



Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons

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We studied movement patterns and the use of navigational beacons in the jumping spider *Phidippus clarus* (Salticidae). *Phidippus clarus* does not build prey-capture webs, but does construct thick silken nests used as nighttime retreats. We measured the degree of nest site fidelity with individually marked spiders and a grid of artificial nest tubes. Females in August were most site-faithful, followed by July females and then by males. Spiders moved long distances through complexly structured habitats, suggesting that nests are likely to be out of sight of the spiders during the day, and that spiders must use cues other than their nest to navigate. We then tested whether females used beacons to find their nests. In one experiment, spiders colonized nest tubes that were either associated with beacons (orange wooden dowels) or not. They were then released near a test beacon. Spiders experienced with beacons readily approached either their own beacon or a similar, novel beacon in a different location. In contrast, spiders with no experience with beacons were significantly less likely to approach the test beacon. In a second test, spiders tested with novel beacons of the same colour as their own were significantly more likely to approach it than were spiders tested with novel beacons of a different colour. We conclude that *P. clarus* are likely to need navigational skills and are able to use beacons as a method of navigation. Jumping spiders provide a new and tractable model system for the study of navigation and space use.

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Many species make forays away from nests, and then face the challenge of finding them again. Returning to a nest can be accomplished via a number of nonexclusive navigational mechanisms that vary among taxa and situations (Collett & Zeil 1998; Hogarth et al. 2000). One method is the use of beacons or landmarks. Beacons, also known as proximal cues, are close to or part of a destination (Shettleworth 1998). Landmarks, also known as distal cues, guide an individual to a destination but are not inherently part of the destination (Shettleworth 1998). Classic examples of landmark and beacon use include Tinbergen's (1975) study of digger wasps, *Philanthus triangulum*, that learned their nest hole was surrounded by a ring of pine cones. When the ring was displaced, the

wasps continued to search in its centre. Von Frisch (1967) observed that honeybees, *Apis mellifera*, tend to use isolated trees as landmarks when returning from a foraging excursion, even when doing so takes a bee off its direct course home. Landmark and beacon use have since been demonstrated in a number of arthropod species, including other solitary and social bees, ants, cockroaches and waterstriders (e.g. Junger 1991; Cheng 2000; Collett et al. 2002; Graham & Collett 2002).

Spiders provide good model organisms for the study of movement, because many species are amenable to both field studies and experimental manipulation. Many prior studies have identified a broad range of factors that influence a spider's decision to move between sites, such as the presence of prey or prey-related cues (Greenstone 1983; Jakob 1991, 2004; Persons & Uetz 1996; Walker et al. 1999; Kreiter & Wise 2001), web destruction (Hodge 1987; Chmiel et al. 2000), interactions with conspecifics (Leclerc 1991; Smallwood 1993; Jakob 2004), sun exposure and thermal extremes (Hodge 1987; Lubin et al.

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1993), predation risk (Lubin et al. 1993) and mate searching (Henschel 2002). Far fewer studies have addressed specifically how spiders navigate, such as the use by some species of polarized light and idiothetic cues (e.g. Seyfarth et al. 1982; Dacke et al. 1999). To our knowledge, there have been no studies of beacon or landmark use in spiders.

Our study species, *Phidippus clarus*, is a jumping spider (Family Salticidae) found in old fields throughout much of North America. Jumping spider behaviour is widely studied, with over 125 studies by R. R. Jackson and collaborators alone, but relatively little is known about their daily movements in the field. Like other jumping spiders (Land 1985), *P. clarus* has one of the most highly developed invertebrate visual systems, and has camera-type eyes (Land 1972) rather than compound eyes. It relies on vision in prey capture (e.g. Jackson 2000; Li et al. 2003), courtship and mate choice (e.g. Clark & Morjan 2001), and aggressive displays (e.g. Wells 1988; Taylor et al. 2001). The most rigorous studies of jumping spider photoreceptors show spectral sensitivity peaks in the green and UV range (Blest et al. 1981; Peaslee & Wilson 1989). Additional information suggests that jumping spiders may have spectral sensitivities in blue-green, yellow and red (DeVoe 1975; Yamashita & Tateda 1976; reviewed in Land 1985). Jumping spiders can also discriminate between a variety of colours associated with aversive levels of heat (Nakamura & Yamashita 2000).

Jumping spiders build silken nests, which are likely to be valuable. Nests provide shelter at night, during inclement weather, and when moulting, mating, ovipositing and guarding young (Jackson 1979). Silk is energetically expensive (e.g. Jakob 1991). Nests are generally placed in sheltered areas that may be limited. For example, *P. audax*, *P. clarus* and *P. princeps* favour the umbels of Queen-Anne's lace, *Daucus carota* (Tessler 1979; personal observation). In some jumping spider species, there is indirect evidence that large individuals will usurp the nests of smaller ones (Plett 1962), suggesting that salticid nests are a costly resource. At least two species of salticids have been observed to leave their nests during the daytime and to return to the same nest at night, *Jacksonoides queenslandicus* in the field (Jackson 1988) and *P. audax* in terraria inside a greenhouse (Popson 1999). However, few data are available on whether jumping spiders move out of sight of their nest during the day. Hill (1979) often found members of several species waiting for prey on flowering plants; this strategy may mean that spiders do not wander from their nests and thus do not need long-range navigational skills. However, Jackson (1988) observed several individuals of *J. queenslandicus* return directly to a nest from positions where the nest was out of view.

We evaluated two sets of data on the behaviour of *P. clarus* in the field. First, we examined natural movements of spiders in the field. We studied both nest site fidelity and the distance that spiders move during a foraging bout; only if they move substantive distances will they require much navigational ability to find their nests again. Second, we also investigated whether jumping spiders can use visual cues in the form of beacons to find their nests.

METHODS

Study Sites

All work was conducted in old fields on or near the campus of the University of Massachusetts, Amherst, U.S.A. containing a variety of grasses, shrubs and flowering plants, predominantly milkweed (*Asclepias syriaca*), goldenrod (*Solidago* spp.), sweet clover (*Melilotus* spp.) and asters (*Aster* spp.).

Site Fidelity

We measured site fidelity by recording whether spiders returned to the same nest on consecutive nights. We took advantage of the fact that some *Phidippus* jumping spiders, including *P. clarus*, readily construct nests inside pieces of tubing (Popson 1999). On 7–8 June 2001, we set up a 30 × 30-m grid of 90-cm-tall surveyor's flags (Ben Meadows, Janesville, Wisconsin, U.S.A.) made of a wire pole with a 7.5 × 6.5-cm plastic flag. Flags were spaced 2 m apart and labelled with their coordinates. We made artificial nest sites (approximately 3.8 cm long, 1.5 cm diameter) of flexible clear plastic plumber's tubing and painted them black with spray paint (Krylon flat black, Sherwin-Williams, Cleveland, Ohio, U.S.A.). We tied tubes to flagpoles with string so that the tubes hung horizontally about 40 cm above the ground. We then allowed a 3-week colonization period for individuals to find nest tubes and construct nests within them.

After the colonization period, we collected spiders from nest tubes by gently squeezing the sides of tubes until they emerged. To identify spiders individually, we used bee tags (2.3 mm diameter; The Bee Works, Orillia, Ontario, Canada) with unique colour/number combinations. We attached tags to the dorsal surface of spiders' abdomens with nontoxic glue by holding the spider with a piece of facial tissue over the cephalothorax. In late June and early July, we tagged some subadults ($N = 24$), but because tags are lost during a moult, we used only adults in our data analysis. We tagged adults throughout the term of this study, and there was no evidence of tags detaching from adults' bodies. We recorded nest tube coordinates and spider sex, and returned marked spiders to their nest tubes.

During the first 3 weeks in July and August 2001, we checked nest tubes twice a day for occupancy. All tubes were checked in the evening between 1900 and 2000 hours. We recorded the presence or absence of silk, the presence of untagged individuals, and the tag number/colour of marked individuals. We also conducted day checks (between 1100 and 1400 hours) of tubes that held tagged individuals during the previous evening's check.

We scored site fidelity as follows. We ignored the first night after marking, because spiders may behave atypically after disturbance. We scored spiders as 'site-faithful' if they were found in the tube during an evening check, absent during the next daytime check, and then back in the same tube in the evening. Thus, only spiders that had left the tube and returned to it were recorded as site-faithful. If spiders were in a tube during two consecutive nights as well as the intervening day, we discarded the data and used the

data from the next day. We scored spiders as 'moving' if they were in a tube on one evening and absent on the next evening, regardless of whether they were in the tube during the daytime check. This category thus also includes spiders that disappeared for other reasons, such as predation or attack by parasitoid wasps (C.D.H., personal observation).

For the first analysis, we used only the first score for each spider (site-faithful or not) so that each individual contributed only one data point to the analysis. We used a contingency table analysis to compare the incidence of site fidelity between males and females in July. We found no males in August, so we compared site fidelity in July and August for females only.

In the second analysis, we calculated average site fidelity for each spider across all observations. We compared male and female averages with a Mann–Whitney *U* test. We used flag coordinates to calculate distances moved by individuals that were found in more than one nest tube. To calculate the mean distance moved by individuals that were not found for several nights, we divided the total distance moved by the number of nights absent.

Focal Observations

Observations were divided evenly between morning and afternoon, and were conducted by the authors and several undergraduate assistants. An observer walked slowly through the fields until a *P. clarus* was sighted. The observer then followed the spider for 5–15 min, or until it was lost from view. We minimized our disturbance of the spiders by following slowly and taking care not to disturb the vegetation that spiders were on. Jumping spiders, when disturbed, pivot and orient their anterior median eyes towards the stimulus. If spiders oriented to the observer repeatedly or for an extended period, we stopped observations and discarded the trial data. We placed surveyor flags at the spider's locations at the start and end of each trial, and used these to measure net distance travelled. Because arthropod movement is temperature dependent, we also recorded ambient temperature.

We recorded the following behaviours using an audio microcassette recorder: stop (body not moving although legs or pedipalps may move), walk (moving the body along by stepping with legs), leap (jumping with body and legs completely off the substrate; used to move between distant stems), prey capture (attacking and subduing prey), feeding (holding prey in chelicerae), interaction with a conspecific, and inside a silken nest. We also noted when spiders were temporarily hidden from view by vegetation. In the laboratory, we scored the audiotapes with behavioural data analysis software (The Observer, Noldus Inc., Leesburg, Virginia, U.S.A.). We established interobserver reliability in the field through training sessions in which two observers simultaneously recorded the behaviour of the same spider. Observers also independently scored the same audiotapes with The Observer. The Observer's reliability analysis indicated that pairs of observers were in agreement more than 85% of the time. We collected data on 20 adult males and 10 adult females. The data were not normally distributed, so we used nonparametric tests to compare movement patterns of males and females.

Beacon Experiment 1

We tested whether female spiders that had experience with a beacon were more likely to approach either their own or a novel beacon than were naïve spiders. For beacons, we used wooden dowels (90 cm long × 0.8 cm diameter), painted orange (Krylon fluorescent orange; peak absorbance 614 nm). The beacons were unlike anything else in the spiders' habitat. In August 2001, we erected 30 vertical dowels by inserting one of their ends into the ground. Dowels were spaced haphazardly within the field, none closer than approximately 10 m, and were hidden from view of other dowels by vegetation. We tied a nest tube, as above, onto each dowel with string so that the tube hung horizontally about 70 cm above the ground. We also slid a 'blinder', constructed from a deli cup lid (12 cm diameter) painted black with a slit cut in the centre, onto each dowel below the nest (Fig. 1) so that the nest tube could not be viewed from the ground, to ensure that spiders would respond only to the beacon rather than to characteristics of the nest tube.

We also established nests that were not associated with beacons. These were hung on small surveyor's flags (a wire pole with a small plastic flag). After allowing a week for the first tubes to be colonized, we began trials. Trials were conducted periodically from August to October 2001.

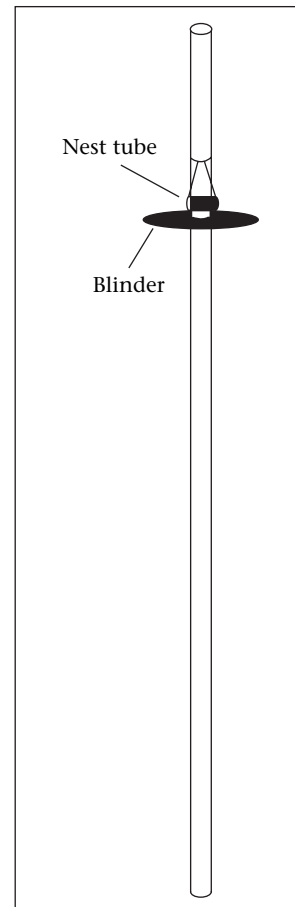


Figure 1. A beacon with a nest tube and blinder.

Because spiders were unmarked, we do not know how long they had experience with a beacon.

Females were divided among the following three treatments. (1) Naïve: spiders were collected from nest tubes on survey flags and tested with a beacon that did not have an occupied nest tube. We used naïve as a shorthand to indicate spiders that did not have recent experience with beacons. However, because spiders were unmarked, they may have had experience with beacons after the beacons were placed in the field and before the start of the trials. (2) Experienced/own: spiders were collected from nest tubes associated with beacons and tested with these same beacons in the same location. (3) Experienced/novel: spiders were collected from nest tubes associated with beacons but were tested with an unfamiliar beacon located at least 10 m away from their home area that did not have an occupied nest tube. These novel beacons looked the same as the beacons with which the spiders were familiar, but they were surrounded by a new constellation of cues. We randomly assigned spiders to treatments and tested 15 female spiders in each group. After a spider had been used in a trial, it was captured to avoid retesting it and its nest tube was replaced by a clean one.

Trials were conducted between 1100 and 1500 hours. We located spiders in nest tubes and collected them as previously described. We held spiders in clear plastic snap-cap vials (5.5 cm long \times 2.5 cm diameter). We placed the vial on the ground 15 cm from the base of the beacon. We then allowed a 5-min acclimation period, during which the spiders could look about through the walls of the vial. We then removed the vial's lid and moved approximately 2 m away to minimize any distraction caused by our presence. Trials began once a spider had ascended the vial.

We recorded observations with a Sony M-527V micro-cassette recorder. We noted whether a spider oriented towards the beacon (swivelling its body to direct its image-forming AM eyes towards it). We scored a trial as 'approached' when spiders reached the beacon and climbed up it. We scored a trial as 'did not approach' when the spider had moved 50 cm from the beacon and was travelling away from it.

Beacon Experiment 2

In beacon experiment 1, female spiders selected their own nest sites, either attached to a beacon or to a surveyor's flag. It is possible that females in the two treatment groups that chose to nest in tubes attached to beacons were likely to move to a beacon during the test trial not because of experience, but simply because they were attracted to the dowels. In 2002–2003, we conducted a second experiment in which all females had experience with beacons, and their task was to distinguish between beacons that differed only in colour. This experiment was conducted in a field adjacent to that used in beacon experiment 1, which had become unacceptably woody. We selected a flat colour (Krylon flat white; peak absorbance 515 nm) and a fluorescent colour (Krylon fluorescent orange; peak absorbance 614 nm), because we wanted to increase the likelihood that spiders could detect the difference between stimuli. We set out 30 dowels of

each colour with attached nest tubes, and let spiders colonize them as in beacon experiment 1. All spiders ($N = 54$) were tested at a novel dowel, but half were tested at a dowel of the same colour as the one on which they had established their nest, and half were tested at a dowel of the other colour. Test dowels were at least 10 m apart and out of sight of the spider's home dowel. Treatments were randomly assigned. All other aspects of the protocol were identical to beacon experiment 1, except that we omitted the blinders during the colonization period, tied nest tubes to dowels with twist ties instead of string, and recorded data with pen and paper instead of audiocassette.

RESULTS

Focal Observations

Observations lasted for 10.3 ± 0.85 min (mean \pm SE). Spiders sometimes attached a silk line to a plant before jumping across a gap in the vegetation, but they generally did not leave a silk trail.

Ambient temperature did not differ between male and female sample periods (range 23–34 °C; Mann–Whitney U test: $U = 62.0$, $N_1 = 20$, $N_2 = 9$, $P = 0.1869$). There was no correlation between temperature and rate of movement (distance moved (m) during observation period/duration of observation period (min)) for females (Spearman rank correlation, corrected for ties: $r_s = 0.596$, $N = 9$, $P = 0.0919$) or males ($r_s = -0.034$, $N = 20$, $P = 0.9922$), and therefore we ignored temperature in further analyses.

Data were skewed, so we used nonparametric statistics (Table 1). The median net distance that spiders moved was 0.25 m, but distance ranged widely (0–20 m). Males spent more time moving and moved at a faster rate than females. Females were seen foraging (attacking or feeding on prey) more often than were males. There was no sex

Table 1. Male and female behaviour during focal observations

Behaviour	Sex	Range	Median	U	Tied		
					Z	N	P
Walking (% time in view)	M	0.3–73	28.3	27	–3.212	20	0.0013
	F	0–19.3	4.0				
Feeding (% time in view)	M	0	0	80	–2.034	20	0.05
	F	0–90.4	0				
Interacting (% time in view)	M	0	0	90	–1.414	20	0.66
	F	0–14.7	0				
Net movement rate (cm/min)	M	0–204	6.0	18.5	–3.634	20	0.0003
	F	0–2.4	0.4				
Leaping (leaps/cm travelled)	M	0–200	10.9	50.5	–0.233	18	0.8154
	F	0–33.3	15.5				

Data were not normally distributed, so statistics are from Mann–Whitney U tests.

difference in the number of leaps that spiders made as they moved through the vegetation. Few spiders interacted, and interaction rate did not differ between the sexes.

Site Fidelity

Of 102 marked spiders, 83 provided data on site fidelity. Nineteen were not seen again after marking. In our first analysis (in which we used only the first measure of site fidelity for each individual), 61% of females ($N = 74$) showed site fidelity. Males were found only in July, and the sample size was much smaller ($N = 9$). We found a significant difference in site fidelity between July males and July females (G test: $G_2^2 = 18.651$, $P < 0.0001$) and between July and August females ($G_2^2 = 13.604$, $P < 0.0002$; Fig. 2). August females showed more site fidelity than expected (91% observed versus 57% expected), and males showed less fidelity than expected (22% observed versus 56% expected).

We also analysed average site fidelity for each individual over multiple observations, as many as 12 per individual. Females returned to their nests, on average, in 61% of the observations, whereas males returned, on average, in 11% (Mann–Whitney U test: tied $Z = -2.282$, $P < 0.03$). Of 102 marked spiders, 40 (29 females and 11 males) were seen in at least two different tubes. Some spiders ($N = 14$) were found in different tubes on consecutive nights. Others ($N = 26$) disappeared for varying durations before appearing in a new tube; for these, we calculated average daily movement. The first group had significantly higher per night movement rates than did the second (Mann–Whitney U test: tied $Z = -4.822$, $P < 0.0001$), suggesting that spiders that were absent for several nights either did not move consistently each night, or moved back and forth in the same area. We therefore discarded distance data for multiple days and examined only spiders for which we had data from consecutive nights. Mean \pm SE distance moved was 12.5 ± 1.92 m ($N = 14$). Males and females did not significantly differ, but sample sizes were extremely small (female: $N = 11$, mean = 11.5 ± 7.81 ; males: $N = 3$, mean = 16.3 ± 1.13 ; Mann–Whitney U test: $U = 11.0$, $P = 0.3918$).

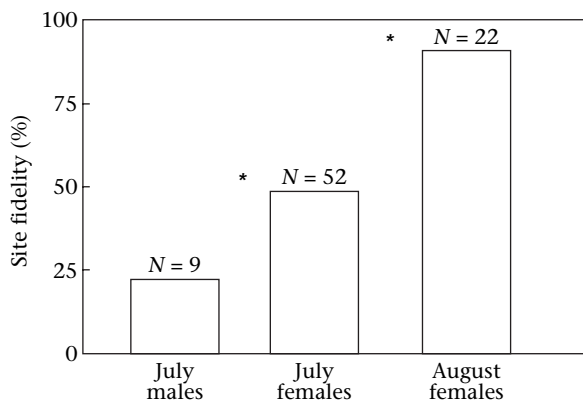


Figure 2. Site fidelity of male and female jumping spiders, expressed as the percentage of spiders that did and did not return to nests after exiting them during the day. * $P < 0.001$.

Beacon Experiments

There were significant differences between the three treatment groups (G test: $G_2^2 = 10.04$, $P = 0.0066$). Most spiders that were not experienced with beacons did not approach beacons. There were no differences between spiders tested with a familiar beacon versus those tested with a novel beacon ($G_1^2 = 1.243$, $P = 0.2644$; Fig. 3).

Four spiders, all from the naïve group, failed to orient to the test beacon at any time. Spiders with experience might be more likely to be looking for a beacon, and thus more likely to orient to one. Spiders often climbed to the top of the vial and pivoted about, and then immediately approached a beacon after they oriented to it. It is also possible, however, that some spiders simply did not see the beacon because of the direction that they exited the vial: the primary eyes have high acuity but a small visual angle (Foelix 1996). When we omitted spiders from the analysis that never oriented to a beacon, the patterns of results did not change (G test: $G_2^2 = 8.359$, $P < 0.02$).

In beacon experiment 2, spiders tested with a novel beacon of a familiar colour were significantly more likely to reach it than were spiders tested with a novel beacon of an unfamiliar colour (G test: $G_1^2 = 11.528$, $P < 0.0009$; Fig. 4). In this experiment, only one spider (experienced with a white beacon and tested with orange) failed to orient. When it was dropped from the analysis, results did not change ($G_1^2 = 10.652$, $P < 0.002$).

Colour itself had no effect on performance. Of spiders tested with a novel colour, 40% ($N = 15$) of spiders reached the orange beacon and 33.3% ($N = 12$) reached the white beacon (G test: $G_1^2 = 0.128$, $P = 0.7210$). Of spiders tested with a familiar colour, 83.3% ($N = 12$) reached the orange beacon and 80% ($N = 15$) reached the white beacon (G test: $G_1^2 = 2.016$, $P = 0.1557$).

DISCUSSION

Phidippus clarus jumping spiders appear to require navigational abilities. Females displayed site fidelity, in that

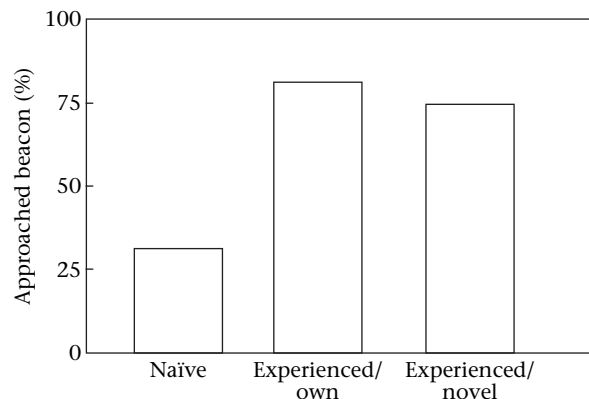


Figure 3. The percentage of spiders that moved to a beacon during a trial in the field. Spiders were either naïve to beacons, experienced with beacons and tested with their own beacon, or experienced with beacons and tested with a novel but similar beacon. $N = 15$ per group.

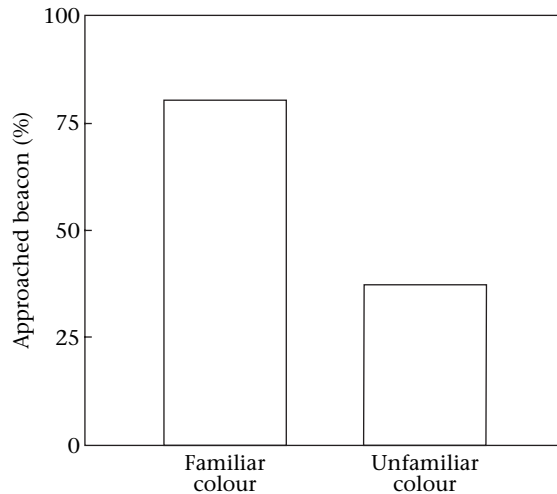


Figure 4. The percentage of spiders that moved towards a novel beacon during a test trial in the field. Beacons were either of a familiar colour or of a novel colour. $N = 27$ per group.

about 50% of marked spiders returned to their nests on consecutive nights in July and 90% did so in August, when most egg sacs are laid. Males did not show site fidelity unless paired with females. Many individuals moved long distances during our focal observations. This behaviour, along with living in a heterogeneous habitat composed of thick vegetation, suggests that at least some spiders are likely to get out of sight of their nests during the daylight foraging period. Our beacon experiments show that spiders can use visual cues to recognize the area around their nest.

It is striking that spiders responded strongly to novel beacons that looked the same as the beacon that held their nest (compare experienced/own and experienced/novel groups in Fig. 3 with familiar colour group in Fig. 4), even though novel beacons were in different locations with a new array of potential distracters, including, for example, different plants and orientation to the sun. Beacons may have been preferred cues for several reasons. First, they were very close to the nest; using beacons that are closely associated with a goal is less computationally demanding than using distal cues (see discussion in Shettleworth 1998). For example, bees emphasize the information from landmarks that are close to the goal (reviewed in Collett & Collett 2002). Second, beacons were very noticeable (at least to our eyes) against the lush green background of plants. Detection of distinctive landmarks is generally the first processing step for using visual landmarks (Möller 2002). It may even be that spiders select nest sites near easy-to-remember objects. Some ants deliberately choose foraging routes near objects that can be used as beacons, possibly to facilitate route memory (Graham et al. 2003). Spiders that select nest sites that are easy to locate from afar may reduce time spent searching for them.

We offered a fairly straightforward challenge to *P. clarus*: spiders needed only to aim at a single beacon to complete a short journey back to their nest. It is possible that spiders, like many insects, can use landmarks and beacons

in more complex ways (e.g. Collett 1996). Elegant experiments have demonstrated that insects perform systematic flight manoeuvres to acquire information about their nest location (Zeil et al. 1996), learn global landmark–landmark relationships (Pastergue-Ruiz et al. 1995) and chain together separate segments of a route, each guided by different snapshots of landmarks (Collett & Collett 2002; Durier et al. 2003). Many of these skills have been found for animals, such as ants and bees that follow long and reasonably stable routes (Collett et al. 2003). We do not know whether *P. clarus* or other jumping spiders habitually reuse routes or whether they simply learn about the appearance of the area around their nest. We often see *Phidippus* spp. waiting for prey on flowering plants, and they may well travel between their nest and a plant for the duration of its flowering.

What, exactly, did spiders learn about the beacons? Insects have been shown to use numerous visual features, including colour, size, edge orientation and symmetry (Collett & Collett 2002). *Phidippus clarus* needed only colour to distinguish between beacons in beacon experiment 2, but we do not know whether they did so using hue, brightness, saturation, or polarization cues. Interestingly, bees use colour to distinguish targets only when the image subtends more than 15° , but otherwise use achromatic cues (Giurfa et al. 1996, 1997). In our study, the beacons were very close: the beacon below the blinder subtended a visual angle of approximately 75° from the spiders' release points. Also, because the spatial resolution is much higher in jumping spiders than in bees (Land 1985), the task of returning to a coloured beacon should presumably be easier for jumping spiders. Although other studies have shown that spiders used colour to discriminate between nearby cues (Popson 1999; Nakamura & Yamashita 2000), to our knowledge, there are no such studies involving distant cues.

Besides visually based beacons, jumping spiders may use other navigational mechanisms, some of which have been identified in other spider families. For example, the wandering spider *Cupiennius salei* (Ctenidae) has been shown to return to a starting location using only the memory of idiothetic information gathered by the lyri-form organs (Seyfarth et al. 1982). Funnel-web spiders (Agelenidae) use a combination of external and idiothetic cues (Görner & Claas 1987; Görner 1988). Individuals of some spider families, including Gnaphosidae, navigate with the help of canoe-shaped tapeta in their secondary eyes that detect polarized light (Dacke et al. 1999; Marshall 1999). Jumping spiders lack these tapeta and their ability to use polarization is unknown. Lycosid spiders also lack specialized tapeta, but navigate via polarized light detected by their anterior median eyes (Ortega-Escobar & Muñoz-Cuevas 1999). A striking example of a long-distance return movement is that of the dancing white lady spider, *Leucorchestris arenicola*. These spiders wander over 90 m from their nest across open, featureless dunes of the Namib Desert, and then take a significantly more direct path back. The mechanism for this ability is still unknown (Henschel 2002; Nørgaard et al. 2003). Still other species follow silken trails. Minch (1978) discovered that *Aphonopelma chalcodes* (Theraphosidae)

move approximately 15–20 cm away from their burrows when foraging. On their outbound path, they constantly attach silk draglines to the substrate and follow these when returning. In contrast, *P. clarus* rarely laid down draglines except when preparing to leap across a gap. They also moved through grasses and small shrubs that flexed constantly in the breeze, which would render draglines unreliable for more than short periods of time. Thus, we suspect that chemical cues incorporated into silk are not routinely used by *P. clarus* for navigation.

Spiders provide a good model system for examining sex differences in spatial learning in an arthropod. Differences are well known in mammals (reviewed in [Ecuyer-Dab & Robert 2004](#)) but are much less well known in insects and, to our knowledge, have not been examined in spiders. [Gaulin & FitzGerald \(1986, 1989\)](#) argued that, for mammals, the sex with the larger home range size should have better spatial memory. In our study, adult males travelled significantly further during focal observations than did females, but did not show nest site fidelity unless paired with females. However, this result does not exclude the possibility of male navigational abilities. Males sometimes visit more than one penultimate female and also display mate choice (C.D.H., unpublished data). It is possible that males use landmarks or beacons to navigate back to favoured females. We have not yet tested adult male *P. clarus* with beacons, because they disappear rapidly from the population within a few weeks after female maturity (C.D.H., unpublished data), but this would be an interesting next step.

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References

- [Blest, A. D., Hardie, R. C., McIntyre, P. & Williams, D. S.](#) 1981. The spectral sensitivities of unidentified receptors and the function of retinal tiering in the principal eyes of a jumping spider. *Journal of Comparative Physiology*, **145**, 227–239.
- [Cheng, K.](#) 2000. How honeybees find a place: lessons from a simple mind. *Animal Learning & Behavior*, **28**, 1–15.
- [Chmiel, K., Herberstein, M. E. & Elgar, M. A.](#) 2000. Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. *Animal Behaviour*, **60**, 821–826.
- [Clark, D. L. & Morjan, C. L.](#) 2001. Attracting female attention: the evolution of dimorphic courtship displays in the jumping spider *Maevia inclemens* (Araneae: Salticidae). *Proceedings of the Royal Society of London, Series B*, **268**, 2461–2465.
- [Collett, M., Harland, D. & Collett, T. S.](#) 2002. The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees. *Journal of Experimental Biology*, **205**, 807–814.
- [Collett, T. M. & Collett, M.](#) 2002. Memory use in insect visual navigation. *Nature Reviews*, **3**, 542–552.
- [Collett, T. S.](#) 1996. Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *Journal of Experimental Biology*, **199**, 227–235.
- [Collett, T. S. & Zeil, J.](#) 1998. Places and landmarks: an arthropod perspective. In: *Spatial Representation in Animals* (Ed. by S. Healy), pp. 18–53. Oxford: Oxford University Press.
- [Collett, T. S., Graham, P. & Durier, V.](#) 2003. Route learning by insects. *Current Opinion in Neurobiology*, **13**, 718–725.
- [Dacke, M., Nilsson, D. E., Warrant, E. J., Blest, A. D., Land, M. F. & O'Carroll, D. C.](#) 1999. Built-in polarizers form part of a compass organ in spiders. *Nature*, **401**, 470–472.
- [DeVoe, R. D.](#) 1975. Ultraviolet and green receptors in principal eyes of jumping spiders. *Journal of General Physiology*, **66**, 193–207.
- [Durier, V., Graham, P. & Collett, T.](#) 2003. Snapshot memories and landmark guidance in wood ants. *Current Biology*, **13**, 1614–1618.
- [Ecuyer-Dab, I. & Robert, M.](#) 2004. Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition*, **91**, 221–257.
- [Foelix, R. F.](#) 1996. *Biology of Spiders*. Oxford: Oxford University Press.
- [Gaulin, S. & FitzGerald, R.](#) 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist*, **127**, 74–88.
- [Gaulin, S. & FitzGerald, R.](#) 1989. Sexual selection for spatial-learning ability. *Animal Behaviour*, **37**, 322–331.
- [Giurfa, M., Vorobyev, M., Kevan, P. & Menzel, R.](#) 1996. Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *Journal of Comparative Physiology A*, **178**, 699–709.
- [Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. & Menzel, R.](#) 1997. Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *Journal of Comparative Physiology A*, **180**, 235–243.
- [Görner, P.](#) 1988. Homing behavior of funnel web spiders (Agelenidae) by means of web-related cues. *Naturwissenschaften*, **75**, 209–211.
- [Görner, P. & Claas, B.](#) 1987. Homing behavior and orientation in the funnel-web spider, *Agelena labyrinthica* Clerck. In: *Ecophysiology of Spiders* (Ed. by W. Nentwig), pp. 275–297. Berlin: Springer-Verlag.
- [Graham, P. & Collett, T. S.](#) 2002. View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *Journal of Experimental Biology*, **205**, 2499–2509.
- [Graham, P., Fauria, K. & Collett, T. S.](#) 2003. The influence of beacon-aiming on the routes of wood ants. *Journal of Experimental Biology*, **206**, 535–541.
- [Greenstone, M. H.](#) 1983. Site-specificity and site tenacity in a wolf spider: a serological dietary analysis. *Oecologia*, **56**, 79–83.
- [Henschel, J. R.](#) 2002. Long-distance wandering and mating by the dancing white lady spider (*Leucorchestris arenicola*) (Araneae, Sparassidae) across Namib dunes. *Journal of Arachnology*, **30**, 321–330.
- [Hill, D. E.](#) 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. *Behavioral Ecology and Sociobiology*, **5**, 301–322.
- [Hodge, M. A.](#) 1987. Factors influencing web site residence time of the orb weaving spider, *Micrathena gracilis*. *Psyche*, **94**, 363–371.
- [Hogarth, L. A., Roberts, W. A., Roberts, S. & Abroms, B.](#) 2000. Spatial localization of a goal: beacon homing and landmark pilot-

- ing by rats on a radial maze. *Animal Learning & Behavior*, **28**, 43–58.
- Jackson, R. R.** 1979. Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. *Journal of Arachnology*, **7**, 47–58.
- Jackson, R. R.** 1988. The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae, Salticidae) from Queensland: intraspecific interactions, web-invasion, predators, and prey. *New Zealand Journal of Zoology*, **15**, 1–37.
- Jackson, R. R.** 2000. Prey preferences and visual discrimination ability of *Brettus*, *Cocalus* and *Cyrrba*, araneophagic jumping spiders (Araneae: Salticidae) from Australia, Kenya and Sri Lanka. *New Zealand Journal of Zoology*, **27**, 29–39.
- Jakob, E. M.** 1991. Costs and benefits of group living for pholcid spiders: losing food, saving silk. *Animal Behaviour*, **41**, 711–722.
- Jakob, E. M.** 2004. Individual decisions and group dynamics: why pholcid spiders join and leave groups. *Animal Behaviour*, **68**, 9–20.
- Junger, W.** 1991. Waterstriders (*Gerris patudum* F.) compensate for drift with a discontinuously working visual position servo. *Journal of Comparative Physiology A*, **181**, 47–58.
- Kreiter, N. A. & Wise, D. H.** 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia*, **127**, 417–424.
- Land, M. F.** 1972. Mechanism of orientation and pattern recognition by jumping spiders (Salticidae). In: *Information Processing in the Visual Systems of Arthropods* (Ed. by R. Wehner), pp. 231–247. Berlin: Springer-Verlag.
- Land, M. R.** 1985. The morphology and optics of spider eyes. In: *Neurobiology of Arachnids* (Ed. by F. G. Barth), pp. 53–78. Berlin: Springer-Verlag.
- Leclerc, J.** 1991. Optimal foraging strategy of the sheet-web spider *Lepthyphantes flavipes* under perturbation. *Ecology*, **72**, 1267–1272.
- Li, D. Q., Jackson, R. R. & Lim, M. L. M.** 2003. Influence of background and prey orientation on an ambushing predator's decisions. *Behaviour*, **140**, 739–764.
- Lubin, Y., Ellner, S. & Kotzman, M.** 1993. Web relocation and habitat selection in a desert widow spider. *Ecology*, **74**, 1915–1928.
- Marshall, J.** 1999. Visual function: how spiders find the right rock to crawl under. *Current Biology*, **9**, R918–R921.
- Minch, E. W.** 1978. Daily activity patterns in the tarantula *Aphonopelma chalcodes* Chamberlin. *Bulletin of the British Arachnological Society*, **4**, 414–415.
- Möller, R.** 2002. Insects could exploit UV–green contrast for landmark navigation. *Journal of Theoretical Biology*, **214**, 619–631.
- Nakamura, T. & Yamashita, S.** 2000. Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *Journal of Comparative Physiology A*, **186**, 897–901.
- Nørgaard, T., Henschel, J. R. & Wehner, R.** 2003. Long-distance navigation in the wandering desert spider *Leucorchestris arenicola*: can the slope of the dune surface provide a compass cue? *Journal of Comparative Physiology*, **189**, 801–809.
- Ortega-Escobar, J. & Muñoz-Cuevas, A.** 1999. Anterior median eyes of *Lycosa tarentula* (Araneae, Lycosidae) detect polarized light: behavioral experiments and electroretinographic analysis. *Journal of Arachnology*, **27**, 663–671.
- Pastergue-Ruiz, I., Beugnon, G. & Lauchaud, J.-P.** 1995. Can the ant *Cataglyphis cursor* (Hymenoptera: Formicidae) encode global landmark–landmark relationships in addition to isolated landmark–goal relationships? *Journal of Insect Behavior*, **8**, 115–132.
- Peaslee, A. G. & Wilson, G.** 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). *Journal of Comparative Physiology A*, **164**, 359–363.
- Persons, M. H. & Uetz, G. W.** 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*, **51**, 1285–1293.
- Plett, A.** 1962. Beobachtungen und Versuche Zum Revier und Sexualverhalten von *Epiblemum scenicum* C1. und *Evarcha bancardi* Scop. (Salticidae). *Zoologisches Anzeiger*, **169**, 292–298.
- Popson, M.** 1999. Finding the way: learning in a jumping spider (*Phidippus audax*). M.S. thesis, Bowling Green State University, Bowling Green, Ohio, U.S.A.
- Seyfarth, E. A., Hergenröder, R., Ebbes, H. & Barth, F. G.** 1982. Idiopathic orientation of a wandering spider: compensation of detours and estimates of goal distance. *Behavioral Ecology and Sociobiology*, **11**, 139–148.
- Shettleworth, S. J.** 1998. *Cognition, Evolution, and Behavior*. Oxford: Oxford University Press.
- Smallwood, P. D.** 1993. Web-site tenure in the long-jawed spider: is it risk-sensitive foraging, or conspecific interactions? *Ecology*, **74**, 1826–1835.
- Taylor, P. W., Hasson, O. & Clark, D. L.** 2001. Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals. *Behavioral Ecology and Sociobiology*, **50**, 403–413.
- Tessler, S.** 1979. A study of the retreat-sites of jumping spiders (Araneae, Salticidae) nesting on Queen Anne's lace (*Dacus carota carota* L.). M.S. thesis, Purdue University, West Lafayette, Indiana, U.S.A.
- Tinbergen, N.** 1975. *The Animal in Its World: Field Studies*. Cambridge, Massachusetts: Harvard University Press.
- Von Frisch, K.** 1967. *The Dance Language and Orientation of Bees*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.
- Walker, S. E., Marshall, S. D., Rypstra, A. L. & Taylor, D. H.** 1999. The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). *Animal Behaviour*, **58**, 515–520.
- Wells, M. S.** 1988. Effects of body size and resource value on fighting behavior in a jumping spider. *Animal Behaviour*, **36**, 321–326.
- Yamashita, S. & Tateda, H.** 1976. Spectral sensitivities of jumping spider eyes. *Journal of Comparative Physiology*, **105**, 29–41.
- Zeil, J., Kelber, A. & Voss, R.** 1996. Structure and function of learning flights in bees and wasps. *Journal of Experimental Biology*, **199**, 245–252.