude of that increase (Table 1). However, the relationship of initial web area to increase in web area did differ between Low and High Prey spiders (Fig. 2). Linear regression showed that much of the variation in web size increase was explained by the initial size of webs in High Prey spiders (R^2 = 0.727, $F_{1,9}$ = 24.00, P < 0.001) but not in the Low Prey Treatment (R^2 = 0.036, $F_{1,10}$ = 0.38, NS).

Prey capture. There was no difference between treatments in the number of *D. melanogaster* captured (Table 1). The number of flies captured varied with web area in High Prey spiders but not in Low Prey spiders (Fig. 3). Linear regression showed that much of the variation in prey capture was explained by the sizes of webs in High Prey spiders (R^2 = 0.709, $F_{1,9}$ = 21.94, P < 0.025) but not in Low Prey spiders (R^2 = 0.014, $F_{1,10}$ = 0.14, NS).

DISCUSSION

The ability of web-building spiders to function as predators is intimately linked to production of webs. Orb-weaving spiders can manipulate the sizes (WITT 1963, HIGGINS & BUSKIRK 1992, SHERMAN 1994) and architectures (EBERHARD 1986, CRAIG 1987) of webs as either evolutionary or behavioral responses to changes in prey density or type. Previous work on sheet web-building eresids *Seothyra hensheli* Dippe-

naar and *Stegodyphus lineatus* (Latreille) found that hungrier spiders built larger webs (Lubin & Henschel 1996, Pasquet et al. 1999). Yet, little is known about how most web-building spiders manipulate webs in response to prey (Eberhard 1990).

We examined how a cribellate tangle web spider, *D. volucripes*, responded to short-term variation in prey capture through changes in web architecture. We found no difference between treatments in the area of silk added to webs over the 9 days of our experiment (Table 1). However, investment in new webbing was proportional to the amount of existing web in High Prey spiders (Fig. 2), as all individuals increased web area by about 50%, even though initial web area varied within the High Prey treatment by as much as 400%. Low Prey spiders were more variable. Low Prey spiders with the largest initial web sizes increased web size by about 20-80% during the experiment, an increase similar to that of High Prey spiders, while the two Low Prey spiders with the smallest initial webs increased web area by 250% and 300% respectively and four others with small webs also had increases in web area that were large enough to fall outside of the 95% confidence interval predicted by High Prey spiders.

We were unable to relate any of the differences in web investment between or within treatments to sizes of spiders (measured as cephalothorax width), dry mass of spiders, or body condition (as calculated by Pasquet et al. 1999). However, our measurement of dry mass cannot be taken as an unbiased measure of foraging status during the web architecture experiment because spiders were able to ingest an uncontrolled amount of prey during the prey capture experiment.

Spiders are generally considered to be food-limited predators (Anderson 1974, Riechert & Luczak 1982, Wise 1993). There are at least three reasons why spiders, or any other predator, may catch fewer than a sufficient number of prey at a site. (1) Spiders may be foraging in a poor quality habitat and could increase foraging success by moving to a higher quality site. (2) Average patch quality may be high but also exhibit high temporal variability, requiring spiders to wait out periods of below normal prey capture. (3) Patch quality may be adequate but the foraging efforts of spiders too low to catch available prey, which can be alleviated by increasing foraging effort.

Once *D. volucripes* had established webs on the "trees" in the field, they showed great site fidelity. Only two of 25 individuals dispersed from webs during the experiment. This suggests that these tangle web-building dictynids may not respond to variation in prey density by changing sites as readily as do some orb weavers (Janetos 1986). Turnbull (1964) found that immature tangle web-building theridiids (*Achaearanea tepidariorum*) changed sites readily until prey capture was sufficiently high when initially released within a room. But, Turnbull did not examine if spiders in established webs would also change sites, and studies on both eresids and linyphiids suggest that non-orb web spiders have a high degree of site fidelity (Leclerc 1991, Pasquet et al. 1999). This suggests the hypothesis that individual spiders might have had two different behavioral responses available with which to confront low prey capture in our experiment. Some spiders may have used a "foraging intensive" strategy where increased investments in webs allowed spiders to better intercept available prey, at the expense of current protein and energetic resources. This strategy may be particularly likely if spiders have previously invested relatively little in webs. Other spiders may have adopted a "foraging conservative" strategy where spiders either decreased metabolism to wait until prey density increased (Anderson 1974, Nakamura 1987) or allocated resources to reproduction (Higgins 1990, Sherman 1994), both at the expense of webs.

Because spiders cannot know why they are not catching prey, we suggest that individuals in the Low Prey treatment adopted one of two different strategies, based in part upon an assessment of their previous foraging effort (i.e. amount of silk in webs). In particular, the two Low Prey individuals with the smallest initial webs showed the disproportionately largest investments in silk during our study. In contrast, Low Prey individuals with relatively larger initial investments in foraging (i.e. larger initial web sizes) did not show a disproportionately large increase in webs. In fact, two of the three Low Prey individuals with the largest initial webs also showed the smallest proportionate increase in webs during the experiment. Thus, spiders with small initial investments in webs might have adopted the "foraging intensive" strategy while spiders with large initial investments might have adopted the "foraging conservative" strategy. However, we have no data to specifically address whether or not the metabolism of spiders varied with investment in webs. We were also not able to quantify directly the reproductive efforts of spiders during the experiment because we could not reliably distinguish egg sacs laid prior to the experiment from those produced during the web architecture experiment.

Manipulation of investment in webs as a means to alter foraging effort requires that web architecture affects prey capture. We found a strong relationship between number of prey captured and size of webs, under standardized prey density, for High Prey spiders (Fig. 3). Therefore, *D. volucripes* can manipulate foraging effort in a predictable manner by altering web architecture. There was no clear relationship between web size and prey capture in Low Prey spiders (Fig. 3). The generally poor prey capture by these spiders might be explained by differences in investment in webs between Low Prey individuals during the web architecture experiment. Webs built by spiders adopting a "foraging intensive" strategy were relatively small (due to their initial small size) but contained a high percentage of fresh silk while those of spiders adopting a "foraging conservative" strategy were relatively large (due to their initial large size) but had little fresh silk. Although cribellate capture silk can retain stickiness for long periods in the laboratory (OPELL 1993), silk in the Insectary during our experiment seemed to be quickly coated with dust and debris as silk spun on the previous day appeared much thinner and less visible than did older silk (pers. obs.). Therefore, larger webs were likely to encounter more prey but retain prey poorly whereas smaller webs with lots of fresher silk encountered fewer prey but were stickier, so that neither strategy resulted in optimal prey capture once prey density was "increased".

We have shown that *D. volucripes* adjust their web architecture based upon previous foraging success. Unlike many studies (HIGGINS & BUSKIRK 1992, PASQUET et al. 1994, SHERMAN 1994, LUBIN & HENSCHEL 1996), we did not find that hungrier spiders invested overall greater amounts of silk in webs. Instead, High Prey spiders invested a proportionately constant amount of silk in webs while the amount of silk invested in webs by Low Prey spiders was more variable. Some Low Prey spiders with small initial webs invested large amounts of silk in webs (200-300% increases) while others, with large initial webs, invested a very little new silk in webs. This suggests that *D. volucripes* may use previous foraging effort (measured as web size), as well as previous foraging success (measured as prey captured), when making foraging decisions. These results may be a consequence of the interdependence of future web architecture on the state of the current web, which is not removed daily as are orb webs. This allows tangle web spiders to maintain a certain level of foraging investment without further energetic input (i.e. by adding little new silk to

their webs). However intriguing, the potential state-dependent nature of investment in webs by spiders needs to be more rigorously examined.

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