

FITNESS BENEFITS OF RETREAT-SITE SELECTION: SPIDERS, ROCKS, AND THERMAL CUES

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Abstract. Although animals are widely assumed to select habitats in ways that enhance organismal fitness, there are few empirical data to demonstrate this link. We studied flat rock spiders (*Hemicloea major*, Gnaphosidae) from eastern Australia, where these highly modified (dorsoventrally flattened) spiders live under loose surface rocks on sandstone outcrops. Field surveys showed that the rocks used as diurnal retreat sites by spiders were relatively thin with low canopy cover and a rocky substrate and therefore were likely to experience high temperatures and large thermal fluctuations. Laboratory trials suggest that this nonrandom rock use is a direct response to thermal cues; juvenile spiders selected warmer over cooler retreat sites. To investigate consequences of habitat selection on fitness-related traits, we maintained cohorts of juvenile spiders at cycling-temperature regimes corresponding to those measured in the field under rocks that were fully, partially, or never exposed to direct sunlight (diel thermal ranges of 16.2°–37.8°C, 15.5°–31.2°C, and 15.2°–24.3°C). Survival rates were high for all groups over the eight-week study, but hotter conditions accelerated growth and development. Our data thus confirm that thermal cues are used in retreat-site selection and that selection of warmer retreat sites will confer fitness benefits to flat rock spiders.

Key words: Australia; bush-rock; development; Gnaphosidae; growth; habitat use; *Hemicloea major*; rock outcrop; sandstone; substrate; temperature.

INTRODUCTION

The selection of habitat by mobile organisms can have major consequences for an animal's biology, from defining the extent of interactions with the environment and other biota (Sih et al. 1992) to conferring significant fitness advantages (Jaenike and Holt 1991). For example, the specific habitat selected will influence the range of abiotic conditions (thermal, hydric, structural, etc.) and biotic interactions (with conspecifics, competitors, predators, prey, etc.) that the organism encounters, either or both of which may form the basis for retreat-site selection (Martin 2001). Despite abundant data describing patterns of habitat use, the benefits of nonrandom use generally remain speculative (Kirsch 1996, Martin 2001). Few studies have considered in detail the mechanisms responsible for habitat selection, and fewer still have investigated the fitness consequences of these behaviors.

Because many attributes of habitats are highly correlated, the empirical demonstration that an animal is disproportionately found under certain conditions does not demonstrate any causal mechanisms for habitat selection (Manly et al. 1993). Instead, the organism's "decision" about habitat use may be driven by its response to some other unmeasured variable that happens to correlate with the one that has been quantified. To

determine whether or not the animal actually uses the quantified cue to discriminate among habitats, we need to conduct manipulative experiments, providing the animal with alternatives that differ only in the attribute of interest. Even more problematic is the question of adaptive advantage; that is, in what ways (if any) does the animal benefit from selecting this habitat attribute?

Spiders are a diverse and well-studied group of terrestrial predators, although generalizations about habitat use by spiders are complicated by their wide diversity in foraging strategies (Wise 1993). Many studies on habitat use by spiders have focused on web-building species, consistently identifying habitat complexity and prey availability as major determinants of web-site selection (Halaj et al. 1998, McNett and Rypstra 2000). Habitat complexity and prey abundance also influence habitat use by cursorial species (e.g., the wolf spider *Schizocosa*; Wagner and Wise 1996) with additional complications introduced by density-dependent effects of cannibalism and territoriality (Moya-Laraño et al. 2002). Direct links between foraging (prey availability and consumption) and measures of reproductive success (e.g., egg production) also have been shown for a number of spider species (Vollrath 1987, Wise 1993).

Thermal conditions are known to influence habitat use by spiders, primarily through the influence of prey availability on the positioning of webs (Riechert and Tracy 1975, Henschel et al. 1992), although effects of temperature on hunting success are variable and seemingly system-specific (Riechert and Tracy 1975,

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Schmalhofer and Casey 1999). Temperature affects many life history traits of spiders, including rate of development, survival, number of moults to maturity, adult size, longevity, and reproduction. Optimum temperature ranges and the way in which temperature affects these traits are highly variable among species (Li and Jackson 1996). Laboratory studies have shown that higher temperatures within a defined range enhance growth and development for some spider species, directly affecting fitness (Vollrath 1987, Li and Jackson 1996).

Questions about habitat use can be asked in many systems, but some systems are more amenable to study than others. One that facilitates research involves organisms that spend much of their time sequestered within retreat sites. We studied a cursorial, dorsoventrally flattened spider that lives under loose surface rocks. Many attributes of such retreat sites might be important in habitat selection. Thermal regimes are critical determinants of habitat use by reptiles in such habitats (Huey et al. 1989, Schlesinger and Shine 1994, Webb and Shine 1998a), and it seems likely that thermal cues will play a role in habitat selection for any ectotherms specialized for life under rocks, including spiders (Huey 1991, Goldsbrough et al. 2003).

In this study we integrate field and laboratory investigations to examine habitat use by *Hemicloea major*, with the aim of identifying both the proximate (causal) and ultimate (fitness) mechanisms responsible for nonrandom habitat. First, we compared rocks used by spiders in the field to nearby rocks that were not used, to see if they differed in a variety of rock attributes, including those that would influence thermal regimes. Second, because so many other factors correlate with thermal cues in the field, we kept spiders in the laboratory and offered them a choice of retreat sites differing only in thermal properties to test whether temperature per se was a cue for habitat selection. Last, we investigated consequences of alternative thermal regimes (simulating sun-exposed vs. shaded rocks) for the survival, growth, and development of spiders, to see if selection of warmer rocks might enhance organismal fitness. Such linkages between habitat selection and fitness are frequently postulated but have rarely been demonstrated.

MATERIALS AND METHODS

Study species

Hemicloea major (the “flat rock” or “major pancake” spider) belongs to the “flattened sac” tribe of the Gnaphosidae (Brunet 1996, Main 2000). These large (adult female body length 2.0–2.5 cm, adult male body length 1.5 cm) spiders are nocturnal, open-range hunters, with a highly flattened body and laterigrade legs (i.e., all legs fanned out to the side, tarsi facing forward; Main 1976, Brunet 1996). They are usually found under loose rocks or in crevices on sandstone

outcrops in New South Wales and southern Queensland and granite outcrops in southwestern Australia (Child 1977, Brunet 1996, Main 2000). The females attach opaque, white to grey disc-shaped egg sacs to rock substrates (Child 1977, Brunet 1996).

Use of rocks in the field

We looked under all rocks small enough to turn (length < 0.6 m) in a 200 × 100 m area of sandstone outcrop in Muogamarra Nature Reserve, New South Wales, Australia (33°33' S, 151°11' E) on 10 June 1998 and located 23 rocks occupied by spiders (“spider rocks”). We examined rock selection at two spatial scales.

Microhabitat.—We randomly selected one nearby rock for each of the spider rocks by numbering the six nearest rocks >7 cm in length within a 1.5 m radius of each spider rock (excluding any other spider rocks) and rolling a die. For each rock we recorded length (longest axis), width (longest axis perpendicular to length), and thickness (longest axis perpendicular to plane defined by length and width, all ±5 mm); percentage of the substrate composed of rock, sand, or soil; mean depth of substrate (from series of probes exploring entire area under rock); maximum and minimum heights to which the rock was embedded; percentage of canopy cover directly over the rock; percentage of cover of the rock by other materials that would block direct sunlight (“noncanopy cover,” e.g., soil, leaf litter, fallen timber, other rocks); exposure to sunlight (classified as: shaded, unshaded, or semi-shaded); and distance to the nearest rock with length >7 cm. The level of exposure to sunlight provides an indication of the period of sun and shade on a rock throughout the day due to aspect and the nature of surrounding vegetation.

Macrohabitat.—We sampled 28 rocks selected at random over the entire outcrop, without reference to the locations of spiders, to quantify habitat availability at a coarser spatial scale.

We conducted discriminant function analysis (DFA; Blackith and Reyment 1971) using SYSTAT (version 7.0.1 for Windows; SPSS, Chicago, Illinois, USA) to compare spider rocks to nearby random rocks and to compare the latter group to random rocks on the entire outcrop. Rock types were compared using squared Mahalanobis distances between group centroids, aided by graphical representation of the first canonical variable obtained from the DFA. Step-wise DFAs were used to identify the smallest subset of rock characteristics that would discriminate between rock types as successfully as the full set of rock characteristics (i.e., improving or maintaining the misclassification error rates).

Rock selection in laboratory trials

Study animals and their maintenance.—Fourteen juvenile flat rock spiders were used, all from a single egg sac deposited in the laboratory by a female from Ku-

ring-gai Chase National Park, New South Wales, Australia (33°42' S, 151°14' E). The egg sac was housed with the adult female in a room at 20° ± 1°C (mean ± 1 SE), with light and heat (gradient of 20°–37°C within each cage) between 0600 and 1800 hours. After juveniles emerged from the egg sac they were kept at ambient room temperature and housed individually in small plastic vials (11 cm high, 5 cm diameter) covered with muslin. Shelter was provided by strips of paper, two lying flat (1.5 × 1.5 cm) and two against the side of the vial (1.5 × 5 cm). Once per week, the spiders were fed first- and second-instar field crickets (*Teleogryllus commodus*) ad libitum (10–15 crickets/vial) and given water on a saturated ball of cotton wool. A dry dog food pellet was placed in each vial to provide food for the crickets. At the time of the experiment, the spiders were all in their first instar (i.e., although these spiders may moult while in the egg sac, we defined a first-instar spider as one that had not moulted since emerging from the egg sac).

Experimental procedure.—We conducted the experiment in eight open-topped plastic tubs (60 × 37 × 21 cm) in a room at 20° ± 1°C. Crevices for use as retreat sites were constructed at both ends of each tub by placing single terra-cotta tiles directly onto the floor of the tub. Heat was provided by a lamp fitted with a blue 40-W bulb positioned under one end of each tub. Black paper and opaque PVC tape prevented light from coming through the tub floor. One hour before dusk, we switched on the heat lamps, heating the crevice at one end of each tub to 37°C. The other crevice remained at room temperature. These temperatures are within the range of those recorded for crevices under 4 cm thick sandstone rocks in full sun and full shade during spring in the Sydney area (Webb and Shine 1998b). Treatments were assigned to tiles at different ends of the tubs in a preset fixed order. Each spider was used in only one experimental trial.

Dusk was simulated between 1800 and 1830 hours using three overhead 60-W bulbs, set to switch off sequentially after the fixed ceiling lights. Just before dusk, an inverted plastic vial was placed over spiders to temporarily restrict them to the center of the tub, preventing them from haphazardly selecting a retreat site whilst the room was still light (see Downes and Shine 1998). A clear perspex (plexiglass) lid was placed over the tub and sealed around the edges using a strip of urethane foam tape. We lifted the plastic vials off the spiders using attached lengths of cotton within 15 min of the onset of darkness, fixing them in a suspended position overnight such that they were unavailable as habitat for the spiders. The heat lamps were switched off at 2030 hours (we extended the period of heat beyond dusk to mimic heat retention in rocks). Dawn was simulated the following day (between 0630 and 0700 hours, reversing the procedure for dusk) to ensure the spiders could select diurnal retreat sites under conditions similar to natural light conditions (see

Kavanau 1962, 1969, Schlesinger and Shine 1994). The final retreat site for each spider was recorded soon after dawn.

Following each trial, the tiles were discarded and the tubs were scrubbed in hot water and allowed to air-dry to ensure that no chemical residues confounded later experiments. We used a chi-square goodness-of-fit test to evaluate the hypothesis that equal numbers of spiders selected heated and unheated retreat sites.

Thermal effects on growth and development

Maintenance of juveniles.—Spiders from two cohorts were used in the experiment. Cohort A emerged from an egg sac collected from Ku-ring-gai Chase National Park (33°37' S, 151°15' E) and cohort B emerged from an egg sac deposited in the laboratory by a female collected from Olney State Forest, New South Wales, Australia (33°7' S, 151°14' E). Prior to hatching, the egg sacs (with adult female, in the case of cohort B) were kept at 20°C, with light and heat (gradient of 20°–37°C within each cage) between 0600 and 1800 hours. The juveniles were housed in vials as in the previous experiment. At the beginning of the experiment the spiders in cohort A were three months old and in their first or second instar, and the spiders in cohort B were two weeks old and all in their first instar.

Experimental procedure.—The spiders were reared in three programmable cycling-temperature incubators (Clayson IM 550R, 45 × 45 × 45 cm internal dimensions; Clayson, Narangba, Queensland, Australia) for eight weeks. Each incubator simulated the thermal regime of a rock crevice in spring with one of three levels of shade: unshaded (hot), semi-shaded (warm), or shaded (cold). Details of the temperature regimes and allocation of spiders to treatments are given in Table 1. The temperature treatments closely mimicked thermal regimes experienced by the spiders in the field (mean thickness of spider rocks was 3.48 cm; temperature regimes based on data recorded by Webb and Shine [1998b] for 4 cm thick sandstone rocks in spring). Fluctuating temperature regimes that simulate conditions in the natural environment were used, as the magnitude of thermal variance can influence spider development and reproduction, even at the same mean temperature (Li and Jackson 1996). Light was provided between 0600 and 1800 hours (to simulate day length in spring) using a pearl 40-W bulb. To provide humidity for the spiders, open containers of water were placed in the bottom of each incubator (surface area of water = 1288 cm² per incubator). Thermocouples (Hobo XT temperature loggers; Onset Computer, Pocasset, Massachusetts, USA) and relative humidity loggers (Hobo RH relative humidity loggers; Onset Computer) were placed in the incubators (in vials set up as for the spiders) and set to record temperature and humidity at ten-minute intervals. Due to incubator failure, temperature in the hot treatment dropped below 5°C for 3 hours during the night at the beginning of the eighth week

TABLE 1. Thermal regimes of the three treatments in the eight-week laboratory experiment conducted at the University of Sydney, Australia, investigating thermal effects on growth and development, and allocation of spiders from two cohorts to the treatments.

Treatment	Rock type simulated	Temperature range (°C)	Absolute temperature extremes (°C)	Mean temperature (°C)	Relative humidity range (%)	Sample size (first instar, second instar)	
						Cohort A	Cohort B
Hot	unshaded	16.2–37.8	15.1, 42.1	23.0	53.8–91.3	15 (9, 6)	18 (18, 0)
Warm	semi-shaded	15.5–31.2	15.3, 32.4	20.4	59.4–92.3	0	18 (18, 0)
Cold	shaded	15.2–24.3	14.6, 25.9	18.0	77.0–98.5	16 (10, 6)	18 (18, 0)

Notes: Numbers in parentheses indicate the numbers of first- and second-instar spiders from each cohort allocated to each treatment. One spider died during the experiment (cohort B, hot), and four escaped (one from cohort A, hot; two from cohort B, hot; one from cohort B, cold). Temperature and relative humidity ranges reported are the mean daily maxima and minima recorded during the experiment. Temperature and humidity data recorded in the hot treatment during the period of incubator failure (1–2 September 1998) were not used in the calculation of statistics given here.

of the experiment. The appropriate temperature regime was restored within 18 hours of failure.

Every seven days, we recorded the incidence of moulting during the previous week (signified by the presence of a shed integument; these spiders do not eat their own moults). The cotton wool was remoistened and any crickets that had died or been eaten or that had developed beyond the second instar were replaced to ensure that food was never limiting (Li and Jackson 1996) and that similar numbers of live crickets were available to the spiders in each treatment.

We weighed each spider to ± 0.1 mg one week prior to the start of the experiment and at the end of the experiment. Growth was calculated as the change in mass. As a measure of growth at the time of the first moult, we measured the length of the second femur (left side, to ± 0.0125 mm) from the moult shed between the first and second instars for cohort B, using an ocular micrometer in a binocular microscope.

We compared final mass (transformed to the natural logarithm; Sokal and Rohlf [1995]) among the treatments (separately for the two cohorts) using one-factor analysis of covariance (ANCOVA), with final mass as the dependent variable and initial mass (also ln-transformed) as the covariate (Raubenheimer and Simpson 1992). Femur lengths were ln-transformed and compared using one-factor ANOVA. Prior to using ANOVA and ANCOVA in the above analyses, we used Cochran's test to confirm that the assumption of homogeneity of variances was satisfied, and we balanced sample sizes by randomly removing values. Where necessary, pairwise comparisons were made using Student-Newman-Keuls tests. A Kruskal-Wallis one-way analysis of variance by ranks with a correction for tied scores (Siegel 1956) was used to test for among-treatment differences in the degree of development (relative numbers of spiders in each instar) after eight weeks. A significance level of 0.05 was used in all tests.

RESULTS

Use of rocks in the field

Spider rocks vs. nearby random rocks.—Discriminant function analysis showed that spider rocks and

nearby random rocks could be distinguished by the 10 rock characteristics with a success rate of 84% (Mahalanobis $D^2 = 1.18$, $F_{9,35} = 4.57$, $P = 0.0005$). With only six of the 10 variables, the rocks could be distinguished with a success rate of 87% (Mahalanobis $D^2 = 1.13$, $F_{6,39} = 7.31$, $P < 0.0001$). Raw and standardized coefficients revealed that, on average, rocks used by spiders had a higher percentage of rock substrate, over double the canopy cover, were twice as thick, and had double the shelter area of nearby random rocks, and they were relatively far from other rocks. Noncanopy cover was 0% for all of the spider rocks and nearby random rocks.

Random rocks near spider rocks vs. random rocks on the entire outcrop.—At a coarser spatial scale, the two classes of rocks were distinguished by DFA with a success rate of 85% using all 10 rock characteristics (Mahalanobis $D^2 = 1.04$, $F_{10,37} = 3.85$, $P = 0.0012$). With seven of the 10 rock characteristics, the success rate of 85% for distinguishing between the two types of random rocks was maintained (Mahalanobis $D^2 = 1.02$, $F_{7,40} = 5.84$, $P = 0.0001$). Randomly selected rocks that were adjacent to spider rocks were less deeply embedded in the soil substrate (mean maximum and minimum depths embedded were < 1 mm), had a higher percentage of rock substrate (by a factor of three), were less exposed to direct sunlight, had a lower percentage of canopy and noncanopy cover, and were half as thick as rocks selected at random on the entire outcrop.

Rock selection in laboratory trials

Of 14 spiders tested, 12 selected the heated retreat site and two selected the unheated retreat site ($\chi^2 = 11.84$, 1 df, $P < 0.001$).

Thermal effects on growth and development

Survival.—Survival was high in all treatments; only one spider died. Four other spiders escaped during monitoring.

Growth.—Initial masses were similar in the hot and cold treatments for cohort A (ANOVA on balanced data [$n = 14$], ln-transformed, $F_{1,26} = 1.40$, $P = 0.25$) and among the three treatments for cohort B (ANOVA on

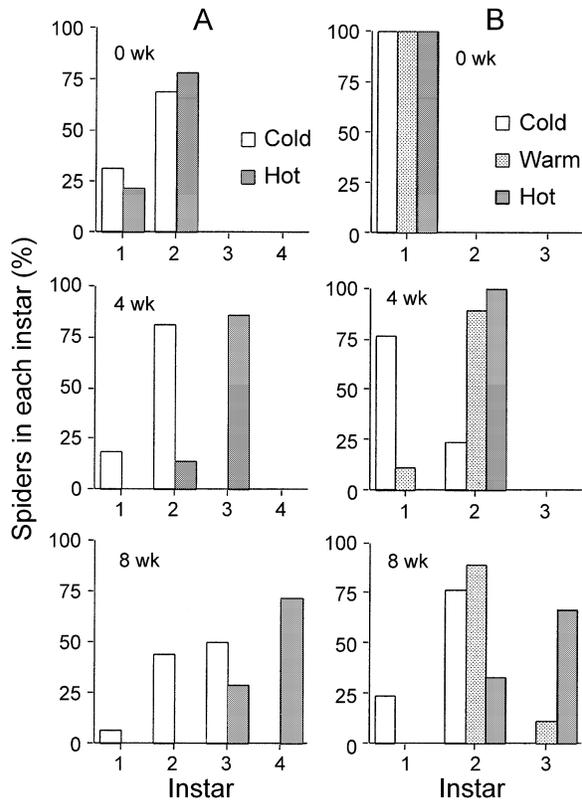


FIG. 1. (A) Number of spiders (as a percentage of the total number in each treatment) in each instar at 0, 4, and 8 weeks for cohort A spiders in the hot ($n = 14$) and cold ($n = 16$) treatments. (B) Number of spiders (as a percentage of the total number in each treatment) in each instar at 0, 4, and 8 weeks for cohort B spiders in the hot ($n = 15$), warm ($n = 18$), and cold ($n = 17$) treatments.

balanced data [$n = 15$], ln-transformed, $F_{2,42} = 0.01$, $P = 0.99$). For both cohorts, the slopes relating initial mass to final mass were homogeneous among treatments (cohort A, ANCOVA, $F_{1,24} < 0.001$, $P = 0.99$; cohort B, ANCOVA, $F_{2,39} = 1.40$, $P = 0.26$). Mean final mass was greater for spiders in the hot (10.5 ± 0.7 mg) treatment than in the cold (4.4 ± 0.3 mg) treatment for cohort A (ANCOVA on balanced data [$n = 14$], ln-transformed, $F_{1,25} = 49.45$, $P < 0.001$). For cohort B, final mass differed among the treatments (ANCOVA on balanced data [$n = 15$], ln-transformed, $F_{2,41} = 19.69$, $P < 0.001$). Mean final mass was greatest in the hot treatment (4.8 ± 0.5 mg), intermediate in the warm treatment (3.7 ± 0.2 mg), and lowest in the cold treatment (2.4 ± 0.2 mg) (SNK, $P < 0.05$ for all).

The mean lengths of femurs measured from the first moult of cohort B spiders did not differ among treatments (hot, 1.054 ± 0.024 mm; warm, 1.088 ± 0.024 mm; cold, 1.054 ± 0.021 mm [means ± 1 SE]; ANOVA on balanced data [$n = 14$], ln-transformed, $F_{2,39} = 0.67$, $P = 0.52$).

Development.—Spiders developed more rapidly under hotter conditions (Fig. 1); for both cohorts, stage

of development after eight weeks varied significantly with treatment (cohort A, Kruskal-Wallis, $H = 17.95$, $P < 0.001$; cohort B, Kruskal-Wallis, $H = 22.31$, $P < 0.001$).

DISCUSSION

Although intuition and optimality theory suggest that animals should select habitats that enhance their fitness (e.g., Bell et al. 1991), data in support of this almost universal assumption are scarce. We found that flat rock spiders in the field used relatively thin rocks with low canopy cover and a rock substrate, that hence were subject to high temperatures and large thermal fluctuations. This pattern of use reflects active selection based on thermal cues because in the laboratory, spiders selected warmer rather than cooler retreat sites. Finally, we demonstrated a benefit to this choice: spiders kept in hotter conditions exhibited enhanced rates of growth and development.

Use of rocks in the field

Our field survey revealed nonrandom use of rocks and contrasting patterns at two spatial scales, indicating considerable heterogeneity in available habitat. On average, crevices under all three groups of rocks sampled on the study outcrop would attain high temperatures due to their low levels of canopy cover and thinness (means of 1.8–4.4 cm). These rocks are far thinner than those classified in previous studies as thin or “hot” rocks (<20 cm thick in Huey et al. [1989], <15 cm thick in Webb and Shine [1998a, b]).

At both macrohabitat and microhabitat scales, spiders used rocks that were largely on a rock substrate and not deeply embedded in soil. For rocks on a rock substrate, thermal regimes inside crevices are determined primarily by rock thickness, degree of shading, and weather conditions (Webb and Shine 1998a, b). Thus, the fact that areas and rocks used by spiders were distinctive in terms of rock thickness, exposure, and canopy cover suggests that spiders respond to thermal cues. Areas of the outcrop used by spiders (containing rocks that were thinner with less canopy cover) would experience hotter-than-average conditions and large temperature fluctuations, but within these areas spiders used rocks that were thicker with more canopy cover, thus avoiding the hottest rocks on the outcrop. Thermal regimes also offer important cues for retreat-site selection by snakes and geckos on the same outcrops (Schlesinger and Shine 1994, Webb and Shine 1998a).

Our findings on factors influencing habitat use in the field are season-specific, because habitat use may vary seasonally for the spiders as it does for other rock-dwelling fauna. For example, some snakes in the same sandstone outcrop systems select thin rocks in exposed positions during cooler months, but move into the forest in summer (Webb and Shine 1998a). Communities of alpine invertebrates in rocky habitats show a seasonal shift in the extent to which microhabitat variables

predict rock occupancy (Sinclair et al. 2001). Hence, although we found strong correlations between rock attributes and rock use by spiders, including attributes that influence the thermal and structural properties of retreat sites, our field study did not reveal the direct causal mechanisms for these patterns.

Rock selection in laboratory trials

Our retreat-site selection experiment demonstrated that juvenile flat rock spiders select their diurnal retreat sites nonrandomly with respect to temperature, preferring warmer retreat sites in the laboratory. We are unaware of any previous experimental studies on the role of thermal cues for retreat-site selection by spiders, but several studies have demonstrated that spiders, especially those adopting web-building foraging strategies, respond behaviorally to thermal cues. For example, burrow-inhabiting lycosids and araneids display complex behavioral thermoregulation that involves basking, altering their orientation to the sun, and seeking sun and shade (Humphreys 1978, 1991). Thermal conditions also influence web-site selection by spiders by affecting prey availability (Riechert and Tracy 1975, Henschel et al. 1992). Investment in sites by *H. major* is not energetically costly compared to that by spiders building webs, creating greater opportunity to explore surrounding habitat to discover the most suitable retreat sites. Little is known about habitat fidelity in flat rock spiders over finer temporal scales, although they have been observed to defend rocks under which they have laid multiple egg sacs (C. L. Goldsbrough, *personal observation*), suggesting that they use individual rocks consistently.

Our experiments demonstrate that juvenile flat rock spiders respond to thermal cues by selecting warm over cool retreat sites. Because this experiment suggests that crevice temperature is important in habitat selection, we can proceed to the next question: what are the advantages and disadvantages of selecting a warmer or cooler crevice?

Thermal effects on growth and development

Our experiment shows that thermal regimes of retreat sites affect the spiders using them. More specifically, the thermal regimes associated with shaded, unshaded, and semi-shaded rocks affect the growth and development of juvenile flat rock spiders. However, we did not detect an effect of an eight-week exposure to these regimes on survival. The thermal regimes used in our experiment encompass the range of temperature conditions likely to characterize natural retreat sites used by spiders in spring (Webb and Shine 1998b), and our experimental setup mimicked diurnal fluctuations as well as mean temperatures (Li and Jackson 1996). Although fitness benefits could not be directly measured in juvenile spiders, survival, growth, and development in early instars are key predictors of fitness at maturity

for many insects with similar life histories (Stiling 1988, Zalucki et al. 2001).

Only one of the 85 spiders died during the experiment, a relatively low mortality for juvenile spiders (Higgins and Rankin 2001). Thus it appears that the thermal characteristics of retreat sites are unlikely to affect survival of juvenile flat rock spiders during spring. Our laboratory experiments also demonstrated that juveniles can withstand temperature extremes of 2.9°C (during incubator failure) and 42.1°C (highest temperature recorded in hot treatment).

Growth was greater under hotter thermal regimes for both age groups of flat rock spiders, suggesting that spiders will grow more quickly if they use an unshaded rock than if they shelter under shaded or semi-shaded rocks. Development was faster at higher temperatures for both cohorts. Thus, development of juvenile flat rock spiders is likely to be enhanced by sheltering under hotter rocks. Faster development has also been observed for spiders reared at higher constant temperatures (Browning 1941, Downes 1993, Li 1995, Li and Jackson 1996).

Although our experiment was designed to modify thermal regimes while keeping other factors constant, factors controlled by temperature also varied. In particular, relative humidity was highest in the cold treatment and lowest in the hot treatment. Thus any apparent effects of temperature could in fact be humidity effects or effects of the two in combination. The same covariation among temperature and humidity will occur in natural crevices and thus is consistent with our interpretation.

In summary, our study shows that flat rock spiders use habitat nonrandomly, such that they are found in warmer than average retreat sites; that juveniles actively select warmer retreat sites in the laboratory; and that juveniles grow and develop faster if kept in hotter conditions. Our data provide a compelling picture of a spider that actively selects retreat sites according to thermal conditions, which confer substantial fitness benefits.

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