



Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider

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(Received 11 April 2002; initial acceptance 10 July 2002;
final acceptance 6 March 2003; MS. number: 7298R)

By making field observations on the movement pattern of the agrobiont wolf spider *Pardosa agrestis* at two spatiotemporal scales, we explored how fine-scale foraging movements scale up to medium-scale habitat use by the spiders. For fine-scale observations, we followed individuals for several metres and for up to 1–2 h. For medium-scale observations we used marking and recapture in live-trapping pitfall grids, which allowed us to detect movements up to 70 m and for 4 weeks. The analysis of fine-scale movement indicated that spiders followed a 'sit-and-move' foraging strategy, which consisted of variable periods of waiting (mean 2.5 min) and brief bouts of movements between the waiting sites. Spiders spent over 90% of the total observation time waiting. Prey capture (or capture attempts) was initiated only from waiting sites. Movement between consecutive waiting sites was more directional than predicted by the correlated random walk model. At medium (2-day) timescales the mean displacement of marked spiders was 7.4 m. Simulations suggested that such a displacement could be achieved if movement observed at the fine scale followed a random path for 2 days. We concluded that movement became less directional with increasing scale. Such a phenomenon might be related to avoidance of revisiting food patches locally and an efficient sampling of the habitat at higher scales. High movement activity in a species that is primarily adapted to ephemeral habitats might increase its likelihood of colonizing new habitat patches.

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Within-habitat movement is a key characteristic of the ecology of animals. Movement through the habitat influences how animals can use resources, interact with other members of the population or become involved in interspecific interactions. Through the quantitative description of movement behaviour we can form mechanistic hypotheses that relate individual movement to higher-level ecological phenomena (Turchin 1991; Wiens et al. 1993).

Wolf spiders (Araneae, Lycosidae) are among the most dominant predatory arthropods in many terrestrial ecological systems (Loksa 1966), including a number of agroecosystems (Nyffeler & Benz 1988; Marshall & Rypstra 1999; Samu 2003). Instead of building a web, these spiders wander over the ground to hunt for their prey. Females carry their eggsacs attached to their spinnerets, and when spiderlings hatch, they climb on their mother's back for about a week's further transport. Wolf spiders can reach abundances as high as 10 adult individuals/m² (Kiss & Samu 2000). Movement characteristics (e.g. colonization ability) largely influence how these generalist predators respond to the spatial

variability of environment and prey (Marshall et al. 2000).

In spite of high field density and the ecological importance of movement, small size and quick/cryptic motion have largely prevented direct field observation of wolf spiders. Hence most of the information available about their feeding, foraging or movement habits comes from laboratory experiments (Samu & Bíró 1993; Toft & Wise 1999; Walker et al. 1999). These studies are burdened with the artificiality of limited prey choice, fixed arena size and simplistic laboratory environment.

As a consequence, there are few reliable field data about the foraging mode and movement behaviour of this important predatory group. The few exceptions comprise mark-recapture studies of coarse-scale resolution (Hallander 1967; Dondale et al. 1969), and studies on the daily movement patterns of these animals (Papi & Syrjamäki 1963; Morse 1997). These studies indicate that wolf spiders are wide-ranging wanderers, able to cover distances of up to 10–20 m/day, and hence have reinforced the earlier view that lycosids actively search and hunt for prey (Savory 1926; Bristowe 1958).

However, further studies have changed this view of wolf spiders as active pursuers of prey. Energetics experiments have revealed that lycosids have extremely low

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basic metabolic rates and high tolerance to starvation (Edgar 1971; Tanaka & Ito 1982), but they consume much more energy when they actively forage (Ford 1977). Since the relative costs of waiting and moving are important determinants of foraging strategies (Schoener 1971; Janetos 1982a), wolf spiders are energetically predestined to be 'sit-and-wait' predators. Field records of low prey capture rates (Edgar 1970; Nyffeler & Breene 1990) and direct laboratory observations of predation and movement (Ford 1978) have also confirmed that lycosids adopt an energy-sparing foraging strategy.

Two studies, however, suggest that wolf spiders are not just sit-and-wait foragers. First, Walker et al. (1999) categorized the more vagile and smaller *Pardosa milvina* as an active forager, and the optional burrower and larger *Hogna helluo* as a sit-and-wait strategist. Second, Morse (1997) pointed out that sit-and-wait and active strategies could be found in different subpopulations of *Pardosa lapidicina*, which occupy contrasting habitats on the sea shore.

Thus it appears that some wolf spider studies claim extensive within-habitat movements, whereas others imply a sit-and-wait strategy with more restricted spider movement. This apparent contradiction might occur because the studies were made at different scales, on different species and under different experimental conditions. We tried to clarify the nature of wolf spider movement by making direct field observations on an exemplar species, under the same field conditions, and at two spatiotemporal scales.

Our aim was to gain information about movement-related behaviour of the wolf spider *Pardosa agrestis* Westring at two observational scales. (1) On a timescale of a few hours we recorded individual movements, foraging events and the structure of occupied microhabitats. From these observations we collected information on foraging behaviour and exact movement pathways. (2) On a timescale of a few days we used mark-recapture tracking of animals in a trap grid to collect information about the extent and directionality of within-habitat movements. (3) We related the two types of information by scaling up fine-scale movement to medium scale. Through the nature of the scaling function we propose a mechanism that connects fine-scale foraging to medium-scale habitat use.

METHODS

Fine-scale Observations

We studied *P. agrestis* on unsprayed alfalfa fields (1.5–2 ha) at the Julianna-major Ecological Station of the Plant Protection Institute, on the northwest border of Budapest, between 1994 and 2000. We made our observations in the active period of the spiders, between 0900 and 1600 hours, from March to the beginning of November.

Pardosa agrestis was the most dominant wolf spider species in the experimental fields. The species is recognizable with practice, and even juveniles can be distinguished from other, less abundant, *Pardosa* species at the

site. Recognition in the field during initial trial observations was confirmed by laboratory identification of the observed specimen (spiders were killed by placing them in 70% ethanol; we then examined their genitalia under a microscope). We observed individuals of both sexes as adults, and also juveniles if they were at least half the size of an adult (adult mean body length \pm SD: females: 7.3 ± 1.74 mm; males: 6.1 ± 1.45 mm). The following five spider categories were distinguished: juvenile, male, non-reproductive female, female with cocoon, female with spiderlings.

The observer followed the spider in the field from a distance of about 2 m, in a squatting posture and moving slowly. Because the observer avoided any sudden movement, spiders behaved naturally, showing behaviours such as moving in every direction, including towards the observer, being stationary, attacking prey, and feeding on it. We therefore assumed that successful observations did not affect the behavioural parameters recorded. If we noticed that we disturbed the spider, that observation was excluded from further analysis. Because of the relatively remote observation, recording fine details of behaviour was limited, although the capture of even a tiny prey, such as a collembolan, was easily detected from the characteristic movement and posture of the spider.

For recording, we used a hand-held computer (Psion Organiser II. LZ 64) which was programmed with the Observer behaviour recording software package (Noldus Information Technology, Wageningen, The Netherlands), so that we could promptly note the movement pattern of the spiders. The configuration consisted of first giving an identity to the spider (ID, stage, sex, reproductive status), then classifying behaviour as movement, waiting and other activities. The program made an exact timing of each behavioural element.

The main 'other activity', feeding, was recorded separately together with the identity of prey. Daily feeding rate of spiders (f) was calculated from Edgar's (1970) formula: $f = Tw/h$, where w is the feeding frequency (i.e. the proportion of observed spiders that we found feeding), T is the total time available for foraging per day and h is handling time.

We recorded bouts of movement ('legs') ending in shorter or longer pauses. We recorded the legs' compass direction (with 45° increments) and lengths (1–5 cm, 6–20 cm, 21–40 cm). Legs longer than 40 cm were rare. During observations we made notes about waiting places according to the type of surface (flat, depression or crevice) and whether they were under the cover of vegetation. We considered an observation to be a sample of a spider's 'daily routine', with an emphasis on movement behaviour. One observation thus consisted of a series of movement elements and other behavioural elements.

To describe expected net displacement (ED) for a walk with n legs under the null hypothesis of random movement we first used the correlated random walk model set up by Kareiva & Shigesada (1983), to obtain the expected value of square net displacement ($E(R_n^2)$):

$$E(R_n^2) = nE(l^2) + 2E(l)^2 \frac{c}{1-c} \left(n - \frac{1-c^n}{1-c} \right), \quad (1)$$

Table 1. Data on pitfall trap grids used in the mark–recapture studies and recapture parameters by sex and study

	Study							
	A		B		C		D	
Start date	16 June 1994		29 July 1995		1 August 1996		1 August 1996	
End date	11 August 1994		13 August 1995		15 August 1996		15 August 1996	
No. of traps	5×5		11×11		11×11		29*,45†	
Trap distance (m)	5		2		3		5	
Area of trapping grid (m ²)	400		400		900		Traps in rows	
Sex	F	M	F	M	F	M	F	M
N (recaptures)	37	79	95	478	128	49	2	5
Maximum recapture distance (m)	18.0	25.0	24.1	24.1	31.9	33.9	40.3	67.5
Mean recapture time in a week (days)‡	2.8	3.6	3.3	3.7	3.6	3.3	4.5	5.0
Mean speed (m/day)‡	2.9	3.0	3.8	3.1	2.2	3.0	8.2	9.6
Maximum speed (m/day)	7.5	20.6	19.0	20.9	20.1	17.0	10.1	13.5

*At 20 m from grid C.

†At 40 m from grid C.

‡Not considering first-day recaptures.

where $E(l)$ is the expected (mean) length of legs, $E(l^2)$ is the expected squared length, and c is the expected value of the cosines of the turning angles. The equation is valid for cases where the distribution of turning angles is symmetric about 0° . However, the results are easier to interpret when ED, rather than $E(R_n^2)$, is calculated. As Byers (2001) pointed out, this cannot be done by simply taking the square root of $E(R_n^2)$. The correct calculation of expected net displacement is:

$$ED = Z\sqrt{E(R_n^2)}, \quad (2)$$

where Z is a correction factor that is dependent on n , and also on the standard deviation of turning angles (SDA). Byers (2001) provided a simulation program that calculates Z . For the present case, because $SDA > 30^\circ$ for all observed spiders, $Z = 0.89$. Separate ED values were calculated for each observation (i.e. for each observed spider) if the observation contained more than three legs. For these cases we made a paired comparison between observed and predicted displacements.

Medium-scale Observations

We examined the medium-scale movement of spiders from a series of mark–recapture studies. These studies were primarily designed to obtain density estimates of the wolf spider population (Kiss & Samu 2000). However, the mark–recapture data sets contain valuable information on the medium-range movement of *P. agrestis*, and this part of the published data together with our unpublished data sets are analysed here.

Between 1994 and 1996 three mark–recapture studies were conducted in alfalfa fields (Table 1). Trapping was done by live-catching pitfalls. Traps were emptied daily, which was logistically the most frequent possible. Small leaves in the bottom of the cups provided shade and humidity as well as hiding places. We marked spiders individually by placing dots of enamel paint on their back with a soft brush. The trapping and marking appeared to have minimal effect on the spiders'

behaviour and mortality; 8% died or were injured and were therefore excluded. Injured, nonvigorous spiders were set free elsewhere. (For further details of the marking procedure see Kiss & Samu 2000.) The spiders were released the same day 1 m to the right of the trap where they were caught. Directly after release the spiders usually moved a few tens of centimetres away from the release point, and then stopped in a shelter. The traps were set up in a grid (Table 1), allowing us to map displacements between recaptures. Technically we distinguish a fourth study, whereby in two trap rows, placed at 20 and 40 m from the trap grid, we tried to recapture spiders leaving the grid.

To gain an overall picture of the movement capacity of *P. agrestis*, we calculated mean distances, speed and recapture time for spiders that were recaptured on day 2–7 after release. We excluded day 1, because on this day the spiders had less time available to move away from the release point.

Scaling Movement from Fine to Medium Scale

The fine-scale observations yielded movement paths of individual spiders, from which we could calculate descriptive parameters, such as the standard deviation of turning angles and the mean lengths of movement legs. We scaled fine-scale observations to higher scale by applying the correlated random walk model as the scaling function. This was done by entering fine-scale movement parameters into the model to arrive at a medium-scale outcome. That is, we hypothesized that medium-scale movement arises from random movement of individuals at a fine scale.

To arrive at a medium-scale prediction, we calculated expected net displacement values for 2 days from the fine-scale movement parameters of individually observed spiders. From the fine-scale observations we considered adult males and females (because in the medium-scale observations only these two categories were studied) for which the observation consisted of more than three movement legs. Then, for each such spider, we made an

extrapolation by calculating ED from their individual original fine-scale parameters, as if the individual spiders moved according to the correlated random walk model for 20 h. To do so, for each spider we calculated the leg length parameters [$E(l)$, $E(l^2)$] and turning angles parameter (c) from the direct observations. From the number of legs each spider made during the direct observation time, we linearly regressed to the number of legs (n) the observed spider would have made during 20 h. We used the correction factor $Z=0.89$. From these parameters we extrapolated to the ED of a correlated random walk for 20 h, using equations (1) and (2).

The 20-h time interval approximated the time available for activity for spiders that were recaptured on the second day in the mark-recapture study. We assumed that *P. agrestis*, like other *Pardosa* species, are active during the day and cease movement at night (Bayram 1996; Marshall et al. 2002). The 20-h estimate for the first 2 days was arrived at by assuming an average of 14 h daylight in the observation period and 8 h for the time we kept spiders in captivity (this was the usual time needed to paint all spiders from the 121 pitfalls).

RESULTS

Fine-scale Observations

Foraging

All observed spiders ($N=106$) showed a characteristic time allocation between moving and being stationary (waiting). Spiders spent most of their time waiting (mean % of observation time \pm SD = $90.3 \pm 16.86\%$), and only a little time moving ($9.7 \pm 17.47\%$). Although all spider categories followed this gross pattern of time allocation, they differed in the proportion of time spent waiting (one-way ANOVA on arcsine-transformed data: $F_{4,101}=11.99$, $P<0.0001$), with a post hoc analysis (LSD test: $P=0.05$) revealing that only males spent significantly less time waiting (males: mean % of observation time \pm SD = $74.3 \pm 26.39\%$) than all other categories (other categories combined: $95.2 \pm 7.74\%$). Individual moving events were rapid, with over 98% of the movements being shorter than 20 s ($\bar{X} \pm$ SD = 3.6 ± 5.86 s). Waiting events were longer and highly variable, but still short (159.6 ± 588.81 s; maximum observed value 95 min).

Waiting time was mainly influenced by the surface type at waiting places. An ANOVA design on log-transformed

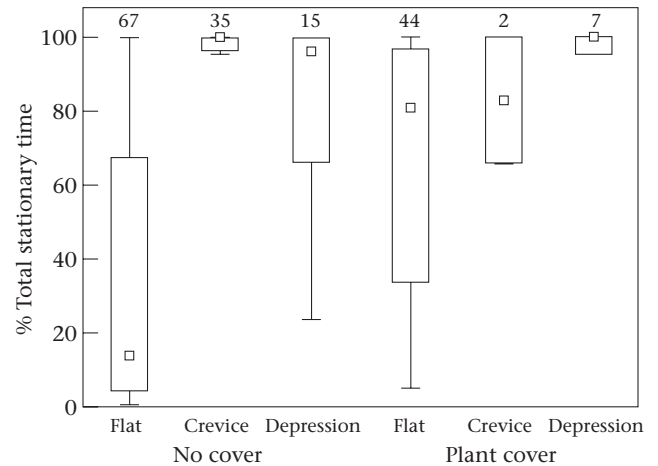


Figure 1. Time spent waiting (percentage of total observation time that individual spiders were stationary) on different types of surface, either on bare ground or under the cover of herbaceous vegetation. Squares show medians, bars 25–75% percentiles and vertical lines minimum and maximum values. Numbers above bars refer to sample sizes.

waiting times (including the effects spider individual (nested within spider category), spider category, surface type, plant cover and surface \times plant cover interaction) revealed that waiting time was influenced only by surface type (ANOVA $F_{2,60}=9.29$, $P=0.0003$; surface \times plant coverage: $F_{2,60}=1.3$, NS), and not by plant coverage ($F_{1,60}=1.1$, NS), spider category ($F_{4,60}=0.78$, NS), or individual spider ($F_{100,60}=0.58$, NS). Post hoc analysis (LSD test: $P=0.05$) showed that waiting times on flat surfaces without cover were significantly shorter than waiting times on other surfaces (Fig. 1). On the other hand, 'flat surface without plant cover' was the most frequently chosen surface for waiting (choice probability 99% lower confidence limit of 'flat-no cover' = 0.763; higher 99% limit of next highest surface type ('flat-plant cover') = 0.137). Thus, spiders frequently used uncovered flat surfaces for short stops, but stayed for longer periods only in more protected places.

During the total observation period of over 45 h, 13 predatory attacks were observed, only three of which were successful (Table 2). No spider actively pursued the prey. In all cases spiders came in 'contact' with the prey, while they were at waiting sites. When spiders sensed

Table 2. Observed events of predatory attack by *P. agrestis* during the total 45 h of fine-scale field observation

Stage	Sex	Attacked prey	Outcome	No. of observations
Juvenile	—	Aphid	Predation	1
Juvenile	—	Chironomid	Predation	1
Adult	Female+cocoon	Collembola	Predation	1
Juvenile	Female	Beetle	Failure	1
Adult	Female+cocoon	Not recorded	Failure	1
Juvenile	Male	Small spider	Failure	1
Juvenile	—	Not recorded	Failure	6
Adult	Male	Not recorded	Failure	1

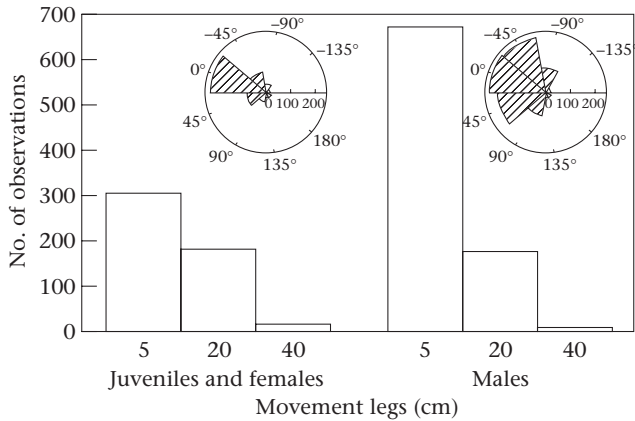


Figure 2. Frequency distribution of the length of movement legs (bar diagram) and the distribution of turning angles between consecutive legs (polar coordinate diagram) by (a) males and (b) juveniles and females (pooled, see text for statistical similarity).

prey (we could not tell whether visually, or by other sensory cues, but see Persons & Uetz 1997, 1998), they approached it by a few centimetres detour from the waiting site, and finished the attack by leaping on the prey. Prey items were varied (Table 2), usually soft-bodied insects (spider in one case), smaller than the spider itself. From these observations feeding frequency of spiders was 2.8%. Using the formula of Edgar (1970), a handling time estimate of 45 min for *P. agrestis* (Nyffeler & Benz 1988), and an estimate of 14 h/day is available for foraging, the feeding rate of *P. agrestis* was 0.53 prey items/day.

Fine-scale movement pattern

The distances covered during movements (cumulative length of legs) were significantly dependent on spider category (ANOVA on log-transformed data: $F_{4,101}=12.58$, $P<0.0001$). Post hoc analysis (LSD: $P=0.05$) revealed that males covered significantly longer paths over 1 h ($\bar{X} \pm SD=21.9 \pm 20.52$ m) than all other spider categories (4.5 ± 6.58 m); there was no difference between the other categories (LSD test). Most movements were short (≤ 5 cm). This movement category included largely short legs of forward movement, but also short detours from waiting sites to attack prey. Females and juveniles used longer legs relatively frequently, while males, in spite of covering much longer paths per unit time, frequently used short legs (Fig. 2). Unfortunately the number of legs we were able to observe differed by sex, stage, probably because of the contrasting size, conspicuousness of coloration and vagility (juveniles: mean number of observed legs $\pm SD=5.3 \pm 5.47$, $N=42$; females: 19.4 ± 19.08 , $N=39$; males: 54.8 ± 72.81 , $N=25$).

Turning angles between two legs showed that spiders performed a forward-oriented movement, that is, the angles were rarely larger than 45° (Fig. 2). The distribution of all observed turning events was centred at 0° ($N=1367$, median 0°), that is, it was balanced between left and right turns. This was also true on the level of spider individuals and spider categories; the central location of turning angles of individual spiders and that of spider categories

did not differ significantly from the common central location of 0° (Van der Waerden test: spider individuals: $\chi^2_{105}=80.15$, $P=0.987$; categories: $\chi^2_4=4.86$, $P=0.302$). However, balanced turning, demonstrated above, can be done with small and large angle turns, and spider categories differed significantly in this respect (central location of absolute angle of turning events by categories was not equal, Van der Waerden test: $\chi^2_4=45.45$, $P<0.0001$), with males most frequently turning at larger angles, followed by females with and without cocoons. The smallest degree of turning (the most forward-oriented movement) was found in females with spiderlings on their back.

In the analysis of directionality of movement, observed displacements of spiders tended to be systematically higher than the displacements calculated from the individual movement path under the correlated random walk hypothesis (paired t test: $t_{57}=5.62$, $P<0.0001$). If a movement is more directional than random, it can be detected from observed displacements being increasingly larger than predicted ones as the number of observed legs increases (Kareiva & Shigesada 1983). In our case, the difference between observed and predicted displacements was positively correlated with the number of legs in all spider categories, although not significantly so for juveniles (Fig. 3).

Medium-scale Observations

The mark-recapture observations allowed us to follow the movement of spiders on a scale up to 70 m and for 1 month, although typical recaptures represented shorter distances and periods (Table 1). During 1 week, spiders could travel distances that were in the size range of habitat patches, and four orders of magnitude larger than their body size (Table 1). Distances moved by spiders recaptured on days 2–7 from release were significantly related to the days to recapture, but not sex or trap distance (Table 3). Spiders in two of the three studies moved without any preferential direction (directions were represented by classifying movement to eight sectors, in all cases leaving out first-day recaptures, because of possible bias from asymmetric release; goodness of fit tests for equal frequencies: study A: $\chi^2_7=2.19$, $P=0.95$; study B: $\chi^2_7=11.36$, $P=0.12$; study C: $\chi^2_7=15.23$, $P=0.03$).

Our next question regarded the speed of this apparent spreading of wolf spider individuals. If daily distances moved by a spider are comparable to the dimensions of the trapping grid, than in a few days spiders can potentially move outside the grid (Fig. 4). Therefore we confined estimates of speed to the first few days. Since first-day recaptures had to be excluded from speed calculations (see Methods), to be conservative we based our estimate on second-day recaptures. We pooled data across studies and sexes, because second-day recapture distances were not dependent on either (Table 3). The distribution shows that in both sexes the mean speed was just below 4 m/day (mean $\pm SD$ combined for males and females = 3.72 ± 3.099 m/day) and that there was a long tail towards higher speeds of up to 20 m/day (Table 1). First-day recaptures can provide further indirect evidence that daily

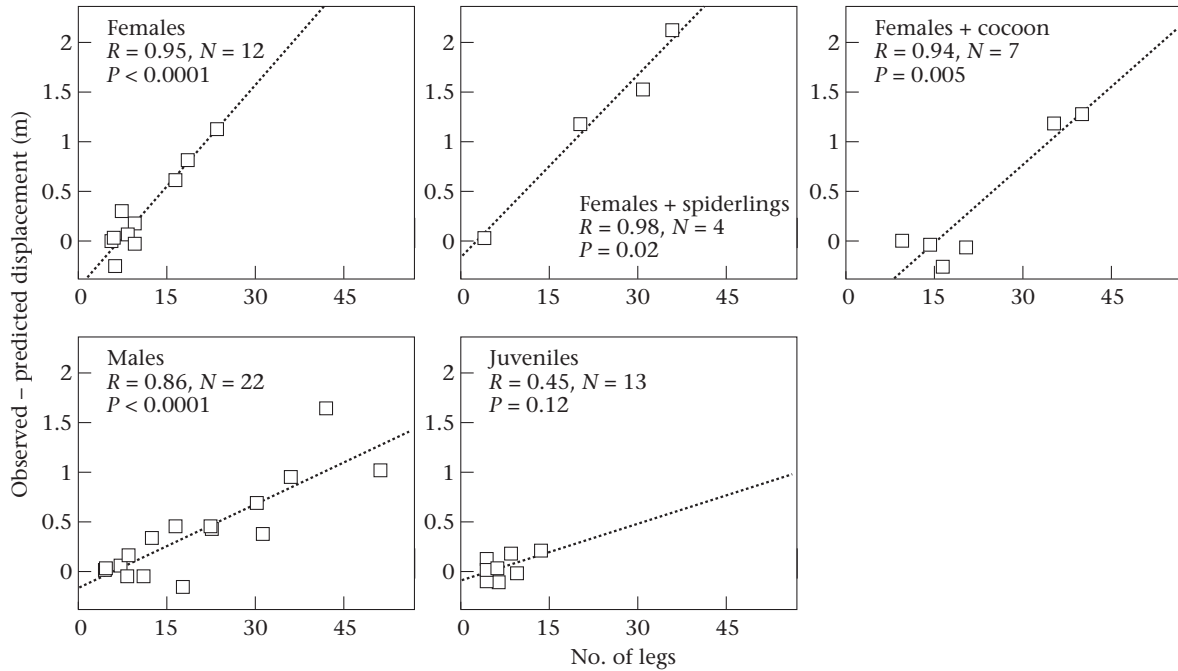


Figure 3. The difference between observed displacements and displacements predicted by the correlated random walk model, as a function of the number of legs of the observed movement path. The relation is presented by spider categories; each data point represents an observation of an individual spider. Females: $Y = -0.42 + 0.07X$; females+spiderlings: $Y = -0.13 + 0.07X$; females+cocoon: $Y = -0.79 + 0.05X$; males: $Y = -0.13 + 0.03X$; juveniles: $Y = -0.05 + 0.02X$.

Table 3. ANCOVA models of recapture distance

Recapture interval	Source	df	Sum of squares	F	P
1 day	Grid	1	600.34	28.92	<0.0001
	Sex	1	111.25	5.35	0.02
	Grid×sex	1	80.98	3.90	0.05
	Error	450	9340.25		
2 days	Grid	1	9.09	0.25	0.62
	Sex	1	0.99	0.03	0.87
	Grid×sex	1	7.39	0.20	0.65
	Error	155	5689.17		
2–7 days	Recapture time	1	746.28	19.52	<0.0001
	Grid	1	53.05	3.76	0.24
	Sex	1	143.77	1.38	0.05
	Grid×sex	1	127.79	3.34	0.07
	Error	356	13 610.35		

The first analysis considers recapture events on the day after release, the second recapture events on the second day after release; the third recapture events 2–7 days after release. The analyses involve three studies, A, B and C, represented by their trap distance value 'grid', which was taken as a continuous covariate (Table 1).

speed is in the 2–5-m range, because first-day recapture distances were significantly negatively dependent on trap distance, but later days were not (Table 3). This means that if only 1 day was available to the spiders, in a grid of larger trap distances they were less likely to reach a neighbouring trap than in a grid of smaller trap distances.

Scaling Movement from Fine to Medium Scale

We used the movement parameters of individually observed spiders in the fine-scale study to extrapolate,

using the correlated random walk model, what displacements could be expected from these spiders if they were observed for 2 days. Then we compared these expected values to displacements observed in animals recaptured after 2 days in the mark-recapture study. Random walking extrapolation resulted in similar expectation of speed as we observed in the mark-recapture study (Table 1). The mean extrapolated speed of spiders ± SD was 4.1 ± 2.97 m/day, with some individuals reaching maximum speeds of up to 14–16 m/day. To test this similarity, we compared the distributions of extrapolated

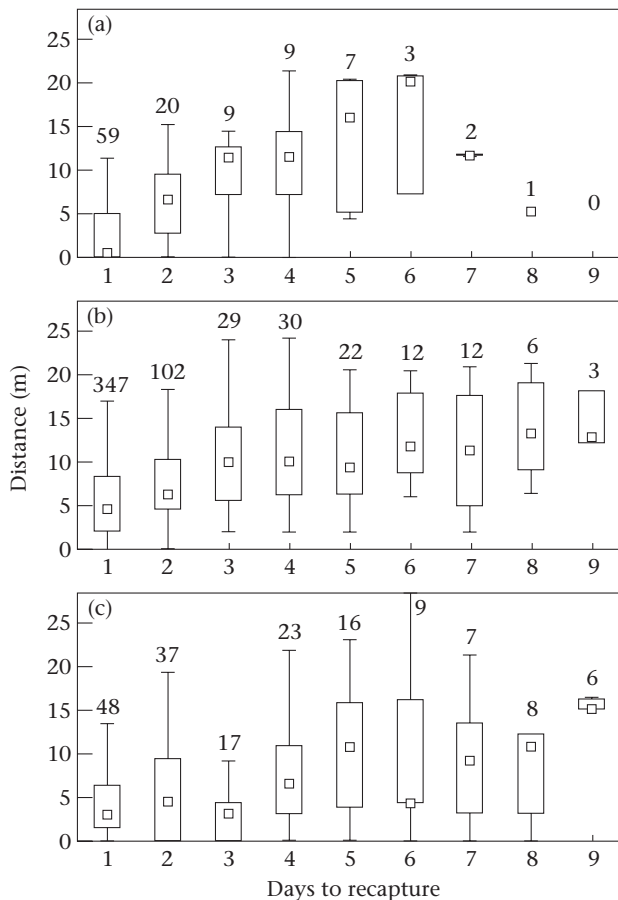


Figure 4. Recapture distance as a function of recapture time. (a) Study A, (b) study B and (c) study C. Table 1 gives trap distances and grid areas for the three mark–recapture studies. Squares show medians, bars 25–75% percentiles and vertical lines minimum and maximum values. Numbers above bars refer to sample sizes.

and observed displacements by sex using a two-tailed Kolmogorov–Smirnov test, with zero displacement observed cases (recapture at the trap of release) being excluded from analysis, because the random walk model cannot have a zero outcome. The respective distributions were not significantly different in either sex (females: $D=0.309$; $N_{\text{extrapolated}}=23$, $N_{\text{observed}}=35$, NS; males: $D=0.245$; $N_{\text{extrapolated}}=22$, $N_{\text{observed}}=104$, NS).

DISCUSSION

The ‘Sit-and-move’ Foraging Strategy

Is *P. agrestis* a sit-and-wait predator? If we consider its time budget, which showed that spiders spent over 90% of the time during their active period stationary at ‘waiting’ sites, and add that all observed predatory attacks started off from such sites, the answer should be yes. However, sit-and-wait and actively foraging strategies represent two ends of a continuum (Janetos 1982a; Uetz 1992). If we consider the extremely sedentary lifestyle of other spiders, especially those that build permanent webs (Enders 1976; Janetos 1982b), and take into account the significance of active elements in *P. agrestis* foraging, we

might take a different view. The spiders did not conform to a traditional sit-and-wait forager: they left waiting sites after a variable, but on average only 2.5-min, period, and frequently relocated themselves. Unlike many other sit-and-wait strategist spiders, *P. agrestis* made no material or energetic investment in waiting sites, nor could we observe any territorial dispute between individuals. Thus *Pardosa* foraging could rather be described as a sit-and-move mixed foraging strategy, where energetically advantageous sitting-and-waiting is combined with an active changing of waiting sites.

The activity level of *P. agrestis* appears to be among the highest of *Pardosa* species. Ford (1978) described *P. amentata* foraging as a ‘sit-and-wait strategy with periodic change of site’ which is essentially the same foraging activity that we found for *P. agrestis*. However, while *P. agrestis* spent 6 min/h moving, *P. amentata* spent only 20 s/h moving. Similarly, Walker et al. (1999) found that *P. milvina* spent only 3.5 min/h moving.

Why does a sit-and-move strategy suit *P. agrestis*? ‘Waiting’ is favoured when the cost of being sedentary relative to moving is low, or spatial variation in patch quality is low (Janetos 1982a). Energetics studies have shown that lycosid metabolism is more suited to wait sedentarily than to move long distances actively (Edgar 1971; Ford 1977). Since this seems to be fundamental to lycosid biology, activity differences seen between closely related species are likely to be adaptations to differing environmental conditions, most probably to prey density.

Wolf spiders are shown to change feeding behaviour actively in relation to prey density (Samu 1993; Samu & Bíró 1993). Other foraging decisions, such as patch leaving time in the wolf spider *Schizocosa ocreata*, depend on a complex of sensory information about prey density (Persons & Uetz 1997, 1998). Not only absolute prey density but also environmental variation in prey availability can influence the position of foraging strategies along the waiting–moving continuum. Spiders living on the soil surface of agricultural areas typically face the conditions of an ephemeral habitat, where periodic disturbances make the ground bare and prey scarce, alternating with spatially and temporally variable occurrences of abundant prey. Risk-prone foragers try to increase overall energy intake by risking high variability, while risk-averse foragers trade off overall intake for lower variation (Real & Caraco 1986). In our view, the sit-and-move strategy of *Pardosa* is a balance between (1) avoiding the high cost of constant moving (Ford 1977), and (2) keeping environmental variation at a tolerable level by relatively frequent relocations. Thus sitting-and-moving, compared with sitting-and-waiting, is a risk-averse strategy, because by increasing the number of patches visited, spiders average the habitat. As the example of orb-weavers shows (Gillespie & Caraco 1987), this may reduce variation in prey intake. Risk aversion, however, has the side effect of low prey capture rate. The presumably more risk-prone *P. amentata* lives in a stable litter habitat, where it is much less active (Ford 1978), and captures twice as many prey per day (Edgar 1970) than *P. agrestis* (Nyffeler & Benz 1988; present study).

All life stage/sex categories in *P. agrestis* could be described as conforming to a sit-and-move strategy. However, in the details of their fine-scale movement, males were undoubtedly different from other categories. Although total time spent moving was not different, males moved about four times further, in shorter legs, and with a wider turning angle distribution. We attribute the differences to the alternative goal of mate finding in males. Their movement may also include the tracking of female silk and pheromones (Hegdekar & Dondale 1969; Anderson & Morse 2001), which are likely to be present on the soil surface of the alfalfa field.

Scale-dependent Movement Patterns

Our medium-scale mark-recapture observations show that *P. agrestis* extensively searches its habitat, covering considerable distances and areas. Despite the methodological difficulties, the replicated experiments resulting in nearly 900 recaptures allowed us to make a conservative estimate of the rate of spreading of spiders within a habitat patch. This spreading on average was 4 m/day, but observed maximum values were three or four times greater. Virtually identical figures were obtained from two other mark-recapture studies of other *Pardosa* species (Hallander 1967; Dondale et al. 1969).

In mark-recapture studies we lose animals from sight for a number of days between release and recapture. Can we infer how spiders search their habitat during that period, using the fine-scale direct observations? We attempted such an inference by extrapolating between scales using the correlated random walk model as the scaling function. These results indicated that over 2 days the movement of spiders appeared to be randomly built up from the directly observed movement units (legs and turning angles). However, at the fine scale (1–2 h) movements were directional.

Based on our scaling exercise, we suggest that with increasing scale, the directionality of *P. agrestis* movement decreases. On the scale of a few minutes spiders either stay at waiting sites, or move linearly. At a 1-h scale, as direct observation showed, the movement path was more directional than random. The function of strong directionality at small scales might be to inhibit the revisiting of already exploited food patches. At the time resolution of mark-recapture observations (2 days), observed displacements were not different from that predicted by random walk. At this scale, revisiting should no longer be an issue, because food patches are refilled, and revisiting probability is low anyway. Thus, at medium scales spiders were probably interested in sampling the whole habitat patch. Such a sampling process, if prey-rich local food patches are encountered, might alter fine-scale movement behaviour, as higher densities of *Pardosa* occur in locally prey-dense areas (Marshall et al. 2000).

Landscape-level distribution studies (Samu & Szinetár 2002) have revealed that *P. agrestis* is a highly habitat-specific species, being densely present in some disturbed habitats, and absent from more mature habitats, even if the two are neighbouring (Samu 2003). We suggest that

the large-scale movement pattern of this species is adapted to the ephemeral nature of its habitats. The high overall movement activity might be one factor of the species' colonization strategy. This would allow it to spread over the typically large habitat patches, such as arable fields, and use suitable habitat corridors or interfaces, between the habitat patches, as well.

Our multiscale study highlights some adaptive features of *Pardosa* foraging behaviour. The sit-and-wait strategy, and especially prey capture from ambush, seems to suit the general *Pardosa* biology the best. However, in *P. agrestis* this strategy has been amalgamated with many active elements, resulting in the mixed strategy of 'sit-and-move'. The movement pattern emerging from the continuous changing of waiting sites was more directional at fine scales, and appeared to be random at medium scales. We suggest that the sit-and-move strategy is suitable for a risk-averse use of unpredictable habitat patches, such as arable fields.

Acknowledgments

We are grateful for the technical assistance of Mrs Erika Botos. We thank Mr László Nemesvári, Mr Imre Fábián and Mr Géza Vörös who made the use of one of the alfalfa fields possible and Drs Ann L. Rypstra, John A. Byers and two anonymous referees for valuable comments on the manuscript. F. Samu and B. Kiss were Bolyai Fellows of the Hungarian Academy of Sciences. The studies were financed by OTKA Grants No. T32209 and F030264 and the NKFP project No. 3B/0008/2002.

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