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THERMAL TOLERANCES AND PREFERENCES OF THE CRAB SPIDERS *MISUMENOPS ASPERATUS* AND *MISUMENOIDES FORMOSIPES* (ARANEAE, THOMISIDAE)

Victoria R. Schmalhofer: Graduate Program in Ecology and Evolution; Department of Ecology, Evolution, and Natural Resources; Rutgers University, Cook College; 14 College Farm Road, New Brunswick, New Jersey 08901–8551 USA

ABSTRACT. *Misumenops asperatus* (Hentz 1847) and *Misumenoides formosipes* (Walckenaer 1837) are diurnally-active, flower-dwelling crab spiders (Thomisidae) commonly inhabiting open fields. In laboratory experiments, both species remained active over a temperature range of approximately 46 °C. The spring-maturing *M. asperatus* tolerated significantly lower temperatures than the summer-maturing *M. formosipes* (CT_{min} = −1.4 °C and 2.2 °C, respectively), while *M. formosipes* tolerated significantly higher temperatures than *M. asperatus* (CT_{max} = 48.2 °C and 45.1 °C, respectively). *Misumenops asperatus* displayed thermal discomfort over a broader range of temperatures (36–44 °C) than did *M. formosipes* (41–46 °C). In a laboratory thermal gradient apparatus *M. asperatus* tended to prefer cooler temperatures than *M. formosipes* (14.4 °C and 18.4 °C, respectively). Regression analysis of literature data for 21 species of spiders showed a significant positive relationship between the thermal preference of a species and its CT_{max}. For their CT_{max}'s, which were high compared to most other spider species, *M. asperatus* and *M. formosipes* preferred low temperatures. The coupling of low thermal preferences and high thermal tolerances displayed by *M. asperatus* and *M. formosipes* is unusual for ectothermic organisms.

Spiders are strict ectotherms (Humphreys 1987; Pulz 1987) and are important predators in many terrestrial systems (Riechert 1974; Wise 1993), yet the thermal ecology of spiders is generally less well understood than is that of their insect prey (Humphreys 1987). Thermal relations (i.e., thermoregulatory behaviors, thermal tolerances and preferences) have been examined in less than 0.1% of spider species (Humphreys 1987), and most research has concentrated on large tropical and subtropical orb-weavers (e.g., Krakauer 1972; Carrel 1978; Robinson & Robinson 1978), desert-dwelling spiders (e.g., Mouer & Eriksen 1972; Seymour & Vinegar 1973; Humphreys 1974, 1987; Riechert & Tracy 1975; Lubin & Henschel 1990; Henschel et al. 1992; Turner et al. 1993), and winter-active species (e.g., Aitchison 1978). Studies of temperate-zone spiders inhabiting moderate environments have generally focused on cold resistance and super-cooling capabilities (e.g., Almquist 1970; Kirchner 1973, 1987; Schaefer 1977; Duman 1979; Bayram & Luff 1993) or temperature effects on growth and metabolic rate (e.g., Anderson 1970; Hagstrum 1970; Moulder & Reichle 1972; Li & Jackson 1996). Fewer studies have examined thermal preferences, upper tolerance limits, or thermoregulatory behaviors of spiders inhabiting temperate regions (for exceptions see Almquist 1970; Sevacherian & Lowrie 1972; Tolbert 1979; Suter 1981; references from Table 2 in Pulz 1987).

Information regarding an animal's thermal tolerances and preferences is necessary to describe the thermal ecology of the animal and to evaluate the thermal suitability of its habitat (Hertz et al. 1993). In the experiments reported here, I examined the thermal tolerances and preferences of two flower-dwelling crab spiders (Thomisidae), *Misumenops asperatus* and *Misumenoides formosipes*. These experiments were part of a larger study investigating temperature effects on crab spider microhabitat selection and hunting performance. Because *M. asperatus* and *M. formosipes* prey primarily on insect pollinators, most foraging opportunities and predation events occur diurnally (Schmalhofer 1996). Compared to nocturnal spiders, which are active when heat stress is minimal, *M. asperatus* and *M. formosipes*, as well as other diurnally-active inflorescence spiders, likely experience greater temperature variability and extremes of temperature. Consequently, diurnal spiders might tolerate greater thermal stress. This study specifically addressed the following questions: 1) What are the thermal tolerances and preferences of *M. asperatus* and *M. formosipes*? 2) When comparing field-active adult female spiders, does the summer-maturing species, *M. formosipes*, display higher tolerances and preferences than the spring-maturing species, *M. asperatus*? 3) How do the thermal tolerances and preferences of these flower-dwelling thomisids compare with the thermal tolerances and preferences of other spiders? 4) Does data drawn from the literature indicate that diurnally-active spiders, in general, have higher thermal tolerances and preferences than nocturnally-active spiders?

Information concerning the thermal relations of *M. asperatus* and *M. formosipes* is of additional interest because thomisids rank among the most diverse families of spiders (Coddington & Levy 1991) and are among the most common cursorial spiders found in the herb stratum of open fields. However, the thermal ecology of this family is virtually unknown, consisting only of a few anecdotal observations (Morse 1979; Lockley et al. 1989).

METHODS

Study animals.—*Misumenops asperatus* and *M. formosipes* are sit-and-wait ambush predators that use their raptorial forelimbs, rather than a web, to restrain prey. In central New Jersey, *M. asperatus* matures in spring (mid-April to early May), females lay a single egg sac in late May or June, and spiderlings emerge in June and July and overwinter as late instar juveniles (pers. obs.). *Misumenoides formosipes* matures in mid-summer (August), females lay a single egg sac in September or early October, and spiderlings generally overwinter in the egg sac (pers. obs.).

Only adult female spiders were used in these experiments. Like many other spiders, male *M. asperatus* and *M. formosipes* seldom capture prey as adults, instead spending their time searching for and guarding prospective mates (Foelix 1996; Dodson & Beck 1993; Pollard et al. 1995). Spiders were collected in Middlesex and Somerset Counties, New Jersey, and voucher specimens have been deposited at the American Museum of Natural History. Experiments involving *M. asperatus* occurred in May and June 1993, and experiments involving *M. formosipes* occurred in August 1993. A given spider was used in only one experimental manipulation.

Because hunger has been shown to influence thermal sensitivity in spiders (Pulz 1987), I maintained the experimental spiders on a diet of one housefly per week for three weeks prior to the initiation of the experiments. This regimen equalized hunger-states among individuals of a given species and maintained spider body mass at relatively constant levels (Anderson 1970; Schmalhofer unpubl. data).

Misumenops asperatus and *M. formosipes* were not acclimated to similar temperatures in the lab prior to testing. Although this confounds species identity with seasonal temperature differences when comparing the two species, I was not attempting to separate these influences, but, rather, was interested in comparing the responses of field-active adults. Also, other researchers (e.g., Sevacherian & Lowrie 1972; Seymour & Vinegar 1973) have found that temperature acclimation does not affect thermal preferences or upper tolerance limits of spiders. However, I maintained spiders at ambient field temperature, rather than a constant temperature, to reduce any possibility of spider responses to experimentally induced temperature changes being influenced by acclimation to an artificial temperature regime. Under natural conditions, the two species experienced different temperature regimes; average daily temperature, based on data collected from the weather station at the Hutcheson Memorial Forest Research Center (HMF) in Somerset County, New Jersey (the site of later field experiments), for 30 days prior to the initiation of experiments was 16.5 ±8.7 °C for *M. asperatus* and 22.8 ±7.9 °C for *M. formosipes*.

Thermal tolerances.—Critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}) describe the highest and lowest temperatures, respectively, at which an animal is capable of displaying coordinated locomotory behavior (i.e., the animal can still escape unfavorable temperatures). An animal's thermal tolerance range is delimited by these critical temperatures. Outside its tolerance range an ectotherm enters a state of heat stupor or cold torpor, which may result in death if exposure to extreme temperatures is prolonged. Critical temperatures of *M. asperatus* and *M. formosipes* were determined by placing spiders confined in petri dishes in a controlled temperature box (VWR Scientific model 2015 low-temperature incubator) initially set to 25 °C. Box temperature was then raised to 50 °C (to determine CT_{max}) or lowered to −5 °C (to determine CT_{min}). Temperature changed at a rate of approximately 1 °C every five minutes. This rate of change was similar to that used in other studies examining tolerance limits (e.g., Almquist 1970; Krakauer 1972; Seymour & Vinegar 1973). For every temperature change of 1 °C, the spiders were prodded to ascertain their ability to initiate an escape response. The last temperature at which a spider responded to prodding (by moving away from the probe, raising its raptorial forelimbs, or grabbing hold of the probe) was recorded as its critical temperature. Spiders were removed from the temperature box once they ceased to respond to prodding. Spiders are known to spontaneously initiate vigorous activity at high temperatures preceding CT_{max}; this activity indicates thermal discomfort as maximal tolerance is approached (Lubin & Henschel 1990). The temperature ranges over which *M. asperatus* and *M. formosipes* displayed thermal discomfort were noted. Five spiders of each species were used to determine CT_{max}, and five different spiders of each species were used to determine CT_{min} (total $n = 10$ spiders per species). Another set of spiders ($n = 9$) was prodded at five minute intervals under constant temperature conditions (25 °C) to ascertain whether a lack of response to prodding was due to habituation rather than temperature.

Thermal preferences.—A temperature arena was established by placing a box (50 cm × 50 cm), the bottom of which was demarcated into numbered squares (2 cm × 2 cm), in a controlled temperature room at 2 °C. Bytac Teflon® paper lined the sides of the box to prevent spiders from escaping. A 650 W photoflood lamp (equivalent color temperature 3400 K) mounted on a ringstand and suspended 1 m above a corner of the arena served as a radiant heat source. A temperature map of the arena was created by determining the temperature of each square within the arena; a spider model (freeze-dried female thomisid) with a fine thermocouple attached to the ventral side of its abdomen was placed in each square and, after two minutes, its temperature was recorded with a Bailey BAT-12 thermocouple thermometer.

Spiders were released singly into the center of the arena, and the number of each square in which a spider stopped and the amount of time it stayed within the square was recorded during a 10 minute period. A spider's preferred temperature (T_p) was determined according to the formula

$$T_p = \Sigma[(T_i)(t_i/t_q)]$$

where T_i is the temperature (°C) of square i, t_i is the time (s) spent in square i, and t_q is the total time (s) a spider was quiescent ($n = 9$ spiders per species). The preferred temperature range of a species was calculated as one standard deviation around its average T_p.

Field temperature.—Temperature data obtained from the weather station at HMF were averaged over three years (1993–1995) to determine average monthly high and low temperatures. These data were compared with the preferred temperature ranges of *M. asperatus* and *M. formosipes*. By graphing the data and calculating the appropriate area encompassed within the high-low temperature curves, a rough estimate of the frequency with which mature female spiders experienced ambient temperatures (shaded air temperature) within their preferred ranges was determined. Average daily temperatures calculated over a ten day period at the beginning and end of a species' adult stage were compared to determine the seasonal temperature shifts experienced by adult *M. asperatus* and *M. formosipes*.

Analyses.—Due to small sample sizes, nonparametric statistics were used to analyze the results. A Mann-Whitney *U* test was used to compare CT_{min} data of *M. asperatus* and *M. formosipes*. Because CT_{max} and thermal preference data of *M. asperatus* and *M. formosipes* were also compared to CT_{max} and thermal preference data of other spider species taken from the literature, Kruskal-Wallace tests were used, and all possible pairwise posthoc comparisons were made using Mann-Whitney *U* tests, with a Bonferroni correction for multiple comparisons (adjusted $\alpha = 0.009$). Spider species for which data were available in the literature were separated into two groups: diurnally active and nocturnally active. For comparative purposes, species that were active both nocturnally and diurnally were counted as diurnally active. Information con-

Table 1.—Critical thermal tolerances (CT_{max}'s and CT_{min}'s) and preferred temperatures (T_p's) of *Misumenops asperatus* and *Misumenoides formosipes*, and the range of temperature over which spiders displayed thermal discomfort. Values are in °C. Critical thermal values and preferred temperatures are given as means (± 1 SD). For CT_{min} data, a significant difference occurs at $\alpha = 0.05$; for CT_{max} and T_p data, adjusted $\alpha = 0.009$.

Measurement	*M. asperatus*	*M. formosipes*	Mann-Whitney *U* test	*P*-value
CT_{min}	−1.4 (0.6)	2.2 (1.8)	−2.660	0.0098
CT_{max}	45.1 (1.3)	48.2 (0.2)	−2.627	0.0086
T_p	14.4 (3.4)	18.4 (5.4)	−1.810	0.0703
thermal discomfort	36–44	41–46		

cerning the activity times of the various species came from the original studies and from Roberts (1995). In cases where information concerning a species' activity time could not be found, the species was presumed to be nocturnally active. Literature values for CT_{max} and T_p were subjected to simple linear regression to determine whether CT_{max} increased with increasing T_p.

RESULTS

Thermal tolerances.—Cessation of spider responses to prodding was due to temperature, not habituation to prodding. Under constant temperature conditions, spiders did not become habituated in 45 consecutive prodding trials. In the CT_{min} and CT_{max} experiments, a given spider was prodded less than 30 times. Also, spider posture changed noticeably when critical temperature was reached. Throughout most of the experimental temperature range, spiders maintained the classic crab spider hunting posture (raptorial forelimbs held outstretched, slightly upraised, and approximately perpendicular to the long axis of the body). Within approximately 1 °C of upper or lower critical temperature, spiders abandoned the classic hunting posture and huddled with their forelimbs held close to the body.

Misumenops asperatus and *M. formosipes* proved to be broadly temperature tolerant. *Misumenops asperatus* had a significantly lower CT_{min} than did *M. formosipes* (Table 1). Conversely, *M. formosipes* had a significantly higher CT_{max} than did *M. asperatus* (Table 1). Spontaneous initiation of escape behavior by spiders (i.e., a spider moved vigorously around the petri dish without prompting from the investigator) was observed during the CT_{max} experiments, and *M. asperatus* displayed thermal discomfort over a wider temperature range than did *M. formosipes* (Table 1). No evidence of low-temperature thermal discomfort was observed during the CT_{min} experiments (i.e., there was no period of spontaneous activity).

Values for the CT_{max}'s of other spider species are presented in Table 2. Comparing CT_{max} values of *M. asperatus* and *M. formosipes* with literature data for diurnally-active and nocturnally-active spiders revealed significant differences (Kruskal-Wallace test: $H = 16.271$, $df = 3$, $P = 0.001$). Diurnal spiders and nocturnal spiders had similar CT_{max}'s, and diurnal spiders and *M. asperatus* had similar CT_{max}'s (Fig. 1). However, CT_{max}'s of *M. asperatus* and nocturnal spiders differed significantly, and *M. formosipes* had a significantly higher CT_{max} than *M. asperatus*, nocturnal spiders, or diurnal spiders (Fig. 1).

Thermal preferences.—Temperature in the experimental arena ranged from 9–57 °C. Spiders encountering hotter areas moved rapidly to cooler areas, holding their bodies well-elevated above the substrate (stilting) until they settled in a cooler section of the arena. Although spiders moved more slowly (relative to the speed at which they vacated hot areas) at the cooler end of the arena, no evidence of cold-trapping (i.e., spider activity was so reduced by the cold that they could not emigrate from cooler areas) was observed. Spiders did not stilt in areas cooler than 30 °C. *Misumenops asperatus* preferred cooler temperatures than *M. formosipes*, but this trend was not significant (Table 1).

Preferred temperatures of other spider species are presented in Table 2. Comparing T_p's of *M. asperatus* and *M. formosipes* with lit-

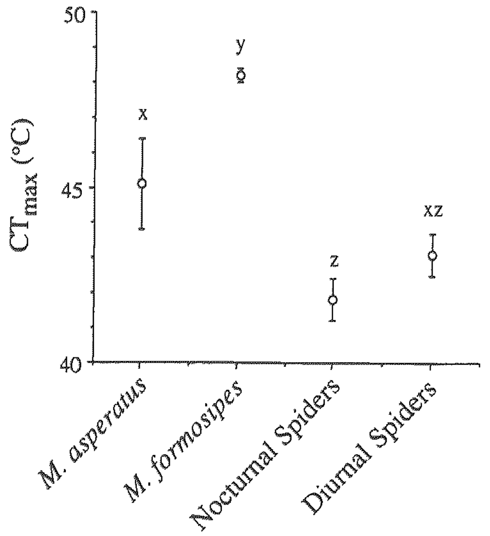

Figure 1.—Critical thermal maxima ($\mathrm{CT}_{\max}$'s) of *Misumenops asperatus, Misumenoides formosipes,* nocturnally-active spiders and diurnally-active spiders. Data for nocturnal and diurnal spiders were taken from Table 2; winter-active species were not included in the analysis. Values with different letters are significantly different using post-hoc Mann-Whitney *U* tests with adjusted $\alpha = 0.009$. Error bars represent one SE for nocturnal and diurnal spiders and one SD for *M. asperatus* and *M. formosipes.* Standard errors could not be used for *M. asperatus* and *M. formosipes* since species averages were calculated from individual values. In contrast, nocturnal and diurnal averages were calculated from species averages, making use of the standard error appropriate.

erature data for diurnally-active and nocturnally-active spiders revealed significant differences (Kruskal-Wallace test: $H = 23.878$, $df = 3$, $P \leq 0.0001$). Preferred temperatures were similar between *M. formosipes* and *M. asperatus,* and between *M. formosipes* and nocturnal spiders (Fig. 2). However, T_p's of *M. asperatus* and nocturnal spiders differed significantly, and T_p of diurnal spiders was significantly higher than that of *M. formosipes, M. asperatus,* or nocturnal spiders (Fig. 2).

Relationship between $\mathrm{CT}_{\max}$ and thermal preference.— Using the literature data shown in Table 2, a significant positive relationship was found between a spider species' T_p and its $\mathrm{CT}_{\max}$ ($F = 6.707$, $df = 1, 19$, $P = 0.018$, $r^2 = 26.1\%$) (Fig. 3). Because *M. asperatus* and *M. formosipes* had unusually high $\mathrm{CT}_{\max}$'s for their T_p's, data for these two species were not included in this analysis. Addition of *M. asperatus* and *M. formosipes* data to the regression resulted in a loss of the significant relationship ($F = 1.615$, $df = 1, 21$, $P = 0.2177$, $r^2 = 7.1\%$). For similar reasons, data for winter-active spiders were also excluded.

Field temperature.—*Misumenoides formosipes* experienced preferred temperatures under field conditions more frequently than did *M. asperatus.* Ambient temperature fell within the preferred temperature range (PTR) of adult *M. asperatus* 43% of the time, exceeded PTR 47% of the time, and fell below PTR 10% of the time (Fig. 4). In contrast, ambient temperature fell within PTR of adult *M. formosipes* 65% of the time, exceeded PTR 10% of the time, and fell below PTR 25% of the time (Fig. 4). During their adult phase, *M. asperatus* experienced an increase in average daily temperature of 5.3 °C, and *M. formosipes* experienced a decrease in average daily temperature of 6.5 °C.

DISCUSSION

Comparing the thermal tolerances and preferences of the spring-maturing *M. asperatus* with those of the summer-maturing *M. formosipes* yielded the expected results. Adult female *M. asperatus,* which experienced lower ambient temperatures than did adult female *M. formosipes,* had a lower $\mathrm{CT}_{\min}$, while *M. formosipes* had a higher $\mathrm{CT}_{\max}$. Thermal preferences of the two crab spider species were similar. Of greater interest is a comparison of the thermal tolerances and preferences of these flower-dwelling spiders with those of other spider species.

There is little information available regarding $\mathrm{CT}_{\min}$ in spiders. In the single study of which I am aware, Hagstrum (1970) reported a $\mathrm{CT}_{\min}$ of 6 °C for a southern California wolf spider, *Alopecosa kochi* (Keyserling 1877) (as *Tarentula kochi* in Hagstrum 1970). Much more data is available concerning lower lethal temperatures and temperature effects on developmental rates (e.g., Almquist 1970; Li & Jackson 1996). Data from other studies indicates that temperate-climate spiders are generally capable of activity at relatively low temperatures. Ford (1978) showed that a European wolf spider, *Pardosa amentata* Clerck 1757, remained active at 5 °C, and Moulder & Reichle (1972) obtained similar results for the litter-spider fauna of a Tennessee *Lirio-*

dendron forest. Aitchison (1984) found that both winter-active and winter-inactive Canadian spiders fed at 2 °C, with winter-active species continuing to feed at temperatures as low as −5 °C. These studies, coupled with the CT$_{\min}$ values calculated for *M. asperatus* and *M. formosipes,* suggest that temperate-zone spiders from moderate climates may generally be expected to have CT$_{\min}$'s near 0 °C.

Misumenops asperatus, and particularly *M. formosipes,* had high thermal tolerances. In general, CT$_{\max}$'s of these flower-dwelling thomisids were more similar to the upper lethal temperatures than to the CT$_{\max}$'s of other spider species (see Table 2). Of the 27 species for which data was available, only six species had comparable CT$_{\max}$'s: *Phurolithus festivus* (C.L. Koch 1835), *Euophrys frontalis* (Walckenaer 1802), *Cyrtophora citricola* (Forskål 1775), *Zelotes longipes* (L. Koch 1866) (as *Z. serotinus* in Almquist 1970), *Hogna carolinensis* (Walckenaer 1805) (as *Lycosa carolinensis* in Moeur & Eriksen 1972), and *Seothyra henscheli* (Dippenaar 1991). *Misumenoides formosipes* had the second highest CT$_{\max}$ recorded for a spider; only *S. henscheli,* an eresid from the Namib desert (Lubin & Henschel 1990), had a higher thermal tolerance. The natural histories of *M. asperatus* and *M. formosipes* may provide an explanation for their unusually high thermal tolerances. These thomisids do not stalk prey, but, rather, position themselves close to a flower's nectaries and/or anthers (pollen-bearing structures) in order to ambush flower-visiting insects (pers. obs.). On the plants used by *M. asperatus* and *M. formosipes,* the floral surface from which nectaries and anthers are accessed by insects is typically exposed to the sun (pers. obs.). Under conditions of high radiant intensity and low wind speed, body temperatures of spiders on sun-exposed floral surfaces can exceed ambient temperature by 15 °C or more (Schmalhofer 1996). A high thermal tolerance would allow *M. asperatus* and *M. formosipes* to continue hunting at ambient temperatures near 30 °C, when floral surface temperatures could be in excess of 40 °C. Ambient temperatures approaching 30 °C are not an uncommon occurrence in late spring and summer in central New Jersey: from April through September in 1993–1995 there were, on average, 52 days per year having a daily high temperature of at least 30 °C.

One would expect that because diurnally-active spiders experience higher temperatures than nocturnally-active species, diurnally-active spiders would prefer higher temperatures. Evaluation of data from the literature showed that this was indeed the case (Fig. 2). However, T_p's of *M. asperatus* and *M. formosipes* were lower than those of other diurnally-active species, and T_p of *M. asperatus* was also lower than that of nocturnally-active species! Pulz (1987) suggested that, barring winter-active spiders, lower thermal preference correlates with lower thermal tolerance. Regression analysis of the available literature data supported Pulz's hypothesis of a positive relationship between T_p and CT$_{\max}$. Interestingly, the CT$_{\max}$'s of *M. asperatus* and *M. formosipes* predicted from the regression equation (40.2 °C and 41.3 °C, respectively) were much lower than the measured values; alternatively, predicted T_p's (32.1 °C and 43.4 °C, respectively) were much higher than the measured values. Thus, depending on how one looks at it, *M. asperatus* and *M. formosipes* have exceptionally high thermal tolerances or exceptionally low thermal preferences. This combination of high thermal tolerance and low thermal preference is unusual for an ectotherm; preferred temperature is usually nearer the upper than the lower tolerance limit (May 1985).

Broad temperature tolerances and relatively low thermal preferences displayed by *M. asperatus* and *M. formosipes* may be viewed as adaptations that facilitate their diurnal predatory lifestyles in potentially thermally stressful habitats (sun-exposed flowers). Hymenopterans and dipterans comprise most of the prey captured by these thomisids (Schmalhofer 1996). Dipterans are well known for their ability to fly at low temperatures (reviewed in Heinrich 1993); and large hymenopterans, such as honeybees and bumblebees, require thoracic temperatures of 30–35 °C in order to fly (reviewed in Heinrich 1993). The capacity to endothermically generate heat by shivering wing muscles allows these bees to fly at low ambient temperatures; honeybees can fly when ambient temperature is as low as 15 °C, and some bumblebees can fly when ambient temperature is less than 10 °C (reviewed in Heinrich 1993). Both *M. asperatus* and *M. formosipes* prey on honeybees, and *M. formosipes* is also capable of capturing bumble-

Table 2.—Literature values for critical thermal maxima (CT_{max}'s), preferred temperatures (T_p's), and upper (T_{UL}), and lower (T_{LL}) lethal temperatures of various spider species. Values are presented in °C. "Code" describes the period of activity and climatic zone inhabited by a species: n—nocturnal hunter, n*—presumed nocturnal hunter (information unavailable), d—diurnal hunter, n/d—hunts nocturnally and diurnally. 1—temperate-zone species inhabiting a moderate environment, 2—presumed to be a temperate-zone species inhabiting a moderate environment, 3—winter-active temperate-zone species, 4—desert species, 5—tropical or subtropical species. Other symbols within the table are as follows: †—average value based on multiple values or the endpoints of a range of values given in the source, HS—heat stupor (this measure is higher than CT_{max} and indicates that locomotor capacity has been lost).

Spider	code	CT_{max}	T_p	T_{UL}	T_{LL}	Source
Agelenidae						
Agelena consociata Denis 1965	d, 5		23.0			table 2 in Pulz 1987
Agelena labyrinthica Clerck 1757	d, 2	41.5†^{HS}	23.5†	45.0		table 2 in Pulz 1987
Araneidae						
Argiope trifasciata Forskål 1775	d, 1			53.7†		table 2 in Pulz 1987
Cyrtophora citricola Forskål 1775	n/d, 5	46.0^{HS}	27.0†			table 2 in Pulz 1987
Clubionidae						
Clubiona diversa O. P.-Cambridge 1862	n, 1	41.4	22.3			Almquist 1970
Clubiona similis L. Koch 1866	n, 1	42.1†	22.3		−9.5†	Almquist 1970
Clubiona trivialis C. L. Koch 1843	n, 1	42.1	16.0		−8.3	Almquist 1970
Dictynidae						
Nigma walckenaeri Roewer 1951 (as *Dictyna viridissima* in Pulz 1987)	n*, 4			48.2†		table 2 in Pulz 1987
Eresidae						
Seothyra henscheli Dippenaar 1991	n/d, 4	49.0				Lubin & Henschel 1990
Gnaphosidae						
Zelotes longipes L. Koch 1866 (as *Z. serotinus* in Almquist 1970)	n, 1	46.4	23.1			Almquist 1970
Linyphiidae						
Bolyphantes index Thorell 1856	n*, 3	39.6^{HS}	4.1			table 2 in Pulz 1987
Frontinella communis Hentz 1850	d, 1	41.8		44.0		Suter 1981
Macrargus rufus Wider 1834	n*, 3	40.8†^{HS}	1.2†			table 2 in Pulz 1987
Oedothorax apicatus Blackwall 1850	n*, 1	40.6†	17.1		−6.8	Almquist 1970
Stemonyphantes lineatus L. 1758	n, 1	40.5	14.4		−11.1	Almquist 1970
Liocranidae						
Agroeca proxima O. P.-Cambridge 1871	n, 1	37.4	19.4			Almquist 1970
Phurolithus festivus C. L. Koch 1835	d, 1	45.6	27.5			Almquist 1970
Scotina gracilipes Blackwall 1859	n, 1	41.4	16.8		−7.1	Almquist 1970

Table 2.—Continued.

Spider	code	CT_{max}	T_p	T_{UL}	T_{LL}	Source
Lycosidae						
Arctosa alpigena Doleschall 1852	n/d, 2			47.3		table 2 in Pulz 1987
Hogna carolinensis Walckenaer 1805 (as *Lycosa carolinensis* in Moeur & Eriksen 1972)	n/d, 4	47.0		48.0		Moeur & Eriksen 1972
Pardosa spp.	n/d, 2			45.0†		table 2 in Pulz 1987
Pardosa lugubris Walckenaer 1802 (as *P. chelata* in Pulz 1987)	n/d, 2		26.2†	47.7		table 2 in Pulz 1987
Pardosa nigriceps Thorell 1856	n/d, 1	39.7	21.0			Almquist 1970
Pardosa pullata Clerck 1757	n/d, 1		23.7†	45.1		table 2 in Pulz 1987
Pardosa pullata	n/d, 1		32.0†	43.0		table 2 in Pulz 1987
Pardosa ramulosa McCook 1893	n/d, 2		28.1†			Sevacherian & Lowrie 1972
Pardosa sierra Banks 1898	n/d, 2		34.6†			Sevacherian & Lowrie 1972
Pirata piraticus Clerck 1757	n/d, 1		29.0†	35.3		table 2 in Pulz 1987
Pirata piraticus	n/d, 1		21.0†			table 2 in Pulz 1987
Trochosa robusta Simon 1876	n/d, 2	40.4^{HS}	24.8			table 2 in Pulz 1987
Trochosa spinipalpis F. O. P.-Cambridge 1895	n/d, 2	39.3	19.2			table 2 in Pulz 1987
Philodromidae						
Philodromus aureolus Clerck 1757	n/d, 1	41.8†	23.1		−10.8	Almquist 1970
Tibellus oblongus Walckenaer 1802	n/d, 1	42.8	19.0		−9.3	Almquist 1970
Salticidae						
Euophrys frontalis Walckenaer 1802	d, 1	45.7	27.5			Almquist 1970
Tetragnathidae						
Nephila clavipes L. 1767	d, 5	41.6				Krakauer 1972
Theraphosidae						
Aphonopelma sp.	n, 4	43.0	29.0†			Seymour & Vinegar 1973
Theridiidae						
Achaeranea riparia Blackwall 1834 (as *Theridion saxatile* in Pulz 1987)	n*, 2			48.0†		table 2 in Pulz 1987
Crustulina guttata Wider 1834	n*, 1	41.8	19.6			Almquist 1970
Dipoena inornata O. P.-Cambridge 1861	n*, 1	43.2	15.5			Almquist 1970
Zoridae						
Zora spinimana Sundevall 1833	d, 1	41.8	19.5			Almquist 1970

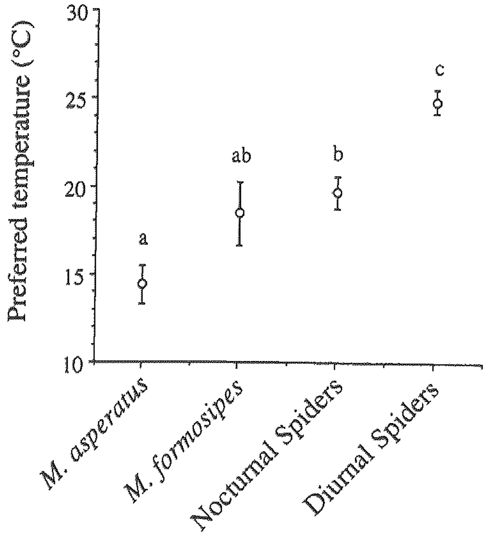

Figure 2.—Preferred temperatures of *Misumenops asperatus, Misumenoides formosipes*, nocturnally-active spiders and diurnally-active spiders. Data for nocturnal and diurnal spiders were taken from Table 2; winter-active species were not included in the analysis. Values with different letters are significantly different using post-hoc Mann-Whitney U tests with adjusted $\alpha = 0.009$. Error bars represent one SE.

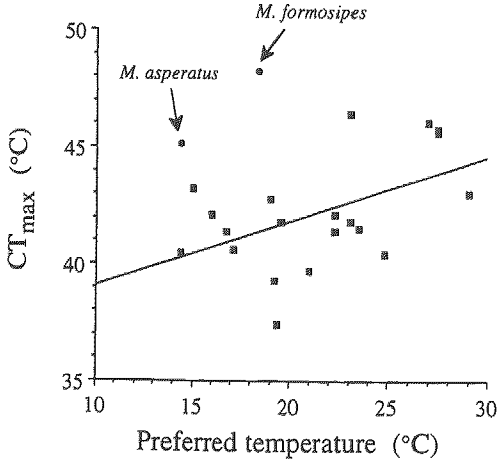

Figure 3.—Linear regression of preferred temperature against CT_{max}. The regression was based on literature data presented in Table 2. Regression equation: $y = 0.275x + 36.26$. Although not included in the regression, for comparative purposes data points for *Misumenops asperatus* and *Misumenoides formosipes* were included in the graph. Squares (■) represent other spiders species, circles (●) represent *M. asperatus* and *M. formosipes.*

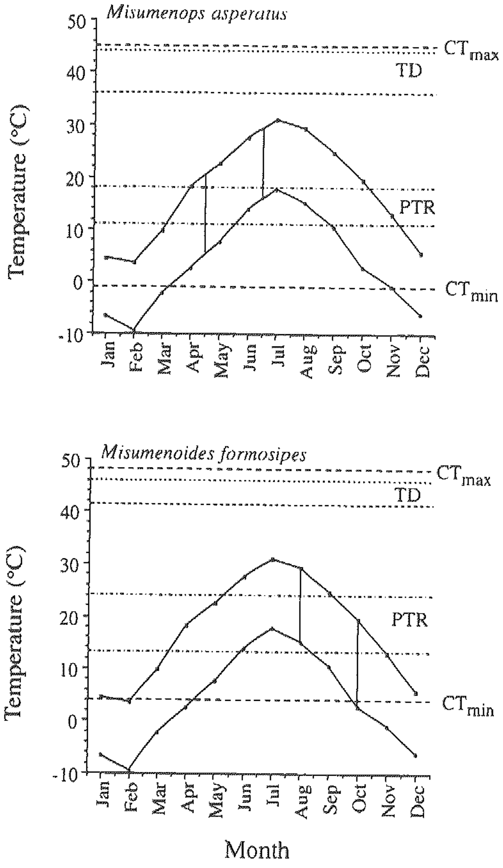

Figure 4.—The relationship between average daily high and low temperatures and the preferred temperature ranges (PTR's) of *Misumenops asperatus* and *Misumenoides formosipes*. Periods of adult activity are demarcated with vertical bars. CT_{max} (upper dashed line), CT_{min} (lower dashed line), and zone of thermal discomfort (TD, dotted lines) are indicated for each spider species. The bounds of a species' PTR (dot-dashed lines) were calculated as one standard deviation around mean T_p.

bees (Schmalhofer 1996). Presumably many of the other bees used by these spiders, such as anthophorids and megachilids, display temperature-flight relationships similar to those shown by honeybees and bumblebees. The broad temperature tolerances shown by *M. asperatus* and *M. formosipes* allow these spiders to increase their foraging time, both daily and seasonally. Coupled with their ability to hunt equally well over a wide range of temperatures (Schmalhofer 1996), and their low thermal preferences, broad thermal tolerances benefit these spiders by affording them the opportunity to hunt prey that is itself active over a wide range of environmental temperatures.

Assuming that an ectotherm benefits by maintaining body temperature within some preferred range of temperature (Hertz et al. 1993), comparing preferred temperature ranges (PTR's) of *M. asperatus* and *M. formosipes* with the average range of temperatures normally experienced by these spiders allows one to make predictions concerning the likelihood that the spiders will experience thermal stress (i.e., unfavorable temperatures that might limit activity or impair performance). Data indicate that *M. asperatus* experiences high thermal stress (ambient temperature > PTR) more frequently than low thermal stress (ambient temperature < PTR), while *M. formosipes* experiences low thermal stress more frequently than high thermal stress. In neither case did average daily low temperature fall below spider CT_{min}. Thus, since ambient temperature did not fall to levels that would inhibit spider movement, *M. asperatus* and *M. formosipes* could alleviate low thermal stress by engaging in behaviors designed to elevate body temperature (e.g., basking in the sun). Normal hunting behavior (i.e., sitting near a flower's nectaries and/or anthers, provided the position was exposed to the sun) would serve to achieve this result.

High thermal stress appears to be more of a concern for these thomisids since ambient temperature typically falls within or above a spider's preferred range, and even when ambient temperature falls within the preferred range, floral-surface temperatures, and thus spider body temperatures, may be much higher, potentially approaching CT_{max}. Most diurnally-active spiders avoid high, stressful temperatures by some behavioral mechanism (Pulz 1987). Ground- or vegetation-dwelling cursorial (non-web-building) spiders can move to shaded areas under twigs, leaves, stones, etc., while web-building spiders may have a shaded retreat associated with the web. In both cases, these spiders still have access to prey when in shade and can continue to hunt. This option of behavioral thermoregulation (shuttling between sun and shade) may not be available to flower-dwelling thomisids if the spiders are to maintain access to prey. Because *M. asperatus* and *M. formosipes* do not strike at prey unless it approaches within a few millimeters of the spider's chelicerae (pers. obs.), spiders must remain near the anthers and/or nectaries in order to have access to prey. In the open field habitats where *M. asperatus* and *M. formosipes* are typically found, the upper surfaces of flowers, where the anthers and nectaries are located, are generally sun-exposed. Thus flower-dwelling thomisids may be faced with a trade-off between maintaining access to prey and avoiding high thermal stress.

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