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# EFFECTS OF TEMPERATURE ON ESCAPE BEHAVIOR IN THE CRIBELLATE SPIDER, *OECOBIUS ANNULIPES* (ARANEAE, OECOBIIDAE)

VINCENT A. COBB

*Department of Biology, The University of Texas at Tyler, Tyler, TX 75701*
*Present address: Department of Biology, Ouachita Baptist University, Arkadelphia, AR 71998*

Although behavioral adjustments have been documented as a mechanism used by insects and reptiles to regulate body temperatures, spiders are also ectothermic and are constrained by their thermal environment (Humphreys, 1974, 1987). Temperature is considered an important factor in the regulation of spider activity (Nørgaard, 1956; Humphreys, 1974, 1978; Riechert and Tracy, 1975; Aitchison, 1984*a*), though Tietjen (1982) reported that temperature had only a slight effect on the total daily activity of the communal spider, *Mallos gregalis*. In addition, some arachnids possess the ability to stay active at extremely low temperatures (Riddle, 1981; Aitchison, 1984*a*, 1984*b*). Specific behavioral activities also can be influenced by thermal gradients. For example, *Theridion saxatile* daily moves egg sacs out of the nest once the temperature has risen to the mid-30°C (Nørgaard, 1956). Other behaviors such as courtship (Costa and Sotelo, 1984; Davis, 1989), web-site choice (Riechert and Tracy, 1975), and locomotory activity (Ford, 1978) are influenced by temperatures.

One way to better understand the effects of temperature on animals is to observe behaviors under differing thermal conditions. For spiders, predator avoidance and escape behaviors provide easily observable behaviors that can be quantified (Tolbert, 1975; Hoffmaster, 1982; Cushing and Opell, 1990*a*). In this experiment, I describe the effect of temperature on the performance of escape behavior in the cribellate spider, *Oecobius annulipes*. It was hypothesized that *O. annulipes* would (1) exhibit reduced performance at lower temperatures, and (2) alter its escape behavior at different temperatures. Performance tests also were administered during both diurnal and nocturnal periods to see if escape behaviors differed with photoperiod.

*Oecobius annulipes* was tested for its ability to escape from a potential predator during October and November of 1988 on the campus of The University of Texas at Tyler. *Oecobius annulipes* was found living on the walls of certain brick buildings and these populations were situated such that their webs were not exposed to direct sunlight. These small spiders, 2 to 3 mm in length, are common under stones and around buildings in temperate climates (Kaston, 1948). The local populations of *O. annulipes* did not live in communal webs as does *O. civitas* Shear (Shear, 1970; Burgess, 1976, 1978). Instead, these spiders have individual webs regularly spaced a few cm apart. Webs of these spiders are small (20–30 mm in diameter) and are attached parallel to the substrate on which they are found; here the web acts as a snare while the spiders remain on the substrate (Kaston, 1948). Webs are attached between bricks, over the cement layer which forms a depression between bricks. This depression allows for routes of entry to, or escape from, the web. Many webs in the population contained one or more egg sacs and spiders often displaced other individuals from webs upon entry. Because of this displacement behavior and potential communal nesting, spiders or egg sacs from a single web could not be associated with a particular individual (Shear, 1970; Burgess, 1978). The common escape behavior of *O. annulipes* is to rapidly flee away from the point of disturbance.

Experiments consisted of disturbing a spider within its web by poking the web from a 90° angle once with a small blunt probe directly above the spider. Spiders that fled from their webs were timed from the initiation to cessation of flight to 0.01 s with a stopwatch. Most spiders fled in a straight line away from the nest. Straight-line distances, from the spider's initial point in the web to its stopping location (flight distance) were measured to the nearest mm. Flight speed (mm/s) was calculated for each individual as flight distance divided by flight time.

Spiders were tested at substrate temperatures of 8, 16, and 23°C. Tests at substrate temperatures of 8 and 16°C were run at night between 2100 and 2400 h. Day experiments were run at 16 and 23°C between 1200 and 1600 h. All substrate temperatures were measured with a Schultheis quick-reading mercury thermometer in which the thermometer bulb was placed directly against the brick substrate. Analyses of variance and group $t$-test were performed on the data using Statview 512+ (BrainPower, 1986).

Of 130 spiders tested, 3 (2.3%) exhibited curved or erratic escape patterns, 5 (3.8%) refused to leave the web they occupied, 8 (6.2%) dropped out of the web to the ground, and 114 (87.7%) fled from their web in a rapid, straight-line fashion. Due to sample size only straight-line escapes were statistically analyzed for temperature effects. However, there appeared to be no relationship of behavior type to substrate temperature, as most of these minor behaviors were observed at all temperature regimes. Thirty spiders were tested at 8°C, 37 at 16°C, 18 during daylight and 19 during night, and the remaining 47 spiders during daylight at 23°C.

Of the spiders tested at 16°C in both day or night, none of the three measured performances were significantly different: mean flight distance = 191.5 mm and 217.2 mm, respectively ($t = -0.65$, $d.f. = 35$, $P > 0.05$); mean flight time = 3.12 s and 3.8 s, respectively ($t = -1.15$, $d.f. = 35$, $P > 0.05$); and mean flight speed = 63.04 mm/s and 58.24 mm/s, respectively, ($t = 0.79$, $d.f. = 35$, $P > 0.05$). Therefore, data from both daylight and night tests at 16°C were pooled for further analyses.

All data on the fleeing behavior of *O. annulipes* at the three temperatures are summarized in Table 1. Mean flight distances of spiders were significantly different between the three substrate temperatures ($F = 3.42$, $d.f. = 2$, $P < 0.05$). Flight distance increased with substrate temperature. However, only 8°C and 23°C were significantly different (Fisher multiple comparison test, $P < 0.05$). The duration of escape, flight times, were significantly different ($F = 4.18$, $d.f. = 2$, $P < 0.05$), but there did not seem to be discernable patterns. The flight speed of *O. annulipes* was significantly faster at the warmest substrate temperature ($F = 52.94$, $d.f. = 2$, $P < 0.001$), even though flight speeds at the lower two temperatures were almost identical (Fisher multiple comparison test, $P > 0.05$).

Predator avoidance and escape tactics are common among spiders and other animals (Foelix, 1982). The variations in these behaviors are many, but for spiders generally consist of "freezing" and relying on cryptic characteristics, running to cover, jumping from webs, shaking webs, leg autotomization, or retaliation attacks (Tolbert, 1975; Foelix, 1982; Hoffmaster, 1982; Cushing and Opell, 1990*b*; Higgins, 1991). In this study, disturbed *Oecobius annulipes* exhibited "freezing" behavior and stayed within the web, ran away from the web, or jumped to the ground substrate from the web. The most common of these behaviors were to run away from the web. Generally, a fleeing spider ran to another nest, displacing its occupant. This could have benefits for the initial fleeing spider because attention of potential predators is diverted to another individual.

Like most ectotherms, spiders have a low metabolic rate (Anderson, 1970) and are influenced by temperature (Humphreys, 1987). Although Humphreys (1974, 1978, 1987) shows that spiders can regulate their body temperature, few studies have examined the effect of temperature on specific behaviors (recent exceptions, Cushing and Opell, 1990*a*, 1990*b*). These studies did not find any effect of ambient temperature on behavior type, but their temperatures generally ranged from 20 to 28°C. I studied temperature differences at lower temperatures (8 to 23°C). Performance instead of behavior types was analyzed. The flight speed of *O. annulipes* was greatest at the higher temperature. No difference was

TABLE 1—Escape behavior performance of *Oecobius annulipes* occupying webs at three different substrate temperatures. Performance values are given as mean, standard error, and (range).

| | Substrate temperatures (°C) | | |
|---|---|---|---|
| Escape performance | 8 ($n$ = 30) | 16 ($n$ = 37) | 23 ($n$ = 47) |
| Flight distance (mm) | 185.4 ± 19.2 (65–419) | 204.7 ± 19.6 (27–450) | 254.3 ± 19.1 (69–600) |
| Flight time (s) | 3.00 ± 0.25 (1.31–5.75) | 3.47 ± 0.30 (0.56–6.50) | 2.54 ± 0.19 (0.56–6.05) |
| Flight speed (mm/s) | 60.61 ± 2.83 (29.62–84.50) | 60.57 ± 3.00 (22.31–101.64) | 106.08 ± 4.35 (39.71–159.28) |

noted at the two lower temperatures. In addition, this study compared spider performance during diurnal and nocturnal periods at the same ambient temperature. No differences were found in the distance of retreat nor in the physiological performance of retreating. This differs from Cushing and Opell's (1990*a*, 1990*b*) work with *Uloborus glomosus* Walckenaer, which showed that this spider changed its types of escape behavior during the day. This study did not examine daily changes in behavior type, but did compare spider performance during diurnal and nocturnal periods at the same ambient temperature. These preliminary data suggest that the types of behavior exhibited during an escape may not change because of ambient temperature differences, but the physiological performance of these behaviors may be altered.

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