

## DETERMINANTS OF FECUNDITY IN *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE)

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### ABSTRACT

The fitness of *Frontinella pyramitela* (Walckenaer) (Araneae, Linyphiidae) is, by definition, a function of its lifetime fecundity and the survivorship of its offspring. In the present study, I sought the major determinants of fecundity in a laboratory setting and then evaluated the results in the context of several published field studies. According to this analysis, the primary determinants are female longevity, foraging success, and size. The data also permitted the calculation of an expected relative contribution to total fecundity of each clutch of eggs: because the fertility rate drops sharply after the second clutch is deposited, early mortality is disproportionately detrimental to lifetime fecundity.

### INTRODUCTION

Darwinian fitness, despite its succinct definition, is notoriously difficult to assess in living organisms (Endler 1986) because three of its principal components, age at first reproduction, lifetime fecundity, and survivorship of offspring (Vehrencamp and Bradbury 1984; Horn and Rubenstein 1984), can seldom all be measured. Nevertheless, differences among animals in any one component are likely to be strongly correlated with differences in fitness, and thus it has become common to study fecundity (number of live births), for example, as an index of fitness (e.g., Emlen and Wrege 1988; Riechert and Tracy 1975).

Scattered in the arachnological literature are numerous reports on aspects of spider fecundity such as eggs per clutch, time between clutches, and fertility. The earlier studies have been reviewed by Turnbull (1973). In more recent literature, a number of authors have reported that ecological variables such as photoperiod (Miyashita 1987a) or foraging success (Riechert and Tracy 1975; Wise 1979; Morse and Fritz 1987), and individual variables such as female size (Fritz and Morse 1985; Killebrew and Ford 1985), contribute to observed intraspecific variability in spider fecundity. Other reports, taken together, have demonstrated the plurality of spider responses to ecological variables: ambient temperature appears not to influence fecundity in one theridiid, *Achaearanea tepidariorum* (C. L. Koch) (Miyashita 1987b), but has a strong influence in another, *Theridion rufipes* Bryant (Downes 1988); similarly, food deprivation does not affect the number of eggs produced either by a linyphiid, *Linyphia triangularis* (Clerck) (Turnbull 1962), or by some species of the lycosid genus *Pardosa* (Kessler 1971),

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but it does affect the number of eggs produced by other *Pardosa* species (Kessler 1971) and by a thomisid, *Misumena vatia* (Clerck) (Fritz and Morse 1985). This variety of responses to the same environmental variables suggests that it may be unwise to generalize (Eberhard 1979).

In the laboratory investigation reported below, I attempted to discover the primary determinants of fecundity in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Linyphiidae). This spider is a small, nearly ubiquitous inhabitant of fields and shrublands in temperate North America. It has been the subject of numerous ecological (e.g., Janetos 1983; Suter 1985), ethological (e.g., Hodge 1987; Austad 1983; Suter and Parkhill 1990), and biophysical (e.g., Pointing 1965; Suter 1984; Suter et al. 1987) investigations.

### MATERIALS AND METHODS

In May of 1988 I captured immature male and female *F. pyramitela* from their webs in old fields in Dutchess County, NY. The spiders were reared to adulthood in isolation from their conspecifics in 473-ml plastic containers at 100% RH, approximately 12:12 photoperiod, and 22-24 °C. They were maintained on a diet of live vinegar flies (*Drosophila melanogaster*), and mean feeding rates varied between 0.62 and 1.55 flies per day (0.81 to 2.02 mg/d). The variation was attributable in part to the spiders' prey capture success and in part to an interaction between the feeding schedule and the timing of ovipositions (feeding is inhibited for 1 to 2 days prior to oviposition). The range of feeding rates brackets Austad's (1989) field estimate of foraging success (1.48 mg/d, equivalent to eight *D. melanogaster* per week) and is lower than my own direct field measure of foraging success (Suter 1985: median = 3.12 mg/d). Females were virgins at the beginning of the study and were allowed only a single mating which occurred within 7 days of the molt to adulthood.

I recorded the matings on videotape (at 2 fps) and then removed the males. The videotaped images provided accurate information about the duration of the insemination phase (Austad 1982; Suter and Parkhill 1990) of each mating. Females that deposited eggs fertilized in those matings ( $N = 57$ ) were transferred to new containers after each oviposition, and their egg cocoons ( $N = 169$ ) were maintained under the conditions outlined above. Egg cocoons were transferred to 70% ethyl alcohol eleven days after oviposition and subsequently analyzed with respect to number of progeny (well-developed eggs or hatched spiderlings), size of progeny (Suter and Parkhill 1990), and unfertilized eggs (no visible evidence of tissue differentiation).

Fourteen pairwise relationships among the variables were evaluated using regression statistics, with  $\alpha = 0.01$  because of the large number of tests. The resulting probabilities were used not to reject explicit hypotheses but rather as a guide to important relationships. Multiple regression of copulation duration, number of clutches, and female mass on lifetime fecundity was not performed because the number of females on which all three independent variables were available was small (18).

Table 1.—Components of fecundity in *F. pyramitela*. Number of progeny, latency to oviposition, and productivity were tested for relationships with other variables. For those comparisons in which the coefficient of determination was significant ( $P < 0.01$ ), the sign of the slope of the tested line is indicated in parentheses.

Relationship	<i>N</i>	$r^2$	<i>P</i>
Total progeny versus copulation duration (see Suter and Parkhill 1990)	40	0.004	0.742
Total progeny versus total number of clutches	55	0.458 (+)	< 0.001
Progeny per clutch versus post-oviposition mass of female	24	0.348 (+)	0.001
Progeny (I) versus feeding rate (flies/day between insemination and first oviposition)	50	0.263 (+)	< 0.001
Progeny (II) versus feeding rate (flies/day between first and second ovipositions)	50	0.314 (+)	< 0.001
Progeny (II) versus latency (II) (second oviposition data only)	50	0.110	0.020
Latency (I) versus food consumption (time and flies consumed between insemination and first oviposition)	51	0.037	0.179
Latency (I) versus post-oviposition mass of female	23	0.282 (+)	0.004
Latency (II) versus food consumption (time and flies consumed between first and second ovipositions)	51	0.136 (+)	0.008
Latency (II) versus post-oviposition mass	28	0.009	0.637
Latency (III) versus food consumption (time from insemination, flies between last molt and first oviposition)	49	0.038	0.182
Eggs per clutch versus clutch order	169	0.365 (—)	< 0.001
Productivity (I, eggs/feeding rate) versus post-oviposition mass of female	24	0.005	0.972
Productivity (II, eggs/feeding rate) versus post-oviposition mass of female	27	0.067	0.181

## RESULTS

The results of this study are summarized in Table 1. Of the 14 relationships tested, six were significant ( $P < 0.01$ ) and had positive slopes. (1) Spiders that lived for many weeks after insemination produced more clutches, and consequently more live progeny, than did spiders that died soon after insemination. Figure 1 characterizes the variation in this relationship between total fecundity and number of clutches produced. (2, 3) The feeding rate achieved by a female strongly affected the number of progeny produced in the immediately succeeding clutch for both the first and second clutches. (4) The number of live progeny in each clutch was strongly related to the mass of the female after oviposition. (5) Larger female mass also increased the delay between insemination and first oviposition, but mass differences were not related to differences in the latency to the second oviposition. (6) Latency to the second oviposition was strongly related to food consumption during the same period, an uninteresting

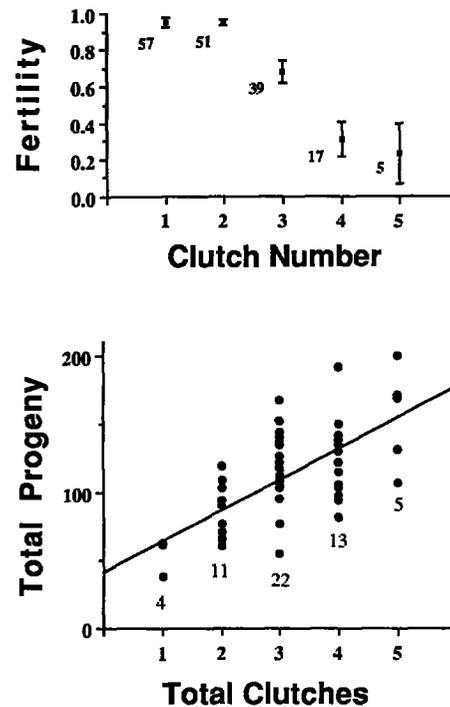


Figure 1.—The fecundity of bowl and doily spiders (lower panel) is closely tied to the number of clutches produced ( $r^2 = 0.458$ ), which is in turn closely related to longevity. This relationship exists despite the rapid decrease in fertility that occurs after the second clutch is deposited (upper panel, and see Suter and Parkhill 1990). Much of the variation seen in the lower panel is probably attributable to the consequences of differences among females in mass and food consumption (Table 1).

consequence of the fact that animals with shorter latencies had fewer days during which to capture prey.

One other relationship was significant but had a negative slope: (7) With respect to number of eggs per clutch, earlier clutches contained more eggs than did later clutches (ANOVA,  $F = 5.97$ ,  $P < 0.001$ ) although most of that variation was due to higher numbers in first clutches (mean  $\pm$  SD clutch size for all clutches,  $42.12 \pm 14.40$ ,  $N = 169$ ; for first clutches,  $53.32 \pm 14.37$ ,  $N = 57$ ); Bonferroni simultaneous confidence intervals for all comparisons in the ANOVA show that only the first clutch is significantly different, at the 0.05 level, from the grand mean). This relationship was previously reported for this species by Austad (1982, 1989).

The latency to oviposition for the first clutch (I) was measured from the date of insemination whereas the latency to oviposition for the second clutch (II) was measured from the date of the first oviposition. It is perhaps not surprising, therefore, to find that latency I was significantly shorter than latency II (I, mean  $\pm$  SD,  $9.62 \pm 3.2$ ,  $N = 47$ ; II,  $11.83 \pm 3.26$ ,  $N = 47$ ;  $t = 3.41$ ,  $P = 0.001$ ), because a female probably begins to synthesize yolk prior to insemination. Similarly, productivity (measured as eggs produced relative to the food intake rate), is lower for the second clutch than for the first, probably because the first clutch contains some pre-insemination yolk [first, mean  $\pm$  SD,  $50.51 \pm 14.42$  eggs/(flies/day),  $N \pm 47$ ; second,  $39.01 \pm 12.99$ ,  $N = 54$ ;  $t = 4.44$ ,  $P < 0.0001$ ].

Eggs per clutch varied linearly with feeding rate over the range of feeding rates (0.81 to 2.02 mg/d) in this study, with a slope of 32 eggs/(mg/d). Thus over the mean 11.8 days between clutches, a spider could produce about 2.7 eggs per mg of prey mass consumed.

## DISCUSSION

The data presented above elucidate the primary determinants of lifetime fecundity in *F. pyramitela* in a laboratory setting: longevity, size, and feeding rate.

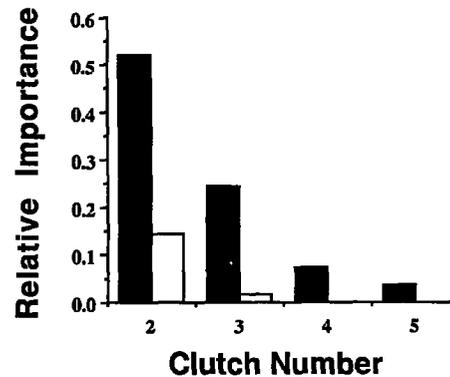
**Longevity.**—Animals that live longer have more opportunities to reproduce, usually, than those that live only briefly. In animals that reproduce repeatedly, lifetime fecundity is particularly sensitive to variation in survivorship. Because the bowl and doily spider is iteroparous, it is not surprising to find that females that live longer produce more clutches and more eggs (Fig. 1, Table 1). In the laboratory, these spiders deposit up to five clutches containing about 42 eggs per clutch [approximately twice the clutch size reported by Austad (1982), but very close to field reports by Austad (1989)] at approximately 11-day intervals. Fertility declines rapidly after the second clutch (Fig. 1) although egg production does not. The sharp decline in fertility after the second clutch (also reported by Austad 1982, 1989) may indicate sperm depletion or senescence, egg senescence, or some combination of these factors.

The implications of these data can be assessed in the context of field survivorship of *F. pyramitela*. Austad (1989) has reported that in field studies, females have surprisingly high mortality rates: his data indicate losses equivalent to 13.5% of the population per day (a probability of mortality of 0.135 per adult female per day). The estimate is about four times higher than my own calculations (0.035 per adult female per day, unpublished data) based on a field demographic study (Suter 1985). Using as bases for calculations the average oviposition latencies reported above and mortality rates of 0.135 (Austad) and 0.035 (Suter), the proportion of females surviving to deposit clutches one through five would be 0.248, 0.045, 0.008, 0.001, and 0.0002 (Austad) and 0.710, 0.466, 0.305, 0.200, and 0.131 (Suter). An estimate of the expected relative contribution of each clutch to lifetime fecundity can be derived from the product of the survivorship probability and the expected number of live young (mean fertility X mean clutch size). Those expected relative contributions, shown in Fig. 2, confirm that longevity, particularly through the first two clutches, is crucial as a determinant of lifetime fecundity in *F. pyramitela*.

**Size.**—Prior to the present study, size variation in *F. pyramitela* was already known to be important in determining the outcomes of agonistic contests both between males (Austad 1983; Suter and Keiley 1984) and between females (Hodge 1987). The data reported above indicate that mass also contributes directly to fecundity per clutch (Table 1, Fig. 1), as it does in many other invertebrates. Thus larger females of this species benefit because (1) their clutches are larger, (2) they retain possession of their webs more frequently (Hodge 1987), (3) they capture more prey biomass per unit time (Janetos 1983), and (4) they may have a somewhat greater resistance to desiccation and other environmental challenges. [The determinants of adult size in this species have not been explored but are obviously important contributors to fitness. Presumably both size at hatching (Suter and Parkhill 1990) and food availability, as well as genotype, are involved.]

**Foraging success.**—Because nutrients are required to produce the yolk that is the primary constituent of spider eggs, the positive relationship between feeding rate and fecundity, and the negative relationship between feeding rate and latency to oviposition, are expected. The relationships probably reflect reality under field

Figure 2.—The expected relative contribution to lifetime fecundity of each clutch. The measure is the product of the probability that the female will survive to oviposit and the expected number of live young (clutch fertility X clutch size) in the clutch, all set relative to the first clutch (1.0). The filled bars are based in part upon an estimate of female mortality (0.035/day) from Suter (1985); the open bars are based upon an estimate of mortality (0.135) derived from Austad (1989).



conditions: clutch sizes and latencies are comparable to those reported by Austad (1989) and the feeding rates in the laboratory are representative of field conditions (Austad 1989; Suter 1985). Both relationships confirm the findings of Austad (1989) and indicate a positive contribution of foraging success to lifetime fecundity. Because feeding rates in this study were not systematically manipulated, however, the range of rates was relatively narrow. I propose to explore the upper limits of food intake in this species to look for both clutch mass and egg number constraints. Such a study would make possible a comparison with the interesting report by Riechert and Tracy (1975) that there is a limit to the number of eggs produced by the agelenid, *Agelenopsis aperta* (Gertsch), but no limit to the total mass of eggs produced.

Janetos (1983) has shown that larger *F. pyramitela* capture larger prey, on average, than do smaller ones. If this relationship holds for all sizes and instars, then larger hatchlings (Suter and Parkhill 1990) would become among the largest of adults and have all of the other advantages of large size to which I alluded above. Clearly a female's foraging success and her size reinforce each other in ways that ultimately augment fecundity.

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#### LITERATURE CITED

- Austad, S. N. 1982. First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution*, 36:777-785.
- Austad, S. N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Anim. Behav.*, 31:59-73.
- Austad, S. N. 1989. Life extension by dietary restriction in the bowl and doily spider, *Frontinella pyramitela*. *Exp. Gerontol.*, 24:83-92.

- Downes, M. F. 1988. The effect of temperature on oviposition interval and early development in *Theridion rufipes* Lucas (Araneae, Theridiidae). *J. Arachnol.*, 16:41-45.
- Eberhard, W. G. 1979. Rates of egg production by tropical spiders in the field. *Biotropica*, 11:292-300.
- Emlen, S. T. and P. W. Wrege. 1988. The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.*, 23:305-315.
- Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton. 336 pp.
- Fritz, R. S. and D. H. Morse. 1985. Reproductive success, growth rate and foraging decisions of the crab spider *Misumena vatia*. *Oecologia*, 65:194-200.
- Hodge, M. A. 1987. Agonistic interactions between female bowl and doily spiders (Araneae, Linyphiidae): owner biased outcomes. *J. Arachnol.*, 15:241-247.
- Horn, H. S. and D. I. Rubenstein. 1984. Behavioural adaptations and life history. Pp. 279-298. *In Behavioural Ecology: an Evolutionary Approach*. (J. R. Krebs and N. B. Davies, eds.). Sinauer Associates, Sunderland, Massachusetts.
- Janetos, A. C. 1983. Comparative ecology of two linyphiid spiders (Araneae, Linyphiidae). *J. Arachnol.*, 11:315-322.
- Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. *Oecologia*, 8:93-109.
- Killebrew, D. W. and N. B. Ford. 1985. Reproductive tactics and female body size in the green lynx spider, *Peucetia viridans* (Araneae, Oxyopidae). *J. Arachnol.*, 13:375-382.
- Miyashita, K. 1987a. Development and egg sac production of *Achaearanea tepidariorum* (C. L. Koch) (Araneae, Theridiidae) under long and short photoperiods. *J. Arachnol.*, 15:51-58.
- Miyashita, K. 1987b. Egg production of *Achaearanea tepidariorum* (C. L. Koch) (Araneae, Theridiidae) in the field in Japan. *J. Arachnol.*, 15:130-132.
- Morse, D. H. and R. S. Fritz. 1987. The consequences of foraging for reproductive success. Pp. 443-455. *In Foraging Behavior*. (A. C. Kamil, et al., eds.). Plenum Press, New York.
- Pointing, P. J. 1965. Some factors influencing the orientation of the spider, *Frontinella communis* (Hentz) in its web (Araneae: Linyphiidae). *Can. Entomol.*, 97:69-78.
- Riechert, S. E. and C. R. Tracy. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. *Ecology*, 56:265-285.
- Suter, R. B. 1984. Web tension and gravity as cues in spider orientation. *Behav. Ecol. Sociobiol.*, 16:31-36.
- Suter, R. B. 1985. Intersexual competition for food in the bowl and doily spider, *Frontinella pyramitela* (Linyphiidae). *J. Arachnol.*, 13:61-70.
- Suter, R. B., G. Doyle and C. M. Shane. 1987. Oviposition site selection by *Frontinella pyramitela* (Araneae, Linyphiidae). *J. Arachnol.*, 15:349-354.
- Suter, R. B. and M. Keiley. 1984. Agonistic interactions between male *Frontinella pyramitela* (Araneae, Linyphiidae). *Behav. Ecol. Sociobiol.*, 15:1-7.
- Suter, R. B. and V. S. Parkhill 1990. Fitness consequences of prolonged copulation in the bowl and doily spider. *Behav. Ecol. Sociobiol.*, 26:369-373.
- Turnbull, A. L. 1962. Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae: Linyphiidae). *Can. Entomol.*, 94:1233-1249.
- Turnbull, A. L. 1973. Ecology of the true spiders (Araneomorphae). *Ann. Rev. Entomol.*, 18:305-348.
- Vehrencamp, S. L. and J. W. Bradbury. 1984. Mating systems and ecology. Pp. 251-278. *In Behavioural Ecology: an Evolutionary Approach*. (J. R. Krebs and N. B. Davies, eds.). Sinauer Associates, Sunderland, Massachusetts.
- 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*, 41:289-300.