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Crab spider hunting performance is temperature insensitive

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Abstract. 1. Laboratory and field experiments showed that the hunting performance of two flower-dwelling crab spiders, *Misumenops asperatus* and *Misumenoides formosipes*, was thermally insensitive over a broad range of temperatures normally experienced by these spiders.

2. In the laboratory, *HP*, a behavioural metric of spider hunting performance, was similar for spiders of a given species over an ≈ 30 °C temperature range.

3. Spiders in the field captured predominantly hymenopterans and dipterans, and field hunting performance, measured as the number of prey captured per spider per day, also proved to be unaffected by temperature.

4. These findings counter the general rule that physiological/ecological performance in terrestrial arthropods is temperature dependent.

5. Freedom from temperature constraints on the capacity of crab spiders to capture prey may be due to the use of venom and/or to muscle physiological adaptations for anaerobic metabolism.

6. Wide thermal performance breadth increases the spectrum of prey available to *M. asperatus* and *M. formosipes* by allowing spiders to hunt prey active during cooler periods of the day as well as those active during warmer periods.

7. Wide thermal performance breadth also benefits *M. asperatus* and *M. formosipes* due to adult phenology; both species experience a seasonal temperature shift during the adult phase.

Key words. Crab spiders, *Misumenoides*, *Misumenops*, predator–prey interactions, spider hunting performance, thermal ecology, Thomisidae.

Introduction

Temperature exerts pervasive effects at all levels of biological organisation (Hochachka & Somero, 1984), and its influence on an animal's physiological capacities ultimately affects ecological performance and even fitness (Huey & Kingsolver, 1989). Many activities in terrestrial ectotherms are temperature dependent (e.g. Huey, 1991; Casey, 1992a), and the body temperature of small ectotherms may be particularly sensitive to rapid temperature fluctuations because their large surface-to-volume ratios facilitate higher rates of heat exchange with the environment (May, 1985). Most terrestrial arthropods, with the notable exception of some endothermic insects such as bumblebees (reviewed in Heinrich, 1993), become increasingly sluggish and inactive as temperature declines (Shapley, 1920, 1924; Rissing, 1982; Joos, 1992). In contrast, spiders are known for their capacity to remain active at low temperature (Moulder & Reichle, 1972; Ford, 1978; Pulz, 1987; Schmalhofer, 1996), despite being strict ectotherms with body temperatures that typically approximate ambient temperature (Pulz, 1987). Some temperate-zone spiders even feed and reproduce in winter (Aitchison, 1984, 1987; Kirchner, 1987).

The relationship between spider hunting performance and temperature is of interest because spiders are important predators in many terrestrial systems (Turnbull, 1973; Riechert, 1974; Wise, 1993). Also, spider fecundity is linked strongly to foraging success (Fritz & Morse, 1985; Morse & Fritz, 1987; Vollrath, 1987; Morse & Stephens, 1996), indicating the ecological and evolutionary importance of hunting performance. Temperature affects spider behaviour in complex ways (Pulz, 1987). The few studies examining the impact of temperature on spider foraging behaviour have

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Table 1. Average ambient temperature during 10-day periods at the beginning and end of the adult stages of *M. asperatus* and *M. formosipes*. Data were taken from the weather station at the Hutcheson Memorial Forest Research Center, Somerset County, New Jersey, U.S.A., from 1993 to 1995. Values given are means (± 1 SD).

	Temperature (°C)			
Dates	Daily high	Daily low	08.00 hours	Daily average
Misumenops asperatus				
26 April – 5 May	21.5 (4.7)	6.1 (4.4)	11.0 (3.4)	12.9 (7.7)
1–10 June	22.9 (6.4)	13.4 (4.8)	18.3 (3.1)	18.2 (6.3)
Misumenoides formosipes				
15–24 August	28.8 (3.3)	15.1 (4.0)	18.9 (3.5)	20.9 (6.8)
20–29 September	21.9 (3.3)	9.1 (4.9)	12.2 (4.3)	14.4 (6.9)

focused on web-building spiders inhabiting desert environments (Riechert & Tracy, 1975; Lubin & Henschel, 1990; Henschel *et al*., 1992; Turner *et al*., 1993; but see Barghusen *et al*., 1997 for a temperate-environment exception). These studies have shown that temperature affects latency to attack (Lubin & Henschel, 1990; Henschel *et al*., 1992), duration of prey capture sequences (Lubin & Henschel, 1990; Henschel *et al*., 1992), web mass (Barghusen *et al*., 1997), and time allocation to foraging (Riechert & Tracy, 1975; Turner *et al*., 1993). None of these studies, however, assessed directly the effects of temperature on a spider's physical ability to subdue and kill prey. Also, temperature effects on hunting by cursorial (nonweb-building) spiders have not been addressed.

This study, which combines laboratory experiments and field observations, is the first to examine the direct effects of temperature on spider hunting performance and shows that two common North American species of cursorial spiders hunt equally well over a wide range of temperatures. The ability to capture prey, as opposed to attack speed, is used to quantify hunting performance because most spiders, including cursorial species, are sit-and-wait predators rather than active pursuers (Uetz, 1992).

Materials and methods

Study animals

Misumenops asperatus (Hentz) and *Misumenoides formosipes* (Walckenaer) are flower-dwelling members of the family Thomisidae (crab spiders). These spiders employ a sit-and-wait strategy to ambush pollinators and other flower-visiting arthropods and use their raptorial forelimbs, rather than a web, to restrain prey prior to envenomation. *Misumenops asperatus* and *M. formosipes* forage diurnally and nocturnally, but most predation events occur during the day because their primary prey, hymenopterans and dipterans, are diurnal (Schmalhofer, 1996). These spiders are distributed widely throughout North America (Gertsch, 1939). In central New Jersey, adults are seasonally separated: *M. asperatus* matures in early spring (late April to early May), and *M. formosipes* matures in mid-summer (mid to late August). Both species experience a seasonal shift in average daily temperature of ≈ 6 °C during the adult stage (Table 1).

Misumenops asperatus and *M. formosipes* are thermal conformers, and, in the field, spider body temperature approximates ambient temperature (Schmalhofer, 1996). Both species tolerate a wide range of temperatures, and maximum voluntarily tolerated temperatures (MVTs) are relatively high: *M. asperatus*, tolerated range = –1–45 °C, MVT = 36 °C; *M. formosipes*, tolerated range = 2–48 °C, MVT = 41 °C (Schmalhofer, 1999). Both species, however, prefer temperatures within the lower half of their tolerated range: *M. asperatus*, preferred range = 11–18 °C; *M. formosipes*, preferred range = 13–24 °C (Schmalhofer, 1999).

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 (Dodson & Beck, 1993; Foelix, 1996). Spiders were collected at seven sites in New Jersey. Experiments involving *M. asperatus* were conducted in May and June 1994 and 1995; experiments involving *M. formosipes* were conducted in August and September 1993 and 1994.

Experimental methods

Spider hunting performance in the laboratory. Crab spiders have a distinctive hunting posture: a spider sits motionless, gripping the substrate with its small third and fourth pairs of legs while the much longer and more robust raptorial forelimbs (first and second pairs of legs) are held outstretched and upraised. In the typical crab spider hunting posture, the raptorial forelimbs are held at an angle of ≈ 90° to the long axis of the body and 45° to the horizontal. Crab spiders occasionally hyperextend their raptorial forelimbs such that the limbs are directed posteriorly (an angle of ≈ 135° to the long axis of the body) rather than laterally. A predation opportunity occurs when prey approaches within the gape created by the spider's outstretched raptorial forelimbs. Prey must generally approach within ≈ 3 mm of a spider's chelicerae before *M. asperatus* or *M. formosipes* will strike (V. R. Schmalhofer, pers. obs.).

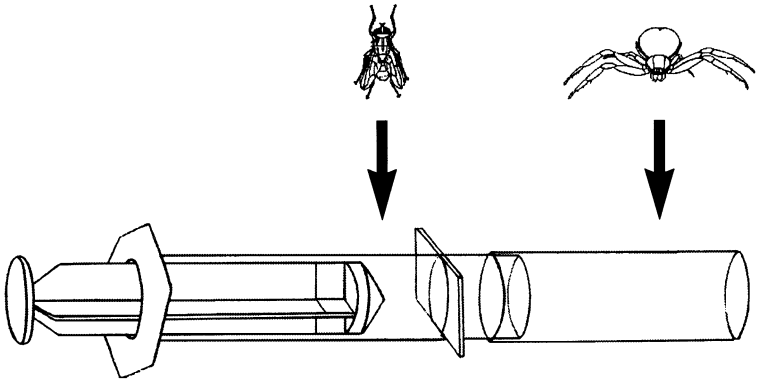

Fig. 1. The arena used in the laboratory experiments. Spider and fly are approximately life size, and the vial–syringe apparatus is approximately two-fifths scale. The spider is shown displaying the typical crab spider hunting posture. The actual space in which the animals interacted was $\approx 32\,cm^3$ (3 cm in diameter, 4.5 cm in length) and provided a surface area similar to that of some of the flowers used by the spiders. The arena was wide enough that spider hunting posture was not compromised; average maximal gape (the distance from the tip of the right forelimb to the tip of the left forelimb if the legs are held out perfectly straight and horizontal) in both species was less than 3 cm (*M. aspertaus* 2.3 cm, *M. formosipes* 2.7 cm), and spiders typically held their forelimbs slightly bent, rather than perfectly straight, so a maximal gape was seldom achieved. The arena also provided sufficient room for flies to take flight.

Musca domestica (L.), the common house fly, served as a representative prey type for these experiments. The temperature of a walk-in environmental chamber illuminated by fluorescent lights was initially set to 25 °C. Spiders and flies were brought in, the chamber temperature was reset to the desired test temperature, and the animals were allowed 60 min to equilibrate. The experimental arena consisted of a large plastic vial fitted over the end of a 60-cm^3 syringe, the tip of which had been removed and in which a slot had been cut to hold a removable partition (Fig. 1). A fly was placed in the syringe, and the partition was slipped into place. A spider was placed in the vial, the syringe and vial were connected, the partition was removed, and the fly was forced into the spider's end of the arena (i.e. it was pushed gently with the syringe plunger). Once a predator–prey pair was introduced into the arena, their interactions were monitored for 5 min or until the spider caught the fly. For each spider, the number of strikes, strike opportunities (defined as the fly entering the area delimited by the spider's raptorial forelimbs and approaching within 3 mm of the spider's chelicerae), whether the fly was captured, and the time required for the spider to capture the fly were recorded. If a fly did not approach within striking range (see strike opportunity) during the 5-min trial, the fly was removed from the arena, and another 5-min trial was begun with a new fly. Each spider was tested at only one temperature ($n = 22$–25 *M. asperatus* per temperature, $n = 30$–35 *M. formosipes* per temperature).

During the laboratory experiments, the vial–syringe apparatus was placed on a dark-brown wooden table. Thus, the visual contrast between the flies and their background was not as great as that occurring under natural conditions, where spiders would encounter prey against a brightly coloured floral background. Although crab spiders are considered visual hunters (Foelix, 1996), having eyes with image-resolving capabilities similar to those of insect compound eyes (Land, 1985), the low contrast between prey and background in the laboratory experiments should not have impaired spider hunting capabilities seriously. *Misumenops asperatus* and *M. formosipes* are successful nocturnal hunters (Schmalhofer, 1996), and their forelimbs are endowed with trichobothria (fine hairs sensistive to air currents and sound), which allow spiders to detect moving prey that is not visually apparent (Foelix, 1996).

Hunting performance (*HP*) in the laboratory was measured according to the equation:

$$HP = ab/c \qquad (1)$$

where a indicates whether or not a spider made a kill (yes = 1, no = –1), b is the number of strikes made by a spider, and c indicates the number of opportunities the spider had to strike at prey. Nonzero positive hunting performance scores indicated successful prey capture, while negative and zero hunting performance scores indicated failure to capture prey. A hunting performance score of 1 reflected perfect responsiveness: a spider struck at prey at every opportunity. Typically, a value of 1 also indicated perfect hunting efficiency: a spider captured the fly at the first opportunity (see Results). Hunting performance scores between 1 and –1 indicated that spiders ignored opportunities to strike at prey that came within range. Values greater than 1 or less than –1 indicated that spiders struck at prey before the prey came within range, potentially causing the prey to avoid the spiders.

The behavioural metric of hunting performance described by eqn 1, rather than time required to capture prey, was chosen as the main method of quantifying hunting performance because the behavioural metric measured both spider responsiveness (the proportion of prey capture opportunities utilised) and predatory effectiveness (whether prey was killed), while time required to capture prey reflected, in part, how long it took the flies to approach within striking range of the stationary spiders. Because hunting performance scores did not approximate a

normal distribution, nonparametric Kruskal–Wallis tests were used to determine whether spider performance varied with temperature. To provide a more complete picture of temperature effects on crab spider hunting performance, analyses of other performance measures (time required to capture prey and whether prey was captured) are presented. The potential effects of temperature on the individual parameters used to calculate the behavioural metric described by eqn 1 were also examined.

Misumenops asperatus was tested at 5 °C intervals from 10 to 40 °C, and *M. formosipes* was tested at 5 °C intervals from 15 to 40 °C. These temperature ranges were selected to correspond to the range of diurnal temperatures normally experienced by adult female spiders. The lower bound of the test range also approximated the lower bound of each species' preferred temperature range. The upper bound of the test range was set at 40 °C because, although ambient temperature seldom reaches 40 °C in central New Jersey, the body temperatures of spiders in sun-exposed positions on flowers can exceed ambient temperature by 15 °C or more under conditions of high radiant intensity and low wind speed (Schmalhofer, 1996) and may therefore approach 40 °C.

For 3 weeks prior to the initiation of the laboratory experiments, spiders were maintained at ambient field temperature on a diet of one house fly per week. This regimen equalised hunger states among individuals, maintained spider body mass at relatively constant levels (Anderson, 1970; V. R. Schmalhofer, pers. obs.), and prevented spider responses to experimentally induced temperature changes from being influenced by acclimation to an artificial temperature regime. This last consideration was of particular importance because the experiments were intended to evaluate the responses of field-active spiders.

House fly locomotor performance. Direct effects of temperature on the prey could result in indirect temperature effects on spider hunting performance. If flies spent less time moving at certain temperatures, and therefore came within striking range less frequently, spider performance could decline. Spider performance might also decline at temperatures at which flies moved more swiftly, assuming that speed of movement correlated with the likelihood of escaping a striking spider. Thus, two measures were used to quantify house fly performance over the experimental temperature range: the amount of time flies were active and walking speed. The amount of time active was measured using the protocol described previously, but with spiders omitted. The amount of time (s) a fly spent moving in the arena during a 5-min period was recorded ($n = 70$ flies, 10 flies per temperature). To measure temperature effects on the rate ($mm\,s^{-1}$) of fly movement, flies were placed singly in small Plexiglas® runs ($1 \times 1 \times 8$ cm) and videotaped for 10 min. The size of the runs permitted the flies to walk, but not to fly; the floor of each run was marked in 5-mm increments. Analysis of the videotape permitted measurement of discrete movement episodes and calculation of an average movement rate for each fly ($n = 70$ flies, 10 flies per temperature). Activity time and movement rate constituted independent data sets because different sets of flies were used to calculate each parameter. ANOVAs were used to determine whether fly performance varied with temperature. In order to satisfy ANOVA assumptions of normality, activity time data were square-root transformed, and movement rate data were log transformed. Differences in fly performance across the experimental temperature range were evaluated using a moderately conservative post-hoc test (Tukey compromise).

Spider hunting performance and prey availability in the field. To measure hunting performance in the field, marked female spiders were released onto flowers of plant species typically occupied by these spiders, and spider activity, prey capture, prey visitation, and ambient temperature were monitored. Potted plants were arranged randomly in a mown field at the Hutcheson Memorial Forest Research Center, New Jersey. Approximately 24 spiders, each with a unique two-digit number marked with red indelible ink on the abdominal dorsum, were released at a given time, and these spiders were monitored between 08.00 and 20.00 hours for 2 or 3 consecutive days. A Campbell Scientific 21X micrologger (Campbell Scientific, Inc., Logan, Utah) was used to record ambient temperature. The micrologger took measurements every 5 s and averaged them over 5-min intervals. Spider hunting performance was measured as the total number of prey captured per day (day = diurnal observation period) divided by the average number of spiders present during that time (some spiders emigrated from the study site). Linear regression was used to determine whether crab spider hunting performance in the field differed with ambient temperature. Because *M. asperatus* and *M. formosipes* generally occupied shaded microhabitats, and wind speeds during the field experiments were typically high enough to keep the body temperatures of sun-exposed spiders to within 3 °C of ambient temperature, spider body temperature closely approximated ambient temperature (Schmalhofer, 1996). Thus, ambient temperature was a reasonable surrogate for spider body temperature.

Linear regression was also used to examine changes in prey availability with changing temperature and to determine whether changing prey availability affected spider prey-capture success. Prey availability was measured as the number of prey visits per floral unit per hour, a floral unit being the area of an inflorescence used by a spider as a hunting arena. Depending on the plant species in question, a floral unit comprised an entire inflorescence (e.g. *Chrysanthemum leucanthemum*) or only a portion of an inflorescence (e.g. a panicle branch of *Solidago* spp.). Rates of floral-unit visitation permitted an estimation of the number of prey encounters experienced by spiders. Prey visitation data were log transformed.

Results

Spider hunting performance in the laboratory and field

Temperature did not affect the hunting performance of *M. asperatus* or *M. formosipes* as measured by the behavioural metric given in eqn 1 (Fig. 2), and temperature did not affect

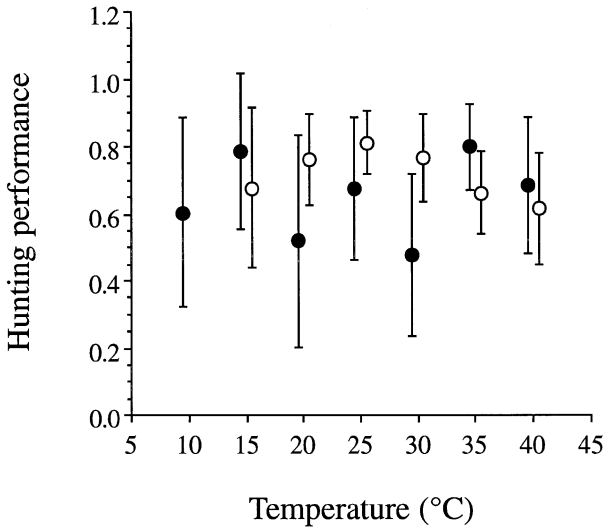

Fig. 2. Hunting performance in the laboratory of *M. asperatus* (●) and *M. formosipes* (○) across the experimental temperature range. Kruskal–Wallis tests indicated that temperature did not affect hunting performance of *M. asperatus* (H = 8.3, d.f. = 6, *P* = NS) or *M. formosipes* (H = 7.3, d.f. = 5, *P* = NS). Error bars = ± 2 SE.

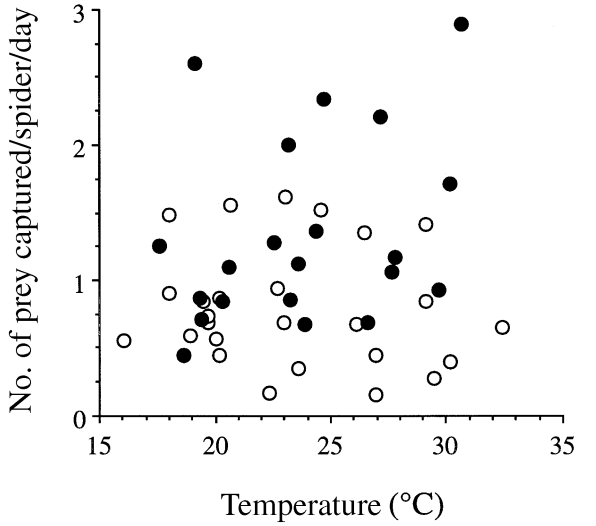

Fig. 3. Hunting performance in the field of *M. asperatus* (●) and *M. formosipes* (○). Linear regression indicated that temperature did not affect the number of prey captured per spider per day by either *M. asperatus* ($F = 2.1$, d.f. = 1,19, $r^2 = 9.9\%$, *P* = NS) or *M. formosipes* ($F = 0.0$, d.f. = 1,24, $r^2 = 0.0\%$, *P* = NS). Each data point represents the average of a diurnal observation period. Similarly, no relationships between prey capture success and ambient temperature were found when the data were separated and analysed according to taxa (e.g. number of Hymenoptera captured per spider per day, number of Diptera captured per spider per day, etc.).

any of the individual parameters (*a*, *b*, *c*) used to calculate hunting performance significantly. The range of hunting performance scores indicated that both spider species were generally successful in capturing prey and were typically perfectly responsive (struck at every opportunity) or under-responsive (ignored some opportunities) rather than over-responsive (struck without opportunity). In some cases, hunting performance scores of 1 resulted from spiders requiring more than one strike opportunity (two opportunities: *M. asperatus* = 12%, *M. formosipes* = 15%; three opportunities: *M. asperatus* = 3%, *M. formosipes* = 4%; percentages refer to the proportion of spiders with a hunting performance score of 1). Although no significant difference was found among the hunting performance scores of *M. formosipes* over the range of experimental temperatures, the pattern apparent in Fig. 2 suggested that differences might have become evident if hunting performance in this species had been tested at more extreme temperatures.

Time required to capture prey (Kruskal–Wallis: *M. asperatus*, H = 10.7, d.f. = 6, *P* = NS; *M. formosipes*, H = 6.9, d.f. = 5, *P* = NS) and the most basic measure of hunting success, whether or not spiders captured prey (Kruskal–Wallis: *M. asperatus*, H = 10.3, d.f. = 6, *P* = NS; *M. formosipes*, H = 6.0, d.f. = 5, *P* = NS), were also unaffected by temperature. In total, 77% of *M. asperatus* and 93% of *M. formosipes* captured flies. A similar proportion of the strikes made by spiders of each species resulted in a kill (*M. asperatus* = 82%, *M. formosipes* = 85%), suggesting that *M. asperatus* made fewer kills because spiders were striking less frequently rather than less effectively.

Predation events occurred very quickly. A successful strike took less than 2 s from initial movement of the spider's raptorial forelimbs towards the fly to full grappling and biting. Spiders generally initiated a strike if a fly approached within 3 mm of the spider's chelicerae; however, some spiders waited until the fly was literally standing on the spider's carapace. There was no noticeable decrease in strike speed (to the human eye) with decreasing temperature. After envenomation, vigorous struggling of the prey typically ceased within 30 s, and flies were completely quiescent (presumably dead) within 2 min. Prey struggles lasted longer on the rare occasions when spiders bit prey on the abdomen; normally the spiders delivered a bite to the base of the prey's head. Spiders held the flies elevated well above the substrate, effectively preventing the flies from gaining any leverage to escape through contact with the ground. Prey were not wrapped in silk at any time. The lack of a temperature effect on any measure of spider hunting performance was particularly striking considering the strong effect of temperature on a fly's capacity to escape a spider, as evidenced by fly locomotory rate (see below).

Field data supported the laboratory results. *Misumenops asperatus* and *M. formosipes* captured primarily hymenopterans (*M. asperatus* 43%, *M. formosipes* 61%) and dipterans (*M. asperatus* 36%, *M. formosipes* 39%); the remaining prey captured by *M. asperatus* (21%) consisted of hemipterans, lepidopterans, and other spiders. No patterns were evident in the timing of prey capture or temperature at which prey capture events occurred for either *M. asperatus* or *M. formosipes*; both spider species captured prey throughout the course of a day and

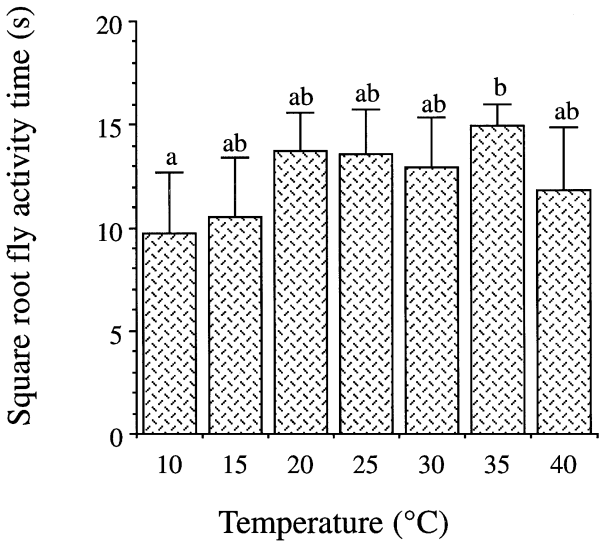

Fig. 4. Effect of temperature on the amount of time flies remained active in the experimental arena. Temperature had a slight effect on the amount of time flies spent moving (ANOVA, $F = 2.4$, d.f. = 6, $P = 0.05$). Values with different letters are significantly different at $\alpha = 0.05$ according to a Tukey compromise post-hoc test. Error bars = + 2 SE. Data were square-root transformed.

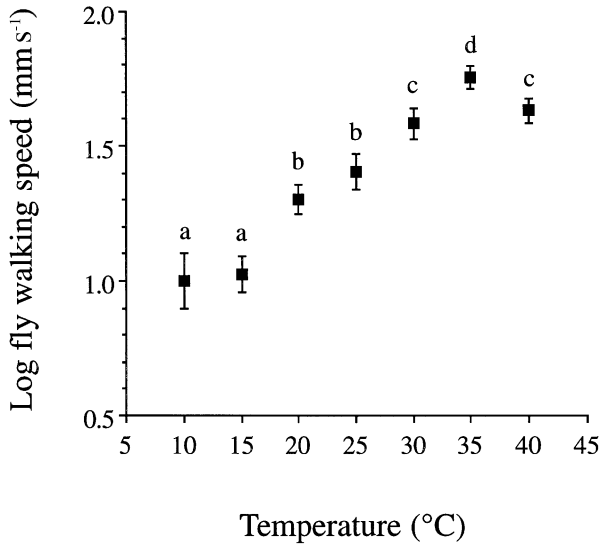

Fig. 5. Effect of temperature on house fly walking speed (mm s^{-1}). Fly walking speed was affected strongly and positively by temperature (ANOVA: $F = 81.9$, d.f. = 6, $P \leq 0.001$). Values with different letters are significantly different at $\alpha = 0.05$ according to a Tukey compromise *post-hoc* test. Error bars = ± 2 SE. Data were log transformed.

at ambient temperatures approaching or exceeding 35 °C and approaching or falling below 15 °C. Overall field hunting performance, measured as the average number of prey captured per spider per day, did not vary with ambient temperature (Fig. 3).

House fly locomotory performance in the laboratory and prey availability in the field

Temperature had a slight effect on the activity time of house flies (Fig. 4). Flies generally spent equivalent amounts of time moving at all temperatures; however, flies were less active at 10 °C than at 35 °C. In contrast, temperature had a strong effect on fly locomotory rate. Fly walking speed increased sharply with increasing temperature, peaking at 35 °C (Fig. 5).

In the field, prey availability increased significantly with increasing temperature (Fig. 6). Neither spider species, however, showed a significant functional response to increasing prey availability (linear regression, number of prey captured per spider per day vs. log-transformed number of prey visits per floral unit per hour: *M. asperatus*, $F = 1.2$, d.f. = 1,19, $r^2 = 5.8\%$, P = NS; *M. formosipes*, $F = 0.5$, d.f. = 1,24, $r^2 = 2.0\%$, P = NS).

Discussion

Clearly, the ability of *M. asperatus* and *M. formosipes* to capture prey was not affected by temperature. This finding contrasts strikingly with the positive temperature-dependence of many performance parameters, such as speed of locomotion, displayed by insects (e.g. Shapley, 1920, 1924; Rissing, 1982; May, 1985; Joos, 1992; Heinrich, 1993; house flies in the present study) and begs the question: what is the physiological basis underlying the wide thermal performance breadth seen in *M. asperatus* and *M. formosipes*? Two mechanisms may be involved: muscle physiological adaptations for burst activity and the use of venom.

Spiders in general are incapable of sustained, intense, aerobic activity because their leg muscles possess few mitochondria (Linzen & Gallowitz, 1975) and typically have a limited haemolymph supply (Paul *et al*., 1991). Thus, spiders rely predominantly on anaerobic glycolysis and phosphate hydrolysis to fuel vigorous activities (Prestwich, 1983, 1988). Animals working at elevated rates use phosphate hydrolysis to fuel very brief activities (≤ 10 s), after which anaerobic glycolysis fuels intense activity (Hochachka & Somero, 1984). For crab spiders, predation events occur as brief, intense struggles. The initial burst of activity, in which a crab spider strikes at, grapples with, and envenomates its prey, requires only a few seconds and is probably fuelled by phosphate hydrolysis. Anaerobic glycolysis probably fuels the lengthier, but still brief (a few minutes), phase that follows, in which the spider waits for its prey to cease struggling before commencing feeding.

In lizards, anaerobic metabolism has been found to be relatively temperature insensitive (Bennett, 1983). If the same relationship holds true for spiders, it might explain the absence of temperature effects on spider hunting performance observed in this study. New evidence, however, suggests that lactic acid

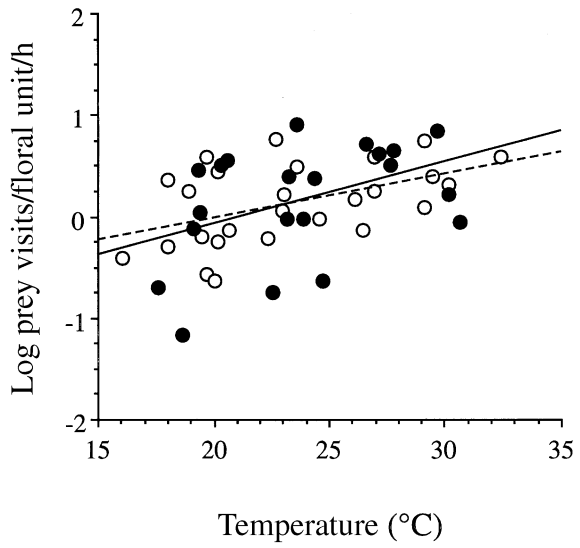

Fig. 6. Effect of temperature on prey visitation rates in the field. Linear regression showed a positive relationship between ambient temperature and prey visitation during both the *M. asperatus* (●) field experiments ($F = 4.4$, d.f. = 1,19, $r^2 = 18.8\%$, $P \leqslant 0.05$) and the *M. formosipes* (○) field experiments ($F = 7.81$, d.f. = 1,24, $r^2 = 24.6\%$, $P \leqslant 0.01$). Each data point represents the average of a diurnal observation period. The solid line represents the regression equation for the *M. asperatus* experiments ($y = -1.31 + 0.06x$); the dashed line represents the regression equation for the *M. formosipes* experiments ($y = -0.90 + 0.04x$).

metabolism (a measure of anaerobiosis) in spiders is thermally dependent (K. N. Prestwich, pers. comm.). It should be reiterated that a behavioural metric of spider hunting performance was measured in the present study. A physiological performance parameter, such as gripping strength or strike speed, might well differ with temperature. Even if this were the case, however, the end result of crab spider–prey interactions (the capture of prey) is obviously not affected.

Use of venom to immobilise prey may play a role in the thermal insensitivity of crab spider hunting performance. Crab spider venom is described as extremely powerful and fast-acting (Gertsch, 1939; Riechert & Harp, 1987; Foelix, 1996). Simply attaining sufficient proximity to potential prey to bite effectively may be enough to ensure a kill. Thus, temperature effects on spider locomotory speed become less important because these spiders are sit-and-wait ambush predators, not stalkers. How quickly prey succumbs depends on the site of envenomation (see Results). Because crab spiders typically bite prey at the base of the head, injecting venom directly into the prey's cerebral ganglia (Pollard, 1993), the fast action of crab spider venom may be a consequence of the spiders targeting a sensitive area of their prey. Leg muscle physiology is still important, however, because a cursorial spider's ability to maintain a hold on prey is critical to prey capture success (Riechert & Luczak, 1982). Even if temperature affects gripping strength, anaerobically adapted leg musculature benefits spiders in terms of mechanical force production. In muscle packing, a trade-off exists between force-producing elements (myofibrils) and energy-producing elements (mitochondria) (Pennycuik & Rezende, 1984; Casey, 1992b). Spider leg muscles comprise less than 0.1% by volume mitochondria (Linzen & Gallowitz, 1975), while mitochondria occupy up to 40% of the volume of insect wing muscles (Sacktor, 1974). Per unit muscle volume, spider leg muscles should be stronger than insect wing muscles, and crab spiders would be expected to have an advantage over their insect prey during grappling.

The capacity to hunt equally well over a wide range of temperatures expands the spectrum of prey available to *M. asperatus* and *M. formosipes* by permitting spiders to capture prey taxa active during hotter portions of the day, as well as taxa active during cooler periods, and those active at night. The ability to capture prey at cooler temperatures is of particular importance because many of the prey taxa available to *M. asperatus* and *M. formosipes* can fly at low temperatures. Large hymenopterans, such as honeybees and bumblebees, are important in the diet of *M. formosipes* (Schmalhofer, 1996). These bees require high thoracic temperatures for flight (≈ 30–35 °C), but are capable of flight at low environmental temperatures because they are endothermic and can generate heat by shivering their wing muscles (reviewed in Heinrich, 1993). Dipterans, used extensively by both spider species, are also well known for their ability to fly at both low and high temperatures (reviewed in Heinrich, 1993).

In addition to daily temperature fluctuations, adult female *M. asperatus* and *M. formosipes* experience seasonal shifts in average temperature (see Table 1). Adult foraging success influences female reproductive output strongly (Fritz & Morse, 1985; Morse & Fritz, 1987; Morse & Stephens, 1996) because 60–85% of a female crab spider's mass is acquired during the adult stage (Morse & Fritz, 1987; Beck & Connor, 1992). Thermal insensitivity of hunting performance permits these crab spiders to cope with a seasonal rise (*M. asperatus*) or decline (*M. formosipes*) in average temperature during the period most critical to reproductive success.

Temperature affects the rate of locomotion of the insect prey of *M. asperatus* and *M. formosipes* as the insects forage on flower-heads. This study showed the strong effect of temperature on the walking speed of a representative dipteran, and hymenopterans probably show similar effects of temperature on walking speed. Even endothermic hymenopterans may be affected by ambient temperature during foraging; when the energetic gains from nectar do not offset the energetic expenditure of maintaining endothermy, endothermy is abandoned and body temperature falls to ambient levels (Heinrich & Heinrich, 1983a,b). Many of the plants occupied by crab spiders are composites (Asteraceae), which have a low energetic reward per flower (Heinrich, 1983). Because of this, crab spiders might be expected to have an advantage in the field at low ambient temperatures when the ability of prey to escape, as evidenced by walking speed, declines. Such an advantage, however, was not observed. Further study is needed to address this issue.

The general perception that temperature constrains the physiological capacities, and therefore strongly affects habitat selection, behaviour, activity patterns, and other aspects of

terrestrial ectotherm performance (Huey & Kingsolver, 1989; Huey, 1991) has been well documented for insects (Shapley, 1920, 1924; Rissing, 1982; May, 1985; Joos, 1992; Heinrich, 1993). It does not, however, apply to two species of crab spider for at least one ecologically important behaviour, hunting performance. Thermal insensitivity of hunting performance has probably been a significant contributing factor in the development of the broad seasonal and diel activity patterns displayed by temperate-zone crab spiders. Given the cosmopolitan distribution of spiders and variety of diel activity patterns (strictly nocturnal, strictly diurnal, or active diurnally and nocturnally) displayed (Turnbull, 1973; Foelix, 1996), it is not unreasonable to suggest that thermal insensitivity of hunting performance may be a common feature of spider ecology. In conjunction with other factors, such as their ability to withstand long periods of starvation (Anderson, 1974; Wise, 1993) and use of venom and silk, the release of spider hunting performance from the limitations typically imposed on ectotherms by temperature may have played a significant role in the expansion of spiders into their current status as a ubiquitous guild of terrestrial predators. Further studies of the relationship between temperature and hunting performance in other spider species are clearly warranted.

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