James D. Wagner · David H. Wise

Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider Schizocosa

Abstract Because cannibals are potentially both predator and prey, the presence of conspecifics and alternative prey may act together to influence the rate at which cannibals prey upon each other or emigrate from a habitat patch. Wolf spiders (Lycosidae) are cannibalistic-generalist predators that hunt for prey with a sit-and-wait strategy characterized by changes in foraging site. Little information is available on how both prey abundance and the presence of conspecifics influence patch quality for these cursorial, non-web-building spiders. To address this question, laboratory experiments were conducted with spiderlings and older juveniles of the lycosid genus *Schizocosa*. The presence of insect prey consistently reduced rates of spider emigration when spiders were housed either alone or in groups. Solitary juvenile *Schizocosa* that had been recently collected from the field exhibited a median giving-up time (GUT) of 10 h in the absence of prey (Collembola); providing Collembola increased the median GUT to 64 h. For solitary spiders, the absence of prey increased by about fourfold the rate of emigration during the first 24 h. In contrast, for spiders in patches with a high density of conspecifics, the absence of prey increased the 24-h emigration rate by only 1.6-fold. For successful cannibals in the no-prey patches, the presence of conspecifics improved patch quality by providing a source of food. Mortality by cannibalism was affected by both prey availability and openness of the patch to net emigration. In patches with no net emigration, the presence of prey reduced rates of cannibalism from 79% to 57%. Spiders in patches open to emigration but not immigration experienced a rate of cannibalism (16%) that was independent of prey availability. The results of these experiments indicate that for a cannibalistic forager such as the wolf spider *Schizocosa*, (1) the presence of conspecifics can improve average patch quality when prey are absent, and (2) cannibalism has the potential to be a significant mortality factor under natural field conditions because cannibalism persisted in prey patches that were open to emigration.

Key words Cannibalism · Emigration · Foraging behavior · Giving-up time · Density dependence

Introduction

Changes in habitat quality alter the rate at which foragers emigrate from a patch. Two important biotic components of patch quality are prey density and exposure to natural enemies (Werner et al. 1983; Stephens and Krebs 1986; Sih et al. 1992). An increase in the density of a cannibalistic generalist predator can reduce patch quality by decreasing the availability of heterospecific prey through more intense exploitative competition, and by increasing the risk of predation via increased rates of cannibalism (Fox 1975; Polis 1988). Alternatively, the presence of conspecifics can also increase patch quality for those individuals that are the successful cannibals. The complexity of these interactions makes it difficult to predict how rates of emigration of cannibalistic foragers from a patch should be affected by changes in both prey availability and the presence of conspecifics.

Wolf spiders (Araneae: Lycosidae) are generalist predators which often exhibit cannibalism (Edgar 1969; Hallander 1970; Yeargan 1975). Most lycosids are mobile foragers that do not construct webs to capture prey. Though categorized as wandering or cursorial spiders, wolf spiders employ a sit-and-wait foraging strategy in which they move between sites but are stationary most of the time (Ford 1977, 1978; Uetz 1979). Distance moved in seeking a new site, and time spent at a foraging site, may depend upon the prey-capture rate (Ford 1978). Indirect evidence suggests that wolf spiders inhabiting the litter layer of deciduous forests frequently have low rates

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of prey capture (e.g., 1 prey item/day; Edgar 1969) and can experience exploitative competition at natural densities (Wise and Wagner 1992).

Species of the lycosid genus *Schizocosa* are widely distributed in North America and are among the most abundant cursorial spiders of the forest floor (Dondale and Redner 1978; Martinat et al. 1993). Previous field and laboratory experiments with fenced enclosures revealed high rates of density-dependent cannibalism among young *Schizocosa ocreata* (Hentz) that significantly decreased when Collembola and crickets were available as prey (Wagner and Wise 1996). The need to use fencing prevented us from determining how changes in prey abundance and spider density affect rates of spider emigration. In addition, use of a barrier may have introduced behavioral artifacts; in particular, spiders may have become concentrated along the fence, leading to inflated estimates of cannibalism. In this paper we report results of laboratory experiments with juvenile *S. ocreata* and *S. stridulans* Stratton designed to measure (1) the extent to which prey availability influences emigration rates of solitary wolf spiders from a habitat patch, (2) how prey availability and the presence of conspecifics interact to influence rates of spider emigration and cannibalism in groups of *Schizocosa* in a habitat patch, and (3) possible behavioral artifacts introduced by constraining spider movements in laboratory and field experiments. Although conducted in the laboratory, these experiments were designed to reveal how prey availability and the presence of conspecifics may affect natural densities of wolf spiders by influencing rates of cannibalism and emigration.

Materials and methods

Experiment 1: giving-up time (GUT) of solitary spiders

This experiment quantified how prey availability influences the time that a solitary spider remains in a patch before emigrating, i.e., the spider's GUT. We examined the foraging behavior of solitary spiders as an aid to interpreting the influence of prey availability on the GUT of spiders in groups of conspecifics. Experiment 1 utilized immature *Schizocosa* collected from a mixed deciduous forest at 300 m elevation in Madison County, Ky., USA. The juvenile spiders were likely a mixture of *S. ocreata* and *S. stridulans*, based upon identifications of mature males from the collecting site. These sibling species can be distinguished only by differences in morphological characters of mature males (Stratton 1991).

The basic experimental unit consisted of two habitat patches between which a single spider could move freely. The patches were covered plastic food containers ($0.02 \text{ m}^2 \times 6 \text{ cm}$) connected to each other by three 17-cm pieces of clear PVC tubing (2.5 cm internal diameter) which juvenile *Schizocosa* readily entered. Collembola (*Tomocerus* sp. Entomobryidae) from a laboratory culture were introduced into one of the two containers; the other container became the No-Prey patch, because Collembola rarely entered the connecting tubes. Collembola are common in deciduous leaf litter, are documented as prey of lycosids (Moulder and Reichle 1972; Manley et al. 1976), and are consumed by *Schizocosa* in the laboratory (personal observation). The bottom of each container was covered with damp peat moss to make the environment suitable for Collembola and to facilitate locating *Schizocosa*. Leaf litter

was not used as a substrate because the position of *Schizocosa* could not have been monitored without disturbing the litter, which might have caused the spider to leave the patch. Each patch had a source of water for *Schizocosa*.

In 15 units, a spider was introduced into the Prey patch; in 15 other units, the spider was placed in the No-Prey patch. GUT was defined as the hours a spider spent in a patch before leaving for the first time, and was calculated as the time elapsed from the start of the experiment to the midpoint of the interval between the census time when the spider was first recorded to have left its original patch and the preceding census time. The spider had to leave the connecting tube before it was considered to be in a new patch.

The experiment was first run in March 1994 with spiders that had been collected the previous autumn and maintained in the laboratory on Collembola and crickets. Concerned that habituation to the laboratory feeding regime may have influenced foraging behavior, we repeated the experiment in April 1994 with freshly collected immature *Schizocosa*. These two separate runs are designated experiments 1A and 1B; average weights ($\pm$ SE) of spiders used were 9.5 ± 0.4 and 12.6 ± 0.2 mg, respectively.

For experiment 1A, the Prey patch was stocked with 20 Collembola, the approximate density in a Maryland deciduous forest where *S. ocreata* is abundant (Wagner and Wise 1996). Before being placed in their patches, spiders were each given 4 Collembola on 4 March; they were placed in their assigned habitat patch at 1100 hours on 7 March. Censusing of spider positions started at 1200 hours and continued at hourly intervals every day between about 0700 and 1830 hours until 1200 hours on 11 March (38 censuses). Spiders were then removed and weighed, and the peat in all patches was searched for Collembola. Final average Collembola numbers in the Prey and No-Prey patches were 14.7 ± 0.8 and 0.4 ± 0.1, respectively.

For experiment 1B, spiders were collected on 19 April 1994. They were each fed four Collembola on 21 April and were introduced into the experimental chambers at 1400 hours on 25 April. Chambers from experiment 1A were used, but the peat had been replaced and the connecting tubes cleaned with EtOH to remove any silk draglines that the previous occupant may have deposited. Since the spiders were larger than those used in experiment 1A, the Prey patch contained 35 Collembola. The experiment was run for the same number of days as experiment 1A, but the containers were censused less frequently. Censusing started at 1500 hours on 25 April and ended, after 22 censuses, at 1000 hours on 29 April. Final average Collembola numbers at the end of experiment 1B in the Prey and No-Prey patches were 19.4 ± 1.2 and 0.4 ± 0.2, respectively.

Experiment 2: behaviors of spiders with conspecifics

The purpose of experiment 2 was to evaluate how prey availability and the presence of conspecifics influence rates of spider emigration and cannibalism. Experimental arenas 12.5 times larger than those in experiment 1 were stocked with or without prey (Collembola and crickets). Each arena was either open to emigration on all sides, or was fenced to prohibit spiders from leaving. In the arenas open to emigration, emigrating spiders were captured and either removed from the experiment, or were returned to the population depending upon the assigned treatment. Contrasting the GUTs from experiment 1 with the rates of emigration in experiment 2 indicates how the presence of conspecifics affects *Schizocosa* residence time in patches markedly different in prey density.

Experimental unit

The basic experimental unit was an uncovered, clear plastic box ($44 \text{ cm} \times 70 \text{ cm} \times 15 \text{ cm}$; floor area = 0.3 m^2). The bottom contained moistened plaster of Paris to maintain high humidity. Because wolf spiders lack true scopulae on their tarsal claws (Foelix 1982), *Schizocosa* could not escape by climbing the smooth walls of the enclosures. Spiders were introduced into a central 0.25-m^2
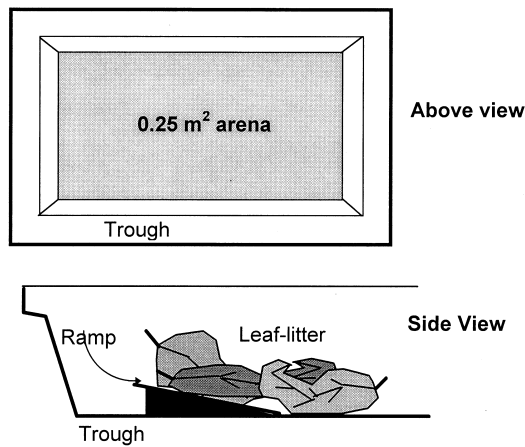
Fig. 1 Experimental unit modified to capture emigrating spiders in the 3-cm wide trough created by the sloping ramp surrounding the arena

arena, which was either enclosed by a metal barrier to prevent emigration, or was surrounded by a sloping ramp that created a trough in which emigrating spiders were captured (Fig. 1). All arenas contained a mixture of beech+oak+tulip poplar+sweet gum leaf litter at a depth (2.5 cm) comparable to that in the field. The litter came from the forest where the *Schizocosa* used in the experiment were collected, and was dried in the laboratory to remove any potential predators and prey.

The arenas were stocked with progeny of 70 adult *S. ocreata* females that were collected with egg sacs on 2 July 1994 from the site of previous field experiments with this species (Patuxent Wildlife Research Center, Prince Georges County, Md.; Wise and Wagner 1992; Wagner and Wise 1996). After several of a female's progeny had started to disperse, we gently coaxed the remaining spiderlings from their mother's abdomen and weighed the brood to determine average spiderling weight. Spiderlings from each brood were then randomly distributed proportionately across treatments, which removed any genetic or weight bias on future spiderling growth and survival, and ensured that spiderling weight and size distributions were equivalent across treatments. Each experimental arena was stocked with 43 spiderlings, a density equivalent to 3 times average field densities (Wagner and Wise 1996). Arenas were misted daily to add a source of water for the spiders. After 14 days, the arenas were destructively sampled and all surviving spiderlings were counted and weighed.

Levels of emigration

In order to (1) measure rates of emigration as a function of prey density and changing spiderling density, (2) determine how the absence of emigration influences rates of cannibalism, and (3) establish whether interactions along a fence barrier artificially elevate rates of cannibalism, we created three levels of spider movement: emigration (E), emigration + compensatory immigration (E+I), and fenced (F). In the E and E+I arenas, emigrating spiderlings fell into the trough that enclosed the arena and could not escape. Troughs were inspected daily for emigrants. In the E treatment, all dispersing spiders were counted and removed from the experiment, whereas emigrants in the E+I treatment were reintroduced to the center of the arena to simulate immigration equal to the rate of emigration. In the F treatment, a 6.5-cm vertical wall prevented emigration from the arena.

Prey abundance

Two prey treatments were established: No-Prey, in which the only food was other spiderlings; and Prey, in which Collembola (*Tom-*

ocerus sp.) and pinhead crickets (*Acheta domestica* Linnaeus) were present. We introduced approximately 240 Collembola/arena, a number comparable to field densities (Wagner and Wise 1996). Collembola were not counted directly but their numbers were estimated by live weight; 0.22 g of collembolans yielded approximately 240 individuals 0.5–3 mm in size. Forty crickets were added on days 1 and 7 to increase the diversity of the spiders' diet and substitute for other prey that occur in the field. All three levels of emigration (E, E+I, and F) were crossed with both levels of prey availability (No-Prey, Prey). The experiment was set up over a period of 2 days and was blocked accordingly.

Measuring rates of emigration and cannibalism

The number of emigrants per day was converted to a daily per capita rate of emigration. Since cannibalism and emigration continually altered spider density, we used a daily estimate of spider density to calculate the per capita emigration rate. The total spiders cannibalized in an arena was the number unaccountably missing at the end of the 14 days. The per capita rate of cannibalism for each arena was calculated by an iterative computer program that determined a rate of cannibalism which yielded the observed final spider density within the time span of the experiment (details of the procedure are given in Wagner and Wise 1996). Based on the calculated per capita rate of cannibalism, spider density on each day was estimated by subtracting the projected number of cannibalized spiders from the spider density of the previous day. In the E arenas, daily spider density was also adjusted by the number of spiders that had emigrated the previous day.

To measure mortality rates from starvation, 30 spiderlings were isolated, without food, in jars (5.5 cm diameter × 7.5 cm) with plaster of paris bases and leaf litter to maintain high humidity. Spiderlings were obtained from 15 different broods. Jars were misted with water daily and on days 7 and 14 were searched for surviving spiderlings.

Statistical analyses

In experiment 1, GUT values did not meet assumptions of normality and equal variances; therefore, the effect of prey was evaluated by the nonparametric Kruskal-Wallis test. Tests for effects of prey availability were one-tailed since we predicted that spiders would spend more time in patches with prey.

Experiment 2 was designed to evaluate: (1) the effect of prey abundance on rates of emigration; (2) the influence of prey abundance and spider emigration on rates of cannibalism, and (3) the impact of a fence barrier on rates of cannibalism. ANOVA of the E arenas evaluated the prey effect on rates of spider emigration. To evaluate the effects of prey, spider emigration, and fencing on spider cannibalism, a series of planned orthogonal contrasts was conducted within the overall design (Rosenthal and Rosnow 1985; Sokal and Rohlf 1995). The influence of prey on cannibalism was evaluated by contrasting rates of cannibalism between No-Prey and Prey and Prey arenas for the F and E+I treatments (Fig. 2). We examined the influence of spider emigration on cannibalism by contrasting rates of cannibalism in arenas where net emigration was prevented – the F and E+I treatments – with rates of cannibalism in the E treatments. The effect of fencing on cannibalism was evaluated by comparing rates of cannibalism between the F and E+I treatments. In both of these treatments, there was no net emigration, and only one type of arena (F) had a physical barrier along which spiders could encounter each other.

Although we did not establish spiders at more than one initial density, declining densities throughout the experiment made it feasible to determine whether per capita rates of emigration were higher when more conspecifics were present. We calculated the correlation between the daily rate of emigration and the daily estimated density within both the E and E+I arenas. A significant positive correlation would be consistent with density-dependent emigration.

Fig. 2 Planned orthogonal contrasts used to analyze the results of experiment 2. *Shaded treatments* (zero coefficients) are not included in a comparison. Replicates from the treatments labeled with the positive coefficients were contrasted with those labeled with the negative coefficient

	Emigration		Emigration + Immigration		Fenced	
	NO-PREY	PREY	NO-PREY	PREY	NO-PREY	PREY
Effects of Prey on Cannibalism	0	0	-1	1	-1	1
Effects of Emigration on Cannibalism	2	2	-1	-1	-1	-1
Effects of Fencing on Cannibalism.	0	0	1	1	-1	-1

Results

Experiment 1A: GUT of solitary laboratory-maintained spiders

Spiders tended to leave sooner from patches without prey (Fig. 3A), but the difference was not statistically significant [$P = 0.07$ (one-tailed), Kruskal-Wallis test]. A substantial number of spiders in both treatments never left the original patch (12/30, treatments pooled). The presence of prey significantly increased the GUT of those spiders that had emigrated by the end of the experiment
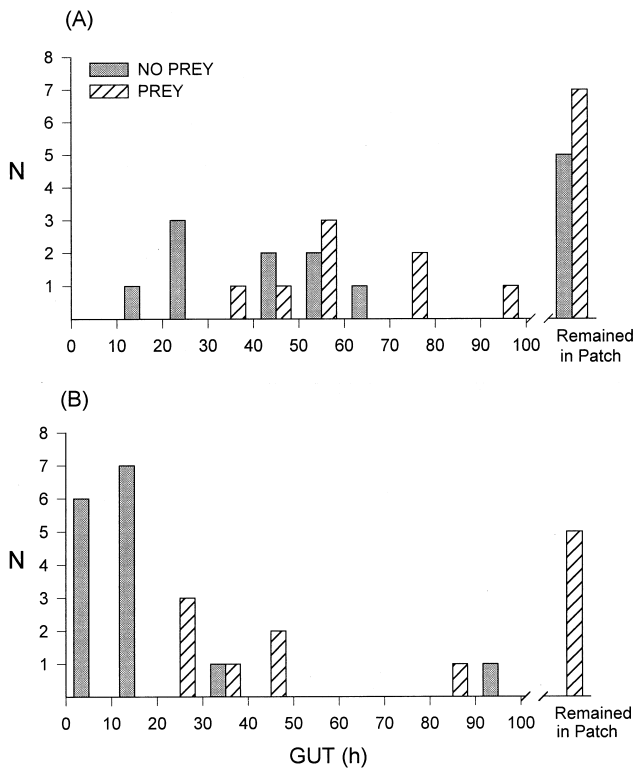

(A)

(B)

Fig. 3 A Effect of prey on the giving-up time (*GUT*) of laboratory-maintained *Schizocosa* (experiment 1A). Median GUT in patches with prey was 97 h, and 52 h in the absence of prey. **B** GUT of freshly collected *Schizocosa* (experiment 1B). Median GUT was 64 h in patches with prey, and 10 h in the absence of prey
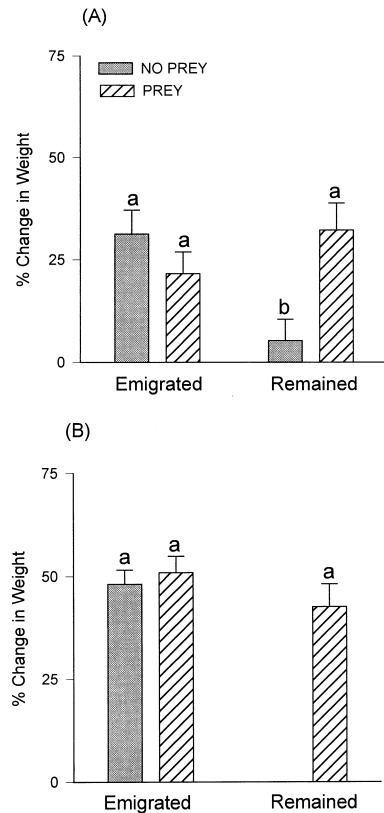

(A)

(B)

Fig. 4 A Weight gain (% increase) of laboratory-maintained *Schizocosa* that exhibited different responses to the presence or absence of prey (experiment 1A). Spiders that remained in a patch without prey did not significantly change weight (5.3±5.2%). All other spiders gained weight, and their gains did not differ significantly. Means (± SE) labeled with the same letter do not differ significantly according to *t*-tests adjusted for multiple comparisons by the sequential Bonferroni method (Rice 1989). **B** Weight gains of freshly collected spiders in experiment 1B. Gains did not differ significantly between categories

[60 ± 7 h versus 38 ± 6 h for patches with and without prey, respectively; $P(t) = 0.013$ (one-tailed), $df = 15$].

The growth of spiders that remained in a patch without prey was not significantly different from zero ($5.2 \pm 5.3\%$), which is consistent with the low number of Collembola that had moved into the No-Prey patches by the end of the experiment. Spiders that remained in a patch with prey, that eventually emigrated from a patch
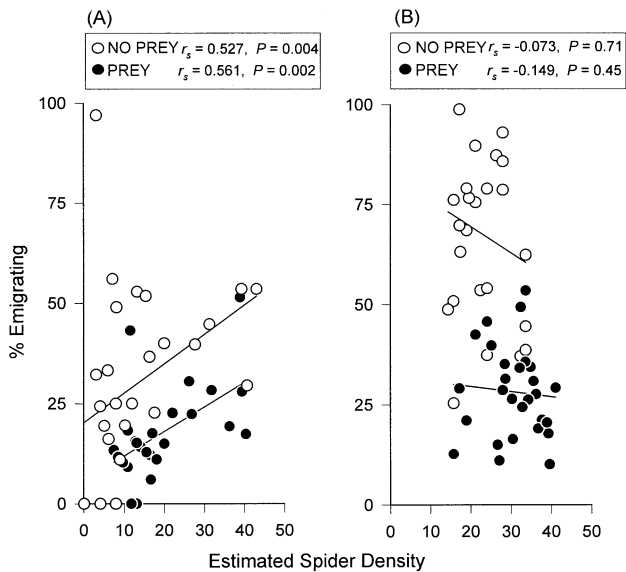
Fig. 5 Correlation, during the first 7 days of experiment 2, of daily per capita emigration rate with estimated spider density in E (**A**) and E+I (**B**) treatments. Values of the Spearman rank correlation coefficient indicate density-dependent emigration in the E treatment, but not from the E+I arenas

Table 1 ANOVA of the effects of prey on rates of emigration. Rates of emigration were arcsin square root transformed

Source	df	MS	F	P
Prey	1	0.1659	21.13	0.006
Block	1	0.0015	0.20	
Error	5			

with prey, or that emigrated from a No-Prey patch to one with prey increased in weight by approximately 25% (Fig. 4A).

Experiment 1B: GUT of solitary freshly collected spiders

The effect of prey on the GUT of freshly collected spiders was much clearer than for the laboratory-maintained spiders in experiment 1A. All spiders in the patches without prey had emigrated by 91 h; the experiment was terminated after the last spider remaining in a No-Prey patch had emigrated. Spiders remained approximately 6 times longer in patches with Collembola than in patches that had no prey [Fig. 3B; $P < 0.001$, Kruskal-Wallis test (one-tailed)]. This difference persisted when GUTs were compared for the subset of spiders that had emigrated by the end of the experiment (40 ± 8 h versus 13 ± 6 h for patches with and without Collembola, respectively). All spiders, irrespective of initial conditions, had increased their weight by almost 50% by the end of the experiment (Fig. 4B).
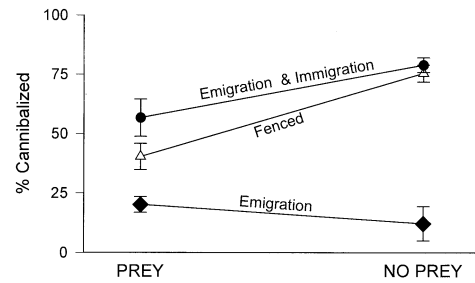

Fig. 6 Fraction of spiders cannibalized during experiment 2. Values are means ± SE

Table 2 ANOVA of the effects of prey, emigration, and fencing on rates of cannibalism. Rates of cannibalism were arcsin square-root transformed. Note that one of the four replicates of the F+Prey treatment was dropped from the analysis because a small opening in the fence barrier allowed a significant amount of emigration

Source	df	MS	F	P
Treatment	5	1358.69	19.09	0.0001
Block	1	0.602	0.01	
Error	16			
Contrasts				
Prey effect	1	1129.53	15.87	0.001
Emigration effect	1	5040.21	70.81	0.0001
Fence effect	1	137.63	1.93	0.183

Experiment 2: behaviors of spiders with conspecifics

Spider emigration

Spiders readily dispersed from both the E and E+I arenas, but access to prey significantly reduced emigration rate (Fig. 5, Table 1). During the first week of the experiment, the average daily emigration rate from arenas without prey was $49 \pm 4\%$ of the spider population. In contrast, the presence of Collembola and cricket prey in the arenas halved the average rate of spider emigration to $23 \pm 2\%$.

Spider density had equivocal effects on spider emigration. In the E arenas, where compensatory immigration was absent and spider density rapidly declined in response to both emigration and cannibalism, spider emigration was strongly density dependent, with an approximate halving of per capita emigration rate with a 75% decrease in spider density (Fig. 5A). However, in the E+I arenas, where spider density declined only in response to cannibalism, spider emigration remained density independent (Fig. 5B).

Spider cannibalism

In the arenas with no net emigration (E+I and F treatments), mortality by cannibalism was high, and was significantly reduced by the presence of alternative prey. Prey availability reduced mortality by cannibalism from
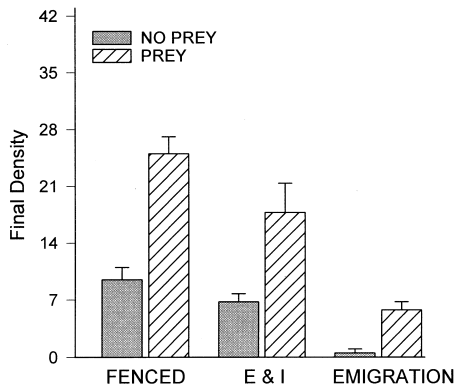
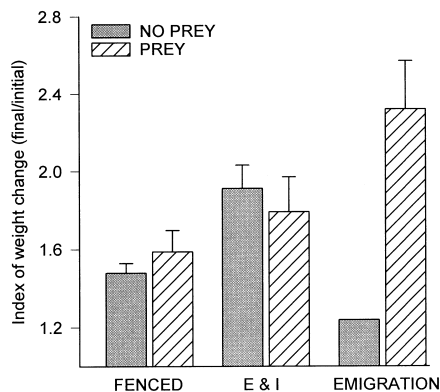**Fig. 7** Final spider density at the end of experiment 2. Values are means ± SE

Fig. 8 Growth of spiders in experiment 2, as measured by the index (mean final weight/arena)/(mean initial weight/arena). Values are means ± SE. All surviving spiders gained weight regardless of prey treatment

79% to 57% (Fig. 6, Table 2). Although rates of cannibalism were significantly lower in the E arenas, where net emigration rapidly reduced spider density, mortality by cannibalism persisted (~ 16%), and was not influenced by prey availability (Fig. 6).

Although fencing elevated rates of cannibalism by preventing emigration, the fence barrier itself did not directly increase cannibalism. Rates of cannibalism in F arenas were not significantly different from those measured in the E+I arenas (Fig. 6, Table 2). In fact, these statistically nonsignificant differences between treatments were opposite the direction expected: rates of cannibalism tended to be lower in the F arenas.

Final spider density

The presence of prey increased final spider density in all treatments (Fig. 7). In the open system with no immigration – the E arenas – the availability of Collembola and crickets increased final numbers of *S. ocreata* by an order of magnitude. Without prey, nearly all of the spiders had emigrated by the end of the experiment (final density ~ 0.5 spiders/arena) With prey available, approximately

seven spiders/arena remained, never leaving the 0.25-m² area during the 2-week period. Cannibalism was the only determinant of final density within the closed-system treatments (F and E+I arenas). In these arenas, when prey were present, final spider density was approximately 21 spiders/arena, which was 3 times the final spider density of No-Prey patches.

Final weight

Average spiderling weight increased in all treatments, regardless of prey availability (Fig. 8). Surprisingly, providing Collembola and crickets did not significantly increase spiderling growth within the F and E+I arenas ($P = 0.70$, $df = 14$). In the No-Prey arenas, spiderlings obtained energy solely from cannibalism and did not suffer a reduction in growth.

In the E arenas, adding prey dramatically increased spider growth rate (by about fivefold), probably because the rapid emigration of spiders in the No-Prey arenas resulted in spider densities too low for cannibalism to sufficiently compensate for the absence of prey.

Starvation

Spiderlings that were housed individually without food exhibited a high initial rate of survival, with 97% (29/30) still alive at day 7. After the second week, mortality by starvation had significantly increased. By day 14, only 17% (5/30) of the starved spiderlings remained alive. This result indicates that in the No-Prey arenas, practically all mortality during the first week of the experiment was the result of cannibalism. Previous research demonstrated that spiderlings exhibited a 95% survival rate when fed only one Collembola per week (Wagner and Wise 1996). Given this fact and the high rates of growth and mortality in No-Prey arenas, it is reasonable to conclude that cannibalism was the dominant cause of mortality during the entire experiment.

Discussion

Predicting a cannibalistic forager's GUT from a patch is difficult since each forager can be a competitor, predator, and/or potential prey. The results of these laboratory experiments suggest that both prey availability and the presence of conspecifics interact to influence emigration rates of *Schizocosa*, a sit-and-wait cannibalistic forager. For solitary spiders, the rate of emigration during the first 24 h was 4 times higher in patches without compared to those with Collembola prey. In contrast, when spiders were in patches with a high density of conspecifics, the absence of prey increased emigration rates by only 1.6-fold in the first 24 h. Thus, for a cannibalistic forager such as *Schizocosa*, the presence of conspecifics can improve average patch quality when insect prey are absent.

In order to evaluate better the implications and generality of these findings, we first consider potential behavioral artifacts resulting from our experimental protocols before exploring the implications of our results in more detail.

Behavioral artifacts: evidence for and against

Laboratory investigations of behaviour can provide insights into how animals behave under natural conditions only if the simplified laboratory environment does not introduce behavioural artifacts. Experiment 1 uncovered an important artifact that can easily be eliminated, and experiment 2 demonstrated that a potentially critical artifact is absent.

Long-term confinement of *Schizocosa* in the laboratory with regular feeding alters foraging behavior. In patches with prey, recently collected *Schizocosa* tended to leave sooner than laboratory-maintained spiders (64 h vs 97 h, respectively). Habituation to the laboratory environment had a much greater effect on the GUT of spiders placed in patches lacking prey, since spiders fresh from the field left these patches much sooner than did the laboratory-maintained *Schizocosa* (10 h vs 52 h, respectively). The different behaviors of spiders in experiments 1A and 1B suggest that it would be worthwhile to study the consequences of long-term experience on foraging behavior and, furthermore, that results of behavioral studies with spiders that have been housed in the laboratory for a substantial portion of the life cycle should be interpreted cautiously. Clearly, it would be prudent to study foraging behavior in the laboratory with animals recently collected from natural populations whenever possible.

Ecological field studies often rely on enclosures to create 'managed environments' (Hairston 1989). In previous field experiments with 1- and 2-m^2 fenced portions of the forest floor (Wise and Wagner 1992; Wagner and Wise 1996), capture rates of *S. ocreata* in pitfall traps placed along the wall were 2 times higher than in traps set in the center of the plots (unpublished data). We became concerned because this difference in trapping rate apparently reflected higher spider activity along the walls of the enclosure, which might have increased opportunities for cannibalistic attacks, yielding an overestimate of mortality from cannibalism. The results of experiment 2 reveal that fence barriers do not increase mortality from cannibalism (F versus E+I arenas), and that the high rates of cannibalism among *S. ocreata* measured in field and laboratory enclosures (Wise and Wagner 1992; Wagner and Wise 1996) are not artifacts of fencing. Of course the opportunity to emigrate from an area can significantly reduce rates of cannibalism (E versus E+I arenas); however, this does not indicate that all experiments utilizing enclosures overestimate rates of cannibalism. Results in the E arenas, an extreme situation where emigration occurred in the absence of immigration, may have little relevance to natural systems, since emigration typically is coupled with immigration, i.e., emigrants become immigrants to other habitat patches.

Experimental enclosures that prevent both emigration and immigration simulate an environment where emigration = immigration (e.g., the E+I arenas). Consequently, experiments utilizing enclosures may not overestimate natural rates of cannibalism if emigration is balanced by immigration in nature.

Effect of prey availability on the rate of emigration of *Schizocosa* from a habitat patch

Availability of prey has a major impact on how quickly juvenile *Schizocosa* leave a small patch of habitat. The presence of Collembola reduced the rate of emigration of solitary spiders during the first day of the experiment from approximately 90% to 25% (rates derived by comparing numbers of recently collected spiders with GUT < 30 h in the two treatments; Fig. 3B). Because a nonlitter substrate was used in experiment 1, results with solitary spiders cannot be extrapolated directly to the situation in the field. Nevertheless, in experiment 2, the younger juveniles, which foraged in a natural leaf litter substrate with conspecifics, exhibited a qualitative response to prey that was similar to that of the solitary, older juveniles on a peat substrate. The presence of alternative prey in the arenas with 43 *Schizocosa* also reduced the emigration rate during the first 24 h (46% to 29%; rates for No-Prey and Prey arenas, respectively, E and E+I pooled).

It is reasonable to speculate that for the solitary spiders, the decision to remain or leave a foraging site was based primarily upon whether or not they had consumed prey within a certain amount of time. This interpretation is consistent with Ford's (1978) finding that mature female *Pardosa amentata* (Clerck) (Lycosidae) increased the time they remained at a site by 50% when they were given an item of prey. It is also possible that sensory cues contributed to the effect of prey on GUT. Other researchers have noted that adult *S. ocreata* alter their GUT within 0.03-m^2 laboratory arenas on the basis of visual cues in the absence of actual prey consumption (Persons and Uetz 1996). Despite the potentially complex physiological and sensory cues involved in patch choice, it is clear that prey availability substantially influences the length of time that immature *Schizocosa* will remain in a small area. Prey availability also clearly influenced GUT of spiders in groups, but the presence of conspecifics affected the manner in which alternative prey influenced GUT.

Effects of conspecifics on emigration rate

The effects of conspecific density on emigration rates in *Schizocosa* involve potentially complicated interactions between food supply and the intensity of exploitative competition, and exposure to, and gains from, cannibalism. The presence of other spiders clearly influenced the response of juvenile *Schizocosa* to differences in prey availability. This can be seen by comparing emigration rates of

solitary and grouped spiders. Despite differences between experiments 1 and 2 in substrate, patch area, and arena construction, emigration rates in the presence of nonspider prey were remarkably similar (25% and 29% for 24-h emigration rates of solitary and grouped spiders, respectively). However, emigration rates in the absence of prey differed between solitary spiders and spiders in groups (90% and 46%, respectively).Thus, depriving solitary spiders of prey increased the emigration rate fourfold, whereas the absence of prey increased the per capita emigration rate by only 1.6-fold when conspecifics were present.

Why did spiders without Collembola or crickets emigrate at half the rate in the presence of conspecifics? It is reasonable to hypothesize that cannibalized conspecifics provided enough food to the successful cannibals to increase the cannibals' GUT for the patch. In treatments in which net emigration was prevented, final spider weights did not differ between arenas with and without insect prey. Thus, growth of *Schizocosa* solely from cannibalism was equivalent to growth based on a prey of Collembola, crickets, and conspecifics.

The presence of conspecifics is clearly not advantageous to all individuals, because at higher spider densities, per capita prey levels are lower and exposure to cannibalism is higher. Field experiments have revealed negative effects of spider density on growth rates of *S. ocreata* spiderlings, suggesting the potential importance of exploitative competition for prey (Wise and Wagner 1992; Wagner and Wise 1996), and previous laboratory experiments have revealed that rates of cannibalism among young *S. ocreata* are strongly density dependent (Wagner and Wise 1996). In agreement with these patterns, daily emigration rates over the first week in the E arenas were clearly density dependent. In contrast to this pattern is the clear absence of density-dependent emigration in the E+I arenas. However, the continual reintroduction of emigrants prevented spider densities from declining below about 15 spiders/arena, which may have obscured a correlation between emigration rate and spider density. It is also possible that the absence of density dependence in this treatment is an artifact of continually reintroducing subordinate individuals predisposed to emigrate. Previous studies have indicated that *S. ocreata* juveniles and adult males exhibit leg-waving displays when encountering a conspecific (Aspey 1975, 1976; called *S. crassipes* by Aspey). Adult male *S. ocreata* form dominant-subordinate hierarchies (Aspey 1976), though it is unknown whether *Schizocosa* spiderlings exhibit similar behavior. Future experiments could clarify whether a constant but random proportion of the spider population emigrated daily, or whether it was a subpopulation of subordinate individuals that reemigrated each day that they were reintroduced.

Control of density in natural *Schizocosa* populations

These laboratory experiments demonstrate that prey availability and the presence of conspecifics influence rates of cannibalism and emigration in juvenile *Schizocosa*, which should lead to differences in population density in natural habitat patches. Furthermore, the results of experiment 2 demonstrate that the immigration of conspecifics can increase average patch quality when prey availability is low.

In the field, emigrants from one patch are a potential source of immigrants into other patches. However, in the natural environment in which habitat patches differ in quality, size, and separation, migration rates into and out of patches will not always be identical. We created the extreme situation in our E arenas, where all immigration was prevented; rates of cannibalism in the E arenas were still high and independent of prey availability. The persistence of cannibalism at the extreme situation, in which prey were present and spider density could decline due to emigration (E + Prey arenas), suggests that under natural field conditions, cannibalism can be a significant mortality factor regulating densities of *Schizocosa*.

It has been shown that relative size differences often determine the outcome of cannibalistic interactions (Polis and McCormick 1987; Van Buskirk 1989; Orr et al. 1990). Consequently, both levels of prey abundance and the size distribution of the cannibals should interact to dictate the size of individuals which emigrate from, or remain in, the foraging patch. In future studies with cannibalistic predators it would be fruitful to focus on this interaction.

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