Effect of temperature on hatching and nest site selection in the Green lynx spider, *Peucetia viridans* (Araneae:Oxyopidae)

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Abstract

1. Thirty-seven *Peucetia viridans* egg sacs were incubated at 15, 17.5, 20, 25, 30, 32.5 or 35 °C. Hatching time was inversely proportional to temperature, and no hatching occurred at the extremes (15, 17.5 and 35 °C).
2. Mean incubation temperature of egg sacs in natural field habitats was 20.0 ± 0.6 °C and mean time until hatching was 30.8 ± 0.8 days.
3. Physical models of egg sacs placed in the field indicated natural incubation sites could vary by as much as 10 °C during the daytime and as little as 1 °C at night. As expected, incubation sites were warmest near the ground and the coolest at the top of vegetation.
4. Regardless of egg sac model placement, predicted hatching time only varied by 2–3 days throughout the incubation period.
5. Natural egg sac placement sites of *P. viridans* occurred near the top of vegetation indicating females were not selecting the warmest available microhabitats for egg incubation.
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1. Introduction

Small organisms have a large surface-to-volume ratio, allowing for a high rate of heat exchange with the ambient environment and facilitating rapid changes in body temperature (May, 1985; Pulz, 1987). Through behavioral thermoregulation, small ectothermic animals (e.g., arthropods) can quickly alter their body temperature (Heinrich, 1993). However, unlike most life stages, the eggs of animals cannot behaviorally thermoregulate, and are subjected to the temperatures of their ambient environment. Therefore, oviparous females should oviposit in environments with adequate temperatures for embryonic development. Nest sites need to allow for proper egg development, and be suitable for the survival of the adult if the female remains with the eggs (Morse, 1985).

In spiders, and many other invertebrates, temperature can be the most critical environmental factor influencing the rate of embryonic development (Downs, 1988).

Temperature affects not only development, but also many other behavioral and physiological factors (Foelix, 1996; Humphreys, 1987), including courtship (Davis, 1989), escape speed (Cobb, 1994), web building locations (Reichert and Tracy, 1975), feeding (Aitchison, 1984), prey capture (Turner et al., 1993), web construction (Henschel et al., 1992), oviposition intervals (Downs, 1988), development and survival (Li, 1995, 2002; Li and Jackson, 1996), and nest site selection (Henschel et al., 1992). Temperature can also affect growth and development of juvenile spiders (Goldsbrough et al., 2004), however, the role temperature plays in egg and embryo development has received relatively little attention to date (Downs, 1988; Li and Jackson, 1996 for review). Many of these studies concentrated on a few Asian species, which limits our understanding of temperature and developmental relationships of spiders in other climatic and geographic regions. In addition, these latter studies were laboratory experiments and did not measure temperatures experienced by spiders or their egg sacs in a natural environment.

Many spider species produce one or a few clutches each year, therefore selection of a nest site that promotes the

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survival of the young is crucial (Foelix, 1996). Most spider oviposition studies have been conducted on web-building spiders that incorporate their egg sac into the web. Orb-weaving spiders base their selection of a nest site on food availability (Bilde et al., 2002) and habitat complexity (McNett and Rypstra, 2000). Spiders may also take the costs of predation and web building into account when selecting a nest site (Uetz, 1992, 1996; Pasquet et al., 1999).

Nonweb building spiders do not have web-associated costs, and can therefore forage in one place and lay an egg sac in another (Morse, 1985). *Frontinella pyramitela* is a web-building spider that does not use its web as an oviposition site. *Frontinella pyramitela* instead chooses leaf litter for an oviposition site, with gravity, moisture, and substrate type acting as a driving force (Suter et al., 1987). This spider species is therefore not limited by its web location for selecting a proper nest site. *Misumena vatia*, a crab spider, forages on milkweed flowers, but chooses leaf size characteristics on nonflowering milkweed plants to construct nests. For reasons still unknown for many species, spiders use various characteristics in choosing an ideal nest site (Morse, 1985). Green lynx spiders, *Peucetia viridans*, generally place egg sacs near the top of flowering plants and shrubs in late summer (Whitcomb et al., 1966; Arango et al., 2000). Such locations expose egg sacs to relatively warm temperatures and suggest that temperature may be influential for egg development and the timing of hatching.

Peucetia viridans, a large green spider, 12–16 mm in length with females being larger than males, occurs throughout the southern United States, Mexico, and Central America (Brady, 1964). Females lay a single egg sac in late summer (Whitcomb, 1962) and then remain with their egg sac until they are hatched, providing protection from predators (Fink, 1986, 1987; Willey and Adler, 1989). Egg sac construction occurs overnight, taking several hours to complete (Whitcomb, 1962). When the egg sac is first constructed it is light green in color and becomes gray or straw color within 24 h (Whitcomb, 1962). Spiderlings emerge from the egg sac as a second instar and disperse through ballooning to a place where they eventually overwinter.

This study was conducted to determine how incubation temperature affects the hatching time in *Peucetia viridans* and to examine how temperature affects nest site selection in the natural environment. We hypothesized that warmer temperatures would shorten the time until hatching, and that nest sites placed closest to the ground in full sun exposure would have the shortest incubation periods.

2. Methods

2.1. Effect of temperature on hatching time

Thirty-two gravid *P. viridans* were collected from fields in Rutherford and Wilson counties in Tennessee between August and September of 2003 and 2004, and housed at Middle Tennessee State University. Gravid females, along with a stem from the vegetation they were found on, were maintained in 0.95 L canning jars covered with cheesecloth at 21.5 °C. Females were monitored daily until an egg sac was observed. Once laid, the egg sac was placed in an environmental chamber (Percival I-36LL) set at one of the following temperatures; 17.5 ($n = 7$), 20 ($n = 10$), 25 ($n = 9$), 30 ($n = 9$), 32.5 ($n = 8$), or 35 °C ($n = 6$). Egg sacs were checked daily for spiderling emergence.

2.2. Monitoring egg sac temperature in the environment

From August through October in 2004, 37 newly laid *P. viridans* egg sacs were located in fields and monitored for incubation temperature. These egg sacs were identified by locating gravid females in the field and were monitored daily until an egg sac was observed. New egg sacs could be identified by their light green color. Egg sac height on the vegetation was recorded and the female was removed from her egg sac. Temperatures of the egg sacs were recorded at 10 min intervals using a single-channel datalogger (LogIt LTC) and a 30 ga type T thermocouple wire was inserted into the egg sac. Because of widespread predation on the first 8 monitored egg sacs, the female spider was returned to her egg sac to guard against predation in all subsequent egg sacs that were monitored. Egg sacs were observed daily until the emergence of spiderlings or until the egg sac was predated.

2.3. Development of an egg sac model

During July 2004, a physical egg sac model was developed to monitor potential temperatures that real egg sacs could experience in the field. Beads composed of glass, plastic, bone, and two different sizes of wood (16.6 mm diameter and 10.4 mm diameter) were used as potential egg sac models. Two beads of each type were painted, one jade green (Krylon # 3509) and the other pebble (Krylon # 3520). These two colors were selected because they approximated the actual color of real egg sacs. One hole in the bead was sealed before being painted, and a 20 ga type T thermocouple wire was inserted and sealed in the other hole.

The two potential egg sac models, along with two real egg sacs, were placed at a height of 1.0 m in an exposed, outdoor location, for 48 h over two sunny days. Temperatures were monitored at 30 s intervals using single-channel dataloggers (LogIt LTC). The model having temperatures that most closely matched the temperatures of the real egg sacs was used to determine potential temperatures that real egg sacs could encounter in the field.

2.4. Determining potential extreme temperatures using egg sac models

The height of an egg sac in the field and the degree of sun exposure potentially could affect egg sac temperature. To determine the temperatures available for egg sac placement by gravid spiders, six egg sac models were placed in the

field, at heights of 0.1, 0.5, and 1.0 m, with three egg sac models placed in complete shade, and three other models placed for full sun exposure. Model egg sac temperatures were recorded at 15 min intervals using a multi-channel datalogger (Campbell Scientific 23X) and 20 ga type T thermocouple wire.

To provide constant shade for the egg sac models, three wooden stakes, each slightly higher than 0.1, 0.5, and 1.0 m were placed in the ground and covered with a piece of white styrofoam (40 × 20 cm) so that the models would not be exposed to direct sunlight. The egg sac models were secured 2 cm below the styrofoam allowing air to circulate around the egg sac model, and permitting it to remain at ambient temperature. Egg sac models in the exposed treatment were attached at the same three heights on a single wooden stake placed vertically into the ground.

2.5. Statistical analysis

A second-order polynomial regression was used to define the relationship between incubation temperatures and days until hatching. Daily mean temperatures of egg sacs in the field were used to predict a hatching time for each egg sac by using the regression equation from the laboratory hatching rate experiment. A paired t-test was used to compare actual hatching time to predict hatching time. The temperatures model egg sac was compared to the mean temperatures of two egg using a paired t-test and Pearson product moment correlation. To determine if nest site selection affected hatching time, the same regression equation was applied to the mean temperatures from egg sac models and used to predict the time until hatching.

3. Results

3.1. Incubating egg sacs in the laboratory

Hatching occurred successfully in temperature treatments of 20, 25, 30, and 32.5 °C, with the most hatching success at 25 and 30 °C (Fig. 1). Hatching was fastest at 32.5 °C (mean = 12.25 ± 0.5 days). The 30 °C treatment had a mean hatching time of 15.56 ± 2.01 days. The 25 °C temperature treatment had a mean hatching time of 19.56 ± 1.24 days. The temperature treatment where hatching time was the longest was at 20 °C (mean = 33.25 ± 1.26 days). No hatching occurred at 35, 17.5, or 15 °C. The number of days from oviposition until hatching was inversely related to incubation temperature and this relationship is described by the regression equation of $y = 0.1264x^2 - 8.1575x + 145.28$ ($r^2 = 0.93$) (Fig. 2). This equation was then used to predict hatching times for field *P. viridans* egg sacs and egg sac models.

3.2. Monitoring egg sac temperature in the environment

The temperatures of 37 egg sacs were monitored in the field. Of those egg sacs, 19 were predated upon, three egg
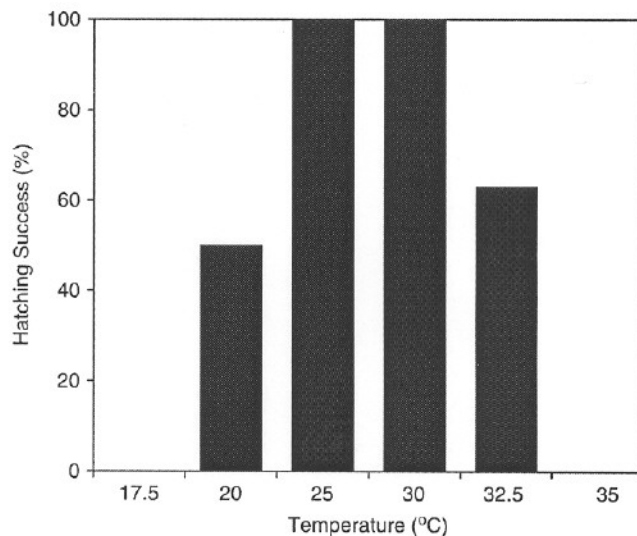

Fig. 1. Effect of incubation temperature (constant 12:12 LD cycle) on hatching success in *P. viridans*.
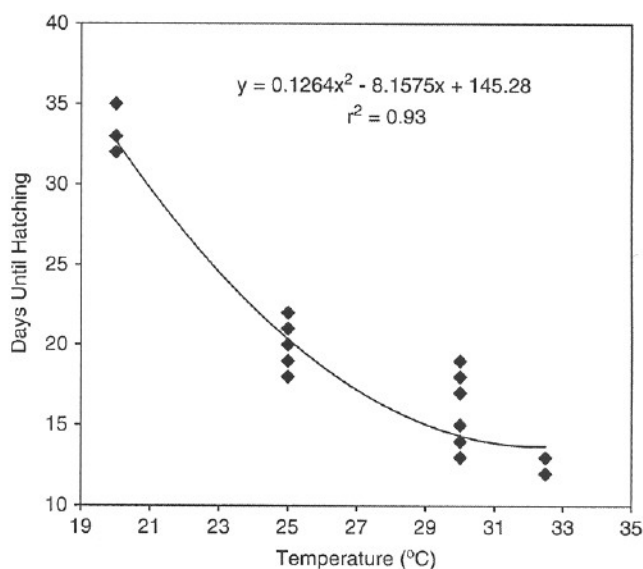

Fig. 2. Effect of incubation temperature (constant 12:12 LD cycle) on time until hatching of *P. viridans* ($n = 23$). No hatching occurred at the 15, 17.5, and 35 °C treatments.

sacs did not hatch, four egg sacs were moved by the mother to another location, and 11 egg sacs hatched successfully. Nine successful egg sacs were monitored for their entire incubation period. The other two egg sacs were monitored for 7 and 15 days. Predation was directly related to the female guarding the egg sacs with 100% predation occurring when the female was removed from the first eight egg sacs monitored. Three egg sacs were guarded for a short time before the mother disappeared, at which point all three were predated upon. Eight of the 19 (42.1%) egg sacs that were guarded were also predated upon, but the time until predation was significantly longer than the
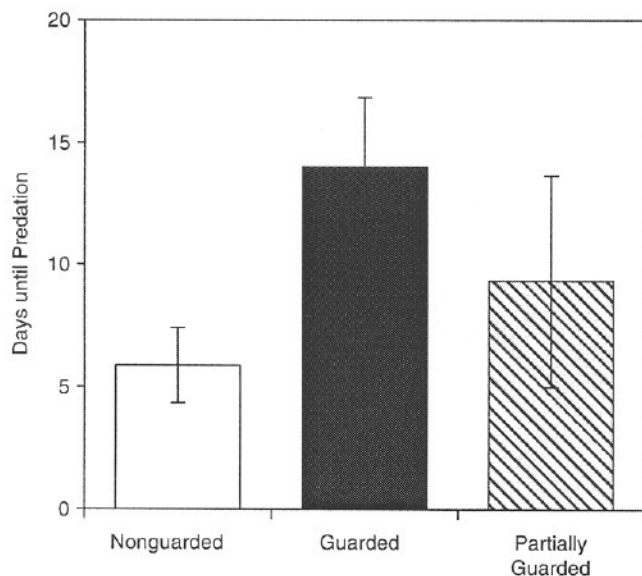
Fig. 3. Time until egg sacs were predated for nonguarded egg sacs ($n = 8$), guarded egg sacs ($n = 8$), and partially guarded egg sacs ($n = 3$). Data are expressed as mean ± 1 SE.

Table 1
Actual and predicted hatching times (days) of *P. viridans* egg sacs monitored in the field for the majority of the incubation period

Egg sac ID	Incubation temperature (°C)	Actual hatching time	Predicted hatching time
9	19.2	32	35.3
16	20.7	28	30.6
18	18.9	39	36.3
19	19	31	35.9
20	22[a]	32	27
22	19.3	29	34.9
26	19.2	33	35.3
33	20.2	35	32.1
37	17.3	39	39.5
Grand mean ± SD	19.5 ± 1.32	33.1 ± 3.9	34.1 ± 3.7

[a] Temperature was only monitored for the first two weeks early in the season, thus the measured mean temperature is likely to be higher than would be expected for the entire incubation period.

nonguarded and partially guarded egg sacs ($t = -2.518$, $df = 14$, $p = 0.025$). The time until predation did not differ between partially guarded egg sacs and nonguarded egg sacs (Fig. 3).

Egg sacs were located on a variety of different plants, including *Grindelia lanceolata* (Narrowleaf Gumweed), *Eupatorium hyssopifolium* (Hyssop-leaved Thoroughwort), *Rudbeckia hirta* (Blackeyed Susan), *Daucus carota* (Queen Anne's Lace), *and Solidago nemoralis* (Grey Goldenrod), and were always found near the top of flowering plants or the peripheral branches of small trees. Two egg sacs were found inside a bundle of *G. lanceolata* leaves held together with silk. Another egg sac was found inside a curled leaf that was still attached to the plant. Mean height at which all egg sacs were located was 103 cm (range = 53–196). The mean temperatures of the nine egg sacs that were monitored in their entirety were used to calculate a hatching time. When the regression equation was used to predict hatching time using real egg sac mean temperatures, no significant differences ($t = -0.786$, $df = 8$, $p = 0.454$) were found between the predicted hatching times and the actual hatching times (Table 1).

3.3. Development of an egg sac model

All potential model egg sac temperatures were within ca. 5 °C of the real egg sacs. To determine which egg sac best matched the thermal characteristics of the real egg sacs, only a 2 h portion was used for evaluation. The sage (green) painted large wooden model (henceforth called the large green wood model) most closely represented the thermal characteristics of the real egg sac graphically (Fig. 4), and was used as the egg sac model in the field. The mean
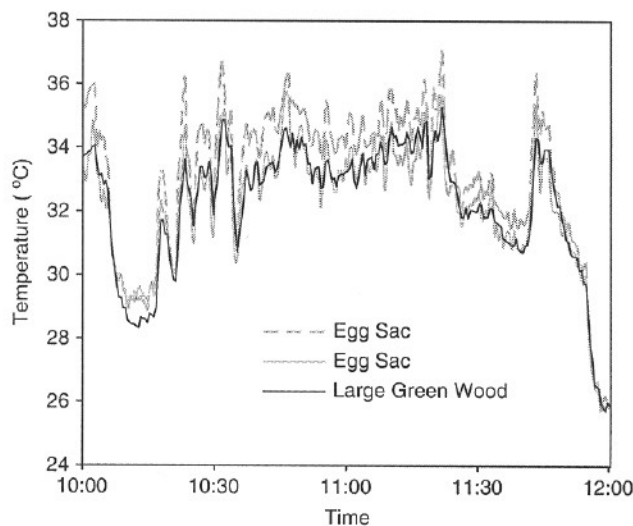

Fig. 4. Temperatures of the large green wood model and two egg sacs monitored for 120 min during a clear sunny day on 9 June 2004.

temperature of the two real egg sacs was correlated to the temperature of the large green wood model ($r^2 = 0.71$, $p < 0.001$). However the mean temperatures of the egg sacs and model were significantly different (paired $t_{5974} = -10.236$, $p = < 0.001$, mean difference = $-0.287 \pm$ SD). The differences in mean temperatures were well within the error range of the datalogger used, therefore biologically, there was no difference between the real egg sacs and the model egg sacs.

3.4. Determining potential extreme temperatures using egg sac models

As expected, the egg sac model with the highest mean temperature was the 0.1 m exposed egg sac, and the coolest model was the 1.0 m shaded egg sac. During the day, the

Table 2
Daily mean temperatures for model egg sacs on a representative warm day and cool day

Egg sac model (m)	Warm day (°C)	Warm day predicted hatching time	Cool day (°C)
0.1, shaded	21.2	29.2	12.0
0.5, shaded	20.8	30.3	11.7
1.0, shaded	20.8	30.3	12.0
0.1, exposed	22.3	26.2	12.6
0.5, exposed	21.6	28.1	12.2
1.0, exposed	21.8	27.5	12.6

Predicted hatching times were calculated only for the warm day because the cool day temperatures were out of the range of the regression model (no hatching was observed at 15 (°C)).
Warm day temperatures were from 8 September 2004.
Cool day temperatures were from 16 October 2004.

warmest exposed model was sometimes 5–10 °C warmer than the coolest egg sac model. At night the warmest egg sac was the model at 1.0 m shaded and the coolest was the 0.1 m exposed model. The difference between the warmest and coolest egg sac at night was only 2–4 °C. Because the temperature differences during the day were greater than at night, the warmest egg sac model during the daytime (0.1 m exposed model) was also the warmest model over a 24 h period (Table 2). However, during a summer day the mean temperature differences between all three egg sacs are <2 °C. Later in the year (i.e. October), when days were cooler, the difference between the warmest and coolest egg sacs was even less (Table 2). Because of the small temperature differences between the models, predicted hatching times based on potential egg sac placement were found to be relatively small.

4. Discussion

Incubation temperature in the laboratory had a large impact on hatching time in *Peucetia viridans*. Warmer temperatures decreased hatching time to as little as two weeks, while cooler temperatures could prolong the hatching time to more than 30 days. Temperature only had a positive affect on hatching between the temperatures of 20.0 and 32.5 °C, and at temperatures beyond those extremes, development did not occur. Under natural conditions, temperature would be expected to influence nest site selection for *P. viridans*. However, the data collected in this study has found evidence to the contrary.

Model egg sacs placed in the field indicated that egg sacs placed close to the ground with no cover would encounter the warmest available temperatures. Egg sacs at this height would develop at a faster rate than if they were placed in other potential locations. However, most egg sacs are not found fully exposed or below 50 cm. Typically egg sacs occurred underneath flowers or leaves giving the egg sac partial exposure. This demonstrates that egg sacs are not normally placed in complete sunlight where the warmest

temperatures are available. Consequently, sites selected for oviposition do not promote rapid hatching any more than other potential nest sites. When the temperatures of all model egg sacs in both of the treatments are examined, no mean temperatures were found to exceed the temperature where development did not occur in the lab. Therefore, there would not be any adverse temperature effects in placing an egg sac close to the ground. The egg sac model at 100 cm, which is the model closest to the actual mean egg sac height for *P. viridans*, was cooler than the model egg sacs closer to the ground for both the shaded and exposed treatments. If the only factor affecting placement of egg sacs was temperature, gravid females should select a nest site closer to the ground to enhance development, and in fact they do not.

Although temperature does play a role in determining hatching time of *P. viridans*, other factors must also influence nest site selection. Few studies have determined the factors influencing nest selection in spiders, especially in spiders that do not use webs as a nest site. *Frontinella pyramitela*, lays its egg sac in a completely different environment than that of *P. viridans* (Suter et al., 1987). *Frontinella pyramitela* builds an aerial web, but lays its egg sac near the ground, in a moist, protected environment. *Misumena vatia* also selects nest sites away from their foraging site. *Misumena vatia* selects an oviposition site near the top of a plant, and in more nonflowering plants than flowering plants (Morse, 1985), suggesting a predator avoidance strategy, while still allowing the mother to feed. These studies illustrate that species may utilize a variety of behaviors and environmental factors in selecting a nest site.

P. viridans egg sacs that were not guarded were extremely susceptible to predation from ants. Previous studies on *P. viridans* have shown that females guarding egg sacs greatly decrease the chances of egg sac predation (Fink, 1987). Placing egg sacs higher on a plant, in temperatures less optimal for development, could further reduce predation from ants because the egg sacs are located further from the soil surface. Also, because *P. viridans* is an ambush predator, placing the egg sac at this height may allow the guarding mother to feed on pollinators, while still guarding the egg sac. *P. viridans* seemingly uses a variety of factors to select a nest site, some of which may include temperature, risk of predation, and a proper environment for adult survival. Although this study did not target factors other than incubation temperature, it is clear, more studies are needed to more accurately determine what factors affect nest site selection and what the relative contribution of these individual factors are on the spiders that remain with egg sacs.

Laboratory developmental rate determination accurately predicted the time until hatching if temperatures were reported as a daily mean as opposed to individual temperatures. Because we only found successful hatching at incubation temperatures of 20, 25, 30, and 32.5 °C, the regression model will not accurately predict hatching times <20 or >32.5 °C. In actuality, daily mean egg sac

temperature in Middle Tennessee fell within this range, but individual temperature extremes sometimes fell out of our predictable range. Therefore, a daily mean temperature was used to predict hatching times instead of individual temperatures.

Obviously, selection of a proper nest site in spiders is required for the survival of offspring. However, few studies have determined the factors that spiders use to select a nest site, especially in species that do not use their web as an oviposition site. For at least *P. viridans*, other factors appear to be utilized in a trade-off with incubation temperature for assuring hatching success.

Acknowledgements

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