

Kinship and familiarity affect recognition and foraging in the wolf spider, *Pardosa milvina* (Araneae: Lycosidae).

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ABSTRACT

KINSHIP AND FAMILIARITY AFFECT RECOGNITION AND FORAGING IN THE WOLF SPIDER, *PARDOSA MILVINA* (ARANEAE: LYCOSIDAE).

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Recognition of familiar and related conspecifics can be crucial for altruistic behaviors. In spiders, a reduction in cannibalism has previously been used as evidence of kin recognition. The goal of this study was to examine the changes in activity and foraging for the non-social wolf spider, *Pardosa milvina* (Araneae: Lycosidae), as novel proxies for recognition and to provide evidence for altruism. Activity and foraging by juvenile spiders were explored on chemotactile cues (silk, excreta, feces) from related and/or familiar spiders. The activity of spiders included time spent moving, speed, and duration on familiar or kin cues. Foraging included the maximum consumption of crickets and rate of capture on non-kin, kin, familiar non-kin, and familiar kin cues. *Pardosa* spent more time ambulatory on kin cues than familiar cues. Additionally, animals foraging on kin cues decreased consumption while those foraging on familiar cues increased consumption. Capture rates increased on familiar cues, but tended to decrease on kin cues. These results suggest that immature *Pardosa* utilize chemotactile cues to distinguish kin and familiar conspecifics and may exploit this recognition to increase their indirect fitness. These results also align with a recent producer-scrounger foraging model that considers within-group relatedness as a key to understanding exploitation by kin. Together these results indicate a foraging strategy that may help to explain the early evolution of sociality in spiders.

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Introduction

Social and altruistic behaviors are often evolutionarily based on kin selection. Altruistic individuals incur a cost in order to ensure a benefit to another individual (Hamilton 1972). Despite the selective conundrum, apparently altruistic behaviors are seen across many taxa from mammals (Mateo 2003) to insects (Hamilton 1972). In high-density populations with frequent encounters, the ability to recognize individuals is crucial to allocate resources to related and honest individuals (Sherman 1977 and Wilkinson 1984). Kin selection theory predicts that benefits will be focused towards relatives to increase indirect fitness without costs to direct fitness. Kin recognition can involve assessment of genetic relatedness compared to self through perceived and expressed traits (Waldman et al. 1988). Thus, the ability to identify related individuals will allow for altruism to be directed to kin.

Although social living is found across a variety of taxa, it is rare in spiders and occurs in only a few dozen species of the almost 38000 described (Whitehouse and Lubin 2005). There are two proposed pathways for the evolution of sociality in spiders: subsocial or communal foraging. The subsocial pathway results from extended maternal care of spiderlings. The communal pathway involves aggregations around resources, particularly those that may be unreachable by a single web (Whitehouse and Lubin 2005). The communal pathway to sociality depends on benefits from group web foraging including capturing larger prey, more efficient prey capture, and the ricochet effect (see Lubin and Bilde 2007; Avilés 1997, and Whitehouse and Lubin 2005). Thus, communal spiders can be considered foraging groups, which utilize each other to gain benefits.

Foraging groups are structured around the ability of some individuals to exploit resources found by others in the group at a lower cost. Exploitive behavior is taxonomically widespread and is often known as kleptoparasitism or scrounging in behavioral ecology (Barnard 1984). Although exploitation can be detrimental to exploited individuals, it is most likely a consequence of group living (Giraldeau and Caraco 2000). The producer-scrounger group foraging model considers the costs and benefits to the producer (forager who finds the resource) and scrounger (exploiter of the found resource) (Giraldeau and Caraco 2000).

Recently, Mathot and Giraldeau 2010 developed a model that considers within-group relatedness as a component of producer-scrounger decisions. This model posits relatedness as a factor that mitigates the costs of exploitation. For the exploiter, the net benefit of exploiting kin is low due to loss in inclusive fitness, but there is a gain in inclusive fitness by the exploited individual since its relative receives resources. In order to maintain the net benefit of kin exploitation, the producer can impose significant costs on non-kin exploiters. The Mathot and Giraldeau model was tested using the producer controlled zebra finch (*Taeniopygia guttata*) system. In flocks of related individuals, there was higher scrounging and lower levels of aggression than flocks of unrelated birds. These results support the model and suggest that producers can be kin-selected to allow scrounging by relatives.

The goal of this study was to examine the potential for kin selection to affect foraging in a solitary spider. Specifically, we used the wolf spider, *Pardosa milvina* (Araneae: Lycosidae). *Pardosa* can reach high densities in the field around patches of

food (Marshall et al. 2000). This species is also food limited and strongly affected by the density of conspecifics (Buddle et al. 2003). Previous work has also shown that *Pardosa* display reduced cannibalistic tendencies towards related individuals (Anthony 2003). Another wolf spider, *Hogna helluo* (Araneae: Lycosidae), also shows reduced cannibalism in sibling pairs of immature spiderlings (Roberts et al. 2003). The high densities in the field, importance of the presence of conspecifics, and kin recognition all indicate that foraging interactions are frequent within *Pardosa milvina* and may be influenced by relatedness.

We utilized the chemosensitivity of *Pardosa* to examine changes in spider activity as a proxy for recognition. *Pardosa* are chemically aware and able to interpret information about prey, predators, and conspecifics from chemotactile cues (silk, excreta, and feces) (Rypstra et al. 2009). We used activity on cues from non-kin, kin, and familiar conspecifics to verify recognition. We predicted that *Pardosa* would recognize kin and familiar spiders from chemical cues as in Anthony 2003. Next, we tested foraging effort on chemical cues from all combinations of related and/or familiar spiders. If the producer-scrounger model of Mathot and Giraldeau applies to *Pardosa*, we predict a reduction in foraging effort in the presence of kin cues as an indication of exploitation tolerance and increased foraging effort in the presence of non-kin cues as costs imposed to the potentially unrelated scrounger. We also expect that familiarity will mediate exploitation and be used to assess the threat of a conspecific.

Methods

Study Species

Female adult *Pardosa* with egg sacs were collected from the soybean fields at the Ecology Research Center (Oxford, Ohio, Butler County) in April and May 2011. The offspring from each female were grouped as a family. Females were maintained in the laboratory on two crickets, *Acheta domesticus* (Orthoptera: Gryllidae), once a week. After hatching, spiderlings were allowed to remain on the mother's abdomen until after dispersal. We used 9 clutches (A-I) and various numbers of spiders from each clutch (A:15, B:13, C:13, D:7, E:29, F:28, G:14, H:10, I:16). Each spiderling was placed in an individual home (8 cm diameter X 8 cm high) with a soil substrate and given *Sinella curviseta* (Collembola: Entomobryidae) ad libitum for food. Spiderlings were given an identifier, which contained the common family letter and a unique number. Once spiderlings were large enough to eat crickets, each was moved to a new individual container (12 cm diameter X 14 cm high) with soil substrate. Unless otherwise noted, spiderlings were maintained on 2 pinhead-sized crickets (less than .25 centimeters) twice a week. All laboratory spiders were kept in an environmental chamber on 12:12h light:dark cycle at 25°C and 70% relative humidity.

Cue Deposition

Cue deposition was similar in the recognition and foraging experiments. Any differences in timing or feeding are noted in the respective sections. Cue spiders in familiar treatments deposited cues in a small container (13 cm diameter X 24 cm high). The bottom of the container was lined with filter paper (12.5 cm diameter) and a moist

cotton ball was added for moisture and humidity control. The spider was kept in the container for approximately 24 hours to deposit cues. Cues used in the recognition and foraging experiments were deposited in a large container (19 cm diameter X 16 cm high) lined with filter paper (18.5 cm diameter) and contained a small moist cotton ball. Familiarization occurred by exposing the animal to the cues of another spider in the small container for either 24 hours (recognition) or 48 hours (foraging) before experimentation.

Recognition

All cue spiders were fed 2 pinhead-sized crickets 48 hours prior to depositing experimental cues. Spiders in the familiar treatment deposited cues 24 hours after feeding. Cues were used within 8 hours of deposition completion. The subject spiders were fed 2 pinhead-sized crickets approximately 48 hours prior to experimentation. Thus, subjects from both treatments had the same hunger level during the trial.

For the recognition trials, filter paper in a two-choice arena contained cues from 1) a kin spider: same family, but not familiarized 2) a familiar spider: non-family spider cues to which the subject spider was familiarized or 3) unfamiliar and non-kin spider cues. Trials were kin vs unfamiliar/non-kin (n=23) and familiar vs unfamiliar/non-kin (n=26). All spiders were juvenile and ranged from 22 to 43 days since dispersal. Some spiders were used multiple times as either a cue and/or subject spider. Spiders were allowed at least 1 week on the non-experimental feeding schedule before being reused.

The filter paper containing cues from the large container were cut out and taped to another piece of filter paper (24.0 cm diameter) with a neutral zone between the two sets of cues (Figure 1). A circular plastic tube (19.0 cm diameter) was placed on top of the

filter paper in such a way to minimize gaps on the outer edges. Spiders were introduced for a 1-minute acclimation period under a clear tube in the neutral zone before the trial began.

We placed the arena under a video camera in an isolated booth and monitored activity in a laboratory room. We quantified behavior between the two sets of cues using an automated digital collection system (Videomex-V, Columbus Instruments, Columbus, Ohio, USA). Changes in movement were automatically recorded every second, requiring a movement of at least one body length movement to be scored as locomotion. Spider behavior was outputted every 30 seconds and summed over a 30-minute trial period.

We measured the following behaviors for each spider: 1) time spent in locomotory activity 2) time spent in non-locomotory activity (movement of legs or rotations of the body which did not score as a displacement) 3) total distance travelled and 4) speed of movement. The position of the cues on the left or right of the test apparatus was randomized. The acclimation tube and outer tube were wiped with 70% ethanol after each test and allowed to dry. The filter paper was only used once.

We calculated the proportions of the total time that the spider spent engaged in locomotory or non-locomotory activity on each half of the arena and transformed these proportions by taking the arcsine of the square root to achieve normality (Neter et al. 1985). We also calculated the mean speed as the distance travelled divided by the time spent walking. We compared values for each cue treatment (non-kin/unfamiliar cue, familiar cue, kin cue) using an analysis of variance, (ANOVA), with individual spider entered as a random effect. These analyses were conducted in JMP 9.0.

Foraging

Differences in foraging were experimentally examined on unfamiliar/non-kin (n=19), unfamiliar kin (n=19), familiar non-kin (n=18), and familiar kin (n=19) cues. All spiders that were used for producing cues were fed 2 pinhead-sized crickets 5 days prior to depositing experimental cues. Spiders that were part of either the familiar or familiar kin treatments deposited cues in the small container on the third day after feeding. Cues were deposited following the same conditions as in the recognition trials. Cue spiders were placed in their individual home for one day and after this intermission they deposited experimental cues in the large container. All subject spiders were fed 1 pinhead-sized cricket 3 days before the foraging trials. Subject spiders in the familiar and familiar kin treatments were familiarized for 48 hours prior to experimentation. The carapace and abdomen width and the weight of each subject spider were measured within one hour before the trial.

The large containers (19 cm diameter X 16 cm high) were used as arenas in the prey capture studies. After the cue spider was removed, 5 pinhead sized crickets were added to the arena. The subject spider was added under a clear overturned vial to the center of the arena. After a one-minute acclimation period, the spider was released into the arena.

The first 5 minutes of the trial were continuously observed until the first capture occurred. Spiders that did not make a capture were also noted. We recorded the total number of crickets consumed over the 90-minute trial. Spiders were weighed and measured within 1 hour of completion of the trials to determine weight changes. Some

spiders were reused as cue and/or subject spiders after at least one week on the non-experimental feeding regime.

We examined the effect of relatedness and familiarity as well as any interaction between them on the number of prey captured in a logistic regression. We used a proportional hazard survival analysis to determine if relatedness or familiarity affected the timing of prey capture during the first five minutes when we had continuous observations. Finally, we determined whether there were separate or combined effects on consumption, as indicated by the change in weight of the animals over the course of the experiment. To control for the differences in prey capture across trials, we compared weight change in an ANCOVA with number of prey captured as the covariate.

Results

Recognition

Of the four metrics we tested only the proportion of time spent in locomotory activity differed among cue types. *Pardosa* spend significantly greater proportion of their time ambulatory on cues from kin animals than on cues from familiar animals ($p=0.017$; Table 1). All other analyses of the Videomex output were non-significant.

Foraging

Both familiarity and relatedness affect foraging effort (Table 2, Figure 2, 3). On cues from a familiar animal, *Pardosa* capture more prey ($p=0.0448$; Figure 3c,d) significantly faster ($p=0.0008$; Figure 2). They captured fewer prey ($p=0.0093$; Figure 3b,d) and tended to take longer to do so on cues from kin, although the difference was of borderline significance ($p=0.0581$; Table 2). At the end of the 5-minute observation

period, close to 90% of the spiders foraging on familiar non-kin cues had captured a cricket, while only 40% of spiders on unfamiliar kin cues had a capture (Figure 2). In 60% of the foraging trials on unfamiliar kin cues, the subject spider consumed 0 crickets (Figure 3b). In contrast, the subject spider consumed 0 crickets in only 20% of foraging trials on familiar non-kin cues (Figure 3c).

The number of crickets consumed was related to the overall weight change, but there was also an interaction between cue source and the weight change (Table 2). This interaction created lines with different slopes dependent on cue source for the relationship between weight change and number of prey consumed (Figure 4). Animals on cues from familiar spiders gained more weight across prey densities than on cues from unfamiliar animals (Table 2).

Discussion

This study shows that foraging decisions in *Pardosa milvina* are dependent on the relatedness and familiarity of conspecifics. Specifically, *Pardosa* behave competitively towards familiar conspecifics and forage cooperatively with related spiders. *Pardosa* view familiar spiders as competitors, but this competition can be reduced by relatedness. The moderation of competition through relatedness provides evidence for altruism. Thus, these results are the first to show altruism through changes in foraging in a solitary spider. The results from our recognition experiment also validate previous studies on recognition in *Pardosa* (Anthony 2003). This recognition allowed foraging decisions to be based on conspecific presence.

We saw a difference in foraging effort in prey capture rate and consumption that is consistent with the Mathot and Giraldeau 2010 producer-scrourger model. We saw reduced foraging effort around kin and increased effort around non-kin. The difference in foraging behavior between non-kin and kin cues represents tolerance for related scroungers and the added costs to unrelated scroungers imposed by producers (subject spider). In this producer-controlled scenario, the subject spider can impose costs to potential scroungers. Although the scroungers are not present with the producer, chemical cues are an indicator of the presence or previous presence of a scrounger. Since consumption was lower on kin cues (Figure 3b), the subject spider is leaving more prey for the potentially related scrounger. The increased consumption of prey on non-kin cues is an indicator of the costs imposed upon non-kin scroungers by the producer (Figure 3a). In essence, the producer assesses the possibility of a scrounger being present and quickly begins to take advantage of the resources when that scrounger is unrelated.

Although *Pardosa* exhibit a decrease in foraging effort in the presence of kin, the spiders continue to act as voracious competitors. If spiders were simply evaluating the relatedness of conspecifics based on chemical cues, we would not expect to see a strong effect of familiarity. However, we found that familiarity was explicitly important in consumption and prey capture rate (Table 2). The presence of chemical cues from a spider, which the subject recognizes as hungry, indicates a threat. Around a familiar animal, the subject spider consumed more prey and began to consume prey faster (Figure 2 and Figure 3c,d), indicating the immediacy of the competition threat.

Both kinship and familiarity mediate the foraging effort in *Pardosa*. Thus, the combination of a familiar and related animal represents a situation where the spider must balance competition and potential cooperation by imposing few costs, but also competing for available resources. This trend is easily seen in proportion of spiders that did not consume any crickets during the 90-minute trial (Figure 3). The proportion of spiders forgoing all prey is highest for the kin treatment and drops significantly for the familiar kin treatment (Figure 3b,d). However, the number of spiders consuming zero crickets is still higher in the familiar kin treatment than the non-kin treatment (Figure 3 a,d). Thus, the subject spider mediated the cooperation and competition by limiting costs to kin, but still competing with relatives that pose a threat.

A similar relationship is seen for the differences in weight gain if focused just on the consumption of 3 crickets (Figure 4). There is a larger weight change in familiar non-kin and familiar kin treatments than for unfamiliar non-kin and unfamiliar kin treatments (Table 2). The greatest weight change was for the familiar non-kin treatment (Figure 4). The threat of competition from the hungry familiar spiders causes more to be extracted from the cricket. Here, spiders are assessing familiarity of a potential competitor, but also imposing high costs to this non-kin scrounger. By extracting more from crickets, any scrounger that would eventually find it would be left with a less nutritious cricket. In contrast, when the scrounger could potentially be related, the producers leave more of the cricket behind for the scrounger.

Although *Pardosa* are solitary foragers, the assessment of cues indicates a balance between cooperation and competition. This balance is one of the crucial aspects of the

evolution of sociality in spiders (Lubin and Bilde 2007). Most social spider species show group foraging and all show prey sharing (Lubin and Bilde 2007). Although these behaviors are cooperative, competition between nestmates for feeding sites on prey does exist (Lubin and Bilde 2007). The presence of a complex balance between cooperation and competition in *Pardosa* reveals a potential selection regime for sociality. This foraging strategy may select for association with kin at high population densities and food limitation. However, according to this foraging strategy, altruism will decline as the groups become familiar with each other.

Appendix 1: Figures

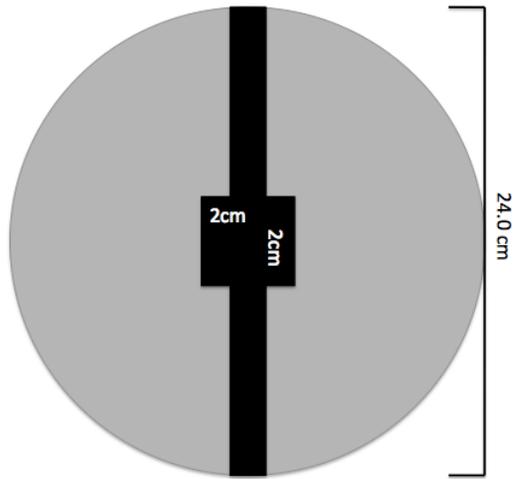


Figure 1: The experimental arena set-up. The black area represents the neutral zone which was free of cues. Each side contained a different chemotactile cue type depending on the treatment.

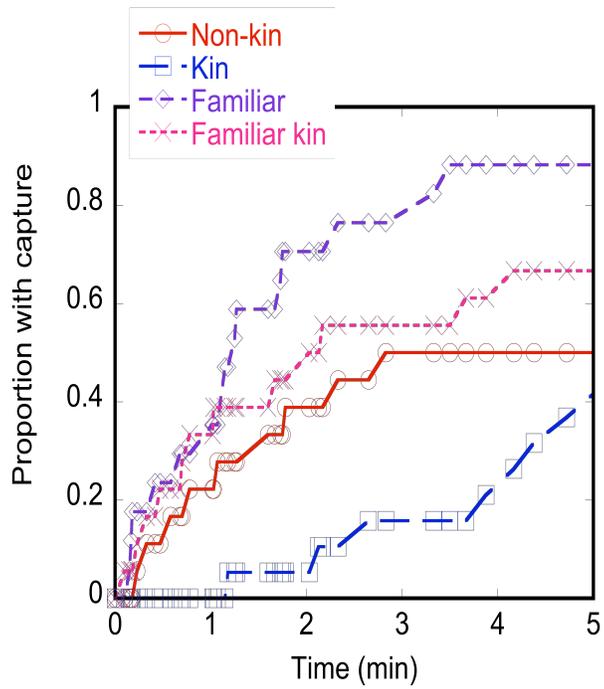


Figure 2: The proportion of *Pardosa milvina* that had captured a cricket within the first 5-minute observation period. Prey capture rate was positively affected by familiarity ($p=0.0008$) and tended to be negatively affected by kinship ($p=0.0581$).

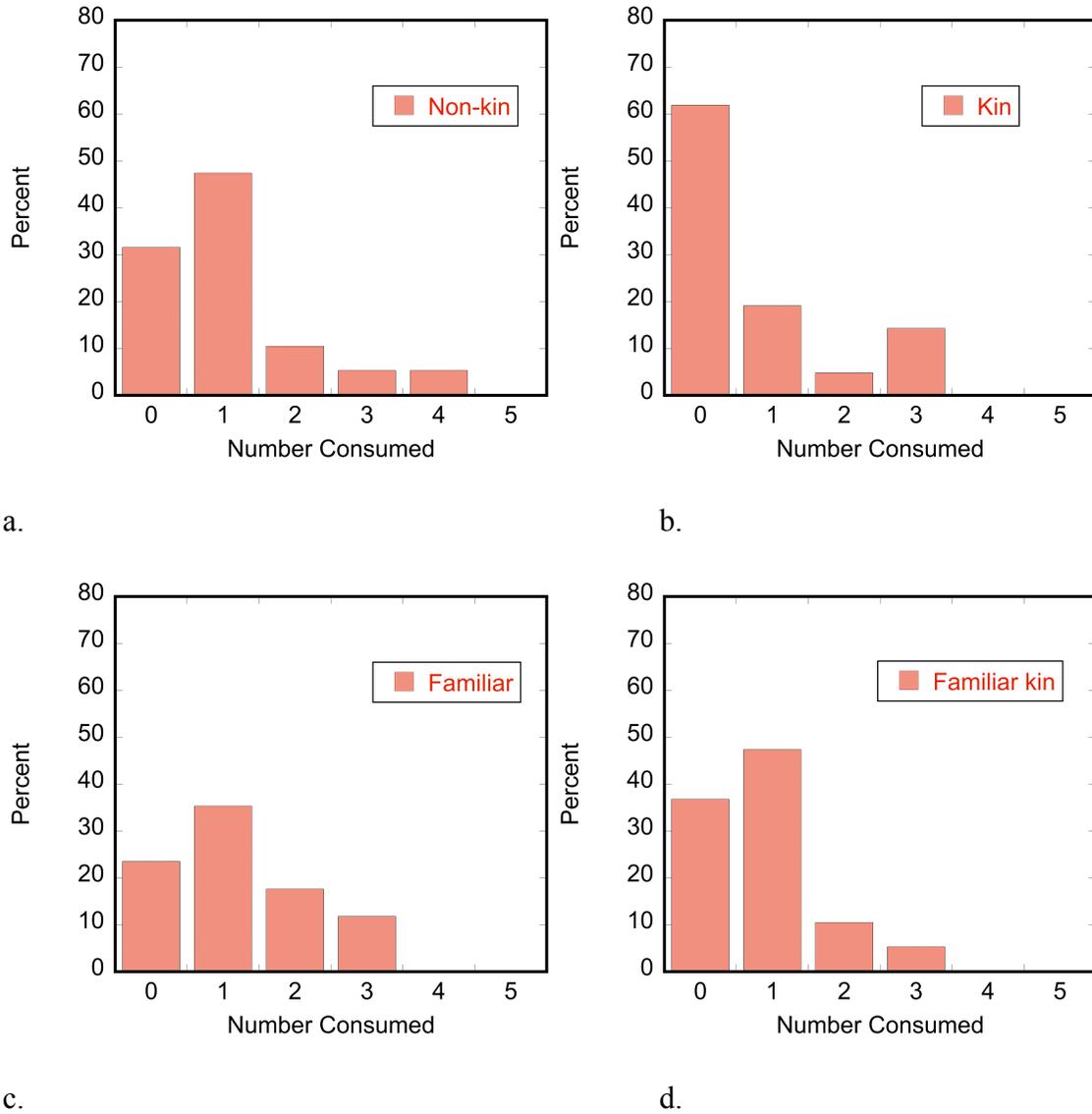


Figure 3a-d: The percentage of trials in which *Pardosa milvina* had consumed 0, 1, 2, 3, 4 or 5 crickets on (a) unfamiliar non-kin, (b) unfamiliar kin, (c) familiar non-kin, and (d) familiar kin. The number consumed was positively affected by familiarity ($p=0.0093$) and negatively affected by kinship ($p=0.0448$).

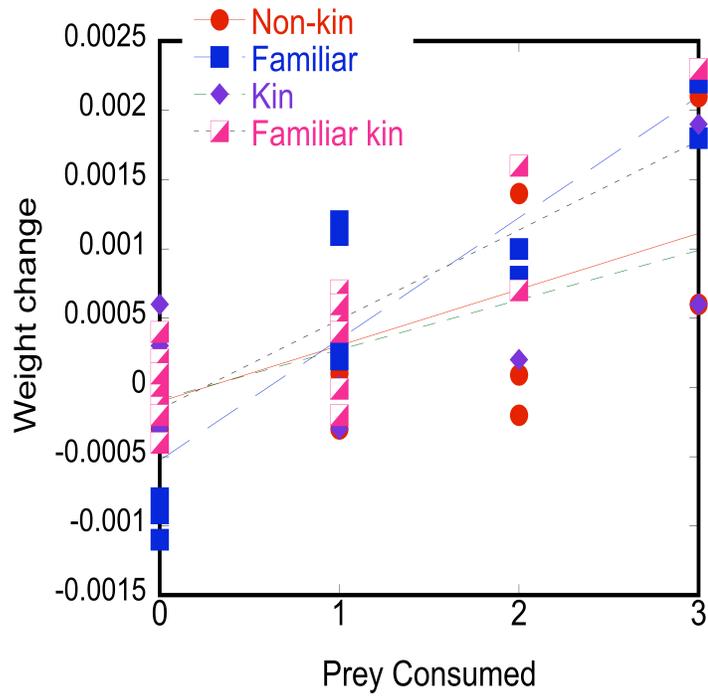


Figure 4: Weight change for subject spiders as affected by number of prey consumed and cue source. Animals on cues from familiar spiders gained more weight across prey densities than on cues from unfamiliar animals.

Appendix 2: Tables

Table 1: Activity metrics recorded (Mean \pm S.E.) for *Pardosa milvina* in a divided arena with cues from an unrelated unfamiliar conspecific on one side and cues from either an unrelated familiar animal or a relative on the other side. Statistics are provided for ANOVA run with cue source as treatment and individual entered as a random effect. Metrics indicated with the different letters are significantly different based on Tukey HSD pairwise comparisons.

Behaviour	Control	Familiar	Kin	F	df	p
Total distance travelled (cm)	420.4 \pm 33.4	391.0 \pm 40.4	473.4 \pm 73.9	1.03	2	0.366
Proportion of time spent in locomotory activity	0.31 \pm 0.01 A,B	0.26 \pm 0.02 A	0.36 \pm 0.03 B	4.33	2	0.017*
Proportion of time in non-locomotory activity	0.47 \pm 0.02	0.42 \pm 0.04	0.53 \pm 0.04	2.323	2	0.106
Speed (cm/sec)	0.95 \pm 0.06	1.02 \pm 0.10	0.98 \pm 0.08	2.09	2	0.135

Table 2: Results of analysis of data on the effects of kinship and familiarity on foraging by *Pardosa milvina*. Logistic regression was used to examine the number of prey consumed (Figure 3), a proportional hazard model was used to explore the time it took animals to capture the first prey item (Figure 2) and ANCOVA with the number of prey consumed as the covariate was used to test for treatment effects on the weight that animals gained during trials as a surrogate for actual prey intake (Figure 4).

Behaviour	Factor	Degrees of Freedom	Test statistic	p
<i>Logistic regression</i>			<i>X²</i>	
Prey Consumption	Kin	1	6.76	0.0093*
	Familiar	1	4.02	0.0448*
	Interaction	1	0.01	0.9195
<i>Proportional hazard model</i>			<i>X²</i>	
Time until first capture	Kin	1	3.59	0.0581
	Familiar	1	11.27	0.00088*
	Interaction	1	0.00	0.9867
<i>ANCOVA with number consumed as covariate</i>			<i>F</i>	
Weight change (after-before)	Kin	1	1.72	0.1440
	Familiar	1	9.16	0.0010*
	Interaction	1	0.28	0.7606

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