SEASONAL HABITAT SHIFT IN AN INTERTIDAL WOLF SPIDER: PROXIMAL CUES ASSOCIATED WITH MIGRATION AND SUBSTRATE PREFERENCE

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ABSTRACT.   During most of the year, the wolf spider *Pardosa lapidicina* Emerton 1885 occupies tidal cobble beaches surrounding Narragansett Bay, RI, USA, but in late autumn part of the population moves into adjacent forest litter to overwinter. We monitored these movements with drift fences and pitfall traps from 1996–1999 and evaluated the possible roles of ambient temperature, rainfall, humidity and storm events. We tested substrate choice over the season as a proxy for migratory tendency, both in the laboratory and the field, focusing on the roles of temperature and photoperiod. The timing of peak migration differed among years (S.D. = 15.5 d). Minimum weekly temperature, weekly rainfall, percent relative humidity and storm events did not explain the variation in migratory times. However, significantly more spiders migrated during weeks with below-freezing temperatures than in weeks without them. Leaf litter, which has less variable temperatures than beach cobble, may provide a refuge from extreme temperatures during winter. Spiders maintained at cold temperatures in laboratory experiments chose leaves over beach cobble significantly more often than did those in warm temperatures. The time of year that spiders were collected also influenced their probability of choosing leaf substrate in the laboratory. Photoperiod, on the other hand, did not significantly influence substrate preference. This study helps to uncover how environmental cues influence seasonal movements across a habitat boundary.

Keywords: Acclimation period, photoperiod, substrate, temperature

Migration is a common behavioral response to seasonal change in temperate-zone organisms, providing them with the opportunity to exploit otherwise unavailable seasonal resources or escape temporarily inclement conditions (Tauber et al. 1986; Dingle 1996). The timing of these movements, often from one habitat type to another, is essential to the survival and reproduction of the migrant. Thus, seasonal migration likely requires both the use of environmental cues to indicate optimal timing of movement and major shifts in behavior, such as substrate choice preference. Two environmental variables, temperature and photoperiod, frequently indicate the oncoming habitat deterioration for temperate-zone terrestrial species and play a major part in their seasonal movements (Schaeffer 1977; Delisle and McNeil 1987; Han and Gatehouse 1991;

Tanaka 1997). These cues help migrants to anticipate or respond directly to seasonally deleterious aspects of their environment, such as low temperatures and freezing conditions, by triggering physiological and behavioral changes (Tauber et al. 1986).

Although long-distance movements like those of some birds and butterflies capture much of the attention surrounding migration, considerably shorter movements by less mobile animals are likely a frequently occurring phenomena. Despite the short distance, these migrants may cross abrupt physical boundaries, including such markedly dissimilar habitats as marine or freshwater-influenced to terrestrial locales (Svensson & Janzon 1984; Takada 1995; Madsen & Shine 1996), epilithic to benthic habitats (Kornijow 1992) and elevational gradients (Kimura & Beppu 1993). Crossing the boundaries exposes migrants to novel substrate. To survive in a drastically different environment, the migrants are often forced to make behavioral changes, potentially including a changed preference for sub-

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strate in the 'new' environment. Whether this change in preference occurs, and how it may be related to actual migratory tendency, has not, to our knowledge, yet been tested.

We studied the effect of photoperiod, temperature, humidity and storm events on the timing of migration by the intertidal wolf spider *Pardosa lapidicina* across a marine intertidal-terrestrial boundary. We further asked how substrate choice is associated with seasonal movement in the field, and how important seasonal cues such as temperature and photoperiod influence substrate preference. Populations of *P. lapidicina* in Bristol County, RI, USA, spend all but the winter months on cobble beaches immediately above the tide line, but in November and December some individuals retreat from the beach to the adjacent forest where they overwinter. Though not a lengthy move (5–15 m, Morse 1997), it spans two totally different adjacent ecosystems (see Polis & Hurd 1996). The spiders are exposed to substrates of strikingly contrasting texture and conductance (stones and pebbles vs. leaves): one familiar, one novel. Although short-distance movements (<1 m) from vegetation to ground hibernacula are common in spiders, larger seasonal movements of several meters are rare (Schaeffer 1977).

Winters in the study area vary markedly in their severity (Morse 1997). For example, snow and ice covered the beach from January through mid-March in 1994, making it uninhabitable for spiders during that time, whereas the 1995 winter was snowless, allowing a small number of spiders to persist on the upper beach throughout the winter (Morse 1997). We hypothesized that as a result this beachside species should respond variably to changing seasons (Hopper 1999; Tammaru et al. 1999; Comeau et al. 2002). During cold winters, temperature extremes, storm events and freezing weather the rocky shore may become extremely deleterious to the spiders (Morse 1997). Under these conditions, *P. lapidicina* should benefit from anticipating the onset of winter and leaving the beach. During mild winters, the spiders may benefit from delaying migration temporarily or indefinitely and feeding on the beach.

We hypothesized that spiders would use photoperiod as an indicator of the onset of winter, but might only respond with movement if temperatures reached some minimal threshold. Furthermore, we expected that large winter storm events would force spiders to leave the beach. Humidity has been shown to influence seasonal movements in another species of wolf spider (Eubanks & Miller 1993), probably due to their high susceptibility to desiccation. Although very dry conditions are unlikely at our study sites because fresh water drains from upslope towards the shore, we expected that humidity could play a role in the seasonal movement of these spiders. In terms of substrate choice, we hypothesized that substrate preference would be closely related to predilection to migrate, since migration required moving to a novel substrate. We therefore predicted that the cues affecting substrate preference would mirror those cues influencing migration in the field and that substrate could be used to examine those patterns experimentally. Preliminary evidence suggested that cold temperatures increase the preference of wolf spiders for leaf substrate (J.M. Kraus, unpubl. data).

To test these hypotheses, we used a combination of field observations and experiments in the laboratory and field. We monitored the movements of these spiders from cobble beach to forest leaf litter using drift fences and pitfall traps during the autumn over four fall seasons (1996–1999). We then examined the relationship between migration and common seasonal cues or deleterious events that might affect the spiders on the beach (temperature, photoperiod, moisture, storms). To investigate the relationship between migration and substrate preference, we ran substrate choice experiments in the field and compared the results with migration patterns. We tested for the influence of photoperiod and temperature on substrate preference in the laboratory to establish the role of these common migratory cues on substrate preference. We used temperature probes to measure the thermal conditions in cobble and leaves before, during and after migration, since consistently warmer temperatures might convey benefits for migrating into the leaf litter in winter.

METHODS

Study subjects.—*Pardosa lapidicina* in Bristol County, RI, USA have a one-year life cycle. During the reproductive seasons of spring and summer, the spiders regularly follow the receding tide into the intertidal area

where they prey primarily upon small Diptera and Collembola (Morse 1997). Spiders disappear from the low intertidal in mid-October. Density on the high intertidal and supratidal decreases in late November and December as numbers caught in the forest leaf litter increase (Morse 1997). Spider density on the beach remains low from December–March, although a portion of the population overwinters on the upper beach. In March and April the density on the beach increases again, as the spiders migrate back to the beach, and then decreases a last time as that cohort dies after reproducing in June and July. These spiders were never found in the forest or forest-beach interface until the fall when they made their decision to overwinter in the forest or on the beach (Morse 1997). It appears that they do not contact the forest environment until the late fall, unless a storm event inundates the beach. Like other *Pardosa* species (Vogel 1971; Lowrie 1973; Fujii 1974), *P. lapidicina* are small, cursorial and nomadic. They are dark-colored and 6–9 mm in length, with the females somewhat larger than the males (Kaston 1948). By migration time in November, they weigh 15–45 mg (J.M. Kraus, unpubl. data). In the study area individuals overwinter as juveniles, usually in the penultimate or antepenultimate stages (Morse 1997). We have no evidence that they overwinter as adults. Morse (1997) estimated about 2000 spiders entered winter in 1993 along a cobble beach 120 m long (17 spiders/m transect). Voucher specimens of *P. lapidicina* have been deposited in the National Museum of Natural History, Smithsonian Institution.

Study area.—We studied the spiders at two sites on the Haffenreffer Estate of Brown University, Bristol Co., RI. The research area consists of a cobble beach and adjacent forest on the west shore of Mt. Hope Bay, a partially sheltered arm of Narragansett Bay. Most cobble rocks range from 10–30 cm in diameter, and larger stones and bedrock protrude in some places (Morse 1997). The cobble bed is several rocks deep. The forest consists predominately of hackberry *Celtis occidentalis*, red oak *Quercus rubra* and red cedar *Juniperus virginiana* under 20 m, with bittersweet *Celastrus orbiculatus*, greenbrier *Smilax* sp., and poison ivy *Rhus radicans* often climbing into the canopy. Other than the vines, ground cover is sparse, but a heavy layer of leaf litter

persists throughout the year (Morse 1997). Ambient temperatures on the beach within 1–2 m of the forest may drop from over 20 °C in early November to −17 °C by late December. Study sites were separated by over 100 m, and by boulders and vegetation (see Morse 1997 for details).

Seasonal movement.—To monitor spider movement from beach to forest, 15 m drift fences were used at two forest sites 5 m from the cobble beach/forest interface and parallel to it. The fences, ca. 0.5 m high, consisted of heavy clear plastic sheeting that was supported by rebars driven into the ground approximately 1 m apart. The bottom of the plastic sheeting was buried under several cm of soil. *Pardosa lapidicina* are non-burrowing wolf spiders and it is very improbable that they could have moved under the fences. Pitfall traps, 1 liter plastic containers of 12 cm diameter, were sunk flush with the ground at approximately 1 m intervals on the beach side of the fences to trap individuals moving directly away from the beach and on the forest side of the fences to measure lateral movement around the fences. Leaves and small stones were added to the bottoms of the traps to provide cover and to discourage cannibalism. The total number of spiders captured was used as an index of migration over that trap period. The weekly ratio of spiders captured on the forest side to total catch was used as a conservative estimate of nonmigratory spider activity in the forest.

Trapping began in late October, based upon preliminary data on the timing of seasonal movements (Morse 1997), which showed no capture of spiders by hand searching in the 5 m strip of forest above the beach and by using pitfall traps 3 m into the forest from early September until 14 November in 1993 (Morse 1997). Additionally, an intensive search of the forest from May–November 1994 (0.1–10 m above the beach) turned up no individuals until 6 November (Morse 1997). Drift fence traps were monitored weekly from late October or early November through mid to late December 1997–1999, and twice weekly in 1996. Spiders were brought to the laboratory, weighed, sexed and then released on the landward side of the fences. Rate of recapture in the fences was estimated in 1997 by marking spiders caught in the fences at the beginning

and end of November with orange micronite dye (Morse 1997) and noting their recapture.

Ambient temperature was recorded at the time of all censuses and field experiments. Daily minimum temperature, maximum and minimum relative humidity, weekly rainfall and storm events of the local region were obtained from recorded NOAA (National Oceanographic and Atmospheric Administration) weather station data at the T.F. Green Airport in Providence, RI, 17 km to the WNW (NOAA 1996–1999). All statistical analyses were performed using SAS statistical software (SAS Institute, Inc. 1989) unless otherwise noted. The relationship between temperature, rainfall and humidity measurements taken between trapping periods and spider movement at the end of that period was examined using NOAA data to investigate the potential influence of these factors on migration during 1996–1999. The effect of storm events and days below freezing were independently evaluated using Wilcoxon non-parametric statistics to evaluate the one-way hypothesis that larger migrations would occur during weeks of storm events and freezing weather.

In 1999, one temperature probe from a HOBO H8 data logger (Onset Computer Corp., Bourne, MA, USA) was placed in each of four habitat types at a central site: ambient in shade 1 m off ground 5 m into the forest, ambient in open 1 m off ground at the beach-forest edge, under leaves 5 m into the forest, and under rocks on the upper part of the beach. The probes recorded ambient temperature every 10 min from early November to late December. Daily temperature variation (s^2) was compared among microhabitats using a 1-way ANOVA. Differences among means were then tested using the Ryan-Einot-Gabriel-Welsch multiple range test.

Substrate choice in the field.—Substrate choice experiments were performed weekly for 14 weeks in the field during 1997 using spiders hand-collected from the upper beach (20 per trial), and in 1997 and 1999 using those captured in pitfalls that week (7 test periods in 1997, 5 test periods in 1999). The substrate choice arenas were plastic tubs (32 cm $\times$ 18 cm $\times$ 10 cm), one half lined with beach cobble and the other half with forest leaf litter. Fresh substrate was used for each run. Spiders already in the leaf litter were extremely difficult to locate by hand (Morse

1997), and as a result only spiders caught in forest pitfalls were used for the already-migrated spiders in the substrate choice experiments.

Substrate choice arenas were placed at the intersection of the cobble beach and forest leaf litter perpendicular to the tide line. The containers were alternated so that the cobble faced the forest in half of the arenas and the leaves faced the forest in the other half, thus controlling for the effect of orientation on spider movement. Spiders were placed in the containers at the interface of the leaves and the substrate, and their location was recorded after 3 h. Pilot studies indicated that the spiders explored the container actively for the first 1.5 h, after which their rate of movement greatly declined (D.H. Morse pers. obs.). The 3 h acclimation period was used as a conservative estimate of the time needed for the spiders to explore their habitat thoroughly and make a choice. If the spider escaped before the end of the experiment, it received a ''no choice'' rating and was removed from the analysis. We used logistic regression to examine whether substrate choice varied over time (both by year and month collected), migration status (1997) or substrate orientation.

Substrate choice in the laboratory.—In Fall 1999, we investigated the effects of temperature and photoperiod on substrate preference under controlled laboratory conditions using a 2 $\times$ 2 $\times$ 5 factorial design: two levels of temperature (cold/warm), two levels of day length (short/long) and five time periods (12–15 Sept., 5–7 Oct., 4–7 Nov., 21–23 Nov., 13–15 Dec.). Substrate choice was measured in the same arenas used in the field. Treatments were replicated 30 times for a total of 600 spiders. The collection dates were chosen to reflect dates before, during and after migration in the field.

Spiders were collected at each of the four collection dates from the beach and immediately acclimated for 8 d before the experiments were run in the experimental arenas. Treatment conditions were maintained in two environmental chambers, one cold (4—6 °C), one warm (22—28 °C). Within each chamber a lightproof partition separated short (9 h, 40 min) and long (12 h, 40 min) day-length conditions. One 20 watt earthlight bulb in each side of the chambers provided appropriate day length. Temperature and photoperiod were not

alternated among chambers over the duration of the experiment due to mechanical constraints. The cold/short treatment simulated temperature and light conditions in mid-November, when previous data indicated the peak migration occurred (Morse 1997). The warm/long treatment simulated conditions in mid-September. The cold/long and warm/short treatments served as controls to separate the independent effects of temperature and photoperiod on substrate choice. The statistical model included temperature, photoperiod, time, and all interactions and was evaluated using a generalized linear model to perform logistic regression on binomial data (PROC GENMOD). All factors were considered fixed because they were set a priori by the investigators to sample different populations.

On each collection date we obtained 120 spiders from the beach 50 m or more from the drift fences, and maintained them individually in 15 dram vials (6.0 cm long, 3.5 cm diameter) with a 3 cm $\times$ 3 cm moistened square of paper toweling. Thirty spiders were randomly assigned to each treatment immediately after collection and remained in the chambers for an 8 d acclimatization period. On the third and sixth days of this period, they were all fed one *Drosophila melanogaster*, and their toweling was moistened to maintain uniform humidity. Instances of feeding (whether the fly was consumed) and molting were recorded. We analyzed the main effects of the treatment and collection date on whether an individual molted or fed, using logistic regression (PROC GENMOD).

On the eighth day, experimental arenas were prepared in the same way as the field experiments and then placed in the environmental chambers for 1 h before the spiders were introduced to bring their materials into equilibrium with the air temperature. Spiders were placed, one per container, at the interface of the cobble and leaves (on a rock and under a leaf), and substrate choice was recorded after 3 h. If the spider did not move (which was extremely rare) or if it escaped before the end of the experiment, it received a ''no choice'' rating and was removed from the analysis. The spiders were released at their original field site during the following week.

All substrate choice trials for both field and laboratory were analyzed with a chi-square test for goodness of fit to examine whether the substrates were chosen in equal proportions. Data were summed over the whole season when sample sizes for a week's trial were not adequate for individual analysis (Sokal & Rohlf 1995).

RESULTS

Seasonal migration.—Yearly drift fence captures (1996–1999) totaled 59, 66, 38 and 28 individuals, respectively, peaking between early November and early December in different years (Fig. 1). Drift fence data were summed over both fences for all analyses due to low sample size. The difference in day length between the two extremes (2 Nov. 1997 and 6 Dec. 1998) was 64 min. The percentage of spiders captured on the side of the fences facing the beach changed over the years, but was consistently more than 2 times as large as the proportion captured behind the fences: 1999, 82% in front; 1998, 71% in front; 1997, 96% in front; 1996, unknown. Also, the overall rates of recapture behind the fences were low. Of the 33 spiders that were marked after being captured at the fences on 2 Nov. and 30 Nov. in 1997, only one was recaptured (3%) after being released behind the fence.

No significant relationship occurred between numbers that migrated and minimum ambient temperature in the week preceding a collection at the pitfall traps (correlation analysis, $R = -0.13$, $n = 44$, $P > 0.05$), but migration did occur significantly more frequently during periods containing episodes of freezing weather (Wilcoxon 2-sample one sided exact test, $n_{above\ freezing} = 15$, $n_{freezing\ or\ below} = 29$, $P = 0.047$; Fig. 2). Neither weekly rainfall (correlation analysis, $R = 0.13$, $n = 44$, $P > 0.05$), nor percent relative humidity (correlation analysis, available for 1996–1997 only; min $R = -0.17$, $n = 27$, $P = 0.41$; max $R = -0.24$, n = 27, $P > 0.05$) correlated significantly with migration, and migration did not occur more frequently during weeks with storm events than those without storms (Wilcoxon 2-sample one sided exact test, $n_{storm}=7$, $n_{no\ storm} = 39$, $P > 0.05$). Although the mean temperature was similar at all microhabitat sites, the variation (s^2) in daily temperature within fallen leaves was more than three times less than in the cobble, in the shade above the leaves, or in the sun above the leaves in 1999 (Table 1).

Substrate choice in the field.—A total of 280 spiders collected from the beach were
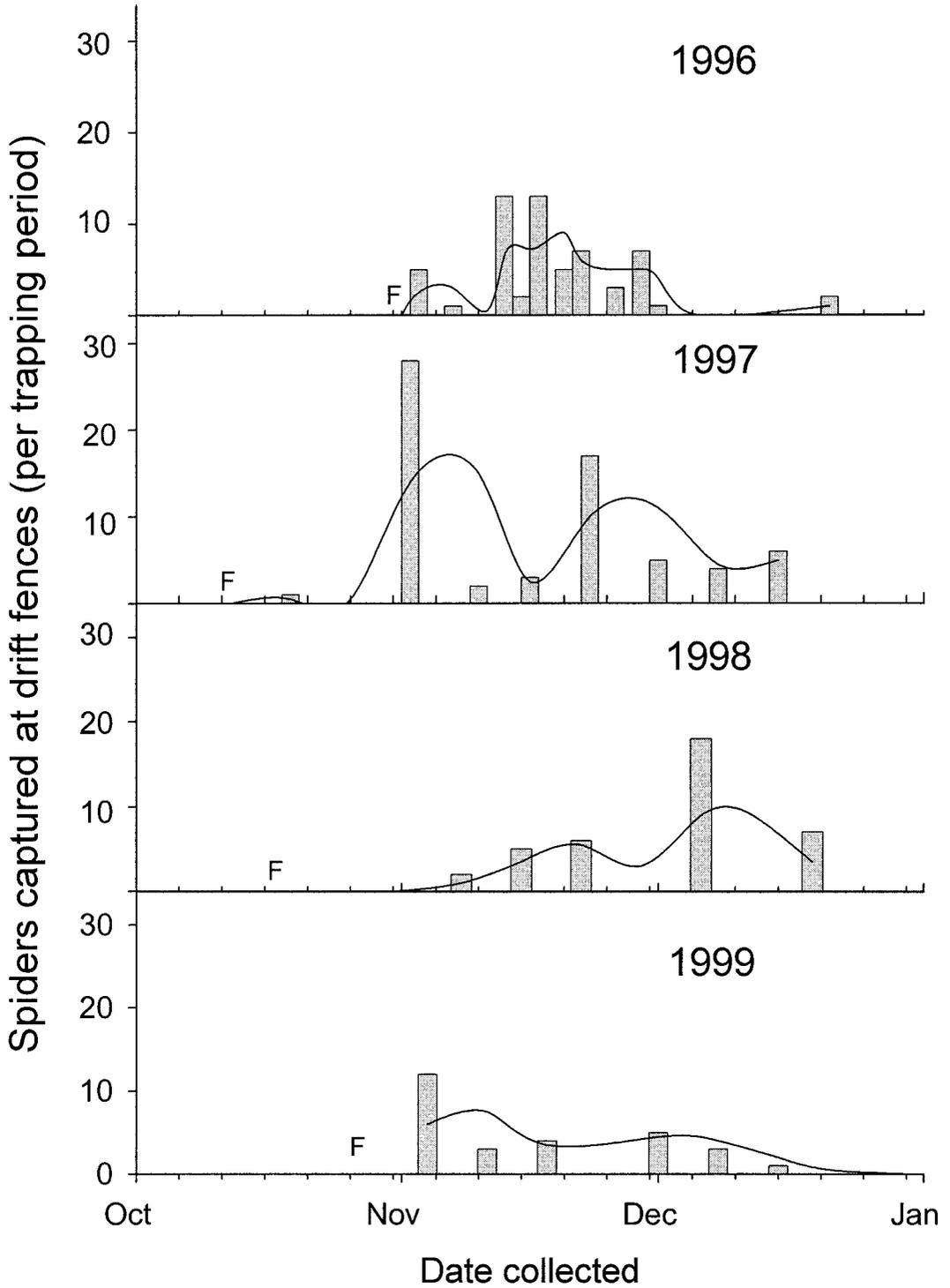
Figure 1.—Number of spiders captured at the two drift fences, 1996–1999. Sample sizes were too low to analyze each fence separately. Bars represent number captured during trapping period (ranging from several days to a week). Lines are running average number of spiders captured over two trapping periods. "F" indicates first date of trapping. Traps ran continuously throughout season. Initiation of trapping was dictated by preliminary data.
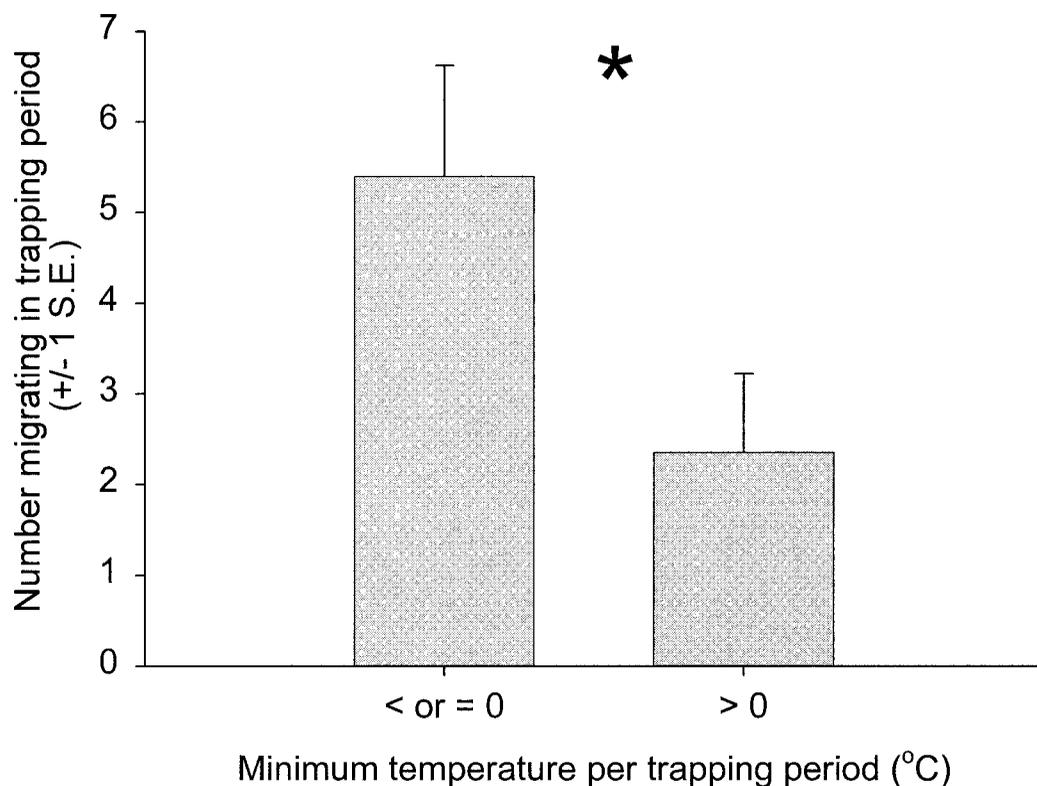
Figure 2.—Comparison of number of spiders (+ S.E.) captured at drift fences during trapping periods with minimum temperatures above freezing (0 °C) versus at freezing and below (1996–1999). Asterisk indicates significant differences between categories at $P < 0.05$.

tested for substrate choice in 1997; 74 escaped before choice was recorded and none failed to make a choice. In 1997 and 1999, a total of 37 and 42 spiders collected from the forest drift fences were tested for substrate choice; 4 escaped before choice was recorded in 1997, no spiders escaped in 1999. No spiders in either year failed to make a choice after the 3 h acclimation period. For the field experiments on substrate choice in 1997 and 1999,

Table 1.—Average daily temperature (°C) and variance in 1999 at four microhabitat sites at the beach-forest interface: under leaves, under cobble, ambient shade, and ambient sun.

Microhabitat	Daily temperature	Variance
Leaves	7.2	1.4
Rocks	6.4	9.4
Shade	6.2	8.0
Sun	6.2	7.8

substrate choice was not predicted by month collected, orientation of substrate, or whether the individual had migrated (1997 only), (logistic regression, $P > 0.05$ in all cases). There was a marginal effect of year on the probability of choosing leaves ($x^2 = 3.51$, $df = 1$, $P = 0.06$). The proportion of individuals choosing leaves over cobble varied over the experimental period in both 1997 and 1999. Spiders collected from the forest in 1997 and 1999 showed an increase in leaf choice in the experimental arenas when migration occurred in the field, discounting the 2 Nov. movements forced by storm-driven beach inundation (Figs. 3, 4). In 1997, the beach-captured individuals increased their leaf choice in late October, before migration occurred in the field (Fig. 3).

Spiders collected from the beach chose cobble significantly more often than leaves in every set of substrate choice experiments (23 total), both in the field and laboratory (x^2 test for goodness of fit, Bonferroni-adjusted, $k =$
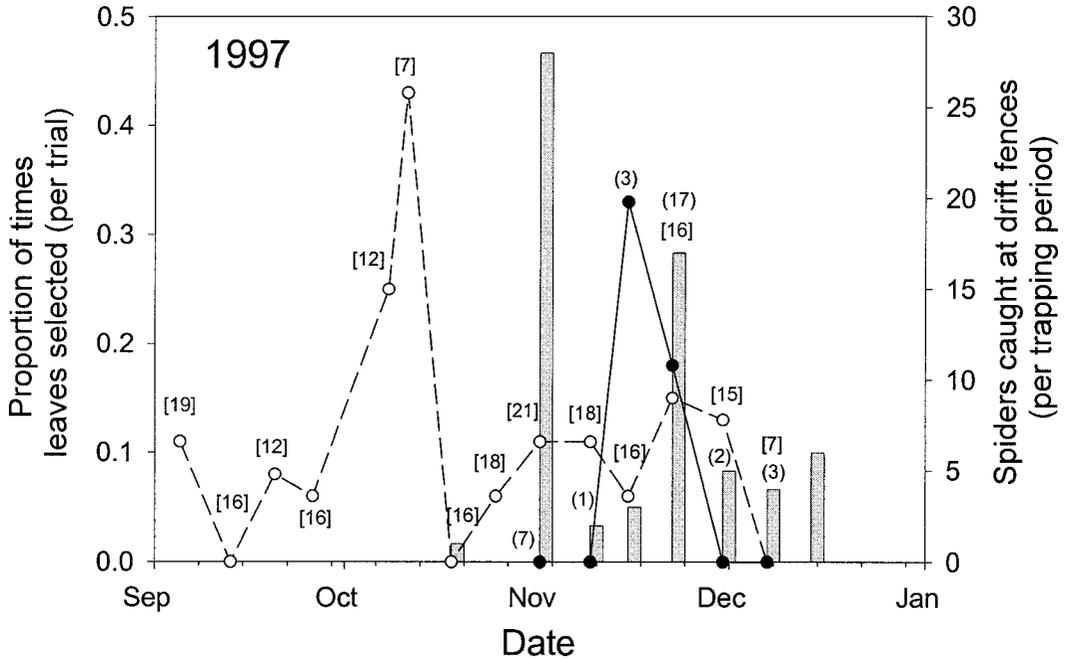
Figure 3.—Results of field substrate choice trials in 1997 showing how substrate choice changes with migratory tendency. Open circles = substrate preference of spiders captured on beach, closed circles = substrate preference of spiders captured at drift fences, and bars = number of spiders captured in drift fences over season. Sample size for substrate choice experiments above each data point: number of spiders captured on beach in brackets, number captured at drift fence in parentheses.
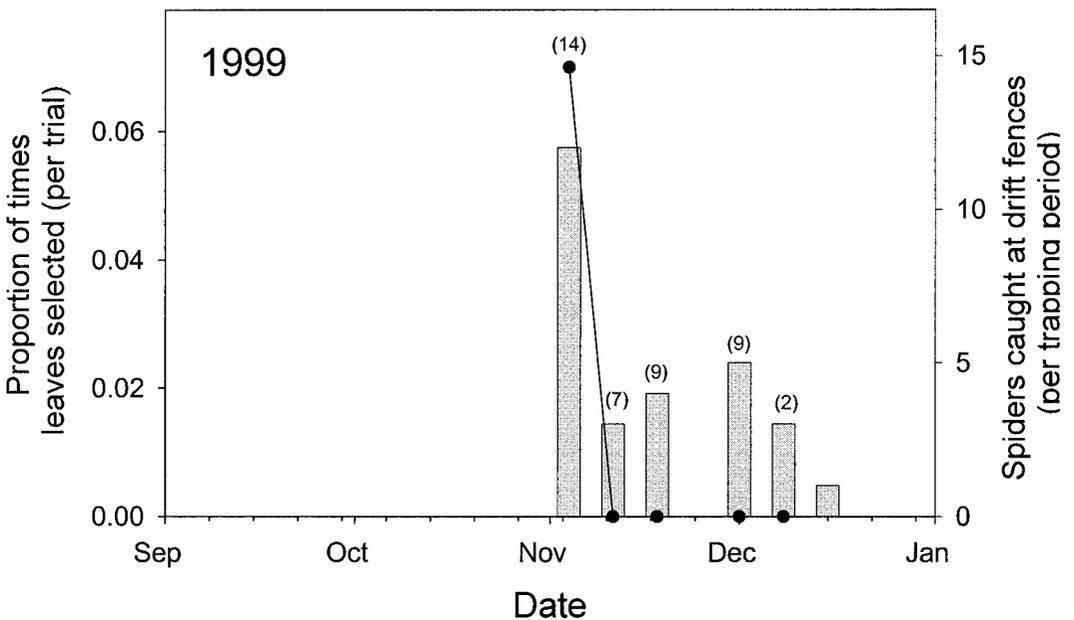

Figure 4.—Results of field substrate choice trials in 1999 showing how substrate choice changes with migratory tendency. Closed circles = substrate preference of spiders captured in drift fences, and bars = number of spiders captured in drift fences over season. Sample size for substrate choice experiments above each data point.
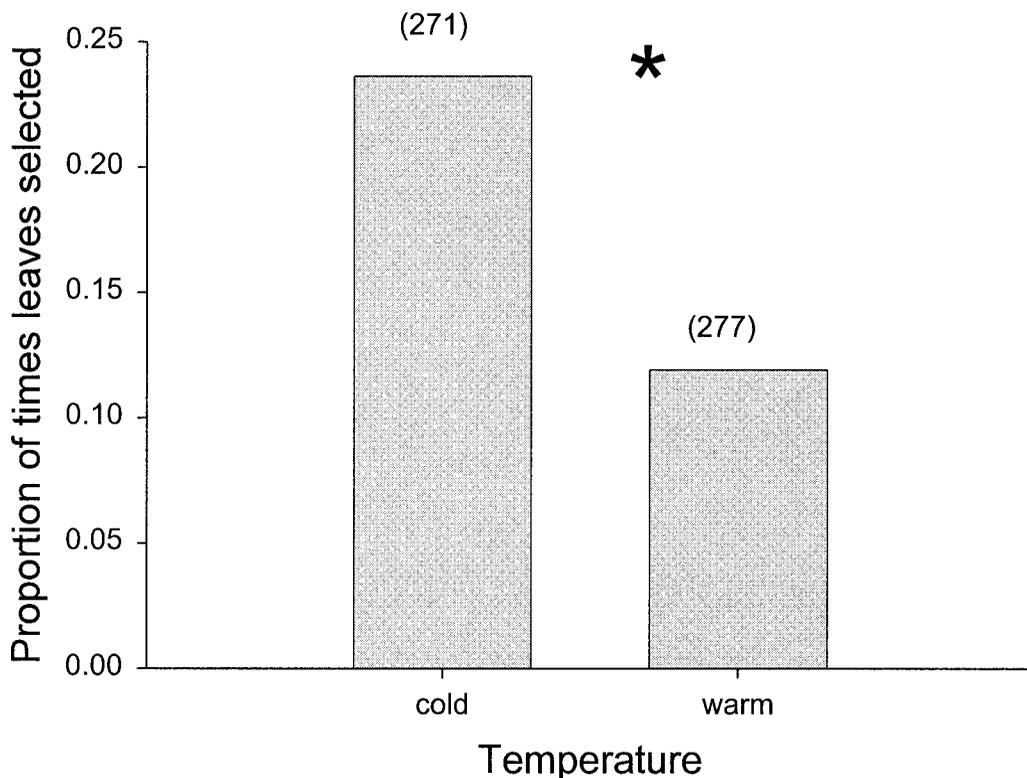
Figure 5.—Laboratory experiments on beach-captured spiders in 1997, showing effect of temperature collected on substrate choice. Sample size for each data point in parentheses. Asterisk indicates significant differences between temperatures at $P < 0.05$. The interaction between temperature and data collected not significant.

23, $P < 0.002$ for every week's trial). Weekly sample sizes of the forest-captured individuals often were inadequate for analysis ($n = 1–18$) because the replicates were limited by the numbers that were caught in pitfall traps that week, but the pooled yearly results showed that the vast majority also selected cobble (29 of 33 in 1997; 41 of 42 in 1999), both highly significantly different from a 50:50 ratio ($x^2_{1,1}$ = 12.5, 20.0; $P < 0.001$, < 0.001: x^2 tests for goodness of fit).

Substrate choice in the laboratory.—A total of 604 spiders were tested in the laboratory experiment over the 5 sample dates. There were 56 deaths or escapes and 6 incidents in which the spider apparently made no choice, 29.4 ± 2 spiders were tested per treatment with the exceptions of 4 treatments that contained only 19 or 20 replicates. Those treatments, late November/warm short and long daylength, and September/cold short and long daylength, had reduced replicates due to

alternate use of the spiders and an experimental error. The main effects of temperature and collection date on substrate choice were significant (temperature $x^2 = 9.24$, $df = 1$, $P = 0.002$; collection date $x^2 = 10.6$, $df = 4$, $P = 0.03$). Preference for leaves peaked in cold conditions and for spiders collected in Oct. (Figs. 4, 5). Post-hoc pairwise contrasts revealed that spiders collected in Oct. had a significantly different substrate preference from those collected in Dec. (Bonferroni adjusted P-value, $P < 0.005$) and were marginally different from those collected in early and late November ($P < 0.05$). Photoperiod did not significantly affect substrate choice ($P > 0.05$). The two-way and three-way interactions among photoperiod, temperature and collection date were also not significant ($P > 0.05$).

Temperature and date collected significantly affected whether an individual molted or fed (Table 2). The incidence of molting and feed-

Table 2.—Proportion of spiders molting and feeding during laboratory experiments in 1999. Molting and feeding are significantly affected by temperature and collection date. Sample sizes in parentheses.

Collection date	Proportion molting		Proportion feeding	
	Cold	Warm	Cold	Warm
OCT 5–7	0.02 (66)	0.35 (66)	0.50 (66)	1.00 (66)
NOV 4–7	0.00 (62)	0.02 (64)	0.56 (66)	1.00 (64)
NOV 21–23	0.00 (62)	0.03 (40)	0.21 (42)	1.00 (40)
DEC 12–15	0.00 (63)	0.00 (61)	0.10 (63)	0.66 (61)

ing decreased over the season and occurred more often in warm conditions (for molting: temperature $x^2 = 46.0$, $df = 1$, $P < 0.001$, date $x^2 = 59.1$, $df = 4$, $P < 0.001$; for feeding: temp $x^2 = 291.9$, $df = 1$, $P < 0.001$, date $x^2 = 108.1$, $df = 4$, $P < 0.001$). Photoperiod had no effect (for molting: $x^2 = 0.4$, $df = 1$, $P > 0.05$, for feeding: $x^2 = 1.1$, $df = 1$, $P > 0.05$).

DISCUSSION

Seasonal migration.—*Photoperiod and temperature:* Our use of drift fence captures as a measure of directional migration and not general activity is supported by the lack of drift fence captures in early fall when warm weather increases activity, the large disparity between spiders caught in front and behind the drift fences (greater than 70% captured in front), and the low recapture rate of spiders in fences (3% in 1997). The timing of *P. lapidicina* movement and the numbers of spiders moving from the cobble beach to the adjacent forest as measured by the drift fences varied among years (Fig. 1). Date of peak movement occurred between early November and late December (S.D. = 15.5 d) during 1996–1999, which is at least 1.5 times as variable as the timing of seasonal migration in some fish and birds (S.D. = 2–10 d; Comeau et al. 2002). For most seasonal responses in arthropods, photoperiod is used to cue the physiological changes that determine the timing of major life history events (Tauber et al 1986). Many organisms use absolute day length (Tauber et al. 1986; Delisle & McNeil 1987), change in day length (Beck 1980) or both to differing degrees (Han & Gatehouse 1991), to anticipate seasonal changes in their environment. The high variance in timing of migration over the years argues against a singular role of photoperiod in this system, but it seems unlikely that photoperiod played no role in migration given its seasonal nature.

It appears that temperature has an effect on migration: low temperatures may thus increase the migratory response of *P. lapidicina* to seasonal change, while mild temperatures decrease it. Only about half as many spiders were captured at the drift fences during the relatively warm autumns of 1998 and 1999 (the 82nd and 96th coldest of the past 100 years), as during the relatively cold autumns of 1996 and 1997 (the 19th and 34th coldest; NOAA, 1996–1999). Furthermore, a greater number of spiders migrated during weeks when temperatures dipped below freezing, perhaps to avoid contact with ice on the beach (Schaeffer 1977), although minimum ambient temperature did not correlate with movement. During mild winters, more individuals apparently overwinter on the very edge of the cobble-forest boundary (< 5 m into forest) or on the beach itself (Morse 1997). Although it is unclear what their relative survival is compared to those that migrate, if these spiders continue feeding on the beach it could give them a size advantage at the beginning of the following season. Ultimately, retreating to leaves during colder seasons may afford the spiders protection from extreme conditions because of the less variable temperatures in the microhabitat under leaves. Leaf litter has been previously found to be a preferred microhabitat for spiders in the winter because of its low thermal conductivity and temperature fluctuation (Schaeffer 1977)

Other temperate zone arthropods exhibit seasonal responses to low temperatures (Delisle & McNeil 1987; Han & Gatehouse 1991; Eubanks & Miller 1992). For example, the length of the prereproductive periods of true armyworm moths *Pseudaletia unipuncta* (Delisle & McNeil 1987) and oriental armyworm moths *Mythimna separata* (Han & Gatehouse 1991), which determine their predisposition to

migrate in the autumn, increase under cold temperature or short photoperiod regimes. These responses suggest that cold temperature may directly determine an animal's propensity to migrate. The mechanism for temperature driving this propensity may be either direct, by affecting rates of growth and development, or indirect, by inducing a physiological syndrome that prepares the insect for coming seasonal changes (Tauber et al. 1986).

Rainfall, humidity and storm events: Seasonal change in habitat preference of non-burrowing lycosids has been previously documented in temperate forests. Eubanks & Miller (1992, 1993) suggested that the habitat shift of *Gladicosa pulchra* in the late summer and early fall was affected by rainfall (surrogate for soil humidity). Rainfall and ambient humidity appeared to have no influence on the habitat preference of *P. lapidicina*. This difference may be explained by the geographical ranges of the two populations. *Gladicosa pulchra* was studied in the southern U.S., where winters are much milder, and desiccation has a larger probability of affecting survival. In addition, the fresh water flowing across portions of our study sites would further reduce dessication risk for the spiders.

Storm events did not correlate with movement in the field. However, the large early peak in 1997 (on 2 Nov., 28 individuals were captured) occurred after a large storm in which the tide inundated the high beach (J.M. Kraus & D.H. Morse, pers. obs.).

Substrate choice as a proxy for migration?—We expected that if substrate preference did play a role in spider migratory decisions, that spiders would be more likely to choose leaves after they had migrated. This expectation was not met: in 1997, 4 out of 29 (14%) spiders that had migrated and 24 of 185 (13%) that had not migrated chose leaves. Although the overall proportion of individuals choosing leaves was not affected by migratory status, it appears that individuals captured at the drift fences show their highest leaf preference within a week of peak migration, not including storm forced movements in 1997 (Figs. 3, 4). On the other hand, beach-captured spiders chose leaves most frequently a month prior to peak migration (1997, Fig. 3).

We predicted that spiders that had not yet migrated would exhibit a strong preference for leaf substrate during the fall migration. Although being in migratory condition does not necessarily result in preference for leaf litter, since spiders that have already migrated still chose cobble a majority of the time, the peak in preference for leaf litter coincided with high migration rates over two years. This result suggests that migration is somehow associated with substrate preference. Collectively, the field-conducted substrate choice experiments, coupled with the pattern of migration, suggests that change in substrate preference is related to seasonal movement from beach cobble to forest leaf litter in the field. To verify this connection, similar comparisons need to be made over more years, using a larger number of replicates.

Month of collection and substrate orientation had no effect on spider substrate choice in the field. The marginal effect of year on substrate choice in the field is most likely attributable to the small number of replicates in 1999.

Substrate choice and environmental cue.—The results of the laboratory substrate choice experiments suggest that temperature, which may affect the number of individuals migrating in the field, also influenced individual substrate preference. Individuals maintained at cold temperatures selected leaf substrate significantly more often than those kept at warm temperatures (Fig. 5). There are two possible explanations for this pattern. Spiders in cold conditions may simply choose the warmer substrate (leaves), especially if they have not yet acclimated to cold temperatures in the field. Alternatively, the spiders may have been physiologically primed, perhaps by photoperiod in the field, to respond to cold temperatures by changing their substrate preference. An additional condition in which the substrate was cooled before being placed with warm spiders or warmed before being placed with cooled spiders, would have allowed us to establish whether the spiders were undergoing a physiological change that affected their preference or if they were simply responding to the tactile cues they were receiving at that moment. Given that the spiders decreased feeding and molting as the season progressed (Table 1), and the main effect of date collected on spider choice (leaf preference peaked in Oct., Fig. 6), we suggest that a physiological change had occurred and the spiders' choices
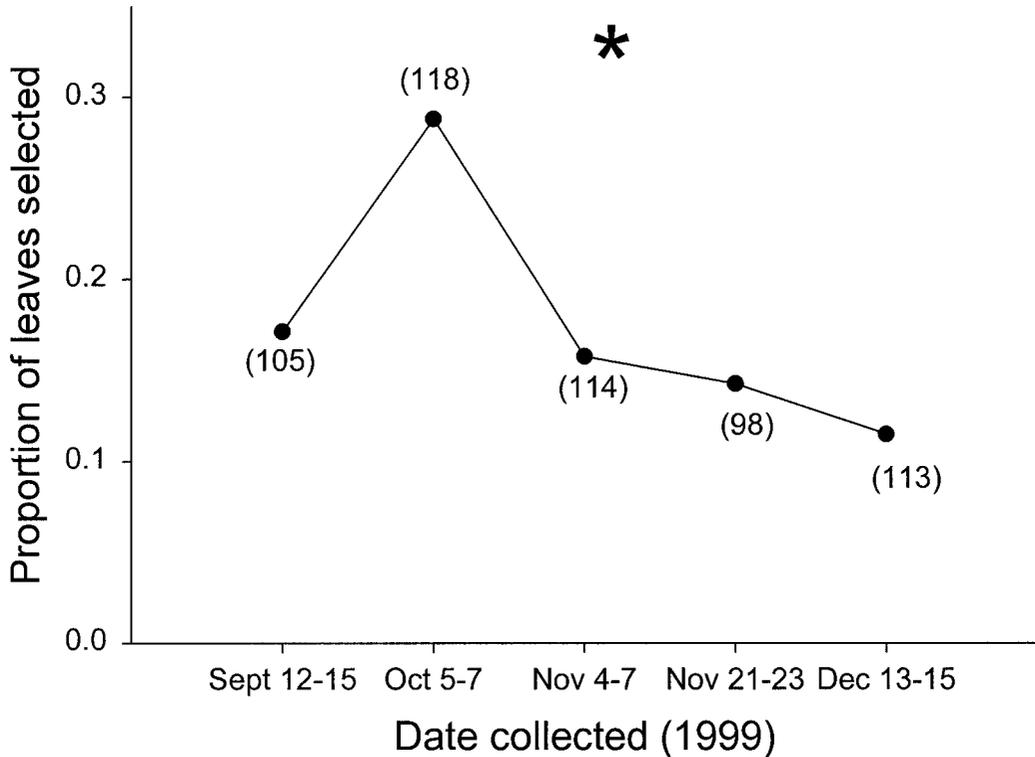
Figure 6.—Laboratory experiments on beach-captured spiders in 1999, showing effect of date collected on substrate choice. Sample size for each data point in parentheses. Asterisk indicates significant differences between dates at $P < 0.05$.

were most likely driven by an interaction between physiological and tactile factors.

Photoperiod showed no effect on substrate preference in our laboratory experiments. This result was surprising because of the role that photoperiod traditionally has played in triggering physiological changes that allow temperate organisms to respond to the onset of winter (Tauber et al. 1986; Kumar 1997). It is possible that *P. lapidicina* do not use photoperiod to make substrate choice decisions. Alternatively, the experimental design may not have tested an aspect of photoperiod (such as change in day length) to which the spiders respond, or the 8 d acclimation period at the beginning of the experiment was inadequate. There is some evidence for the latter explanation, since the date at which spiders were collected from the field affected substrate choice in the laboratory (Fig. 6). Spiders collected in October were almost twice as likely to choose leaves in the laboratory as those collected at any other time. Apparently the

spiders were at least partially making their substrate choice decisions based on conditions in the field.

On the failure of some individuals to migrate.—The striking difference between the rocky intertidal and adjacent forest litter may inhibit *P. lapidicina* that encounter the interface from moving across the boundary. Since the spiders were born on the beach in the spring and early summer (Morse 1997), they are naïve to the forest environment, having previously experienced no more than occasional leaves. This background is consistent with leaves never being favored by a majority of individuals in the experiments, even though they provide a less variable temperature regime than the beach cobbles.

Although we have not quantified costs of migrating to the leaf litter, we have trapped both arachnid and shrew predators at the drift fences (Morse 1997 pers. obs.). In other communities prey moving across habitat boundaries have been shown to enhance the num-

bers of predators there (Polis & Hurd 1996; Hering & Platcher 1997; Henschel et al. 2001). This cost may inhibit movement for *P. lapidicina*. Spiders may also continue to reap a benefit from access to food on the beach. Laboratory data suggest, however, that this benefit would be most significant early in the season, since the spiders undergo a two-fold decline in overall feeding rate and cease molting as the season progresses, even if maintained in warm temperatures (Table 1). Further, individuals captured on the beach during November and December are slightly lighter than ones caught in the forest (J.M. Kraus pers. obs.) and have ceased gaining mass by this time (D.H. Morse pers. obs.).

Depending on the year, most of the spiders may eventually cross the beach-forest interface, but some do not unless driven to it by physical factors such as ice and high water. Although they might change their choices with experience and time, the performance of the naïve individuals is the relevant variable here, since it represents the normal condition for an individual first encountering the habitat boundary.

ACKNOWLEDGMENTS

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