

UTILIZATION OF RESOURCES BY THE MALE GOLDEN ORB-WEAVING SPIDER *NEPHILA CLAVIPES* (ARANEAE)

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ABSTRACT

Two experiments were performed in order to evaluate the influence of female *Nephila* on various aspects of male activity. In the first experiment, the possible benefits of females' presence were measured in terms of male longevity. In the second, food deprived and sated males were offered a choice of mating or feeding with a receptive female.

In the first experiment, groups of individually-housed males were provided with: regularly fed females with which to mate and share prey and silk, freshly killed prey and female silk with no female, female's silk alone, or nothing at all. Solitary males provided with prey and silk lived longer than those in other groups: feeding on silk alone did not affect longevity. Males provided with females lived longer than those without. No significant relationship between body size and longevity was noted in either summer.

In the second experiment, two groups of male *Nephila* were deprived of food for a week. One group was then fed prey partially eaten by a female. Males were then placed on females' webs with prey to determine the influence of deprivation on orientation towards prey or female. Males generally preferred to mate first, even when deprived of food for a long period of time. Observations were made to determine if specific pre-copulatory behaviors exist, and body jerking (violent, rapid shaking with first two sets of legs often jumping on and off the silk) was observed to occur primarily before mating. Other indicators of arousal, such as abdomen wagging or shaking, and exploratory behaviors such as plucking or probing, occurred equally often before mating and feeding.

INTRODUCTION

For most orb-weaving spiders, mating occurs on the female's web, as the adult male ceases building and repairing his own web and adopts a strategy of searching for mates (Christenson and Goist 1979). Though the adult male orb-weaver is not generally considered a predator, he has ways of meeting nutritional needs: feeding on prey that the female has captured (Robinson and Robinson 1980; Christenson et al. 1985), the occasional appropriation of webs from conspecific or related species and trapping prey there (Eberhard, Barreto, and Pfizenmaier 1978), and ingestion of female silk (Vollrath 1980). Female silk ingestion by males have been observed in *Nephila clavipes* (Linnaeus) (Vollrath 1980), in *Leucauge mariana* (Keyserling) (Eberhard pers. comm.) and *Verrucosa arenata* (Walckenaer) (Levi 1976).

It is not clear what males gain from feeding while on the female web. The strategy of searching for a female consumes energy, as does competition between males. The largest male on a given female's web may take up a position in the support strands near the hub, directly above the female (Christenson and Goist

1979). Hub males feed on prey trapped by the female more frequently than do the smaller males who remain on the web periphery (Christenson and Goist 1979).

It is logical to expect that feeding on prey would increase male longevity, but the payoff from silk ingestion is not as clear. In *Araneus diadematus* (Clerck), nearly all of the material the female needs for new web construction can be gotten from consuming, often within a few minutes, the previous day's web (Peakall and Witt 1976). It appears in this case that ingested silk is used for silk production (Foelix 1982); however, silk from naturally occurring webs may be coated with pollen and other microorganisms which may be nutritionally valuable (Smith and Mommsen 1984).

The first question we ask (from census data) is how frequently do males ingest silk and prey and do hub and peripheral males differ in rates of ingestion. Second, we ask (in Exp. 1) if silk and/or prey ingestion influences male and sperm longevity. We exposed males to four feeding conditions: males housed continuously with a regularly fed female, males housed alone but provided with freshly killed prey, males housed alone with female silk, and housed with no prey or silk. As feeding is a variable which contributes to body size, we also asked if male body size is related to longevity.

Female *Nephila* are receptive to the advances of the male in two situations: immediately upon completing her final molt, and when feeding throughout adulthood (Christenson and Goist 1979, Christenson et al. 1985). Robinson and Robinson (1980) note that males feed on the female's prey item or copulate with the female while she is feeding. Virtually nothing is known about the regulation of this male choice, to feed or to mate. The third question we ask (in Exp. 2) is if the immediate feeding status of the male influences his tendency to mate or to feed. Males that were food deprived or recently fed were placed with adult females who were feeding and thus sexually receptive.

As mating may occur while the female is feeding in many species, there is a potential confusion between male courtship behavior and male pre-feeding behaviors. As there is little predation on males by females (Christenson et al. 1985), it is likely that there are cues from which females may be able to distinguish potential mates from potential prey. The fourth question we pose (in Exp. 2) is do males respond differently when mating or feeding on the female's prey item.

METHODS

Census data.—To estimate the frequency of silk and prey ingestion by males in an unrestrained population, free-ranging but individually marked males ($n = 116$) and females ($n = 99$) were observed daily through July and August, 1984, at the Tulane University Hebert Center near Belle Chasse, Louisiana. Incidences of silk and prey consumption by hub and peripheral males were recorded as part of a daily census. A total of about 1425 male/census datum points was gathered. A day's set of observations for each male was considered one male-day. The following summer, 517 additional free-ranging males at Jean LaFitte National Historical Park in Barataria, La. were also observed for incidents of silk and prey consumption. These males were not marked and not followed daily.

Experiment 1—Male and sperm longevity.—In 1984, thirty-eight adult male *Nephila clavipes* were gathered at the Tulane University Hebert Center between

14 and 16 July. In 1985, 45 additional males were gathered at the Barataria site, between 4 and 9 July. All subjects had just completed their final molt, determined by change in palp structure and body coloration, and at least one sperm web was present on their web. Thus, all subjects were of approximately the same age—within a day or two of the final molt. Cephalothorax-abdomen length and tibia-patella lengths were recorded.

Subjects were housed in $123 \times 62 \times 62$ cm boxes, completely enclosed with Fiberglas screen. Males that were to be housed with females were placed one to a box with a randomly selected mate. The subjects in the other groups were housed in three Fiberglas-screened boxes, subdivided into twelve $30 \times 30 \times 30$ cm cells. Each group was housed in a separate box, one male per cell.

Ten subjects were randomly assigned to each of four groups: **Female group**, in which the female was supplied daily with one or two mealworms; **Prey-Silk group** which every other day received a mealworm and female web silk mostly from the viscid spiral; a **Silk group** which every other day received only female silk; and a **Nil group** which received nothing. Subjects to be housed alone were placed in cells counterbalanced by size so that each box contained four small, medium, and large males. Males with a cephalothorax-abdomen length of up to approximately 8.0 mm were classified as small, between approximately 8.0-10.0 mm medium, and greater than 10.0 mm large.

Prey-Silk subjects received web and prey taken from an unrestrained female *Nephila* between 0800 and 1000 hours. A single mealworm was placed in a female's web, and after approximately fifteen minutes of feeding by the female, or when the prey appeared dead, part of the non-sticky barrier strands were removed and a wooden dowel cross (20 cm between the tips of the arms) was swept through the viscid spiral and rotated several times, winding most of the spiral onto the cross. This provided a thick net of support for the mealworm. The cross was then placed upright in the center of the appropriate male's cell. Silk subjects received a cross with female silk obtained in a similar manner, and Nil subjects were given a plain dowl cross.

On the day of prey and/or silk replacement, a one-minute observation of each male was made every hour, beginning fifteen minutes after the last male had been fed. There was approximately four observations each day in which incidents of prey or silk consumption were recorded. A day's set of observations for each boxed male was considered one male-day. Every morning, a census was taken in which feeding, deaths, or disappearances were noted. Data were collected until every animal had died or had disappeared.

Sperm analyses.—One subject from the Prey-Silk group, and one from the Nil group (1985 subjects) were returned to the laboratory every other week for three weeks (total of three from each group) to determine any effect upon sperm development within the palp. Six males were also removed from the Female group over the same period of time. Sperm were evaluated with a Leitz® phase-contrast microscope following methodology described in Christenson, Schlosser, Cohn and Myers (1986).

Ants attracted to the partially eaten prey were a problem, and it was impossible to determine whether missing subjects had escaped, or had died and been carried off. Statistical analyses were conducted on the data from confirmed deaths.

Experiment 2—Male feeding and mating courtship.—Twenty adult male *Nephila* were gathered approximately 20 km south of Belle Chasse at the Jean

Lafitte National Historical Park in Barataria, LA, during August, 1985. Previous mating experience was unknown. They were housed individually in $123 \times 62 \times 62$ cm boxes completely enclosed with Fiberglas screen. Ten adult female *Nephila* were also collected at the Barataria site and housed singly in additional enclosures. Reproductive history of these spiders was also unknown.

All of the males were deprived of prey for one week. On the day of testing, the females were given mealworms and allowed to feed for 15 min, whereupon the mealworms were removed and placed singly in plastic vials. Males were then placed in a vial either alone (unfed group; $n = 10$), or with a partially eaten mealworm for 15 min of observed feeding (fed group; $n = 10$). Individual males were moved to a female's web in which a fresh mealworm had been placed just below the hub. The following male behaviors were recorded during a 30 min period: abdomen wag (tip of abdomen), shake (vibrating the entire body while maintaining contact with the web with all eight legs), body jerk (more violent, rapid shaking with first two sets of legs often jumping on and off the silk), probing and plucking (with forelegs).

To insure that the behaviors were oriented towards prey or female, only behaviors that occurred within the five minutes before copulation or a feeding bout were included in the analyses. During this five minute period, behaviors were scored as 1/0, a 1 given if the behavior occurred, a 0 if not. This was done because of the difficulty in recording each occurrence of some behaviors, for example wags, where a series was recorded as "repeated wags", without an actual count.

RESULTS

Male feeding: Description and frequency.—Males who consumed silk gathered in their chelicerae silk from the upper portions of the viscid spiral or from the outer barrier strands. This silk was formed into a small ball which was continuously worked in the chelicerae until consumed completely in about one hour. Female *Nephila*, in contrast, consume silk at a much faster rate. Portions of their webs are taken down and ingested all within a few minutes. The following are very conservative assessments of the frequency of male ingestion of female silk, since the silk ball is clearly visible only for 15 or 20 minutes after it is formed.

During the census of unrestrained animals, there were nine recorded incidents of silk eating in 240 observations of peripheral *Nephila* males, and six in 1185 observations of hub males over the 1984 summer census of free-ranging males at the Hebert center. There was a significant difference in the rate of observed consumption of silk between hub and peripheral males ($X^2_1 = 19.332$; $p < 0.001$). Peripheral males consumed silk at a rate of 3.7 per 100 male-days. Hub males consumed silk at a rate of one per 200 male-days.

In observations of free-ranging males at the Barataria site (1985), silk ball ingestion was recorded 20 times in 415 observations of hub males, and 9 times in 106 observations of peripheral males. A Chi-square analysis of these data showed no difference in the proportion of hub vs. peripheral males who ate silk ($p = 0.35$). The rate of observed consumption of silk by hub and peripheral males was approximately 8.5 per 100 male-days.

The 1984 census of free-ranging males at the Hebert center resulted in approximately sixty observations of prey items in female's webs. Of these female webs with trapped prey, four observations of males feeding were made. The rate of observed feeding on prey by free-ranging males in this population was approximately seven per 100 male-days.

Feeding and longevity.—There were approximately 1100 male-days of observations of boxed males with access to prey (Prey-Silk, and Female groups). The rate of prey consumption by all boxed males was approximately two per 100 male-days. There were 22 observations of boxed males feeding upon prey (12 in 1984 and 10 in 1985). Fifteen of these observed feedings occurred in males housed with females (seven in 1984 and eight in 1985). The rate of observed feeding males housed alone (Prey-Silk group) was approximately two per 100 male-days. The rate of observed feeding males in boxed males housed with females was also approximately two per 100 male-days.

Over both seasons, two observations of silk eating were made in the Prey-Silk group, and two were made in the Silk group. The rate of observed silk consumption was approximately one per 250 male-days. This was substantially lower than the rate obtained for free-ranging males (eight per 100).

Mean longevity of the males is reported in Table 1. A one-way ANOVA conducted on 1984 males which were housed singly was significant ($F_{2,17} = 5.4531$, $p = 0.015$). Neuman-Keuls analyses of the three groups showed a significant difference between the Prey-Silk and Nil groups ($p = 0.012$), and between the Prey-Silk and Silk group ($p = 0.039$), but not between the Silk and Nil groups ($p = 0.322$). Though the males in the Male-Female group lived almost two weeks longer than the Prey-Silk group, this difference was only suggestive ($p = 0.08$).

In 1985, a significant difference in longevity was found only between the males with females versus those without ($F_{3,21} = 23.855$; $p < 0.0001$). Neuman-Keuls analyses indicated no significant differences in longevity past final molt between the Prey-Silk and Silk groups ($p > 0.99$), Prey-Silk and Nil groups ($p = 0.41$), or the Silk and Nil groups ($p = 0.33$). The mean longevity of the males indicated a slight trend in the predicted direction, identical to the more significant results obtained the previous summer (Table 1).

Effect on sperm.—Analysis of the sperm in palps from deprived and fed males showed no obvious differences in either their number or structure. Slide preparations of sperm from fed and deprived males were filled with coiled sperm.

Size and longevity.—Size was not significantly correlated with longevity in any of the groups. The mean body length for the 30 individually housed males collected at Belle Chasse was 8.8 mm and the mean tibia-patella length was 6.8 mm. The Barataria males' mean body length was 8.9 mm, and mean tibia-patella length was 6.9 mm. When body length and tibia-patella length were correlated with days of survival past final molt, no significant relationship was found in any of the groups.

Male choice: To feed or to mate.—Of twenty males in this study, fifteen preferred to mate first, four preferred to feed first, and one neither fed nor mated ($X^2_2 = 16.3$; $p < 0.001$). Feeding status did not influence males' orientation towards prey or female ($p = 0.36$); they generally preferred to mate even after having been deprived of food for a week. Of ten males in the Fed group, nine mated first, one fed first, and one male neither fed nor mated during the

Table 1.—Mean longevity for males in each group in each season of observation (days). *n* refers to the number of confirmed deaths in each group, SD = standard deviation.

	Nil Group			Silk-Only			Prey-Silk			With Female		
	\bar{x}	<i>n</i>	SD	\bar{x}	<i>n</i>	SD	\bar{x}	<i>n</i>	SD	\bar{x}	<i>n</i>	SD
1984	22.1	9	7.3	27.3	6	5.3	38.8	5	14.5	52.6	8	13.1
1985	21.6	6	7.2	23.3	7	11.7	28.9	8	8.0	68.8	4	12.7

observation period. Of ten males in the deprived group, seven preferred to mate and three preferred to feed before any other activity.

Male responses when feeding versus mating.—The following analyses were based on 15 males who mated and four who fed when placed on the web with their females. Only data from the males' first activity (either mating or feeding) were counted, although one male (sated) fed first then mated, and three males (deprived) mated first, then fed. The data from the male who neither fed nor mated were dropped from the analyses. Only three males fed without first mating during the observation period, one from the sated group, and two from the deprived group. Abdomen wagging, body jerking, probing, shaking, and plucking were observed in both groups. Their appearance was not dependent upon their feeding status ($p = 0.94$; $p = 0.90$; $p = 0.91$; $p = 0.81$; $p = 0.21$ respectively). However, when the data were collapsed across treatment, it was possible to evaluate whether or not a behavior would occur significantly more often before the subject mated or fed. Wagging, probing, shaking, and plucking were no more likely to occur before mating than before feeding ($p = 0.28$; $p = 0.83$; $p = 0.21$; $p = 0.11$). Body jerking, however, was almost exclusively pre-copulatory and was observed prior to feeding only three times, twice after the male had first copulated ($X^2_1 = 8.872$; $p = 0.003$). Only one incident was observed in which a male copulated without first body jerking.

DISCUSSION

Results indicate that feeding on prey increases male longevity. This should increase the likelihood that a male lives until the female becomes sexually receptive or until he can move from female to female. The costs to the hub male of feeding are minimal since few males are killed by a female while trying to feed on her prey, and since hub males are killed by the female no more frequently than smaller, peripheral males (Christenson and Goist 1979). Silk ingestion, in contrast, appeared to have little affect on male longevity, at least with our subjects who were confined to a cage and not allowed to move long distances. This implies that naturally occurring microorganism attachment to female silk is insufficient to make a significant impact on the longevity of adult male *Nephila*.

Conservative estimate of silk consumption by the boxed males may have been partially responsible for the difference in observed silk ingestion between boxed and free-ranging males, as the Fiberglass screen made it difficult to observe whether the males were consuming silk. Another possibility may be greater silk and/or energy requirements in free-ranging males. As ingested silk is primarily used to produce new silk (Foelix 1982), less would be needed by males whose locomotor activity is reduced through confinement.

The data indicate a substantial difference in the rate of observed silk consumption between the 1984 Belle Chasse census data and the 1985 Barataria data. There are three possible explanations for the difference. First is that there was a seasonal variation in the severity of winter, 1985 being severe and killing most overwintering instars. Prey availability, growth rates, and feeding patterns could have been affected. Second, perhaps there are population differences between the Belle Chasse and Barataria animals. Mating and egg-laying do seem to begin earlier in the summer in the Barataria population. Third, although unlikely, differences in methodology could account for the discrepancy between the Belle Chasse and Barataria data. Belle Chasse males were marked and followed daily over the summer, while the Barataria males were unmarked and from different areas of the park. It is not clear what, if any difference this could make in terms of observation of silk consumption, but it does merit noting.

Males live longer when housed with females. This underscores the importance of females in controlling resources important to male reproductive success. This advantage may be due to female protection from potential predators such as ants, and/or to enhanced ability to feed as prey are located near the female. Vibratory and/or chemical cues provided by the female undoubtedly assist the male in locating available prey (Krafft 1982). The absence of these cues in the three groups of males housed alone might reduce the opportunities to feed in the Prey-Silk group, despite the presence of freshly killed prey.

As a male on a female's web will spend a great deal of energy monitoring her as well as his environment (Christenson and Goist 1979), his nutritional requirements will be higher than that of a male housed alone in a relatively confined space. This may also partially account for the greater number of observed feedings in males housed with females. As the rate of observed prey consumption was approximately the same, however, other as yet undetermined benefits of the presence of females may contribute to increased male longevity.

There was a somewhat large difference in the rate of observed feeding between boxed and free-ranging males. This difference may be related to the frequency of prey availability in each population. The females in the boxes were extremely well fed in comparison to free-ranging *Nephila*. Free-ranging males have fewer opportunities to feed relative to boxed animals, therefore when a free-ranging female is observed with a prey item, the probability of the male attempting to feed with her (as assessed through our census methods) may be higher than what occurs in the boxed animals. It would be necessary to supply free-ranging spiders with prey at a rate comparable to that supplied to the boxed animals in order to obtain a clearer indication on the effect captivity may have on rate of prey consumption by males and females.

Body size is not directly correlated with a specific male's lifespan. However, in a natural setting, size is the predominant factor in determining which male will achieve hub status and the opportunity to feed (Vollrath 1980). It is, therefore, size relative to one's conspecifics on a given female's web which determines mating, feeding, and in part, longevity.

When given a choice between mating and feeding, males prefer to mate. It appears that activities such as abdomen wagging and shaking are not specific pre-copulatory behaviors, but indicative of general arousal. Vibratory signals are integral components of feeding and mating behaviors in orb-weaving spiders (Robinson 1982). Probing and plucking with forelegs were usually observed to

precede contact with either the prey or the female, and probably are used to obtain vibratory cues from the web (Krafft 1982).

The selective occurrence of body jerking suggests that there may be specific pre-copulatory responses in male *Nephila*. The behavior is similar in form to shaking, which seems to be a reaction to arousing stimuli. However, intensity of general arousal is not sufficient to produce the body jerking response, as males do not do it when subjected to significant disturbance. When chased about the web with the tip of a fine paintbrush males will abdomen-wag at a rapid pace, and if tapped lightly with the tip they will shake violently. This activity produces a rapidly vibrating web which makes it difficult to see the animal (personal observations). Body jerking is not observed in these situations and appears to be specific to the mating situation.

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