Martyniuk, J. and D. H. Wise. 1985. Stage-biased overwintering survival of the filmy dome spider (Araneae, Linyphiidae). J. Arachnol., 13:321-329.

# STAGE-BIASED OVERWINTERING SURVIVAL OF THE FILMY DOME SPIDER (ARANEAE, LINYPHIIDAE)

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## ABSTRACT

Overwintering success of the filmy dome spider *Prolinyphia marginata* (Koch) [= *Neriene radiata* (Walckenaer) and *Linyphia marginata* Koch] was observed with respect to stage of development and differences in body weight within a stage. Studies conducted in three different areas measured winter survivorship rates of 60 spiders housed in outdoor cages (Michigan), 243 spiders in outdoor jars (Maryland), and 245 spiders in a combination of cages and jars (New York). The overall proportion of spiders successfully overwintering was 0.31 in New York, 0.69 in Maryland, and 0.75 in Michigan. All three studies showed that older stages (instars) had substantially higher survival rates than younger stages. Comparison between the autumn weights of overwintering survivors and non-survivors indicated that differences in spider weight within a stage had no significant influence on winter survival.

These experimental studies suggest that overwintering mortality may be significant in natural populations of *P. marginata,* and that different overwintering survival rates among stages can alter the composition of the population.

## INTRODUCTION

Not much information is available on overwintering mortality in spiders. Schaefer (1977) studied the winter ecology of several species and found that winter mortality was not correlated with overall generation mortality. Buche

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(1966, cited by Toft 1976) discovered that the smaller stages (instars) of linyphiids do not survive cold temperatures as well as later stages. On the other hand, Schaefer found that only adults of the linyphiid *Centromerita bicolor* suffered substantial winter mortality. Other information is available (e.g. Kirchner 1973, Edgar and Loenen 1974), though we lack much basic data, especially considering the potential importance of winter mortality as a key factor in the dynamics of spider populations. Not much is known about the relative susceptibility of the younger stages to winter conditions, despite the fact that populations of over 70% of temperate spider species overwinter, at least partially, in juvenile stages (Schaefer 1977).

The filmy dome spider, *Prolinyphia marginata* (C. L. Koch) [= *Neriene radiata* (Walckenaer) = *Linyphia marginata,* C. L. Koch], is a sheet-web building linyphiid common in North America. The species overwinters in forest leaf litter (J. Martyniuk and D. H. Wise, pers. obs.), as do many temperate linyphiids (Schaefer 1977, Aitchison 1978). Census data for a Michigan population of *P. marginata* indicate that winter disappearance is significant in this population (Wise 1976). The complex phenology of the filmy dome spider produces an overwintering population that is a mixture of subadult stages, ranging from recently emerged spiderlings to large, late-stage juveniles (Wise 1976, 1984). This mixture of stages reflects within-season differences in the timing of reproduction and development patterns of young spiders, and also reflects the effects of variable prey abundance upon rates of growth and development (Wise 1975, submitted, Martyniuk 1983).

This paper reports the results of three separate studies, each with a different population of *P. marginata.* Considered together, the studies examined the relative overwintering survival of different stages and the influence of weight differences within a stage on winter mortality. Study I was conducted by J. Martyniuk, and Studies II and III by D. H. Wise.

## STUDY I

**Methods.**—The population that was studied occurred on the Nature Preserve of the State University of New York at Binghamton, Broome Co., New York. During February 1981, leaf-litter samples were collected and examined in order to document the presence of *P. marginata* in the leaf litter during the winter. Five 30 cm x 30 cm forest floor plots were excavated and removed (10 cm depth) from known *P. marginata* habitat and transported to the laboratory in plastic bags. Three viable, immature *P. marginata* were found in the samples. It was not possible to determine the exact location of the spiders in the litter due to the disruption of excavation and transportation.

To determine overwintering mortality in *P. marginata,* 145 spiders in 1981-82 and 55 spiders in 1982-83 were individually housed in 400 ml glass jars containing ca 5 cm of leaf-litter and soil. The jars were securely covered with fabric netting and placed next to a wall on an open terrace. A sheet of plywood was suspended 10 cm above the top of the jars, minimizing snow accumulation and possible drainage problems. As a control for this artificial situation, in 1981-82 three 30 cm x 30 cm x 30 cm net cages, each containing soil and leaf-litter with 15 spiders, were embedded 10 cm into the ground in an area known to harbor *P. marginata.*

The mesh size of the cages was large enough to allow snow to accumulate inside. Leaf litter and soil used in the jars and cages were collected from the field and examined for resident *P. marginata* prior to use in experimental containers. Jars were placed outside and spiders were introduced into the cages with the final disappearance of *P. marginata* in the field, 1 November 1981 and 5 November 1982. Likewise, jars and cages were examined for survivors with the reappearance of spiders in the field, 18-28 April 1982 and 15-25 April 1983. Following these monitoring periods, the soil and leaf-litter were inspected in the laboratory for further survivors.

To investigate further the degree of similarity of the jar environment to that of field conditions, jar leaf-litter temperatures were compared to actual leaf-litter temperatures measured in the field. The leaf-litter temperature and snow covered in 13 previously identified *P. marginata* web-sites were monitored from 23 January 1981 to 24 February 1981. Glass-encased mercury thermometers, which had been calibrated with a total emersion, mercury/nitrogen thermometer over a range of temperatures including those encountered in the field, were placed ca 5 cm down in the litter. Litter temperatures and snow covered at these sites were recorded daily (1200 hours), and the total emersion, mercury/nitrogen thermometer was used to record the daily ambient air temperature. Similarly, from 13 January 1983 to 24 February 1983 the litter temperature of a sample jar was recorded every six days (1200 hours) using the total emersion mercury/nitrogen thermometer.

Spiders used in the study were collected one week prior to the start of the experiments. For each collection period (1981 and 1982), a 20 m x 20 m plot was marked in *P. marginata* habitat and all observed individuals were captured. The cephalothorax width of the collected spiders was measured so as to identify the particular stage of development for each individual (Martyniuk 1983). Thus samples for both years reflect the composition of stages in the population entering the winter. No stage I, II or III spiders were found in 1982, whereas 15 stage III spiders were collected in 1981, but escaped shortly after the start of the experiment. Fifteen stage I and 15 stage II individuals, captured in 1981, were combined into one group to increase the sample size. Such variation in population structure is characteristic of this species (Wise 1984). None of the stage VI spiders used in these studies were mature.

To determine if there was a difference in average weight between entering and surviving spiders within a stage, 20 spiders in 1981, and 10 spiders in 1982, all stage V, were individually weighed to provide a direct comparison of the autumn weight between survivors and non-survivors.

**Results.**—Overwintering survival rates for the various developmental stages of *P. marginata* are presented in Table 1. The combined data for all three experiments indicate an average overwintering survival rate of 0.31 (76/245). However, mortality was not evenly distributed among stages. Older stages, V and VI, had a much higher success rate than younger stages ($\chi^2 = 37.03$, $p < 0.001$, 2 X 4 contingency table).

Differences in spider weight within stage V seem to have had little influence on overwintering success. Analysis of Variance shows no significant difference ($F = 1.25$, $p > 0.05$) between the average autumn weight of 19 stage V survivors, 2.6 ± 0.6 mg.

Table I.—Overwintering survivorship of *P. marginata* in jars and cages, Study I.

| | 1981-82 (jars) | | 1981-82 (cages) | | 1982-83 (jars) | |
|---|---|---|---|---|---|---|
| Stage | n | Proportion Surviving | n | Proportion Surviving | n | Proportion Surviving |
| I, II | 30 | 0.03 | - | - | - | - |
| IV | 35 | 0.06 | 15 | 0.13 | 20 | 0.25 |
| V | 55 | 0.42 | 15 | 0.47 | 20 | 0.65 |
| VI | 25 | 0.44 | 15 | 0.40 | 15 | 0.33 |
| TOTAL | 145 | 0.26 | 45 | 0.33 | 0.42 | |

The overwintering field parameters of leaf-litter temperature, snow cover, and ambient air temperature from 23 January 1981 to 24 February 1981 are depicted in Figure 1. Comparison of survival rates in jars and cages, in conjunction with the recording of leaf-litter temperatures, suggests that conditions in the jars adequately mimicked overwintering field conditions. Analysis of variance showed no significant difference ($F = 4.05$, $p > 0.05$) between the average temperature of litter in the field, -2.6 ± 2.3 °C, and the average temperature of litter in the jars -0.1 ± 5.7°C. Elimination of stage I and II data from the 1981-82 jar study, since they were not included in the cage study, produces a survival rate of 0.31 compared to the 0.33 rate found for the field cages and 0.42 in the 1982-83 jar study. Z-score comparisons show no significant differences ($p > 0.05$) between the 1981-82 survival frequencies in cages and jars for stages IV, V and VI.

## STUDY II

**Methods.**—A total of 242 immature spiders was collected from two Maryland populations at the end of October 1982. One population inhabited an oak forest on the Liberty Watershed, 40 km northwest of Baltimore. The second site was a predominately oak forest located 35 km south of Liberty on the Patuxent Wildlife Research Center, near Laurel. Details on the phenology and size structure of both populations appear elsewhere (Wise 1984).

The spiders were assigned to stage based upon the relationship between length of the fourth tibia and developmental stage (unpubl. data). The two youngest stages have been combined for the analysis since only two Stage I spiderlings were collected. Stages V and VI were pooled because many spiders cannot be assigned unambiguously to one or the other of these stages when tibia length is the criterion. The spiders were kept in the laboratory until 10 November, when they were placed individually in 240 ml glass jars containing a layer of vermiculite, crumpled tissue paper to mimic leaf litter and a wire framework for web attachment. The top of each jar was covered tightly with fine-meshed nylon cloth. The jars were placed on shelves on a screened porch in the forest at Patuxent. On 11 November each spider was given three (stages I-II) or six (stages III-VI) fruit flies. On this date all spiders were alive and many were in small webs.

The jars were left on the porch through the winter, and were examined for living spiders on 20 March 1983. By this date *P. marginata* had appeared on webs in the forest at Patuxent.

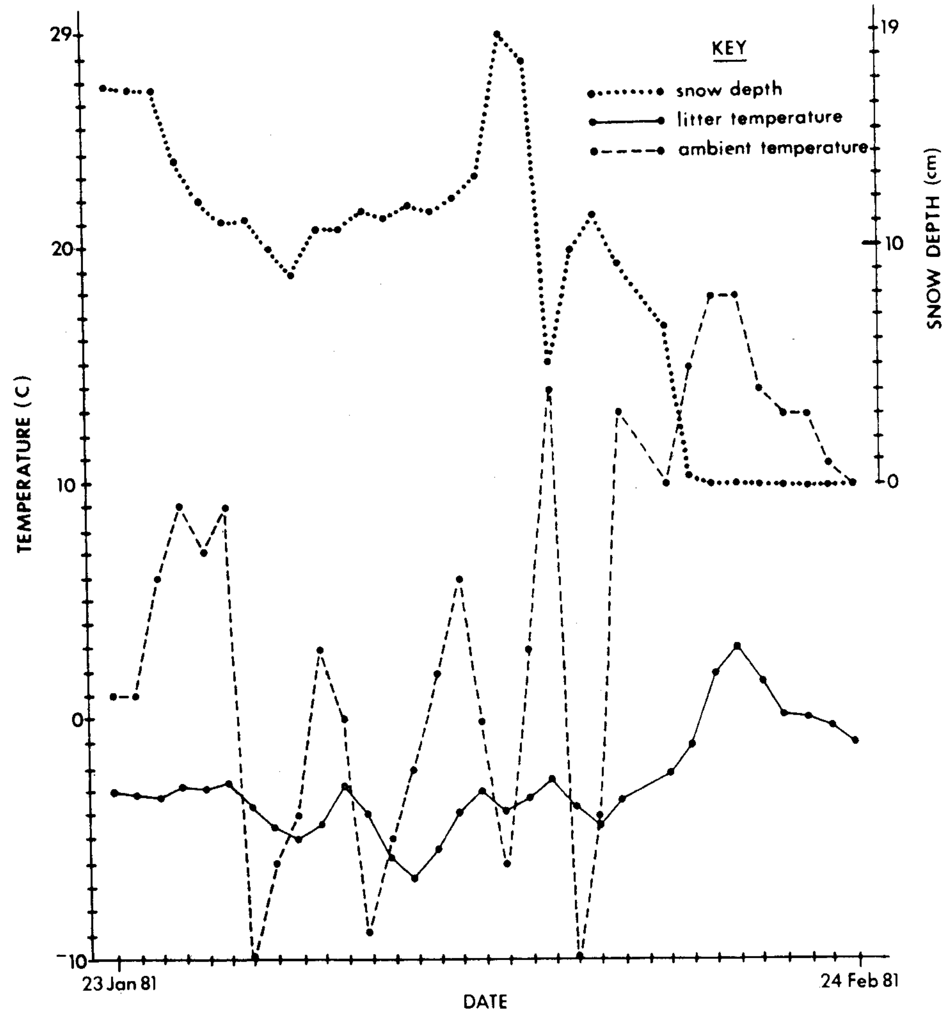

Fig. 1.—The overwintering field environment of *Prolinyphia marginata* from 23 January 1981 to 24 February 1981. Average daily leaf litter temperature, snow cover, and ambient air temperature for 13 sites, Study I.

**Results.**—The overall survival rate (stages I-VI combined) was 0.69 (168/242). Probability of surviving the winter was not the same for all stages ($\chi^2 = 42.8$, $p < 0.001$, 2 x 4 contingency table). The youngest stages (primarily stage II) suffered a markedly higher winter mortality than the larger stages (Fig. 2).

## STUDY III

**Methods.**—The third study was conducted 1972-73 in an oak forest on the E.S. George Reserve, Livingston County, Michigan, in *P. marginata*'s natural habitat. Detailed information on this population of the filmy dome spider appears elsewhere (Wise 1975, 1976).

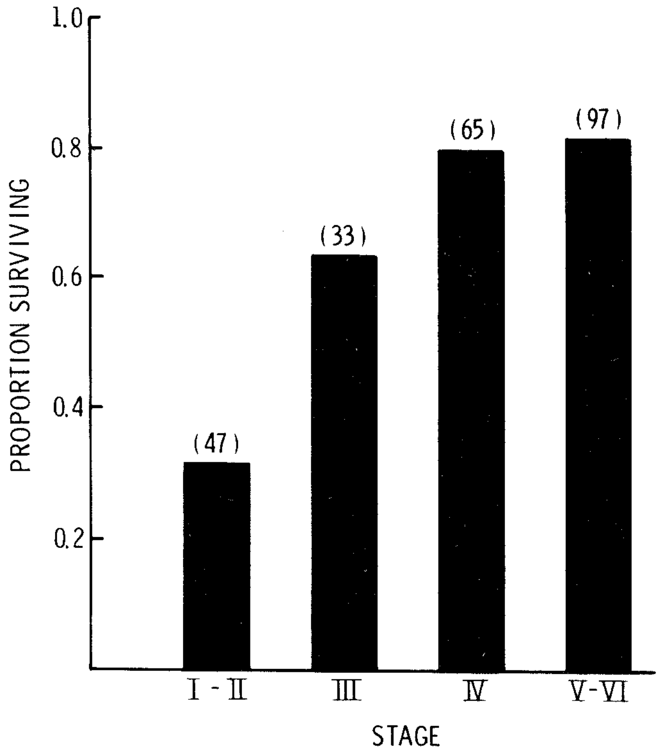

Fig. 2.—Overwinter survival of different stages, Study II.

The overwintering study was part of an experiment to determine the influence of feeding rate on rate of development. Sixty immature *P. marginata* were collected from various sites in the forest, weighed and placed individually in cylindrical cages ca 15 cm high and 10 cm in diameter, made of hardware cloth with openings small enough to retain fruit flies. The tops were covered with nylon cloth. The cages, which contained a layer of soil and leaf litter, were placed in leaf litter on the forest floor. Levels of soil and leaf litter were the same inside and outside the cages.

Each spider was randomly assigned to one of three feeding treatments: High (60 fruit flies/3 days), Medium (6 fruit flies/3 days), and Low (0 fruit flies/3 days); the only prey available to these spiders were very small insects that penetrated the screening, or insects that emerged from the soil). The spiders were fed from 3 August through 27 September. On 6 October they were removed, weighed and returned. Filmy dome spiders are found in webs through the end of October in this part of Michigan (Wise 1976); however, supplemental feeding was not continued through October, primarily because by then the weather is cold enough that feeding and growth in natural populations are probably minimal. The cages were searched for living spiders on 30 March, when *P. marginata* began to appear in webs on natural vegetation.

**Results.**—The overall survival rate over the winter was 0.75 (41/55). The smaller spiders suffered a significantly higher winter mortality rate (Table 2; $\chi^2 = 24.4$, $p < 0.001$, 2 x 3 contingency table). Apparently the size within a stage did not affect survival, since within the Low feeding treatment the October weight

Table 2.—Results of study III.

| Feeding treatment | Low | Medium | High |
|---|---|---|---|
| August 3 | | | |
| No. alive | 20 | 20 | 20 |
| Weight (mg) | 0.90 ± 0.05 | 0.97 ± 0.06 | 0.91 ± 0.06 |
| October 6 | | | |
| No. alive | 18 | 18 | 19 |
| Weight (mg) | 1.59 ± 0.16 | 6.04 ± 0.26 | 5.86 ± 0.33 |
| No. Molts 3 Aug.-6 Oct. | 0.7 ± 0.3 | 2.0 ± 0.3 | 1.8 ± 0.4 |
| March 30 | | | |
| No. alive | 6 | 16 | 19 |
| Weight (mg) | 1.32 ± 0.14 | 4.71 ± 0.21 | 4.50 ± 0.26 |
| Winter survival (%) | 33 | 89 | 100 |

of those that survived the winter did not differ significantly from that of the spiders that died before spring (1.50 ± 1.8 mg and 1.63 ± 0.60 mg, respectively; $t = 0.42$ $p > 0.5$).

The rate of feeding clearly affected growth rate and rate of development, as measured by weight gain and by the number of molts from August through September (Table 2). In addition to being heavier, spiders in the High and Medium feeding treatments were 1-2 stages more advanced than those in the Low feeding group. Since linear dimensions were not recorded, it is not possible to assign the spiders to a particular stage. However, it is clear that the larger spiders in October were more advanced developmentally i.e., they had completed more molts and were closer to adulthood than the smaller spiders.

## DISCUSSION

Depth of the snow cover and condition of the litter affect the microclimate experienced by overwintering spiders (Aitchison 1978). We used outdoor cages in Studies I and III in order to mimic natural conditions as much as possible. Spiders overwintering in jars in studies I and II did not benefit from the insulative effects of snow, and thus their mortality rates may have been higher than in natural populations. However, comparison of survival rates in outdoor cages with those in jars (Study I) suggests that mortality rates in the jars did adequately reflect those under entirely natural conditions. No such comparison is possible for Study II, but there is usually no significant snow cover for most of the winter for the part of Maryland in which this study was conducted. Thus it is unlikely that the physical conditions in the jars in this study caused higher mortality rates than would have been observed in the natural population inhabiting the surrounding forest.

Overall winter survival rates varied between the three studies, from a low of 0.26 in Study I (jars, 1981-82) to a high of 0.75 in Study III. This variation likely reflects both differences in experimental technique and differences in severity of winters between years and sites. Similar variation appears in rates estimated from census data of natural *P. marginata* populations. For example, two estimates of juvenile survival from the first week in October to the middle of April in the Liberty population in Maryland range from 0.24 (115/473; 1980-81) to 0.62 (190/306; 1981-82) (calculated from census data presented in Wise 1981). Direct comparisons of survival in these three studies with census data of natural populations are of course not justified, because estimates in natural populations 1) encompass a longer time span than the period of winter stress; 2) include disappearances due to predation and dispersal; and 3) are subject to sampling error, particularly with the smaller stages. Taken as a whole, though, these experimental results and censuses of natural populations suggest that winter mortality may be a significant factor in the dynamics of *P. marginata* populations.

The markedly lower winter survival of the younger stages, a result consistent with the finding of Buche (1966), is a striking pattern that was found in all three studies. This differential survival increases the homogeneity of the size structure of the population after the winter. For example, in the New York population (Study I) representation in the experimental population decreased from 12% (autumn) to 1% (spring) for stages I and II, and from 29% to 12% for stage IV. Contrastingly, the proportion of stage V spiders increased from 37% to 57%, and stage VI from 23% to 29%. In this situation overwintering mortality not only reduces the overall population density, but also produces a more homogeneous population in developmental stage.

Higher winter mortality rates among the smaller stages may have led to selection against females that mature and reproduce late in the season. *P. marginata* populations display two peaks in adult abundance, one in spring and a second in August. The latter results from progeny of spring adults that develop rapidly (Wise 1976, 1984). These rapidly developing spiders usually mature no later than August. They deposit egg sacs during September and October and die by winter. Maturation and reproduction too close to the onset of winter has likely been selected against, because progeny of late-maturing spiders would face the winter as smaller stages [this aspect of *P. marginata*'s phenology is discussed in more detail in Wise (1984)].

Results of Study I and III suggest that within a stage, differences in weight do not influence overwintering survival. Perhaps physiological changes occurring during development affect the physiology of cold resistance. Alternatively, differences in the relative amount of food reserves, or differences in the surface area-to-volume ratio, may better explain the lower overwintering survival of the younger stages. More experimentation is required to answer these questions. Particularly fruitful would be a detailed examination of the effects of size differences within the smaller stages. The lower survival rate of the smaller spiders in Study III may have resulted at least partly from their feeding history. Perhaps they had fewer energy reserves at the start of the winter than the better fed spiders.

In summary, these three experimental studies suggest that overwintering mortality in natural populations of the filmy dome spider may be particularly important for the smaller stages. Such stage-biased mortality rates have consequences for population structure, and for individual fitnesses of spiders with particular feeding histories and reproductive patterns.

## ACKNOWLEDGMENTS

R. S. Wilcox made helpful comments on an earlier draft of a portion of the manuscript. We would like to acknowledge the support of the State University of New York at Binghamton; the University of Michigan; and the Patuxent Wildlife Research Center, U.S. Department of the Interior, for providing research sites. Study II was supported by a NSF Graduate Fellowship, NSF Grant BG-25986 to the University of Michigan for research in systematic and Evolutionary Biology, and a University of Michigan Graduate Student Dissertation Research Grant. Study III was supported by NSF Grant DEB 81-19309.

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*Manuscript received October, 1984, revised February 1985.*