*Anim. Behav.*, 1994, **48**, 19–34

# The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies

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*(Received 2 February 1993; initial acceptance 8 April 1993; final acceptance 7 May 1993; MS. number: A6461R)*

**Abstract.** This field study analyses reasons behind the changing, nightly web dimensions of the orb-weaving spider *Larinioides cornutus* (Araneidae), thereby providing insight into this species' dynamic foraging strategies. The investigation contrasts with earlier studies which have generally assumed web parameters of individuals to remain constant, constrained by species-specific design patterns. Three web dimensions, area of the catching spiral, total thread length, and mean mesh size, were measured for webs built before and after experimentally supplemented prey consumption and egg production. Nightly variations in web dimensions suggest that hungry spiders invest more effort into foraging, while sated spiders re-allocate energy from continued foraging to egg production. These data demonstrate that the foraging plasticity of individual orb-weavers is greater than previously presumed. More generally, the data lend support to a seldom-tested tenet of optimal foraging theory: the direct relationship between foraging success and enhanced reproductive fitness.

Variations in the structure and design of spider webs have been extensively researched, but historically constrained by the implicit assumption that biologically meaningful variations in spider web construction exist primarily at, or above, the species level. By neglecting conspicuous variations in web morphology between or even within individuals, arachnologists have overlooked an important and poorly understood area of study: individual behavioural plasticity in orb-weaver web construction.

In 1963, Peter Witt first challenged the long-held assumption that a spider's orb-web construction was limited to genetically controlled species-specific design patterns (Savory 1952; Witt & Baum 1960; Risch 1977; Levi 1978; Foelix 1982; Shear 1986). Since Witt's (1963) laboratory study of *Araneus diadematus* (Araneidae) (republished in Witt et al. 1968), other researchers have begun to recognize and investigate web-design variations (Eberhard 1990). Yet, nearly 30 years after Witt's first attempt, Eberhard (1988, 1990) concludes that we are far from knowing the full story behind these variations for even a single species of orb-weaver. Despite the many studies of intraspecific web-design variations, Witt's 1963 laboratory investigation remained, until recently, the only published study to longitudinally examine an individual orb-weaver's web-building response to variable prey environments.

Higgins (1990) and Higgins & Buskirk (1992) have brought the discussion of longitudinal variation in web dimensions for individual spiders back to the topic of energetics. Higgins (1990) conducted field research on the changing foraging investments over time of individual *Nephila clavipes* (Tetragnathidae). She investigated how changes in orb size are associated with moulting and egg production, and found that webs built just prior to moulting and egg production decreased in diameter while mesh size remained unchanged. Higgins & Buskirk (1992) also asserted that spiders experiencing low foraging success constructed larger webs, contradicting Witt's (1963) hypotheses. Although variation in an individual's orb-web design and the underlying causes remain poorly understood, these recent studies, and others addressing behavioural plasticity of animals, strongly argue that individual variation appears to be the rule rather than the exception (for a review see West-Eberhard 1989).

## The Natural History Context for Orb-weaver Behavioural Plasticity

For many orb-weaving spiders, the web represents the primary means of prey capture. To

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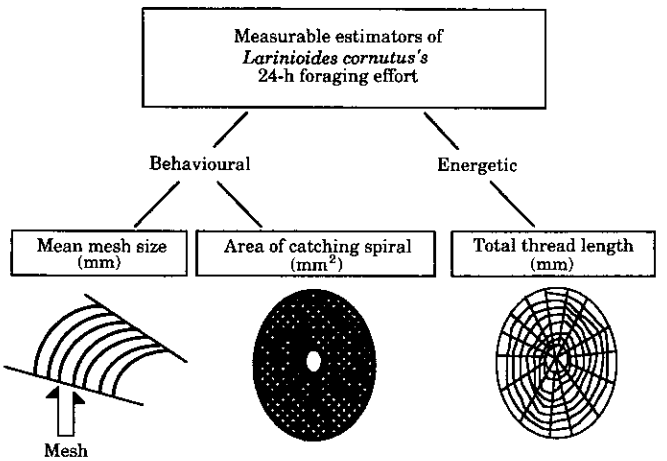


**Figure 1.** The three web dimensions focused upon in this study represent measurable estimators of *L. cornutus*'s 24-h foraging effort. Total thread length represents the material (energetic) investment in a given web by a spider. For any given thread length, spiders can behaviourally manipulate the mesh size and area of the catching spiral of their webs by varying web construction and design. Therefore, these two web dimensions represent estimators of a spider's behavioural investment into its 24-h foraging effort.

ensure a renewed, effective prey capture surface every 24 h, several species of nocturnal orb-weaving spiders, including *Larinioides cornutus* (Araneidae), ingest their previously built web and replace it with a new one nearly every night (Breed et al. 1964; Eberhard 1971; Carico 1986). This renewal is critical because a web's ability to capture food decreases over time as prey and non-prey items contact and destroy both threads and glue (Chacón & Eberhard 1980). By recycling their web's proteins ($\leq$95% efficiency, Peakall 1971; $\leq$32% efficiency, Townley & Tillinghast 1988), spiders make an otherwise energetically costly foraging strategy more affordable. Even so, the web represents a majority of a spider's daily energetic output (Peakall & Witt 1976; Prestwich 1977).

A spider's foraging benefits, costs, and perhaps ultimately, reproductive fitness, may rely in part upon the individual's specific choice of nightly web-design dimensions. Many orb-weavers use their webs to filter flying prey from the air column (Denny 1976; for a conflicting view see Chacón & Eberhard 1980; Eberhard 1986). Which prey type a spider's web will strain from the air depends upon many different factors of that web's design (Uetz et al. 1978; Olive 1982; Eberhard 1986), material (Eisner et al. 1964), and spatial (Janetos 1986) or temporal placement (Ward & Lubin 1992). These web parameters presumably associate with different construction and metabolic costs, although these associations are poorly understood. As benefits and costs vary with different sized webs, theories of optimal foraging would predict that variations found between webs built by an individual should be non-random. How, and why, *L. cornutus* varies its nightly web design, constitutes the subject of this study.

### Interpreting the Orb-web

To more adequately understand an orb-weaver's particular foraging strategy, I use parameters of the orb-web itself as quantifiable estimators of the spider's nightly investment into foraging. For any given web or sequence of webs, the energetic and behavioural investments a spider makes into foraging can be estimated by measuring the total thread length, area of the catching spiral, and mean mesh size (Fig. 1). The 1-h period during which an orb-weaver replaces its web, represents a majority of this sit-and-wait predator's 24-h energetic commitment to foraging (Peakall & Witt 1976; Ford 1977; Prestwich 1977; Tanaka 1989). Web-building has two primary costs: the actual production of silk proteins and the motor costs of construction (Eberhard 1986). Eberhard (1986) refers to these costs as the

'material' and 'behavioural' costs of web production, respectively. Eberhard's terminology differs from that used in this paper. Here, both the 'material' (thread production) and the 'behavioural' (increased metabolic rates associated with thread placement) are considered components of the individual's total 'energetic' investment into foraging.

Spiders can influence the energetic (protein) costs and benefits of foraging by varying their investment of thread during web production. Constructing webs with less thread may save a spider energy, but only with the associated costs of a decreased probability of foraging success caused by a concomitant reduction in the prey capture surface area. On the other hand, spiders building webs with more thread can increase their probabilities of prey capture, but only by increasing their production costs as well. Therefore, the total thread length of a web can be used to represent a spider's energetic commitment to foraging (Peakall & Witt 1976; Ford 1977; Prestwich 1977; Eberhard 1986; Tanaka 1989).

Additionally, a spider can behaviourally manipulate its invested thread length by adjusting the silk density (mesh size) to produce variably sized snares. Changes in web area (Higgins & Buskirk 1992) and mesh size (Uetz et al. 1978) presumably also influence prey capture probabilities. In this way, both the area of the catching spiral and mean mesh size represent a spider's behavioural commitment to foraging. These three web dimensions are interrelated so that, for example, larger webs can be produced by: (1) increasing thread production while maintaining mesh size, (2) widening mesh size while maintaining thread length, or (3) altering both thread length and mesh size. Data presented will show that *L. cornutus* demonstrate all three web manipulation strategies as their foraging and reproductive needs change.

Individual *L. cornutus* were monitored from a field population in upstate New York. Area of catching spiral, total thread length, and mean mesh size were measured for each web built. Changes in these three web parameters from one web to the next indicate that spiders do not simply produce a static web size each night as often previously assumed. I hypothesized that spiders fine tune their web dimensions to meet their changing energetic needs such that web dimensions would be affected by both feeding (an energetic gain) and egg production (an energetic expenditure). More specifically, I tested the following hypotheses.

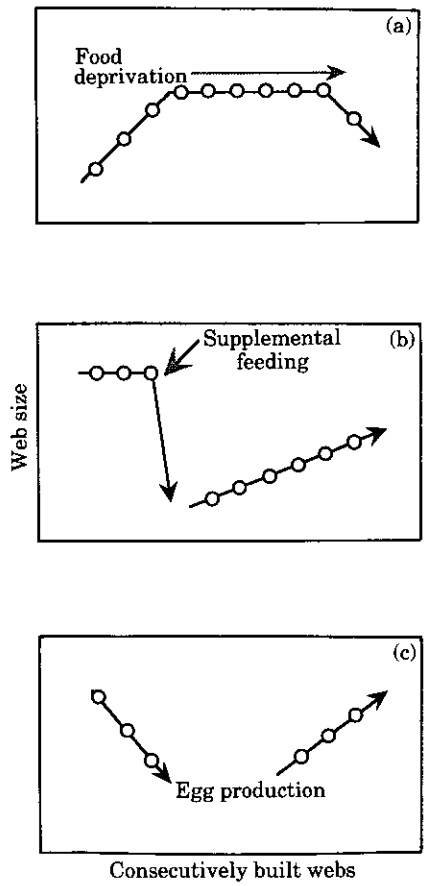


**Figure 2.** Hypothesized changes in the size of consecutively built webs for orb-weaving spiders as a function of (a) food deprivation, (b) foraging success and (c) egg sac production.

(1) During periods of food deprivation, progressively larger webs will be constructed as hunger level increases, until some maximum web dimension is produced. This large web size will be maintained over successive webs until energetic constraints, such as decreasing protein stores as a consequence of loss through web production, force the construction of progressively smaller and smaller webs (Fig. 2a).

(2) After supplemental feedings, web sizes will drop precipitously as sated spiders reduce energy allocated to foraging. Following an initial period of no web construction or construction of small

webs, progressively larger webs will be constructed as hunger levels increase (Fig. 2b).

(3) Increased egg production will be observed as a function of substantial prey consumption. It has been well documented that spiders show a reproductive response to increased prey consumption (Greenstone 1978; Wise 1979).

(4) Smaller webs will be produced prior to egg production as spiders re-allocate their limited energies from prey capture to reproductive output. After egg production, spiders will construct larger webs in an attempt to replenish their energy stores by increasing the probabilities of prey capture, despite associated costs. This trend in web sizes will directly contrast with those trends found before and after prey consumption because egg production depletes, while heavy prey consumption enhances the energy balance (Fig. 2c).

## MATERIALS AND METHODS

### The Subject: *Larinioides cornutus*

I studied adult females of *Larinioides cornutus* (Araneae: Araneidae) in their natural setting from June to September of 1988 and 1989. Originally described by Clerck (1757) and later re-classified as *Nuctenea cornuta* by Levi (1974), this species is now generally accepted as *Larinioides cornutus* (Clerck) (Grasshoff 1983). This species is holarctically distributed typically living on human structures near water (Levi 1974). The back porch and surrounding vegetation of Bullfrog Camp, located on Lincoln Pond of the Edmund Niles Huyck Preserve and Research Station in Rensselaerville, Albany County, New York, supported a population of approximately 50 adults. The Preserve is located at 41°10′ latitude, 74°10′ longitude on the western edge of the Helderberg Plateau at an elevation of approximately 650 m.

Adult females were randomly selected and monitored nightly throughout the summer until their death or disappearance. Flashlights with dark red plastic coverings facilitated observation while neither attracting insect prey, nor disturbing subject's natural photo periods (Foelix 1982). No other artificial lighting existed, so prey levels were kept at naturally low levels. Each subject's abdomen was marked on the dorsal surface with Testor's® non-toxic enamel paint. Spiders did not detectably react to either the painting procedure or the paint itself, nor was there any observed effect of painting on survivorship. Each night throughout the summer marked subjects were monitored from 2000 to 0530 hours.

Spiders generally built webs on vertical support poles meeting the porch ceiling at a 90° angle. Throughout the summer, I chose spiders from the many microhabitats that the porch offered. Movement by spiders when off the web consisted primarily of travel along a connecting drag-line between a silk-lined retreat and the web-hub. Retreats were frequently constructed in cracks, holes, or overhangs about 35 cm above and to one side of the web's hub. This strong site tenacity allowed observations of several subjects for the summer's duration, and few interactions between conspecific females were observed. Competitive interactions, although observed on occasion, did not appear to play a significant role in this study system. Every night at 0000 hours, I recorded the current temperature and the previous 24-h minimum and maximum temperatures. Spiders generally began building webs around 0000 hours, although building times ranged from 2130 to 0430 hours. Web dimensions were measured within 2 h of the web's completion, before it could be damaged by flying insects, inclement weather, or courting males.

### Measuring Web Dimensions

For each web, I took several measurements from which I estimated area of the catching spiral, total thread length, and mean mesh size. For each web (see Fig. 3) I measured to the nearest 5 mm four 'diameters' (vertical, horizontal, and 45° diagonals) from one outermost spiral to the opposite outermost spiral. I measured to the nearest 1 mm two diameters across the hub and surrounding 'free zone' (from innermost spiral to innermost spiral). I counted the number of spirals in each of the web's four cardinal directions, and I totalled the number of radii.

From these measurements I calculated the area of the catching spiral (hub and free-zone area subtracted from the total web area), total thread length, and mean mesh size. Total thread length did not include support threads for the web because these were used over several consecutive webs. I used modified versions of the thread-length equations developed by Baum (as communicated to Breed et al. 1964) and used by Witt et

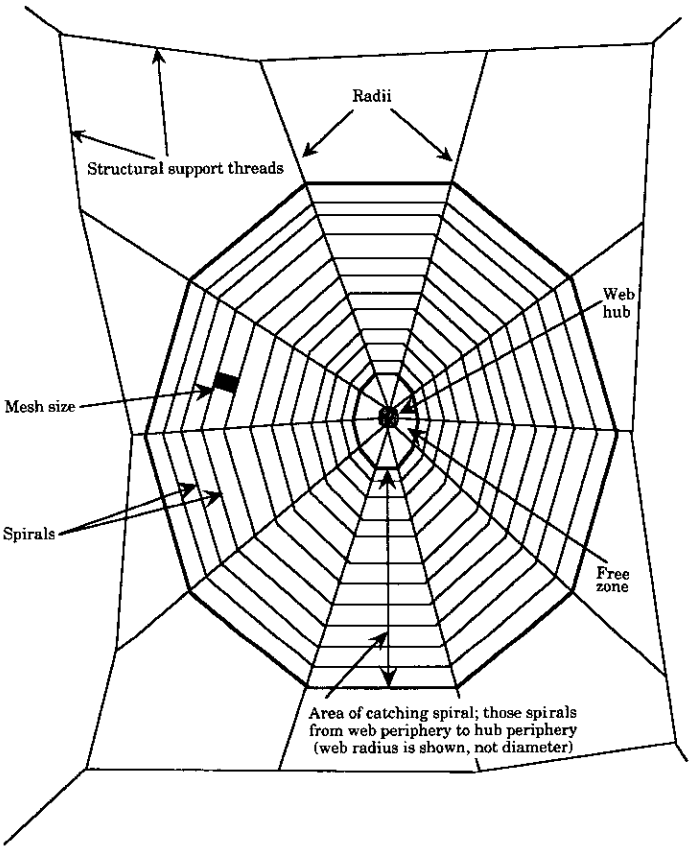


**Figure 3.** Components of a schematic orb-web enumerating and defining measured dimensions and variables.

al. (1968) and mesh-size equations used by Risch (1977). Thread length was calculated as follows

$$\text{thread length} = NR \times (RAD_w - RAD_h) + SPIRALS \times \pi \times (RAD_w - RAD_h)$$

where $NR$ equals the number of web spokes (radial threads), $RAD_w$ and $RAD_h$ equal the average radius of the web and hub, respectively, $SPIRALS$ is the average number of spirals, and $\pi = 3{\cdot}14159$.

### Measuring Natural Prey Densities

Natural prey densities were estimated with sticky traps and by measuring the number of prey 'passively' caught by newly built webs after spiders were removed. Sticky traps were made with flexible plastic sheets treated with Tanglefoot spray and stretched over wooden needle-point hoops 30·5 cm in diameter. Trap design and placement closely approximated the average web area, height, orientation and position. Five such traps were hung from the porch roof and stabilized with weights. On 50 different evenings at 2000 hours, I estimated the prey density of the previous 24 h by counting and removing all prey caught on each trap. I subjectively classified the insects caught into one of seven size classes ranging from gnats to large damselflies. Traps were used to obtain rough estimates of local prey densities rather than to estimate what prey types or amounts the subjects consumed (Eberhard 1990). I counted and classified but did not remove prey contacting 150 webs of known thread length, mean mesh size and area of sticky spiral. Because larger prey could sometimes escape from uninhabited webs, these

measurements allowed for a more accurate, although underestimated, assessment of the total prey consumed by the spiders.

### Supplemental Feedings

On any given summer night, I monitored up to 30 potential subjects (adult females) as they hunted their newly constructed webs. Of those potential subjects, only those that were neither gravid nor sated from a recent prey capture were considered for supplemental feeding. When one of these subjects had built five webs over 5 consecutive nights without significant prey consumption (more than a few class I insects), I supplemented its diet with one or more large prey items totalling 300 mg of prey (wet weight). Because subjects were supplementally fed on different nights throughout the summer, the potential for the uncontrolled environment to confound all the trials in a particular way was strongly reduced. All prey were part of the spiders' natural diet, caught locally, weighed to the nearest 0·1 mg on a Cahn Electrobalance (Model 7500), frozen for easy handling and short-term storage, and then defrosted before introduction to spider webs. The bulk of the supplemental feedings was comprised of dragon-flies (size class VII), *Libellula luctuosa* Burmeister and various other *Libellula* spp., although flies and damselflies (classes IV through VI) of various genera were sometimes used.

I placed the dead prey item(s) midway between the hub and perimeter (randomly chosen quadrant) on newly built and measured webs. I considered the feeding event to be complete when: (1) edible parts of prey items were fully consumed; (2) spiders dropped prey remains from their webs; (3) spiders placed discarded prey in the peripheral support threads of their previous night's web (the night of feeding); (4) spiders ignored artificial vibrations of prey remains which, before feeding, would easily have elicited a predatory reaction; and (5) spiders, neglecting remaining prey, left their web areas during relocation or to oviposit.

### Control Webs: Changes in Web Dimensions with Neither Supplemental Feeding Nor Egg Production

Because spider web dimensions may vary in ways that I hypothesized but for reasons unrelated to feeding or egg production events, I measured 10 consecutively built webs for 27 different spiders that neither consumed prey greater than size class I or II nor reproduced during the observation period. To minimize the potentially confounding influences of prior and subsequent prey consumption or egg production on these results, I maintained conditions of consumptive and reproductive abstinence for an additional 10 days preceding and following the 'control' period. This baseline analysis was conducted with a sample size of 229 webs. This value differs from the potential of 10 webs per spider totalling 270 because several spiders did not build a new web every night ('missing values'=41 of 270 or 15·2%; approximately 8·5 webs per individual). I also analysed these 229 webs to determine what if any effects temperature had on web dimensions.

### Data Analyses

*Selection of webs for analysis*

I measured the five consecutive webs built before and after experimental prey consumption or egg laying. For all treatments and subjects, if abiotic or biotic factors destroyed a web during the 10-web period, the subject was dropped from further analysis. For the feeding experiment, 15 trials were performed using 15 different subjects. Of these 15 feeding trials, I selected eight for further analyses because they did not occur within 15 days of uncontrolled (natural) consumption or reproduction events. The reduction in statistical power of decreasing the sample size by seven (47%) was high, but the system's biology and my hypotheses required elimination of these individuals because natural feeding or egg production could themselves influence web size. This potentially confounding influence would have made it difficult to draw meaningful conclusions concerning the relationship between web size and consumptive or reproductive status.

Similarly, I selected 10 egg-laying events for further analysis from the 21 observed layings over the summer. These 10 spiders produced egg sacs no less than 15 days before or after the nearest heavy feeding event or additional reproductive event. This conservative selection of subjects enhanced the study's resolution by helping to ensure that changes in web dimensions before egg production were not strongly related to or confused with changes in web dimensions after prey consumption and vice versa.

*Analysis period: web-to-web*

While the majority of spiders constructed webs nightly, occasionally a night was skipped. For that reason, I focused my analyses upon consecutive web construction rather than a 24-h period. I measured five consecutive webs built both before and after prey consumption or egg production. These analyses focused upon energy output associated with web construction and neglected energy saved by infrequent web construction, which I considered to be insignificant (Peakall & Witt 1976; Gillespie & Caraco 1987; Higgins & Buskirk 1992). These analyses assumed that daily resting metabolic costs for orb-weaving spiders were negligible (Anderson 1970, 1974).

*Statistics*

I used paired (dependent) sample *t*-tests (two-tailed) to compare web sizes before and after eating or egg production. The mean size of the five webs built before and after the intervention (feeding or reproduction) for each individual spider, represent the paired samples.

I used multiple linear regression (MLR), and step-wise regression analyses to investigate the relative effects of time (first five webs compared with the second five webs), and previous 24-h low and high temperature on dimensions of individual webs for the 27 control subjects. For the step-wise regression analysis, I used an alpha value of 0·05 to enter and remove a variable into the equation.

I used the Lilliefor's test (standardized residuals) for normality to test the parametric assumption of samples being derived from a normally distributed population. I used the Bartlett's test for homogeneity of group variances to test the parametric assumption of equal variances in web dimensions between spiders (Wilkinson 1987). No statistically significant departures from the parametric assumptions of normality or equal variances were found. The probability of committing a type I error ($\alpha$) was set at 0·05 throughout the study.

## RESULTS

### Variable Natural Prey Abundance: Sticky Traps, Orb Webs and Web Location

The supplemental feeding regime used in this study was designed to quantitatively and qualitatively mimic the natural prey consumption rates experienced by individual spiders from this field population. Spiders were commonly observed to eat few or no insects over several nights. However, when a spider finally captured prey, the prey item was frequently larger than the spider herself.

To estimate the natural prey density and variability at the study site, I measured numbers of prey caught each night both by traps and natural webs. Capture rates of insects were quite variable, yet both sampling methods demonstrated that the smallest prey classes were most readily caught and retained. Similar percentages of prey caught by the five traps indicated that there were no discernible micro-habitat differences in prey abundance in the study area. However, individual spiders did experience differential prey capture success (see below). Capture rates for sticky traps varied nightly, ranging, for example, from zero to 50+ class I prey. Eighty-five per cent of all prey caught by the five traps represented the smallest size class (class I: gnats), while 10·5% represented class II (mosquitoes; Fig. 4a). No insects representing classes IV to VII (large visually oriented insects and moths) were caught, although their conspicuous abundance at the study site suggested that low capture success resulted primarily from an imperfect trap design. Unattended spider webs caught prey in similar proportions to the sticky traps, with 150 webs capturing 87% class I and 10·6% class II (Fig. 4b). No obvious trends between web dimensions and passive prey capture by webs (webs with spiders removed) could be discerned, leaving this important component of orb-weaver ecology available for further study (but see Higgins & Buskirk 1992).

While numbers and sizes of prey caught by most spiders were consistently very small, prey capture rates for individual spiders varied considerably. Differences in individual passive web-capture demonstrate the importance of site selection on foraging success. One spider built 18 webs over 18 days, and caught 17 damselflies representing either size class III or IV; two or three damselflies occasionally were found in a single web. In contrast, a spider occupying a web site less than half a metre away caught only two damselflies over the same 18-day period. A third spider frequently caught an average of $10{\cdot}8 \pm 1{\cdot}48$ class I insects for 10 webs, while another's webs averaged $2 \pm 0{\cdot}8$ class I and $1{\cdot}3 \pm 0{\cdot}2$ class II insects per day for 12 days (same period).

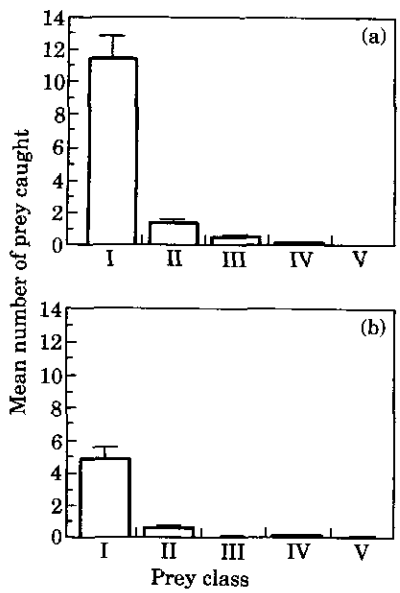


**Figure 4.** Mean (± SE) number of prey caught by (a) five sticky traps over 45 days and (b) 150 webs built by 14 adult *L. cornutus*. Seven prey size classes were estimated: gnats (I), mosquitoes (II), small flies (III), larger flies and small damselflies (IV), larger damselflies and medium sized moths (V), larger moths, horseflies, and large damselflies (VI), and dragon-flies (VII). The absence of values for classes VI and VII reflects the fact that none of these prey could be caught and retained by the traps or webs when spiders were not present, rather than the lack of these prey types in the local environment. Zero values were used and included in the mean values for those times when traps were monitored but no prey of a particular class were caught.

### Baseline Variations in Web Dimensions

To better understand and highlight the changing web dimensions observed in response to both experimental feedings and egg production, I monitored three web dimensions, area of the catching spiral, total thread length, and mean mesh size, as they varied with both temperature and time. The area of the catching spiral was not significantly correlated with either high or low temperature. Step-wise regression analysis showed that thread length was positively correlated with the previous 24-h (nighttime) temperature ($r^2<0{\cdot}02$, $P<0{\cdot}05$), whereas no significant relationship was found with previous high (daytime) temperatures. Mesh size was significantly negatively correlated with previous nighttime temperature (MLR: multiple $r^2=0{\cdot}074$, $t=-3{\cdot}46$, $P<0{\cdot}001$) but not with previous daytime temperature. Although statistically significant, the biological significance of these data remains unknown.

Monitoring the web dimensions of 27 spiders that experienced neither heavy prey consumption nor egg production over time (10 consecutive nights), revealed that these spiders built relatively stable web sizes during this period. Neither area of catching spiral (Fig. 5a) nor total thread length (Fig. 5b) significantly changed when mean values of the first five webs were compared with mean values of the second five webs ($P>0{\cdot}99$ and $P>0{\cdot}6$, respectively). Mean mesh size of webs (Fig. 5c), however, significantly decreased over the 10-web observation period.

### Supplemental Feedings Result in Decreased Web Sizes

Although web dimensions were only weakly affected by temperature and time, area of catching spiral ($mm^2$) and total thread length (mm) significantly decreased after heavy prey consumption compared with pre-consumption web dimensions (Table I). Mean mesh size, however, did not significantly change during this period (Table I). In general, web area (Fig. 6a) and thread length (Fig. 6b) tended to increase prior to supplemental feeding, followed by a steady decrease for these two dimensions. Mesh size (Fig. 6c) did not exhibit any such trends but rather oscillated, with the widest-meshed webs immediately following the feeding event.

More specifically, webs built the first night after supplemental consumption continued to decrease in thread length, while area trailed slightly behind. Area decreased only slowly as spiders produced the widest mesh sizes measured during the experimental period (+5·6%; up from the previously built web). For these webs constructed immediately after consumption, web area decreased but remained relatively large (−13·9%; down from the previously built web's mean value for all eight subjects), while thread length decreased more obviously (−25·4%; down from the previously built web). On the second night after prey consumption, web area (−22·7%), mesh size (−4·97%), and thread length (−7·94%) all decreased in value, with web area and thread length continuing to fall over the remainder of the five-web observation period after prey consumption.

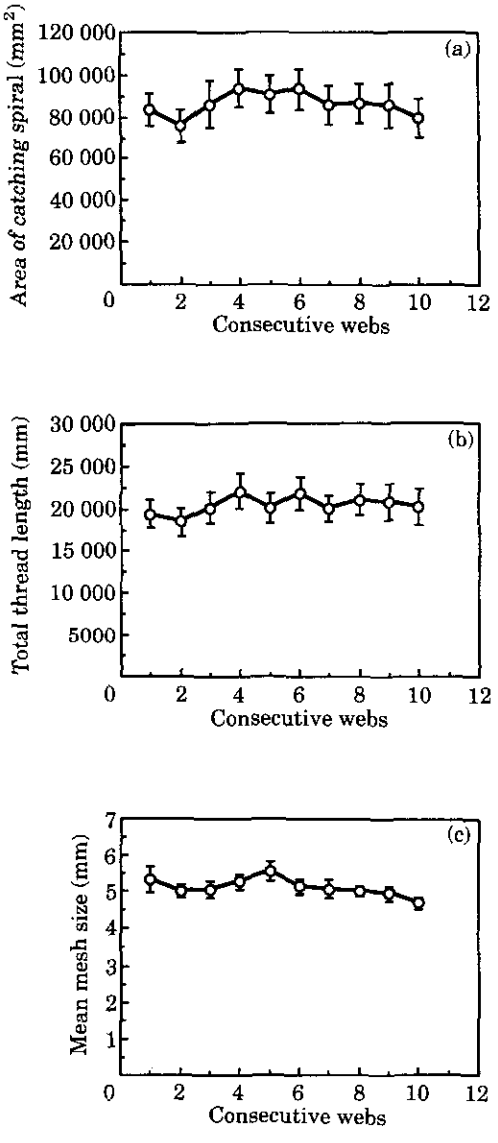


**Figure 5.** Mean (± SE) web dimensions for 10 consecutively built webs of 27 control spiders (*L. cornutus*), influenced by neither prey consumption nor egg production. A total of 229 different webs built by 27 spiders at different times throughout the summer were analysed. Control spiders had neither eaten a substantial amount of food (size>house fly) nor laid eggs for at least 10 days before or after this analysis period. Areas (a) and total thread lengths (b) of the first five webs were not significantly different from the second five webs ($P<0.99$; $P<0.75$, respectively), however, mean mesh size (c) significantly decreased when the first five webs were compared with the second five (−5·86%; paired samples, $t=2.25$, $P<0.03$).

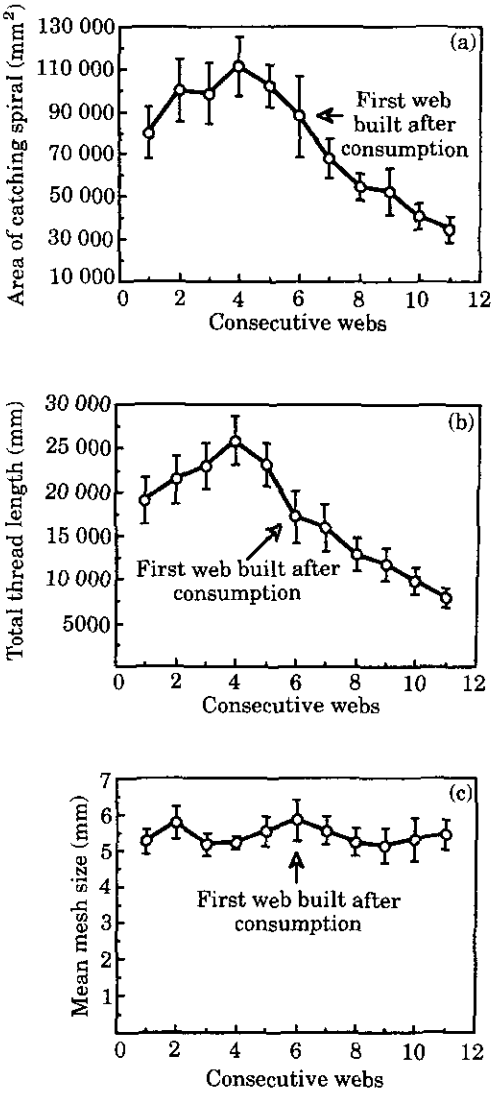


**Figure 6.** Mean (± SE) web dimension for five webs built before and six webs built after supplemental prey consumption by eight adult, female *L. cornutus*. Supplemental feedings were provided after construction of the fifth web. The mean value for the first web built after feeding (web six) had an $N=3$, as only three spiders built on this night. (a) Area of the catching spiral (mm²). (b) Total thread length (mm). (c) Mesh size (mm).

### Web Sizes Increase with Reduced Consumption

The following anecdotal situation may offer preliminary insight into changes of foraging investment when food is unavailable. One subject

**Table I.** Mean (± SE) of means for area of catching spiral, total thread length and mesh size for control webs and for five webs built before and after supplemental prey consumption and egg production

| | Web dimension | *N* | Before | After | % Change | *P** |
|---|---|---|---|---|---|---|
| Prey consumption | | | Five webs built before | Six webs built after | | |
| | Area ($mm^2$) | 8 | 94 471 ± 11 752 | 56 213 ± 4600 | −40·49 | 0·02 |
| | Thread (mm) | 8 | 21 553 ± 2292 | 13 072 ± 1349 | −39·35 | 0·02 |
| | Mesh (mm) | 8 | 5·5 ± 0·3 | 5·3 ± 0·3 | −3·25 | 0·5 |
| Egg production | | | Five webs built before | Five webs built after | | |
| | Area ($mm^2$) | 10 | 69 741 ± 7765 | 69 818 ± 9968 | 0·11 | 0·99 |
| | Thread (mm) | 10 | 17 388 ± 1926 | 18 601 ± 2310 | 6·52 | 0·75 |
| | Mesh (mm) | 10 | 4·4 ± 0·3 | 5 ± 0·3 | 14·49 | 0·01 |
| Control webs | | | First five webs | Second five webs | | |
| | Area ($mm^2$) | 27 | 85 900 ± 3960 | 86 461 ± 4222 | 0·65 | 0·99 |
| | Thread (mm) | 27 | 20 027 ± 795 | 20 894 ± 836 | 4·33 | 0·61 |
| | Mesh (mm) | 27 | 5·3 ± 0·1 | 5 ± 0·09 | −5·86 | 0·03 |

*Paired-samples *t*-test.

(Fig. 7a–c), constructed her webs adjacent to a well-lit house window and experienced nightly prey satiation. The webs she built had areas and thread lengths that were respectively 40 and 20% smaller than the mean web values for 590 webs measured from other members of the study population. After several nights, the inside window-shade was intentionally drawn and prey contact with the web was dramatically reduced to approximately the equivalent of five mosquitoes a night. Nearly a three-fold increase in both web area and thread length resulted over the next 18 days. Over the next few weeks, however, web sizes decreased to the levels observed during the heavy consumption period. This condition of smaller web construction persisted for approximately 10 more days of observation during which the spider produced two egg sacs and was not seen again.

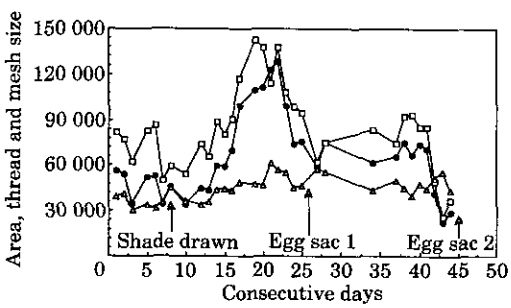


**Figure 7.** Influence of prolonged periods of reduced prey consumption after an initial heavy consumption period for one mature, female *L. cornutus*. This spider naturally encountered heavy prey conditions but maintained web sizes significantly smaller than the mean web values for the experimental spider population ($N$=590 webs). After her prey availability was experimentally reduced to near zero levels, the area of the catching spiral ($mm^2$) (—●—) and thread length (mm × 5) (—□—) increased three-fold during the next 2·5 weeks over their initial levels. Mesh size (mm × 10 000) (—△—) also increased.

### Heavy Prey Consumption Leads to Increased Egg Production

Fifty-eight per cent of those spiders experiencing enhanced prey consumption also experienced enhanced reproductive output. During the summer of 1989, I observed 14 spiders produce 21 egg sacs. Of these 21 egg sacs, 17 were produced after heavy experimental or heavy natural prey consumption. The average interim period between heavy consumption and production of these 17 egg sacs was 4·4 ± 0·6 days (range=8 days) during which an average of 2·7 ± 0·5 webs per spider (range=5 webs) were built. Of the four remaining egg sacs, two were produced by a single spider. These 14 spiders stand out from the other 24 adult females monitored but not observed to reproduce during the summer.

### Effects of Egg Production on Web Dimensions

Egg sac production influenced web dimensions differently than did supplemental prey consumption (Table I). In contrast to prey consumption, average areas of the catching spiral and total thread lengths of webs built after oviposition were not significantly different from those webs built

before. Mean values of mesh size were significantly larger after egg production than before.

In contrast to those web size trends associated with feeding, web area (Fig. 8a) and thread length (Fig. 8b) decreased over the five webs measured prior to egg production, after which thread length showed a shallow increasing trend. Mesh size (Fig. 8c), once again, did not show any significant increasing or decreasing trends before or after reproduction.

The web dimensions of five subjects were measured over eight webs rather than five, following egg production (Fig. 9a–c). Both area and thread length increased significantly for four of the five spiders observed over this post-reproduction period ($P<0{\cdot}05$, $P<0{\cdot}01$, respectively), with these dimensions decreasing for the fifth subject. Mesh size did not significantly change, remaining relatively wide for all five subjects.

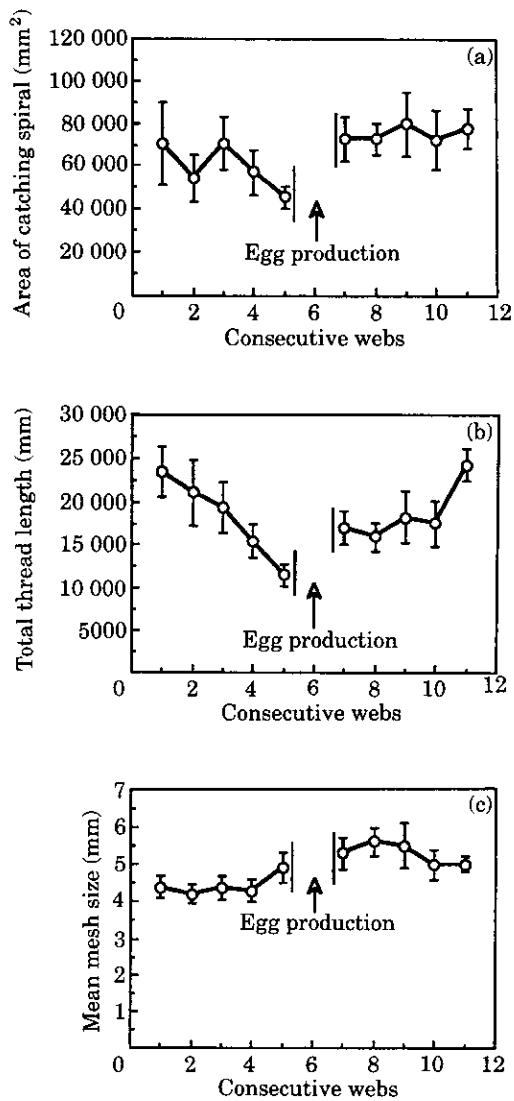


**Figure 8.** Mean (± SE) values of changing web dimensions for five webs built before and after egg production for 10 adult female *L. cornutus*. Web analyses were arranged so that egg production was sequentially placed between the construction of web five and web six to facilitate comparisons between spiders. (a) Area of the catching spiral ($mm^2$). (b) Total thread length values (mm), which decreased 6·52% after reproduction (NS). (c) Mean mesh size values (mm), which significantly increased 14·49% after reproduction ($P<0{\cdot}01$).

## DISCUSSION

This study documents variations in the nightly web design for individual orb-weavers, and explores ecological explanations for the variations found. Results indicate that adult females of *L. cornutus* build larger webs when hungry, and smaller webs when sated. In contrast, these spiders decrease thread length and web area before producing eggs, and increase mesh size thereafter. While explanations focusing on the effects of temperature and/or time may enhance our understanding of certain web-building patterns, these explanations inadequately address the observed complexity of orb-weaver behavioural plasticity. In an attempt to more fully explain this complexity, a closer examination is required of the effects of high energy intake (prey consumption) and high energy output (reproduction) on web-building, and the interaction between the three web parameters. By monitoring patterns of changing web dimensions, one can empirically estimate the relative energetic and behavioural investments each adult female allocates into both foraging and reproduction over its lifetime.

### Foraging Effort During Reduced Prey Consumption

Spiders displayed significant variation in their web parameters in response to their levels of prey consumption. Webs of *L. cornutus* gradually increased in area and thread length when spiders experienced low prey abundance, while these parameters decreased after heavy prey consump-

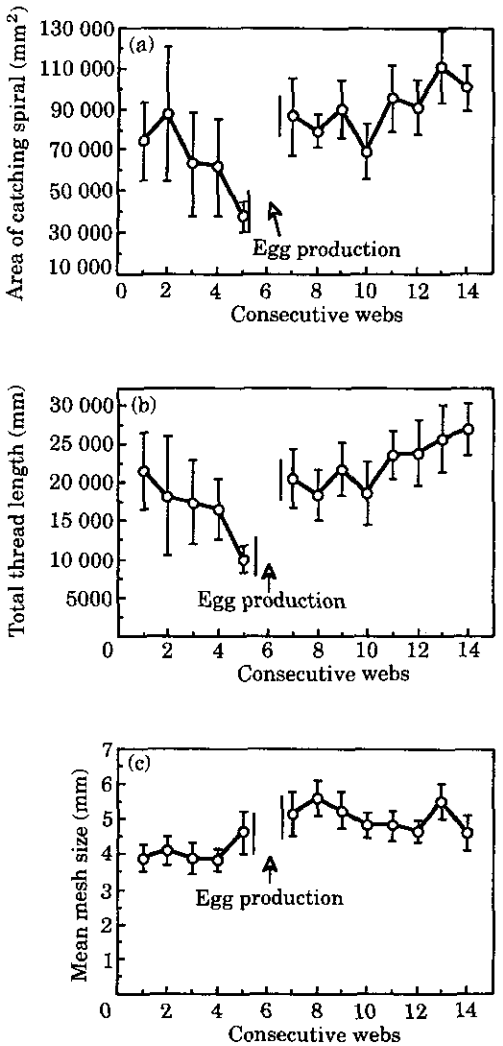


**Figure 9.** Mean (± SE) web dimensions for five webs built before and eight webs built after egg production ($N$=5 *L. cornutus*). (a) Area of the catching spiral (mm²) increased 15·86% after reproduction (NS). (b) Total thread length (mm) increased 37·18% after reproduction (NS). These values were statistically significant after one of the five subjects that built smaller webs after reproduction was removed from analysis. (c) Mean mesh size (mm) increased 23·47% after reproduction ($t$=8·53, $P$<0·001).

tion. In contrast, mesh size did not significantly change over the experimental period regardless of the level of prey consumption. These results suggest that spiders invest more energy into foraging by producing larger webs of greater thread length rather than behaviourally manipulating the available thread length to cover more area by widening mesh size. These findings are consistent with those of Higgins & Buskirk (1992), who recently determined that *Nephila clavipes* increase their web diameters and maintain constant mesh sizes during periods of low foraging success.

Unexpectedly, increasing trends in area and thread length slowed and then reversed by the fifth web built before prey consumption (Fig. 6a, b). At this time, thread length fell more rapidly than web area, while mesh size slowly widened, suggesting that the spiders behaviourally compensated for their diminishing energetic reserves (sensu Witt 1963). This population of *L. cornutus* may have begun to experience stress associated with low prey consumption by the fourth day because of an experimental artefact: to avoid confounding influences from previous consumption events, subjects chosen for supplemental feeding had not eaten more than a few class I or II insects for 2 weeks prior to supplemental feeding. Hypothesis 1 (Fig. 2a) predicted web area and thread length would eventually decrease after such an extended period without food, but whether extended hunger caused the observed decrease remains unknown. Spiders are well renowned for their ability to survive extremely long periods of prey deprivation (Anderson 1970). Therefore, severe energy depletion may be an unlikely cause for these decreasing web dimensions. Yet the ability of spiders to survive without food may be contingent upon strategically decreasing their foraging investments until a time when prey capture probabilities are greater (Hypothesis 1).

Results from 27 control subjects deprived of large prey items imply that spiders faced with low prey consumption were able to maintain their energetic investment into foraging. These spiders maintained their web areas with a stable production of silk during the 10-web observation period, contradicting the predictions of Hypothesis 1. However, mean mesh size significantly decreased during this period, suggesting a more intensified behavioural search effort for the more abundant though less profitable smaller prey (Uetz et al. 1978). If Hypothesis 1 was expanded to include decreasing mesh sizes, in addition to web size, as a form of increased foraging effort, one may more accurately represent the spiders' response to hunger. From this expanded perspective, *L. cornutus* appears to emphasize a behavioural

rather than energetic foraging response to periods of low prey availability.

And yet, one subject (Fig. 7) constructed smaller webs when prey was plentiful and significantly larger webs with increased thread length when prey was scarce. After approximately 3 weeks of strongly reduced prey consumption, enlarged areas and thread lengths began to decrease as energetics presumably constrained this spider's foraging effort (Hypothesis 1). The subject, however, laid two egg sacs during this time, confounding the interpretation of these trends; did area and thread length decrease because of an energetic constraint resulting from gradual starvation or represent a re-allocation of energy from foraging to reproduction? The anecdotal nature of this observation precludes drawing conclusions.

Other studies have documented that hungry spiders tend to build larger webs (Witt 1963; Higgins & Buskirk 1992). Although Witt's conceptual and experimental approaches to studying web variations sharply contrasted with the approaches taken here, our results generally corroborate one another and discrepancies can be explained by examining our methodological differences. Taking a strictly physiological approach, Witt predicted that there would be a direct correlation between feeding success and web size; well-fed spiders would have more energy to produce larger webs after feeding. In contrast, this study's more ecological approach predicted that although well-fed spiders would have more energy to produce larger webs, they would have less need to do so, resulting in an inverse relation between foraging success and web size. Witt (1963) observed that when starved, spiders maintained or increased their web areas and mesh sizes even as thread production decreased, thereby investing behaviourally into foraging when energy levels were low. Additionally, data from a field study with *N. clavipes* (Tetragnathidae) demonstrate that one other orb-weaver species increases web diameters when hungry (Higgins & Buskirk 1992).

### Web Construction After Prey Consumption

Experimental feeding events failed to elicit an immediate drop in web sizes as predicted in Hypothesis 2. Rather, spiders maintained a relatively large web area by increasing mesh size for the first web built after consumption, possibly attempting to exploit the temporary increase in prey availability. Capable of opportunistically gorging on excess food, these subjects retained a relatively large web area with wide mesh while investing 25% less thread into the snares (Fig. 6). By constructing effective, yet energetically prudent webs, spiders may then partition additional resources into growth (juveniles), reproduction, or other life-history requirements (Calow 1981; Pianka 1981; Higgins 1990).

Following this first web built after consumption, both area and thread length continued to drop precipitously as mesh size returned to pre-consumption values. These data contrast with the second part of Hypothesis 2 (Fig. 2b) which predicted that web sizes would drop precipitously after ingestion and then gradually increase with hunger. Rather, energy was divested from foraging thereby reducing the probabilities of continued successful prey capture. The question therefore remains: where did the energy saved from a decreased foraging effort go? Data suggest this energy might have been re-partitioned to egg production.

### Food Limitation and Reproductive Response

Low prey capture rates from both sticky traps and passive webs (i.e. without spiders; Fig. 4) suggest that this study population of spiders experienced low prey availability. The traps and unattended (passive) webs, unable to capture the occasional, large prey item, underestimated the actual diet of the subjects which tended towards a boom-and-bust prey regime. Under such resource constraints where periods of low prey availability may last several weeks, spiders would need to balance foraging effort with reproduction. I hypothesize that *L. cornutus* responded to significant prey consumption events by re-allocating their resources from additional foraging efforts (decreasing thread lengths) into egg production. After significant food consumption, 14 spiders produced one or more egg sacs. This observation supports a large body of literature theorizing and demonstrating a spider's reproductive response to consumption (Wise 1979).

However, spiders can also produce egg sacs without experiencing prior heavy prey consumption. In contrast to the reproductive responses displayed by several subjects, the single individual depicted in Fig. 7a–c, produced two egg sacs after a prolonged period of low prey consumption. This

phenomenon is commonly observed in laboratory and field settings when spiders are maintained with minimal food (A. Cady, personal communication). Thus, it would appear that spiders have an alternative reproductive strategy when faced with extended periods of moderate or total food deprivation; they produce one final egg sac(s) before already depleted energy stores run out.

**Web Dimensions Vary with Egg Production**

Web dimensions showed distinct patterns before and after egg production (an energetic expenditure); patterns that contrast strongly with those before and after prey consumption (an energetic gain). If the inverse correlations observed between energetic state and web size are as meaningful as other experimenters (Higgins 1990; Higgins & Buskirk 1992) and I suggest, one would expect web patterns to be the opposite of those found before and after prey consumption (Hypothesis 4; Fig. 2c), and in general, this was the case. Both area and thread length, but not mesh size, showed decreasing trends before and increasing trends after reproduction. These results support Higgins (1990) who also found a decrease in web diameter but not mesh size in successively built webs preceding egg laying. Mean mesh size significantly increased after reproduction for *L. cornutus*.

After egg production, prey consumption may once again become a priority for many foragers. Without nutritional renewal, their life-expectancy and future reproductive output may be reduced. Construction of a large web represents the best way an orb-weaver can capture a large prey item and thereby replenish its depleted energy stores. The associated costs, however, are high (Eberhard 1986), so depleted spiders should try to maintain their increased foraging efforts through behavioural rather than energetic means (Hypothesis 4; Fig. 2c). Specifically, after egg production, energetically depleted spiders increase their mesh sizes to maintain or increase their web areas while maintaining or reducing thread lengths; a prediction the data support. Wider mesh sizes, however, presumably reduced the chances of capturing smaller insects which comprise a major component of a spider's daily catch (Uetz et al. 1978). After building a few webs and capturing small class I and II insects, mesh sizes did eventually fall back to pre-reproductive values while web area was energetically maintained by longer thread lengths.

By following changes in web dimensions over eight webs subsequent to egg production (Fig. 9a–c), I found that thread lengths continued to increase. Thread production significantly increased for four of the five subjects observed. This increasing trend suggests that post-reproductive spiders allocated their gradually increasing energies into foraging (Witt et al. 1968). The fifth subject, however, decreased her thread production over this post-reproduction period, demonstrating that web construction is highly plastic and still inadequately understood.

**Structural Constraints: an Alternative Hypothesis Considered**

An alternative, more parsimonious, explanation interpreting the trends in thread length found here must be considered in place of the ecological explanation presented above. However, recent studies and conceptual inconsistencies in this alternative weaken the alternative's validity. This alternative explanation focuses upon the structural limitations of the orb-web rather than the life history and foraging strategies of the spider itself. The alternative suggests that a web's thread length varies inversely with the spider's body mass because heavier spiders must support themselves with thicker, shorter, and thereby stronger, threads (sensu Christiansen et al. 1962; *Araneus diadematus*: Araneidae). Data presented above, seem at first approximation to support this perspective; both sated and gravid (i.e. heavy) spiders produced webs with decreasing thread lengths.

Conclusions from the literature are contradictory and inconclusive, possibly because of the inherently confounding variables of weight and size. Some studies have demonstrated a gradual, life-long increase in web area and/or mesh size with increasing body size and weight (Meyer 1953 cited in Witt & Baum 1960; Reed et al. 1970; Denny 1976; Olive 1980; Higgins 1990; Higgins & Buskirk 1992; Ward & Lubin 1992). In contrast, other studies have found no such significant correlation (Leborgne & Pasquet 1987). Work's (1976, 1977) convincing experimental investigation failed to demonstrate a correlation between daily spider mass and thread diameter for *A. diadematus*, thereby weakening the persuasiveness of the alternative explanation.

Most importantly, the logic of the alternative hypothesis is inconsistent with the physiology of

orb-weavers. It proposes that heavier spiders must support their own weight by producing thicker and thereby shorter threads which results in a decreased web area. This causal progression is flawed because a web's structural support and area are (1) determined by different web components and (2) controlled by different silk glands. A web's ability to support a heavy spider lies in the web's frame and radial threads, both of which are produced by the ampullate gland (Andersen 1970; Foelix 1982). Web area, on the other hand, is defined by the area of the catching spiral. These highly elastic and sticky, spiral threads are produced by two other glands, the flagelliform (thread) and aggregate glands (glue) (Foelix 1982). Therefore, the inconsistency of this explanation is as follows: that a heavier spider requiring greater support may increase the diameter and thereby shorten the length of the frame or radial threads, but these reductions are unlikely to have a profound effect on the web area which is more a function of spiral thread production and spacing. The alternative hypothesis is thereby brought further into question.

In conclusion, data presented here suggest that orb-web construction is far more complex and responsive to a spider's dynamic internal state than previously considered. By manipulating the area of catching spiral, total thread length, and/or mean mesh size, spiders appear to fine-tune their web dimensions to specifically address their changing foraging and reproductive needs. Limited energy resources, or more specifically proteins, may be partitioned between foraging and reproduction. It is suggested that future investigations into the behaviour and energetics of orb-weaving spiders consider the significant patterns in web construction that appear to be associated with the spider's dynamic energetic state. Further analysis of web characteristics may greatly increase our understanding of spider foraging behaviour and may contribute to our understanding of the ways animals partition limited energy resources between foraging and reproduction.

## ACKNOWLEDGMENTS

I am very grateful to Stimson Wilcox who saw potential in the earliest stages of my work, and to the following people who helped with earlier drafts: Nancy E. Stamp, Alan Cady, David Sloan Wilson, Linden Higgins, David Murrish, Stim Wilcox, and a very constructive anonymous referee; Denise Gobielle, Ian Vabnick, and Peter Whitlock performed outstanding and tireless field assistance making this study both fun and plausible; Gary Fowler and Kathy Welch provided statistical help; Richard Wyman and the Huyck Biology Preserve and the American Museum of Natural History's Theodore Roosevelt Memorial Fund funded this project; and thanks to my emotional support staff including Richard Feldman, Mary Mengel, Richard Wilkens, Gary Sullivan, Dan Fishman, Larry, and the rest of my family.

## REFERENCES

Andersen, S. O. 1970. Amino acid composition of spider silks. *Comp. Biochem. Physiol.*, **35,** 705–711.

Anderson, J. F. 1970. Metabolic rates of spider. *Comp. Biochem. Physiol.*, **33,** 51–72.

Anderson, J. F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* Hentz. *Ecology*, **55,** 576–585.

Breed, A. L., Levine, V. D., Peakall, D. B. & Witt, P. N. 1964. The fate of the intact orb-web of the spider *Araneus diadematus* Clerk. *Behaviour*, **23,** 43–60.

Calow, P. 1981. Resource utilization and reproduction. In: *Physiological Ecology* (Ed. by C. R. Townsend & P. Calow), pp. 245–270. Cambridge: Blackwell Scientific Press.

Carico, J. E. 1986. Web removal patterns in orb-weaving spiders. In *Spiders: Webs, Behavior and Evolution* (Ed. by W. A. Shear), pp. 306–318. Stanford, Connecticut: Stanford University Press.

Chacón, P. & Eberhard, W. G. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. *Bull. Br. Arachnol. Soc.*, **5,** 29–38.

Christiansen, A., Blum, R. & Witt, P. N. 1962. Changes in spiders webs brought about by mescaline, psilocybin and an increase in body weight. *J. Pharmac. exp. Ther.*, **136,** 31–37.

Clerck. 1757. *Aranei Suicici.* Stockholm.

Denny, M. 1976. The physical properties of spider's silk and their role in the design of orb-webs. *J. exp. Biol.*, **65,** 483–506.

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

Eberhard, W. G. 1986. Effects of orb-web geometry on prey interception and retention. In: *Spiders: Webs, Behavior, and Evolution* (Ed. by W. A. Shear), pp. 70–100. Stanford, Connecticut: Stanford University Press.

Eberhard, W. G. 1988. Behavioral flexibility in orb web construction: effects of supplies in different silk glands and spider size and weight. *J. Arachnol.*, **16,** 295–302.

Eberhard, W. G. 1990. Function and phylogeny of spider webs. *A. Rev. Ecol. Syst.*, **21,** 341–372.

Eisner, T., Alsop, R. & Ettershank, G. 1964. Adhesiveness of spider silk. *Science*, **146,** 1058–1060.

Foelix, R. F. 1982. *Biology of Spiders.* Cambridge, Massachusetts: Harvard University Press.

Ford, M. J. 1977. Energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* Berktau (Linyphiidae). *Oecologia (Berl.)*, **28,** 341–349.

Gillespie, R. G. & Caraco, T. 1987. Risk-sensitive foraging strategies of two spider populations. *Ecology*, **68,** 887–899.

Grasshoff, M. 1983. Larinioides CAPORIACCO 1934, der korreckte Name fur die sogenannte *Araneus cornutus*-Gruppe (Arachnida: Araneae). *Senckenbergiana biol.*, **64,** 225–229.

Greenstone, M. H. 1978. The numerical response to prey availability of *Pardosa ramulosa* (McCook) *Araneae: Lycosidae* and its relationship to the role of spiders in the balance of nature. *Symp. Zool. Soc., Lond.*, **42,** 183–193.

Higgins, L. E. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). *J. Insect Behav.*, **3,** 773–783.

Higgins, L. E. & Buskirk, R. E. 1992. A trap-building predator exhibiting different tactics for different aspects of foraging behaviour. *Anim. Behav.*, **44,** 485–499.

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

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

Levi, H. W. 1974. The orb-weaver genera *Araniella* and *Nuctenea* (Araneae: Araneidae). *Bull. Mus. comp. Zool. (Harv. Univ.)*, **146,** 291–316.

Levi, H. W. 1978. Orb-webs and phylogeny of orb-weavers. *Zool. Soc., Lond. Symp.*, **42,** 1–15.

Olive, C. W. 1980. Foraging specializations in orb-weaving spiders. *Ecology*, **61,** 1133–1144.

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

Peakall, D. B. 1971. Conservation of web proteins in the spider, *Araneus diadematus. J. exp. Zool.*, **176,** 257–264.

Peakall, D. B. & Witt, P. N. 1976. The energy budget of an orb-weaving spider. *Comp. Biochem. Physiol.* (A)., **54,** 187–190.

Pianka, E. R. 1981. Resource acquisition and allocation among animals. In: *Physiological Ecology* (Ed. by C. R. Townsend & P. Calow), pp. 300–314. Cambridge: Blackwell Scientific Press.

Prestwich, K. N. 1977. The energetics of web-building in spiders. *Comp. Biochem. Physiol.*, **57,** 321–326.

Reed, C. F., Witt, P. N., Scarboro, M. B. & Peakall, D. B. 1970. Experience and the orb web. *Devl Psychobiol.*, **3,** 251–265.

Risch, P. 1977. Quantitative analysis of orb-web patterns in four species of spiders. *Behav. Genet.*, **7,** 199–238.

Savory, T. H. 1952. *The Spider's Web.* London: Frederick Warne.

Shear, W. A. 1986. The evolution of web-building behavior in spiders: a third generation of hypotheses. In: *Spiders: Webs, Behavior, and Evolution* (Ed. by W. A. Shear), pp. 364–400. Stanford, Connecticut: Stanford University Press.

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

Townley, M. A. & Tillinghast, E. K. 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component GABamide. *J. Arachnol.*, **16,** 303–320.

Uetz, G. W., Johnson, A. D. & Schemske, D. W. 1978. Web placement, web structure, and prey capture in orb-weaving spiders. *Bull. Br. Arachnol. Soc.*, **4,** 141–148.

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

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *A. Rev. Ecol. Syst.*, **20,** 249–278.

Wilkinson, L. 1987. *SYSTAT: The System for Statistics.* Evanston, Illinois: SYSTAT.

Wise, D. H. 1979. Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae: Araneidae). *Oecologia (Berl.)*, **41,** 289–300.

Witt, P. N. 1963. Environment in relation to the behaviour of spiders. *Archs Env. Health*, **7,** 4–12.

Witt, P. N. & Baum, R. 1960. Changes in orb-webs of spiders during growth (*Araneus diadematus* Clerk and *Neoscona vertebrata* McCook). *Behaviour*, **16,** 309–318.

Witt, P. N., Reed, C. F. & Peakall, D. B. 1968. *Spider's Web: Problems in Regulatory Biology.* New York: Springer-Verlag.

Work, R. W. 1976. The force-elongation behaviour of web fibers and silk forcibly obtained from orb-web-spinning spiders. *Textile Res. J.*, **46,** 485–492.

Work, R. W. 1977. Dimensions, birefringences, and force-elongation behaviour of major and minor ampullate silk fibers from orb-web-spinning spiders—the effects of wetting on the properties. *Textile Res. J.*, **47,** 650–662.