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The Effect of Visual Features on Jumping Spider Movements Across Gaps

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Abstract Our objective was to determine whether an animal's decisions to cross inhospitable open space are influenced by the visual characteristics of targets it can see across the space. We studied jumping spiders (Salticidae) in the genus *Phidippus*. We considered the effect of target size (short vs. tall) and distance (close vs. distant) in no-choice experiments. How often spiders approached close targets, regardless of target size, was not significantly different from how often they approached tall, distant targets, but they approached close targets of either size significantly more often than short, distant targets. When presented simultaneously with short, close and tall, distant targets the spiders' choices did not differ significantly from random. We also tested for the effects of the contrast of targets with their background and found that the spiders crossed open space to reach green, but not white, targets, regardless of background. Finally, spiders were more likely to approach a green grass-like target rather than a target composed of geometric shapes. We conclude that target size, distance and appearance all influence the spiders' willingness to cross open space.

Keywords Perception · movement · gap crossing · spiders · salticidae

Introduction

An animal's movement decisions are often intimately linked to its perceptual abilities. Whether an animal perceives and is attracted to particular features of the landscape influences how it navigates through familiar terrain, allocates time in different areas of its home range, and explores new areas (e.g., Collett and Zeil 1998;

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Patullo and Macmillan 2006). For example, animals may be more willing to cross inhospitable terrain if they can perceive landscape features on the other side, a finding of particular relevance to conservation biologists studying animal movement in fragmented habitats (Andreassen et al. 1998; Gillis and Nams 1998; Zollner 2000).

Many arthropods respond preferentially to visual cues with particular characteristics. Specifically, contrast with the background, size, color and shape have been shown to be important for arthropods in the context of choosing landmarks for navigation (e.g., Dyer et al. 2008; Hoefler and Jakob 2006), identifying suitable shelter (e.g., Björklund 2008) and selecting host plants or flowers (e.g., Björklund et al. 2006; Brévault and Quilici 2007; Horridge 2007; Mayer et al. 2000; Prokopy and Owens 1983). How visual cues influence the decisions arthropods make when encountering unfamiliar terrain is of particular interest. For example, field studies show that arthropod movement between types of habitat patches depends on the nature of the boundary between patches, such as the plant species that form the edge and the contrast between patch types (e.g., Haynes and Cronin 2006; Bonte et al. 2004). To understand precisely which characteristics influence movement requires the experimental manipulation of cue characteristics. The difficulty of designing such experiments is lessened if we study animals that rely primarily on vision.

Investigating how movement decisions are influenced by the characteristics of visual stimuli demands a careful choice of study species. The distance from which an animal is able to detect a particular landscape element, hereafter a target, is called its perceptual range (Lima and Zollner 1996). To date, most of what we know about vision-based perceptual range (target perception) has come from testing small mammals with perceptual ranges on the order of 90–500 m (Mech and Zollner 2002). Species with such long perceptual ranges cannot be studied readily in the laboratory, where target characteristics can be tightly controlled on a scale that is relevant to the animal. Other species better suited to laboratory study, such as many arthropods, typically have only a limited ability to detect targets visually and rely primarily on olfaction (Hoffman 1983; Fahrig and Paloheimo 1987; Nottingham 1988). Although it is possible to study target perception in these species (e.g., Schooley and Wiens 2003), experimental design can be challenging.

Jumping spiders (family Salticidae) offer a tractable model system. Jumping spiders rely heavily on visual information gathered through their two types of eyes. These are the principal eyes, a pair of large, forward-facing eyes that support color vision and especially high spatial acuity, and three pairs of secondary eyes that are especially well suited for motion detection (reviewed in Land and Nilsson 2002; Harland and Jackson 2004; Lim and Li 2006). The role of vision in jumping spider behavior, especially courtship (e.g. Clark and Uetz 1993; Maddison and Hedin 2003) and hunting (e.g., Jackson and Pollard 1996), has been well documented. Much less is known about how jumping spiders use vision to make decisions about moving through the environment.

We studied the movement decisions of three species from the genus *Phidippus*. These spiders are common in mixed vegetation in old fields, an environment that is often patchy, with suitable vegetated habitat separated by inhospitable open space that these spiders are reluctant to cross (Baker 2007). To examine the effect of target characteristics on movement decisions, we presented spiders with a variety of target stimuli in both choice and no-choice tests and measured the spiders' willingness to

cross open space to reach them. We conducted three sets of experiments, each focused on a different set of target features.

First, we manipulated target size and distance. Various insect species (reviewed in Graham et al. 2003) are attracted to tall objects. *Phidippus* spiders also appear to be attracted to tall objects: when 90-cm tall painted wooden dowels were placed in the field, spiders were quick to orient to, approach and climb them (Hoefler and Jakob 2006). We predicted that spiders would move more readily to taller targets compared to shorter targets. In addition, we examined the interaction between target size and distance. Several insects have been shown to use the angle subtended by the image of the target on the retina as an indicator of target size. For example, wood ants (*Formica rufa* L.) trained to use a small wall as a navigational aid will, when presented with a taller wall, adjust their path so as to keep the image of the top of the wall at a particular retinal elevation (Graham and Collett 2002). Additionally, bees (*Apis mellifera* L.) trained by classical conditioning to respond to a disk of a particular size also respond to disks of different sizes, as long as the disks are positioned to subtend the same retinal angle as the original disk (Wehner and Flatt 1977). In the dimorphic jumping spider *Maevia inclemens*, males that display in a low posture court close to the female, whereas males that display in an upright posture court further away. Clark and Uetz (1993) suggest that these two displays present visual targets to the female of almost identical size. On this basis we predicted that in our choice tests, spiders should be equally willing to approach short, nearby targets and tall, distant targets if both targets subtend the same angle at the point where the spider makes its choice.

Second, we investigated the role of contrast of the target with the background. The distance at which an animal perceives a particular target varies with the surrounding environment (e.g., Prokopy and Owens 1983; Zollner and Lima 1999). We tested two target colors against matching and against contrasting backgrounds, and predicted that spiders would move to the contrasting target more often than to the matching target.

Finally, we tested the role of target shape on the spider's movement decisions. Target shape influences movement in ladybird beetles, which selectively approach stalk-like posts (Collett 1988). Flies approach and climb vertical patterns (summarized in Hirsch and Tompkins 1994). This was the rationale for an experiment in which we compared the spiders' responses to targets that superficially resembled the tall grass common in their habitat with targets of the same color and height but composed of geometric shapes, and thus dissimilar to natural objects. Because both their evolutionary history and individual experience was with grass, we predicted that spiders would be predisposed to move more often to targets that were grass-like than to the geometric shapes.

Methods

Study Animals, Collection and Maintenance

We studied adult *Phidippus princeps*, and to a lesser extent *P. clarus* and *P. audax*. All subjects were adult females (7–10 mm in body length). We collected spiders by sweep-netting old fields dominated by goldenrod (*Solidago* spp. L.), Alsike clover (*Trifolium hybridum* L.), and alfalfa (*Medicago sativa* L.) in Amherst, Massachusetts.

Spiders were collected as adults or penultimate. In our sites, *P. clarus* matures in early-to-midsummer, and *P. princeps* in early fall. Maturation of *Phidippus audax* seems to be less synchronized, with some adults present for much of the season. The individuals we worked with were collected in late summer. We conducted experiments with *P. clarus* in July and August 2002, *P. audax* in October and November 2002, and *P. princeps* in September–January in both 2002 and 2003. Experiments were done between 1000 and 1800, with treatments randomized to account for time of day effects.

Spiders were housed individually in plastic boxes (19×13×4 cm high), aerated with holes, that held green wooden dowels and leafy green plastic plants to provide climbing surfaces and mitigate the effect of captivity on behavior (Carducci and Jakob 2000). We provided each with *ad libitum* water in a cotton-stoppered vial and three small crickets (*Acheta domesticus* L.) per week. The laboratory was kept at 25±2°C under a summer light regime of L:D 13:11.

Target Color

We used either green targets or both white and green targets for these experiments. Targets were painted either flat white or “foliage green” (Delta Ceramcoat nontoxic acrylic paint, City of Industry, California). Because some species of jumping spiders can detect UV light (Lim and Li 2006), we measured reflectance spectra of the targets with a spectrophotometer (Ocean Optics, Dunedin, Florida). Visible spectra were recorded under a tungsten-halogen filament, and UV spectra under a deuterium lamp (Ocean Optics, Dunedin, Florida). Green reflected slightly more in the UV range than did white.

Target Size and Distance

We used *P. princeps* to test the effect of target size and distance using two experimental designs. First, in no-choice tests, we released individual spiders at one end of a linear, horizontal arena with a single target at the opposite end. We used white foam-core board (Elmer’s Products, Toronto, Canada) to construct arenas of two lengths: 30 and 100 cm (both 20 cm wide×40 cm high and open at the top). A thin layer of petroleum jelly was applied to the upper 4 cm of the arena walls to prevent spiders from escaping. Arenas had a 2-cm diameter entry hole centered at one end, and targets were positioned at the opposite end. Targets had bases made of green 2-cm blocks of wood. Glued to the four sides of each base was green plastic “grass” composed of flexible plastic strips, tapering from 3 mm in width to a point (Silk Garden Shop, Irving, Texas), either 11.4 or 38 cm long (Fig. 1a). Target heights and arena lengths were chosen so that the tall target in the large arena subtended the same angle at the spider’s starting point as did the short target in the small arena (20.8°). Three replicates of each arena type and of each target type were used equally often throughout the experiment as a control for spurious effects of equipment. We tested large and small arenas and tall and short targets in a 2×2 design. The arenas were illuminated with General Electric 40 W fluorescent bulbs positioned 2.6 m above them, and trials were videotaped from above with a Canon Hi 8 camcorder. Trials were scored live, and videotapes were reviewed to confirm time measurements.

We randomly assigned 60 females of *P. princeps* to one of the four treatments, and tested each spider only once. Each spider was tested individually in trials that

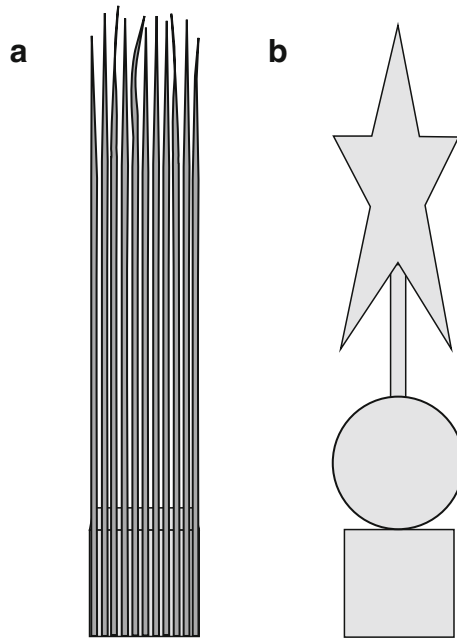


Fig. 1 Two types of targets, a grass-like target composed of a wooden block with plastic grass-like strips glued around each side, either 11.4 cm (a) or 38 cm tall (not pictured), and a target constructed of wooden geometric shapes (b). We measured the willingness of spiders to cross open space in order to reach these targets.

lasted for 15 min or until it climbed onto the target. To release a spider into the arena, we placed it in a 200-cc syringe covered with tape and with its tip removed, stoppered with a cotton ball. The syringe was inserted through the entry hole in the arena, and left undisturbed for 5 min to allow the spider to calm down. The experimenter then removed the cotton ball and gently guided the spider into the arena with the syringe's plunger. After each trial the arena was wiped down with 70% isopropyl alcohol to eliminate potential chemical traces, and allowed to dry.

We scored a spider as reaching a target if it touched the target with its two most anterior legs. We were also interested in whether spiders that perceived a target moved more quickly down the arenas. In no-choice experiments, we measured the latency (sec) from the release of spiders into the arena to their first crossing of an imaginary line 15 cm from the release point. For experiments in which arena lengths were the same, we also tested the latency to reach the target.

Based on results from the first experiment, we designed a choice test in which a short, close target and a tall, distant target were presented simultaneously in a horizontal V-maze (Fig. 2). An entry hole at the point of the V-maze was sized to fit a syringe. After a 5-min acclimation period in the syringe, a spider was released into the maze. A glass barrier blocked access to the corridors but allowed the spider to view both targets. After 10 min, the glass barrier was removed by gently sliding it to one side through a slit in the arena wall. The open slit was then blocked by foam core. The spider was allowed 15 min to make a choice, defined as its two anterior legs touching a target. We tested 40 spiders. To eliminate the effect of side bias, we

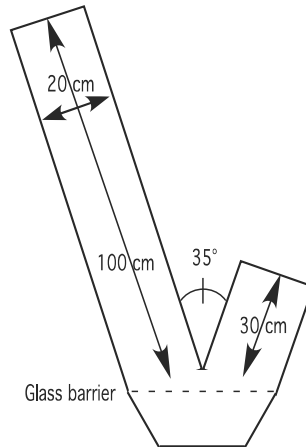


Fig. 2 The arena for the choice test. Walls were 20 cm high except the wall at the end of each corridor and 13 cm of the adjacent side walls, which were 38 cm high. The corridors were interchangeable, and their positions were reversed after every 10 trials.

switched the arms of the V-maze after every 10 spiders. Nine spiders that did not make a choice were dropped from the data set.

Target Color, Contrast and Shape

To tease apart the effects of a target's color and its contrast with the background, we constructed two arena types of the same dimensions as the small no-choice arena described above. The inner walls and floor were painted either white or green. We used targets identical to the short target used in the first experiment, painted either white or green (Fig. 1a). We tested spiders in one of the four combinations of arena and target color. Based on our results, we added a fifth treatment to assess the effect of target shape on spider movement. This target type was composed of 6 mm-thick wooden geometric shapes (Lara's Crafts, Fort Worth, Texas) that a spider would not normally encounter in the wild. Its maximum width and height were the same as that of the short target (Fig. 1b). This target was painted green (Delta Ceramcoat nontoxic acrylic paint, City of Industry, California) and used only in green arenas. Three replicates of each arena and target type were constructed and used equally often throughout the experiment.

Because we had access to *P. clarus* and *P. audax* only briefly, we tested them only in small white arenas. We randomly assigned 30 *P. princeps*, 32 *P. clarus*, and 42 *P. audax* to be tested with either the green or white target. We assigned an additional 45 *P. princeps* to one of the three green-arena treatments (green, white, or geometric green target). All spiders were female and tested only once. We taped the trials and scored the tapes as above.

Statistical Analyses

We analyzed the no-choice test results using logistic regression on JMP for Macintosh (SAS Institute 1995). In each case, the dependent variable was whether spiders reached the target. For the experiment on target size and distance, the

independent variables were arena length, target size, and their interaction. For the experiment on target color, because we tested only *P. clarus* and *P. audax* in white arenas, we analyzed the influence of species, target color, and their interaction for white arenas only. Next, we tested the effect of target, background color and their interaction on movement of *P. princeps* only. Lastly, we tested the effect of target shape (green grass-like target vs. green geometric-shapes target) on the movement of *P. princeps* in green arenas.

Data for latency to reach the 15-cm mark and to reach the target were non-normal. Therefore, for multiple-factor tests, we used nonparametric bootstrap analyses (using code in Jakob et al. 1998, rewritten in C++) and for the comparison between the geometric-shapes target and grassy target, we used a Mann-Whitney U test (Statview, Abacus Concepts 1995).

For the choice test, we used a binomial test to compare the number of spiders that reached the short, close target with those that reached the tall, distant target (expected, 50:50).

Results

Target Size and Distance

In no-choice tests, arena length significantly affected the willingness of *P. princeps* to move to a target: distant targets were less often reached (logistic regression; $\chi^2=7.0$, $P<0.01$; Fig. 3). There was no significant effect of target size alone on spider movement ($\chi^2=1.98$, $P>0.15$). There was a significant interaction between arena length and target size ($\chi^2=4.27$, $P<0.04$): spiders less often reached a distant, short target than any other target and distance combination (Fig. 3). We found no differences in the latency to reach the 15-cm mark (ANOVA; overall mean \pm SE: 138 \pm 31 s; arena length: $F_{1,48}=2.94$, $P=0.096$; target size: $F_{1,48}=0.01$, $P>0.9$; arena length \times target size: $F_{1,48}=0.38$, $P>0.5$).

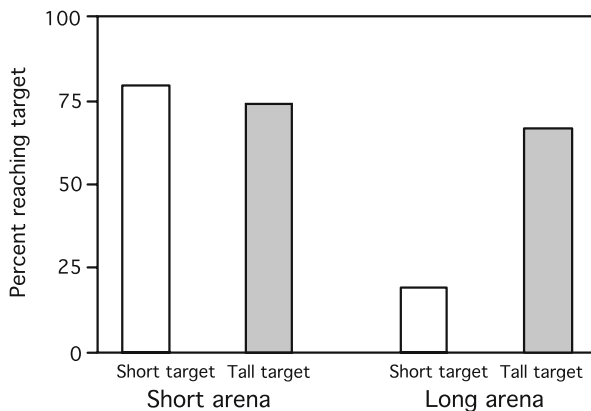


Fig. 3 The percentage of *P. princeps* in no-choice tests that reached short or tall targets in small or long arenas. $N=15$ per treatment.

Of the 31 spiders that made a choice in the choice arena, 14 reached the short, close target and 17 reached the tall, distant target. These results did not differ significantly from an expected value of 50:50 (binomial test, $P>0.7$). These findings suggest that the spiders treated the targets as being equivalent. Our sample size was large enough to enable us to detect large differences at $P=0.05$ (power, 87%, see Cohen 1977), suggesting that we can cautiously conclude that spiders treated these targets equivalently.

Target Color, Contrast and Shape

In the white no-choice arena, the three *Phidippus* species moved to the green target more frequently than to the white target (logistic regression; $\chi^2=21.1$, $P<0.001$). There was no significant difference across species in movement to a target ($\chi^2=2.1$, $P>0.3$) (Fig. 4). In green-target trials, 42 of 52 spiders (80.7%) moved to the target, whereas only 20 of 52 spiders (38.5%) reached the target in white-target trials. We found no significant differences in the latency to reach the 15-cm mark (ANOVA; overall mean \pm SE=89 \pm 17 s; species: $F_{2,93}=1.38$, $P>0.2$; target color: $F_{1,93}=0.05$, $P>0.8$; target color \times species: $F_{1,93}=0.74$, $P>0.4$) or the target itself (overall mean \pm SE=225 \pm 30 s; species: $F_{2,57}=0.92$, $P>0.3$; target color: $F_{1,57}=0.01$, $P>0.9$; target color \times species: $F_{1,57}>1.19$, $P>0.3$).

The contrast between target color and arena color did not significantly affect the propensity of *P. princeps* to reach a green target (logistic regression; $\chi^2=0.007$, $P=0.9332$): irrespective of arena color, *P. princeps* moved to the green target more than the white target ($\chi^2=23.44$, $P<0.001$; Fig. 5). We found no differences in the latency to reach the 15-cm mark (ANOVA; overall mean \pm SE=99 \pm 30 s; arena color: $F_{1,47}=0.13$, $P>0.7$; target color: $F_{1,47}=0.01$, $P>0.9$; arena color \times target color: $F_{1,47}=0.39$, $P>0.5$) or the target itself (ANOVA; overall mean \pm SE=256 \pm 91 s; arena color: $F_{1,47}=0.73$, $P>0.4$; target color: $F_{1,47}=0.28$, $P>0.6$; arena color \times target color: $F_{1,47}=1.64$, $P>0.2$).

Target shape also significantly influenced whether *P. princeps* reached a target (logistic regression; $\chi^2=9.5$, $P=0.002$). Only 5 of 15 spiders (33.3%) moved to the green geometric-shapes target, compared to 81.8% of spiders reaching the green grass target. There were no significant differences in the latency to reach the 15-cm mark (overall mean \pm SE=85 \pm 49 s; Mann-Whitney U, tied $Z=-0.5$, $P>0.6$) or the target (overall mean 341 \pm 81 s; tied $Z=-1.331$, $P>0.15$).

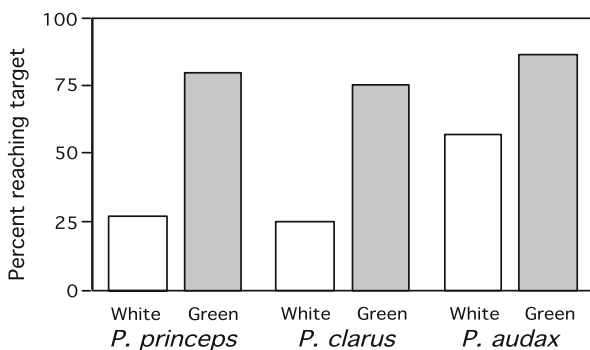


Fig. 4 The percentage of three species of *Phidippus* in no-choice tests that reached green or white targets in white arenas. For each test, $N=15$ for *P. princeps*, 16 for *P. clarus*, and 21 for *P. audax*.

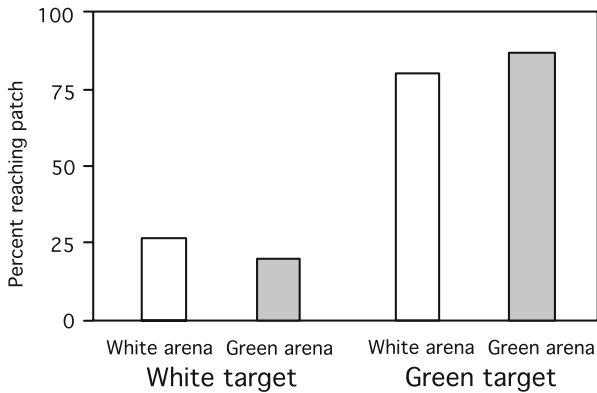


Fig. 5 The percentage of *P. princeps* in no-choice tests that reached green or white targets in green or white arenas. $N=15$ per treatment.

Discussion

The willingness of spiders to cross inhospitable open space was influenced strongly by characteristics of the target on the other side. Distance to the target, the interaction between target size and distance, and the target's color and shape all significantly affected spider movement, but there was no significant effect of how much the target contrasted with the background.

Distance to the target was important: in no-choice tests, spiders crossed open space significantly less often to short, distant targets than to other targets. The spiders either failed to detect short, distant targets or else they detected them, but deemed reaching them not worth the risk of crossing open ground. Our data do not allow us to distinguish between these two hypotheses. However, other research suggests that the visual acuity of *Phidippus* species is sufficient for discerning the targets we used in our experiments. For example, individuals of *Phidippus johnsoni* in the field have been seen displaying to other living conspecific individuals from distances of 50 cm (Jackson 1980) and, in laboratory experiments, *P. johnsoni* and *P. femoratus* sometimes displayed to their own mirror images from over 20 cm away (Harland et al. 1999). These findings from the literature on *Phidippus*, combined with what is known about the exceptional eyesight of salticids in general (Harland and Jackson 2004), give us confidence that the species of *Phidippus* that we studied would have had little difficulty discerning the targets we used.

Spiders in no-choice experiments moved to tall, distant targets as often as to short, close targets that presented a retinal image of the same size. In accordance with those results, spiders presented with a simultaneous choice of tall, distant or short, close targets did not choose one significantly more than the other. Experiments based on classical conditioning are needed to determine whether spiders judge objects that subtend the same visual angle to be identical, as has been found in other arthropod species (see Introduction), or whether taller targets are more desirable and thus worth any increased risk inherent in crossing an open area. Our results do, however, provide

another example of a species whose movement behavior depends on apparent target size, and we suggest that models of animal movement that take into account perceptual range can be made more realistic by including target size as a parameter.

Contrary to our prediction, spiders consistently moved to green grass-like targets and not to white grass-like targets irrespective of their contrast with the background. Perhaps contrast would be more important to the spiders under dimmer light than used in our test conditions. Furthermore, spiders moved infrequently to the green target composed of geometric shapes, so spiders are not responding to green color alone. In short, the spiders responded more strongly to targets that were, to our eyes, more similar than other targets to grass in color and form. We do not know whether this behavior is innate or results from experience with grass, as our spiders were field caught.

It is clear that even slight changes in habitat characteristics can profoundly affect the movement patterns of *Phidippus*. It is likely the same is true for other salticids and other animal species. Understanding which target characteristics entice an animal to cross inhospitable habitat may lead to useful management tools for threatened species or species used as biocontrol agents. For example, planting a line of tall fast-growing trees at the edge of a patch may increase the detection of the patch of habitat or the likelihood that this habitat patch will be identified as suitable. This in turn may help attract colonists.

Although our experiments were conducted in small-scale arenas and over short time periods, we have some indication that the behavior of *P. clarus* is similar under more natural conditions. In field enclosures, *P. clarus* did not cross 4-m gaps separating 1-m² habitat targets over the course of an 11-hour day (Baker 2007). At even larger scales, additional factors may come into play. For example, in root voles, corridors were shown to enhance interpatch movement in a short-term study of home range use (Andreassen et al. 1998), but had less effect when the time scale was long enough to encompass home-range shifts (Andreassen and Ims 2001). Larger-scale field experiments may be especially easy to carry out with jumping spiders. These highly visual animals can be useful in our understanding of the relationship between individual behavior and landscape-level phenomena.

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