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INTERSEXUAL COMPETITION FOR FOOD IN THE BOWL AND DOILY SPIDER, *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE)

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ABSTRACT

Among web-building spiders, bowl and doily spiders *(Frontinella pyramitela)* are unusual because adult males feed frequently. The males rarely build webs, however, and so depend upon females' snares for foraging. In field and laboratory experiments I assessed the impact of male competition on female foraging success and growth rate. During periods when males are abundant, a female is likely to have a male on her web 22% of the time. These cohabiting males capture about 32% of the prey that hit the web despite the female's efforts to capture the same prey. As a result, males decrease female foraging success by about 7% during periods of male abundance. Adult females grow at a rate that increases linearly with increased food consumption–thus the presence of cohabiting males causes a corresponding 7% decrease in female growth rate when males are abundant. The literature on spider foraging and fecundity permits us to calculate that the resultant impact on female fecundity is between 6.1% and 7.0% depending upon what proportion of growth in adult females is attributable to maternal biomass increase and what is attributable to egg production. This detriment to the female is probably outweighed by the high cost of dislodging the male and by a reduction in the probability that the female will be killed by spiders that mimic prey.

INTRODUCTION

Several taxa of insects and spiders effectively reduce the availability of food for host spiders by web parasitism or commensalism (see references in Barth 1982 and Krafft 1982) and some adult female spiders suffer a further effective reduction in food supply because adult males compete for food while in residence on the females' webs (Rovner 1968, Robinson and Robinson 1978, and see references in Kraft 1982). This situation, male use of the female's web for predation, is rare among spiders because in most species the males take no food during adulthood (Bristowe 1958, Savory 1977; in contrast, see Eberhard et al. 1978).

The bowl and doily spider, *Frontinella pyramitela* (Walckenaer), is one species in which the influence of male competition on female growth and fecundity may be particularly severe. This is because 1) males live with females on the females' webs for long periods of time and 2) males capture and feed on prey on those web despite attempts by the females to prevent such activities. This paper describes some aspects of the feeding ecology of bowl and doily spiders and assesses the effect of male competition on female growth and fecundity.

MATERIALS AND METHODS

Spiders.—*Frontinella pyramitela* is a common inhabitant of low vegetation throughout much of temperate North America. Its non-viscid web consists of a bowl-shaped horizontal sheet, an underlying flat sheet, and a barrier or knock-down meshwork of silk that is above the bowl and "doily." The spider lives on the underside of the bowl, dorsal surface downward, and captures prey that are deflected onto the bowl by the barrier silk. The webs are approximately circular when viewed from above and those of adult females have a diameter of about 8 cm. The female spiders are small (4 mm long, 6 mg) and the males are smaller still (3 mm, 3 mg). Mating in this species occurs on the underside of the bowl of the female's web and is preceded by a complex vibration- and chemical-mediated courtship (Suter and Renkes 1982, 1984).

Field Procedures.—Prey capture rates by adult female *F. pyramitela* were assessed in the field (Poughkeepsie, NY, USA) by observations at one-hour intervals at marked web sites. The time of capture, size of prey, and web site were recorded for each captured prey item. More frequent visits to webs were not possible because of the large number of webs that were under observation at a given time. I found that little inaccuracy in quantification of capture rates resulted from hourly observations because spiders fed on most prey items for more than one hour. Prey capture rates were assessed once in 1981 (July) and twice in 1982 (May and July) for a total of 1093 web-hours. Observations spanned all hours of the day and night but periods of inclement weather (during rain, or ambient temperature less than 10°C) were avoided because the spiders temporarily abandoned their webs or were unresponsive to prey at those times.

I performed censuses of occupied *F. pyramitela* webs 16 times during the 1982 season. All adults and late-instar juveniles (greater than 2.5 mm long) were counted and adults' sexes were recorded. The presence of a common theridiid inhabitant of bowl and doily webs, *Argyrodes trigonum* (Hentz), was also recorded. I confined my censuses to a single unmanipulated study area and, within the confines of that area, tried to achieve sample sizes of at least 80 spiders. When the population in the study area was very low, I could not always achieve that sample size.

I measured male-female cohabitation times (the total consecutive time spent by a male on a female's web) both in the field and in the laboratory (see below). In the field, both marked (fluorescent tempera paint on the dorsal surface of the abdomen) and unmarked males were used at marked web sites. Each male was swung by its dragline onto the periphery of a web occupied by a solitary female. There the male would usually begin courtship immediately (Suter and Renkes 1982), mate, and remain with the female for some time. Timing began as the male first contacted the web and continued until he could not be found on the web. Though the initiation of timing was precise, its termination could have been off by 0.5 hour for marked individuals because they were checked each 0.5 hour, and by 0.5 minutes for unmarked individuals because they were checked each 0.5 minutes.

Vestigial-winged (Vg) *Drosophila melanogaster* were used as experimental prey to assess competition for prey between male and female spiders. These flies were used because many similarly sized prey are encountered by *F. pyramitela* in nature (see results) and because they cannot fly and so are readily captured by the spiders. Naturally formed cohabiting pairs of spiders that were neither actively courting nor feeding on prey were presented with a single fruit fly dropped so that it would land approximately midway between the spiders on the bowl of the web. The spider that ultimately fed on the fly was designated the winner despite occasional changes of possession during the frequent stereotyped contests that preceded feeding. I presented a second fly about 1.5 hours later, after the first fly had been entirely consumed and its carcass discarded.

Laboratory Procedures.—Adult female spiders captured on hedges near Poughkeepsie, New York, were placed on glass or wooden hexapods and enclosed in 3.8 l plastic aquaria. Because adult males rarely build webs, males were enclosed in 10 ml test tubes stoppered with cotton. Both aquaria and test tubes contained wet sand which kept the air near 100% RH. I fed vinegar flies to females on their own webs and to males on webs vacated by females. The temperature in the laboratory varied between 21°C and 23°C.

I measured cohabitation times in the laboratory via continuous visual monitoring of unmarked males on females' webs. Methods were identical to those used in the field (above) except that the webs were on wooden or glass hexapods and were continuously lighted. The cohabitation times of 40 pairs were measured in the laboratory and 17 were measured in the field. Because there were no statistically significant differences between field and laboratory results, both sets of results were pooled.

I assessed the relationship between food consumption and growth rate in 30 adult female spiders by feeding the spiders different numbers of Vg vinegar flies each day for eight days. Spiders were weighted to the nearest 0.01 mg at the beginning and end of the study and the weights of egg masses produced during the study were added to the weights of the responsible females. The flies had a group mean weight of 0.96 mg.

The mortality rates of adult male spiders are usually insensitive to food supply because adult males don't eat (see introduction). *F. pyramitela* males do eat, however, and so may suffer increased mortality when food is scarce or unavailable due to competition. To check the relationship between feeding history and mortality rates, I fed variable numbers of vinegar flies to 33 adult males and then withdrew all food. All of the spiders were maintained at 100% RH until their deaths.

RESULTS

Prey-capture Rates.—During 1093 web-hours of observation, *F. pyramitela* females captured 149 prey that varied in length from 0.5 mm to 11 mm. The mean rate of prey capture (0.14 prey per hour or 1 prey every 7.3 hours) did not vary systematically with the hour of the day or with the date during the adults' foraging season. Because many of the hours of observation were not contiguous, I could not directly derive a frequency distribution of times between prey captures from the field data. However, because webs encounter prey randomly with respect to time of day, the distribution of times between prey captures can be approximated from the exponential distribution with μ = 7.3 hours (Schaeffer and Mendenhall 1975). The distribution indicates that 50% of the time a lone female spider will have to wait less than six hours between prey captures, that 75% of the time she will wait less than 12 hours, and that about 10% of the time she will have to go without food for over 25 hours.

Of course, not all captured prey are equally valuable. The insect prey of *F. pyramitela* vary considerably in mass and consequently in nutrient content. Figure 1 shows how prey length varied among prey captured by spiders in the field. More than 80% of all prey captures were smaller than 3 mm—that is, about the size of a female *D. melanogaster* or smaller, and more than half of all prey captures were smaller than 1.5 mm. At the other extreme, the largest prey was an 11 mm beetle.

The prey lengths shown in Fig. 1 are readily converted into mass units using the empirically derived conversion formula given by Suter (1977). I converted the frequency distribution of prey lengths into a frequency distribution of prey masses and then built a two-dimensional matrix whose elements were the products of those mass frequencies and the exponential frequencies (above) of times between captures. The resulting frequency distribution of rates of prey capture (in mg/h) reveals that the median prey capture rate is 0.13 mg/h, that 25% of the time the spiders capture at a rate greater than 0.39 mg/h, and that 25% of the time they capture prey at a rate less than 0.05 mg/h.

Male impact on the female.—The time spent by males on females' webs in the laboratory and in the field varied between 0.37 and 50 hours and showed no systematic differences between the two sites. The frequency distribution of cohabitation times of 57 pairs from both field and laboratory sites is shown in Fig. 2. The distribution has a median of 7.8 hours with more than 20% of the males leaving the webs in less than 2 hours and about 25% remaining on the webs longer than 12 hours. Two of the males were still on webs after 50 hours.

An assessment of the impact of cohabitation on female foraging depends on information about the prevalence of males in a spider population and on the foraging success of the males. Web censuses throughout the bowl and doily spider's active season revealed only one period when males were present (Fig. 3) though in previous years I had seen a second but smaller pulse of males during September. During the peak period of male abundance (May 25 to June 9, 1982), males could be found on 21.9 ± 0.6% (mean ± S.D., N = 3 samples days) of all *F. pyramitela* webs. That apparently skewed sex ratio could have been underestimated because males wander between females' webs and might remain off webs for many hours. To test that possibility I performed a removal experiment. All males (N = 13) were removed from webs in a small population (48 webs) of spiders, and the appearance of additional males was monitored over the succeeding three days. Over those three days, only four males appeared on the 48 female-occupied webs. Thus it is likely that, in a population of bowl and doily spiders, more than 80% of all males in the population can be found on female webs at any given time. (I could not eliminate immigration of males into the test population, so any or all of the males that appeared during the experiment could have been immigrants). I conclude that the sex ratio is only slightly underestimated by counts of spiders on webs.

Also present on *F. pyramitela* webs were both sexes of the theridiid *Argyrodes trigonum*. The mean frequency of web occupancy by *A. trigonum* on three days in late May was 0.19 ± 0.04 (SD); of 487 webs checked, 94 harbored at least one *A. trigonum*.

F. pyramitela males captured 32% (24/75) of all test prey *(Drosophila)* given them in field studies of male-female competition for prey. When the first fly was presented to a cohabiting pair, 37% (20/54) of the time the male captured the fly. Second fly presentations resulted in only 19% (4/21) capture success by males. The difference between first-

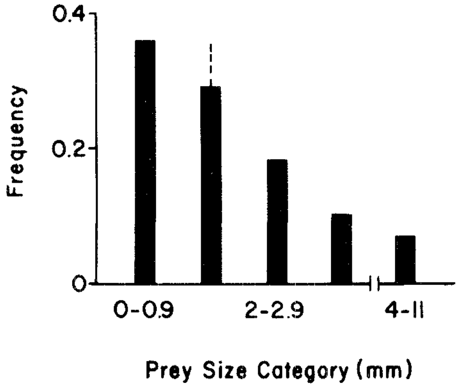

Fig. 1.—Frequency distribution of sizes of prey captured by bowl and doily spiders during 1093 web-hours. N = 149, median = 1 to 1.9 mm (vertical dashed line).

and second-presentation capture success is not significant (χ^2 = 1.50). However, a comparison of the success of males capturing both first and second prey (0/11, 0%) with females capturing both (11/22, 50%) revealed that males are significantly less likely than females to capture two prey in a row when the second prey comes soon after the first (binomial test, $P < 0.001$). During 35 of the presentations of test prey, I noted not only which spider eventually captured the prey but also which spider contacted the prey first. Males were the first to contact the prey 46% of the time (16/35).

Growth rates of females and starvation morality of males.—Figure 4 shows the results of a eight day laboratory study in which I fed vinegar flies to female bowl and doily spiders and measured the spiders' growth rates. The two spiders that received no food during the study lost only 14% of their original mass after eight days. Over the 0 to 0.23 mg/h range of capture rates, spider growth rates increased linearly with capture rates. The linearity of the data indicates that neither satiation nor decreased nutrient utilization occurred at high feeding rates.

Figure 5 shows the frequency distribution of deaths of male spiders as a function of time since the last feeding. Starved males died within 34 days of their last vinegar fly meal if kept at approximately 22°C. Time of death was neither related to the date (i.e. the age of the spider) (runs test, $P > 0.1$) nor to the number of flies consumed prior to withdrawal of food ($r_s = 0.08$, $P > 0.1$) nor to the mass of the spider at the beginning of the study ($r^2 = 0.01$, $P > 0.1$). Only the time spent fasting was strongly related to time of death (runs test, $P < 0.025$).

DISCUSSION

Impact of male competition for prey.—In spiders, as in many other invertebrate groups, fecundity is directly proportional to the mass of the female and to her foraging success (Turnbull 1962, Kessler 1971, Riechert and Tracy 1975, Wise 1975, Van Wingerden 1978). Any limitation of a female spider's food supply, then, results in a limitation of

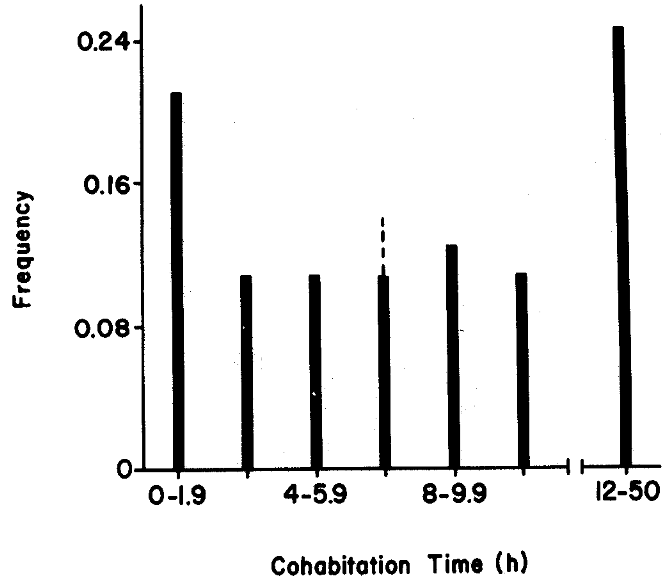

Fig. 2.—Frequency distribution of cohabitation times of pairs of spiders from both field and laboratory observations. N = 57, median = 7.8 hours (vertical dashed line).

her fecundity and a consequent limitation of her fitness. The data presented herein show that male bowl and doily spiders cause a considerable decrease in female foraging success by competing with them for prey items. The competition must also cause a decrease in the females' fecundity and, if females are not all equally tolerant of male cohabitation, a decrease in their fitness.

The impact of male competition on *F. pyramitela* females can now be estimated. During periods of high male:female ratio, a female is likely to have a male on her web about 22% of the time (assuming that cohabitation times are approximately evenly distributed across females). The cohabiting male captures about 32% of the prey that hit the web despite the female's efforts to capture those same prey. Thus during periods of male abundance, males decrease female foraging success by about 7.0% (0.32 X 0.22 X 100).

Though a 7% decrease in prey capture constitutes a major effect of competition, the impact must be much greater for many females in a population of bowl and doily spiders. The number of visits of males to a particular female's web, the time between prey captures at the web, and the sizes of prey are all highly variable, apparently random parameters. And the tenacity of the visiting males, though sensitive to female reproductive status (Austad 1982) and to several identifiable male attributes (Suter, unpublished), is not entirely under the female's control. Some females will therefore lose considerably more than 7% of their food to males during periods of male abundance because they cohabit with more males who stay longer and are more successful at competing for prey. During the remainder of the reproductive lives of the female spiders, male impact is low or nil because males are scarce.

Adult female bowl and doily spiders grow at a rate that depends linearly on the amount of food they consume (Fig. 4). Turnbull (1962), in studies of the fecundity of another linyphiid spider, *Linyphia triangularis*, showed that growth in his mature females was entirely composed of increase in total egg mass rather than increase in maternal tissue biomass. Assuming that is also the case for *F. pyramitela*, the impact of the male competition is then as great on fecundity (or mean egg mass) as it is on the "growth" rate in Fig. 4. In contrast, Kessler (1971) showed that in four species of wolf

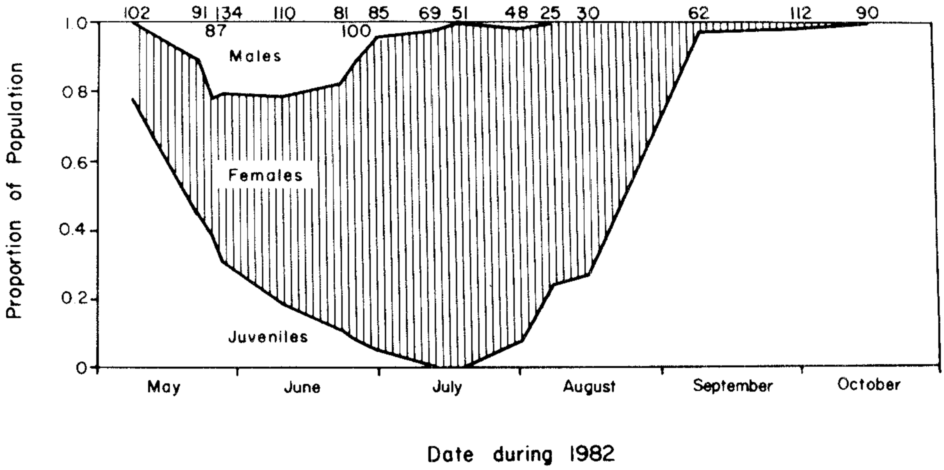

Fig. 3.—Relative abundances of male, female, and immature spiders inhabiting webs during the 1982 season. Numbers at the top of the graph indicate the total number of *F. pyramitela* counted on each census date.

spiders (Lycosidae) about 13% of adult female growth was increase in maternal biomass and the remaining 87% was egg production. If bowl and doily spiders are very similar to the wolf spiders in their reproductive ecology, then 87% (rather than 100%) of the growth deficit would be subtracted from the female's current reproductive effort. In either case, the fecundity deficit caused by the male competition for prey is large—between 7.0% (all growth is egg production) and 6.1% (87% of growth is egg production) during the period when males are most abundant. Figure 3 shows that males are common for about four weeks early in the summer, time enough for the female to produce at least two, perhaps three clutches of eggs (Kessler 1971, Eberhard 1979, Austad 1982) and time enough to encompass a majority of the reproductive life of most females (Austad 1982a). Because the aggregate impact of males varies with their abundance, the 6-7% estimate of their impact at peak abundance overestimates the impact of males during an entire season.

Benefit (to males) of competition for prey.—In most spider species, the males apparently do not feed as adults (see introduction) but rather wander from female to female, from web to web, consuming stored nutrients. If male mortality is high while searching

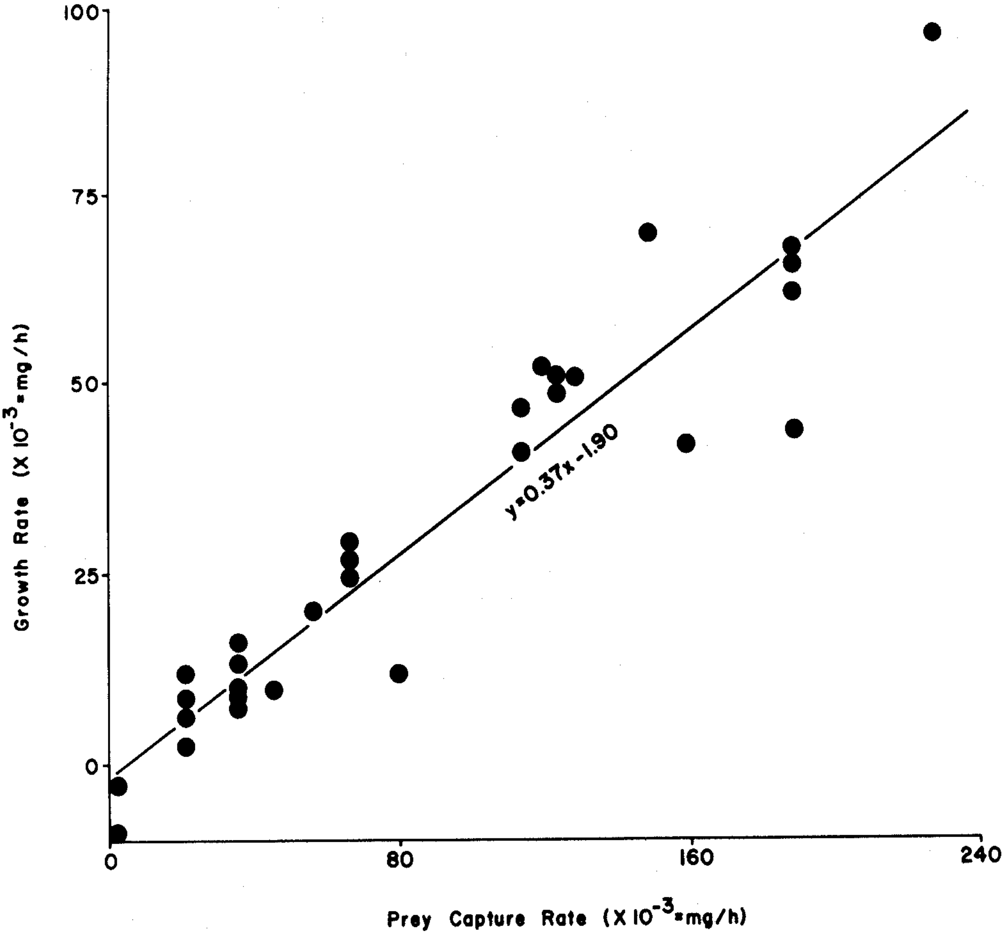

Fig. 4.—Growth rates of adult female bowl and doily spiders as a function of the rate of prey capture. The solid line indicates the best fit to the data (r = 0.947) for the growth of the 30 spiders in the study.

for females, then male foraging would confer no nutritional advantage because the spiders, with their comparatively low metabolic rates (Anderson 1970), would die of other causes before they died of starvation. Thus high off-web mortality is an adequate explanation for the absence of feeding by males in some species of spiders. What explanations can be offered for the existence of vigorous foraging by adult male bowl and doily spiders? 1) Off-web mortality from predators may be low due to crypsis, small size, unpalatability, location of search, etc.; 2) desiccation may be a primary source of male mortality in dry habitats and thus feeding may more appropriately be considered drinking; or 3) intrasexual competition for scarce resources may favor heavier spiders and males can become heavier by eating.

Neither I nor the literature have information on mortality in vagabond male spiders although Robinson and Robinson (1978) suggest that such mortality may be relatively low for small male spiders because of their inconspicuousness. Desiccation certainly is a problem for both sexes of *F. pyramitela* during periods when there is neither rain nor dew formation, and both sexes can be observed to drink as dew forms or when it rains. However, males kept at high relative humidity still feed readily when placed on female webs and this feeding, in the absence of desiccation, prolongs their lifetimes under laboratory conditions (Fig. 5). Thus the threat of desiccation is not a sufficient explanation of male feeding in the bowl and doily spider. Several authors have shown that the results of intrasexual competition among male spiders are biased by mass: the heavier male has a higher probability of winning an encounter (Rovner 1968, Dykstra 1969, Christenson and Goist 1979; in contrast, see Aspey 1977). Austad (1983) and Suter and Keiley (1984) have shown the same mass bias in *F. pyramitela*. It may be, then, that increase in mass

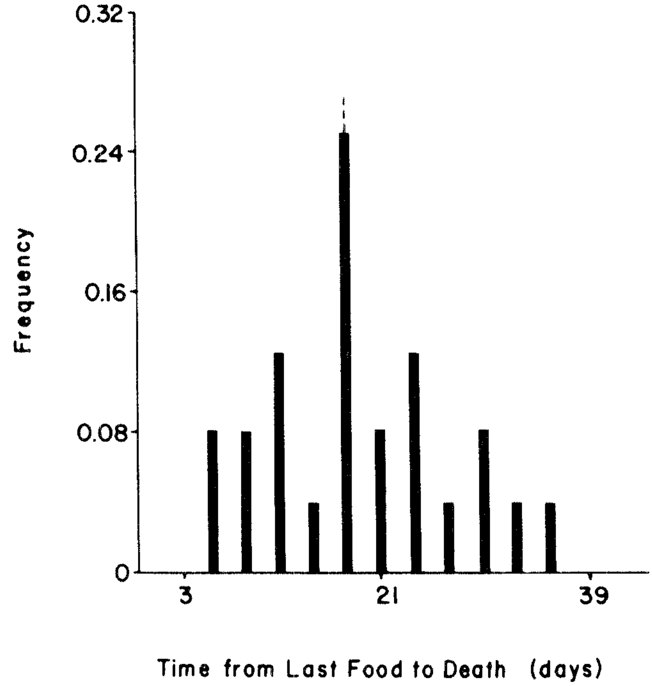

Fig. 5.—Male morality due to starvation. Twenty three males kept at high RH and at approximately 22°C died within 34 days after their last meal (median = 17 days, dashed line). Time of death was neither related to the age of the spider nor to the number of flies consumed prior to withdrawal of food nor to the initial mass of the spider. The time spent fasting was significantly related to time of death (runs test, $P < 0.025$).

through opportunistic feeding is adaptive for males both because it prolongs their lives (above) and because it makes them more formidable opponents during agonistic encounters. Both prolongation of life and success in agonistic encounters would allow a male to inseminate more females than if he was short-lived and a frequent loser.

Benefit (to females) of male cohabitation.–*F. pyramitela* males cohabit with females far longer than is necessary for insemination of the females (Austad 1982) and yet far shorter than is necessary to guard the female and thereby ensure paternity. Indeed, Austad has shown that first male sperm priority is so complete in this species that first males have no need to guard and subsequent males have no paternity to ensure. Those conclusions and our data indicate that the males remain in webs to feed.

A female's tolerance of such prolonged male cohabitation is difficult to understand, then, because her interests are apparently in direct conflict with his. Austad (1984) argues that, at least with respect to multiple matings, the costs of compliance with the male are less than the costs of resistance. His argument was tenable for multiple matings because all known costs to the female were small. The nutrient cost of lengthy periods of cohabitation with males, however, is high.

I propose two explanations for female tolerance of male cohabitation. 1) Males are probably expensive to dislodge. Observations of males and females both during courtship (Suter and Renkes 1984) and during competition for prey indicate that the two sexes are equally agile on the female's web. Thus, though the female is heavier than her mate, she is unlikely to be able to throw him off without expending considerably time and energy in prolonged chase. In this respect, the male's behavior contrasts sharply with his behavior when confronted with another male: when confronted by an aggressive female, the male avoids direct contact by fleeing from the female but remaining on the web; when confronted by another male, the resident male promptly engages in display and fighting behavior that ends when one male flees from the web altogether (Austad 1983, Suter and Keiley 1984). 2) The presence of the male decreases by approximately 50% the probability of female mortality caused by predation by other spiders. Several spiders in the Theridiidae and Mimetidae prey upon bowl and doily spiders. Typically the bowl and doily spider senses the presence of the intruding predator, mistakes it for prey, and rushes to the attack only to be attacked and consumed itself (pers. obs.). When males share females' webs, males and females are equally likely to rush at prey and thus equally likely to rush at predators that mimic prey. In my study areas, *Argyrodes trigonum*, known to be a predator on other spiders (Wise 1982) is very common during the period when male *F. pyramitela* are also abundant and may therefore contribute strongly to mortality during that period. Indeed, I have frequently observed *A. trigonum* feeding on both sexes of bowl and doily spiders. I hypothesize, therefore, that a major benefit to the female of prolonged male cohabitation is the deflection of predation from female to male. I am currently testing this hypothesis in field populations.

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