2003. The Journal of Arachnology 31:278–284

# THE EFFECTS OF SIZE, SEX, AND REPRODUCTIVE CONDITION ON THERMAL AND DESICCATION STRESS IN A RIPARIAN SPIDER (*PIRATA SEDENTARIUS*, ARANEAE, LYCOSIDAE)

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**ABSTRACT.** Within a species, physiological tolerances and thermoregulatory behaviors may vary among ontogenetic stages or between sexes. Such different tolerances can strongly affect the ecology and life history of a species. In a laboratory study, we tested the hypothesis that *Pirata sedentarius* Montgomery 1904 is differentially susceptible to thermal/desiccation stress by size and sex. As predicted, male adults were more susceptible to thermal/desiccation stress than females. Unexpectedly, however, juvenile spiders survived longer under thermal/desiccation stress than adults. Furthermore, female adults without egg sacs displayed a trend toward higher thermal/desiccation tolerance than females carrying egg sacs. These results suggest that for *P. sedentarius*, microhabitat preferences and/or thermoregulatory behaviors may change over the course of development, and may vary between sexes and between females with and without egg sacs.

**Keywords:** Microhabitat partitioning, ontogenetic changes in physiological tolerances

Lycosid spiders are known to exhibit thermoregulatory behavior to increase their body temperatures above ambient conditions, particularly following a meal or while carrying an egg sac (e.g., Nørgaard 1951; Humphreys 1978), and they can actively regulate evaporative water loss (Aspey et al. 1972). However, they are relatively vulnerable to desiccation (e.g., compared to web-building spiders; Foelix 1996), and water loss is accelerated at higher temperatures (Humphreys 1975).

Previous studies have demonstrated size and sex-related differences in both evaporative water loss and preferred temperatures (Sevacherian & Lowrie 1972; Humphreys 1975; 1978). Male and female spiders often display differential patterns of resource and microhabitat use, as males spend much of their time and energy locating females, and females invest much of their time and energy in egg sac production. Among lycosids, different collecting techniques can yield different sex ratios, and males are reported to travel farther and more often than females (Vlijm & Kessler-Geschiere 1967; Cady 1984). Furthermore, among some lycosids, microhabitat preferences differ between juvenile and adult stages (Vlijm & Kessler-Geschiere 1967; Hallander 1970; Edgar 1971; Kronk & Riechert 1979). Hallander (1970) suggests that this differential microhabitat use may protect juvenile wolf spiders from cannibalism by larger conspecifics.

*Pirata sedentarius* is a widespread species in North America (Wallace & Exline 1977), but it has, thus far, received very little attention in the literature. In this study, we used *P. sedentarius* (which appears to be a hydrophilic specialist) to test for differences in physiological tolerance to thermal/desiccation stress among ontogenetic stages (size classes), between sexes and between females with and without egg sacs.

## METHODS

During the summer of 2001, we sampled two one x five m. plots in the Ten Mile Creek streambed between Lincoln Pond (4 ha) and Lake Myosotis (40 ha), on the Edmund Niles Huyck Preserve and Biological Research Station, Albany County, New York. The creek hydroperiod undergoes seasonal fluctuation

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and occasional severe flooding; the creek (~2–3 m wide during sampling) occupies a relatively small portion of the streambed, which consists of an extensive un-submerged cobble area under an opening in the forest canopy. Leaf litter and vegetation were absent in the plots sampled during this study, but the cobble is occasionally interspersed with herbaceous vegetation (e.g., the same area during the following summer; DeVito unpubl. data). This habitat is dominated by three lycosid species *Pirata sedentarius*, *Pardosa lapidicina* Emerton 1885, and *Pardosa fuscula* Thorell 1875, and inhabited by at least two others (*Rabidosa* sp. and *Hogna* sp.). The overall abundance of lycosid spiders decreases dramatically outside the streambed (pers. obs.), which is bounded by mixed deciduous leaf litter habitat.

The plots, which represent only the portion of cobble habitat closest to the creek (i.e., ≤ 5 m), were dominated by *P. sedentarius*; only two individual spiders of any other species were found during sampling. Voucher specimens (adult females and males) have been placed in the American Museum of Natural History.

The two plots were laid out perpendicular to the creek (southward from its edge) where the creek bends westward and is crossed by a stepping stone path. Spider collection in Plot 1 was initiated at 1000 h (ambient temperature = 21 °C; partly cloudy; plot shaded throughout; brief light rain) on July 5, and collection in Plot 2 was initiated at 1500 h (ambient temperature = 24 °C; partly cloudy; plot in sun for part of sampling period) on July 6. The plots were partly shaded by canopy cover during both collecting times, and activity of spiders on the rock surfaces was minimal.

One person (JD) sampled the plots, proceeding outward from the creek edge, with the total collecting time for each plot approximating three hours. Every rock in the plot was overturned and each uncovered spider was collected. Soil samples were collected under each rock where a spider was found; these were transported to the laboratory in PVC jars.

To minimize the effects of captivity (e.g., prolonged exposure to artificial moisture levels) spiders and soil samples were processed immediately upon return to the laboratory. Percent soil moisture was estimated for each soil sample using the gravimetric method. Small samples of soil (~ 30–50 g) were weighed, dried in an oven at 40 °C for eight hours, then weighed again. Percent soil moisture was calculated: (dry mass − wet mass)/wet mass. Mean soil moisture levels were calculated among the samples collected in each square meter of each plot.

Spiders were measured, sexed and divided into the following categories: 1) size class (total body length to the nearest 0.5 mm), 2) sex (juvenile, adult male, or adult female), and 3) reproductive condition (for adult females; egg sac present vs. not present). Spiders were then housed in individual plastic cups covered with fiberglass mesh screen, and placed in a drying oven preheated to 40 °C. This temperature, which probably exceeds the maximal temperatures attained in the streambed (i.e., ~34 °C; DeVito unpubl. data), was tested in preliminary trials because it is standard for drying samples of organic matter over an extended (i.e., eight hour) period. It was ultimately chosen for this study because it was low enough for discrimination among tolerance levels of individual *Pirata sedentarius* but high enough to test the maximal tolerance of *Pardosa lapidicina* and *Pardosa fuscula* within a reasonable (i.e., 14 hour) period.

Time of death was recorded for each spider, rounded up to the nearest ten minutes. Dying spiders assumed a characteristic crenulated posture; death was confirmed by subsequent unresponsiveness to tapping on the container. The tolerance test ended upon the death of the last specimen (290 minutes).

Pearson's correlation was used to test for relationships between soil moisture level, distance from the stream and spider density. Spider survival times at 40 °C were compared between sexes and among size classes using ANOVA (STATISTICA v. 4.5; 1993, Statsoft, Tulsa, OK). We also performed a post-hoc analysis (Chi Square Goodness of Fit Test) of microhabitat use by juvenile size class.

## RESULTS

Neither moisture level nor spider density differed between plots (ANOVA; $F_{1,7} = 0.41$; two-tailed $P = 0.54$ for moisture level, and $F_{1,7} = 1.14$; two-tailed $P = 0.32$ for spider density). Data from plots 1 and 2 were therefore pooled for all subsequent analyses.

As expected, mean soil moisture level in

Table 1.—*P. sedentarius* total abundance in streamside plots.

| | Distance from stream | | | | | |
|---|---|---|---|---|---|---|
| | 0–1 m | 1–2 m | 2–3 m | 3–4 m | 4–5 m | Total |
| Small juveniles (2.0–3.0 mm) | 9 | 6 | 6 | 5 | 3 | 29 |
| Large juveniles (3.5–4.5 mm) | 17 | 10 | 2 | 0 | 2 | 31 |
| Adult females | 7 | 2 | 2 | 3 | 2 | 16 |
| Adult males | 4 | 1 | 1 | 0 | 2 | 8 |
| Total abundance | 37 | 19 | 11 | 8 | 9 | 84 |

each (1 $m^2$) interval decreased with increasing distance from the creek ($r = -0.83$; one-tailed $P < 0.01$; Fig. 1). *Pirata sedentarius* were abundant in the plots (Table 1), and mean spider density was directly related to mean soil moisture level ($r = 0.88$; one-tailed $P < 0.01$) and declined with increasing distance from the creek ($r = -0.7847$; one-tailed $P < 0.01$; Fig. 1).

Survival time (minutes to death at 40 °C) was not normally distributed across the data set (Kolmogorov-Smirnov; d = 0.24; $P < 0.01$). However, after survival time values were log-transformed, the resulting distribution was not significantly different from normal (Kolmogorov-Smirnov; d = 0.10; $P > 0.20$). Log-transformed values were therefore used in all subsequent analyses.

Under the conditions of induced thermal/desiccation stress, juvenile *P. sedentarius* (2.0–4.5 mm) survived longer than adults (ANOVA; $F_{1,75} = 13.1$; $P < 0.001$; Fig. 2). Adult female *P. sedentarius* survived longer than adult males (ANOVA; $F_{1,22} = 37.5$; two-tailed $P < 0.01$), but survival times did not differ between females with and without egg sacs (ANOVA; $F_{1,14} = 3.41$; two-tailed $P = 0.09$). Although adult *P. sedentarius* in this study ranged in size from 4.5–7.0 mm, size had no effect on log survival time while controlling for sex (ANCOVA with sex as covariate; $F_{5,17} = 1.27$; two-tailed $P = 0.32$).

For juvenile *P. sedentarius*, size (TL to the nearest 0.5mm) had a significant effect on log survival time (ANOVA; $F_{5,47} = 6.64$; two-tailed $P < 0.01$). Planned comparisons revealed that small juveniles (2.0–3.0mm) survived longer than large juveniles (3.5–4.5

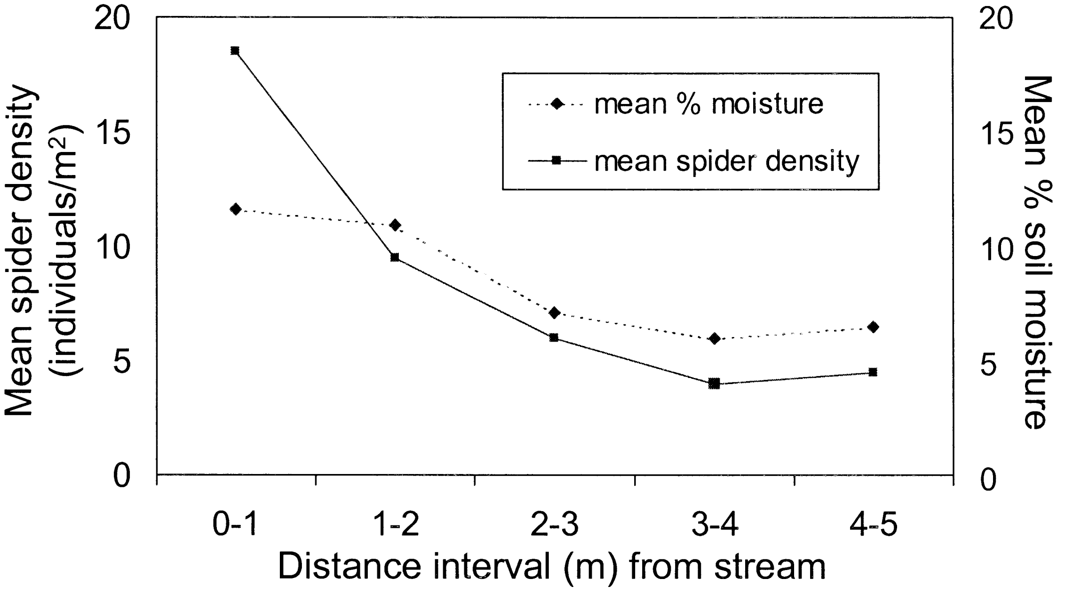

Figure 1.—*Pirata sedentarius* microhabitat use; soil moisture and spider density vs. distance from stream edge.

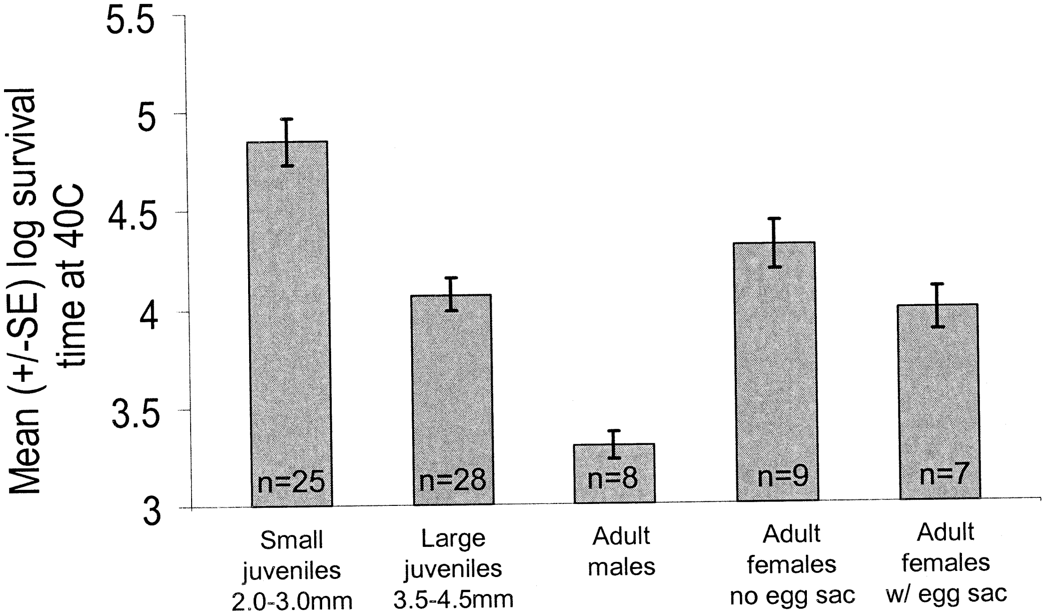

Figure 2.—Effects of size, sex, and reproductive condition on survival time for juvenile and adult *P. sedentarius* under thermal/desiccation stress.

mm) ($F_{1,47}$ = 14.7; two-tailed $P < 0.01$; Fig. 3).

The stress tolerance differences between juvenile size classes prompted us to test the hypothesis that *P. sedentarius* exhibits corresponding ontogenetic changes in microhabitat use. In accordance with this prediction, we found that large juveniles were collected more often than small juveniles in the intervals closer to the creek ($X^2_4$ = 10.6; $P$ = 0.031; Fig. 4).

## DISCUSSION

The high abundance of *P. sedentarius* close to the water is consistent with their relative susceptibility to thermal/dessication stress (e.g., compared to *Pardosa* spp.; DeVito unpubl. data). Furthermore, the streamside habitat may support higher densities of prey items. Humphreys (1975) found that a lycosid spider (*Geolycosa godeffroyi* Koch 1865) was capable of water uptake from a soil substrate with a moisture level above 11%. In our study, the soil moisture levels within the first 2 m of the stream exceed this value.

The differences in thermal/desiccation tolerance found between sexes and among size classes of *P. sedentarius* raised several questions regarding underlying mechanisms and possible ecological significance of the observed effects. The tendency of males to be more prone to thermal/desiccation stress than females is likely related to the considerable difference in body volume (i.e., the volume of the male abdomen being much smaller than the volume of the female abdomen), as large spiders are generally less prone to desiccation than small spiders (Savory 1964). Because male wolf spiders generally travel more widely than females (e.g., Vlijm & Kessler-Geschiere 1967), their increased vulnerability to desiccation is particularly interesting.

The non-significant trend toward higher thermal/desiccation tolerance in females without egg sacs compared to females carrying egg sacs has been confirmed as a significant difference in our more recent study with a larger sample size (DeVito et al. unpubl. data). This finding may reflect a differential ability to withstand physiological stresses based on the amount of energy (i.e., body mass) invested in the egg sac, and resulting differences in abdomen size. Relative thermal/desiccation tolerance may also be influenced by factors such as the time to last feeding, and consequently the size (distention) of the abdomen, and the amount of water currently stored in

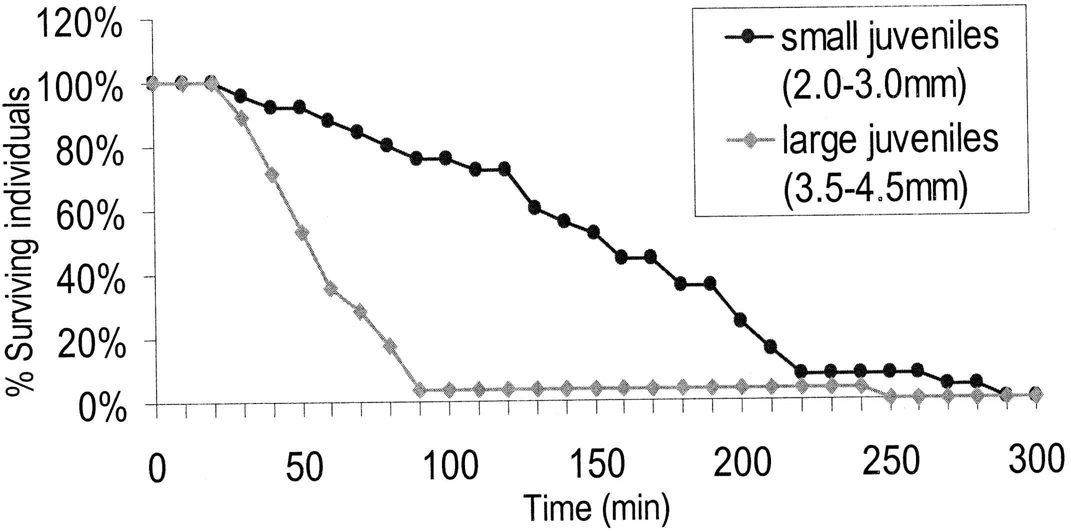

Figure 3.—Survival over time for juvenile *P. sedentarius* size classes under thermal and desiccation stress.

the body. Spiders, which had recently consumed a meal would be predicted to survive longer than hungry spiders under the testing conditions used in this study.

In light of our results, it is surprising that lycosid females (including *P. sedentarius*) carrying egg sacs are more active on sunny days than in overcast conditions (pers. obs.), and that female *Pirata piraticus* Clerck 1757 apparently prefer warmer temperatures when

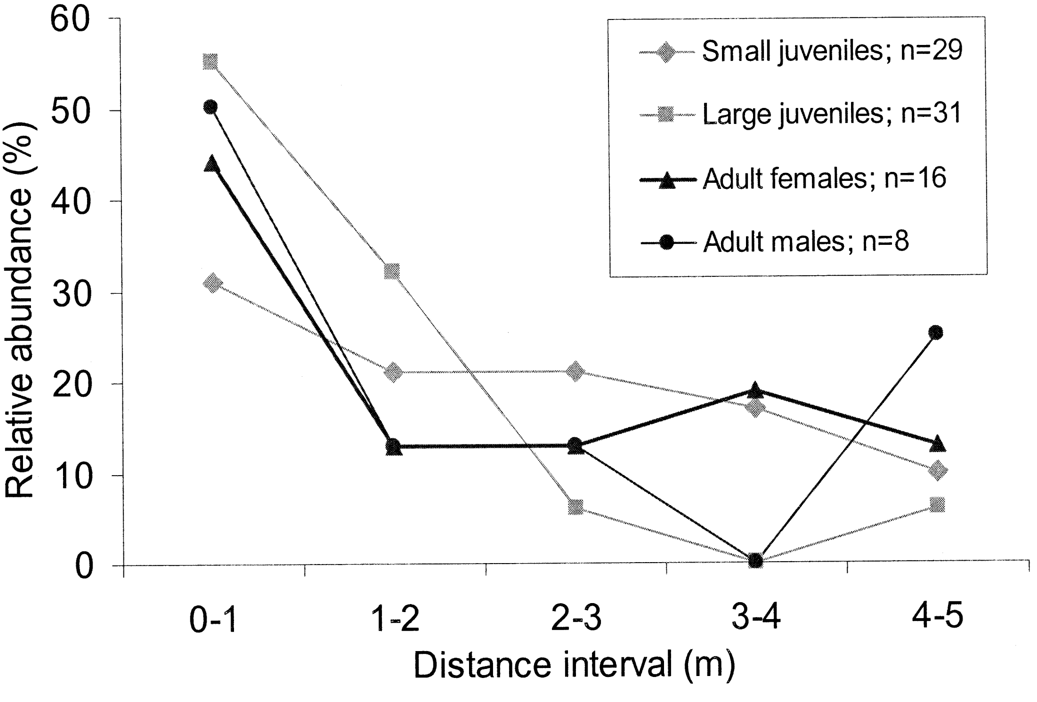

Figure 4.—*P. sedentarius* microhabitat use by sex and size class; proportional abundance vs. distance from stream edge.

they are carrying egg sacs (Nørgaard 1951). Moring and Stewart (1994) also found that spiders (*Pardosa* and *Alopecosa* species) in a streamside cobble habitat in Colorado were more active as light intensity increased.

It seems likely that female lycosids with egg sacs walk a fine line between keeping egg sacs warm enough and protecting themselves from thermal/desiccation stress. The proximity of refugia (e.g., moist soil conditions in cobble habitats) probably plays a very large role in habitat use for streamside lycosid spiders in general. Females carrying egg sacs may further require heterogeneous climatic conditions (e.g., exposed rock surfaces in cobble habitats) to balance the thermal requirements of the egg sac with their own physiological limitations.

Given the general tendency of larger spiders to be less vulnerable to desiccation than smaller spiders (along with the fact that desiccation is accelerated at higher temperatures), the finding that juvenile *P. sedentarius* survive much longer than adults was surprising. This result is not consistent, for example, with the results of Sevacherian & Lowrie (1972), who found that juveniles of two *Pardosa* species preferred lower temperatures than adults.

We speculate that the higher thermal/desiccation tolerance of (especially the smallest) juvenile size classes might be due to the storage of lipids from the yolk sac. Furthermore, the extremely high tolerances of a few individual juveniles may have resulted from individual variation in the timing of molt cycles. Spiders approaching a new molt cycle would have two layers of cuticle, perhaps affording more protection from desiccation, in comparison with spiders that had recently molted. The ontogenetic differences in thermal/desiccation tolerance and microhabitat use observed in this study lead to the implication that small juvenile *P. sedentarius* can tolerate warm, dry conditions more successfully than large juveniles and adults. Such an adaptation would facilitate dispersal from the back of the mother. This possibility is reflected by the parallel habitat use of small juveniles and adult females (Fig. 4).

The tendency of large juveniles to be concentrated at the edge of the water is consistent with their reduced thermal/desiccation tolerance compared to small juveniles. However, if food resources are more abundant closer to the stream, this pattern may alternatively reflect the exploitation of those resources by spiders which 1) can no longer rely on the yolk sac and 2) do not yet need to warm an egg sac or wander in search of females. Future studies should explore the possibility of differential thermoregulatory behavior among size classes, as well as ontogenetic changes in microhabitat use.

## ACKNOWLEDGMENTS

This study was conducted with the assistance of a research grant from the E.N. Huyck Preserve & Biological Research Station. This foundation also provided access to equipment and supplies. Additional funding was provided by the University of Texas at Arlington Biology Department. J. McGuinness instructed J. DeVito in the use of equipment and contributed ideas to the experimental design. S. Beatty instructed J. DeVito in the gravimetric method of measuring soil moisture. C. Amaya and M. Pfeiffer contributed to the interpretation of our results. C. Brown, M. Gerson, M. Nelson and M. Pfeiffer provided critical reviews of an earlier version of this manuscript. P.E. Cushing, M.C. Lowder, D. Mott, G. Stratton, and an anonymous reviewer offered helpful comments during the review process.

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*Manuscript received 22 April 2002, revised 11 December 2002.*