January 2002

Relating the unique sensory system of amblypygids to the ecology and behavior of *Phrynus parvulus* from Costa Rica (Arachnida, Amblypygi)

Eileen Hebets
University of Nebraska - Lincoln, ehebets2@unl.edu

Relating the unique sensory system of amblypygids to the ecology and behavior of *Phrynus parvulus* from Costa Rica (Arachnida, Amblypygi)

Eileen A. Hebets

Abstract: While the unique sensory system and neuroanatomy of amblypygids suggest that olfaction is important in their lives, to date no behavioral data exist to support this suggestion. To gain insight into amblypygid ecology and behavior, an individual mark–recapture study was conducted on the Costa Rican amblypygid *Phrynus parvulus*. Within two 50 by 25 m plots, the distribution and movement patterns of individual amblypygids were recorded for over 2 months. A total of 88 adult individuals (60 males and 28 females) were marked, with an average 51% resighted. Females were resighted more frequently than males (75% females, 40% males). The sexes did not differ in their frequency or movement distance, but females were more likely to be seen on the same tree over time. While both sexes potentially wander in search of mates, females may also be searching for a good crevice, or diurnal hideout. Once a female has mated and laid eggs, she likely remains stationary. Movement patterns and tree choice seem to be dictated by both the presence of conspecifics and environmental factors such as tree surface area, moss cover, and the presence of buttressing. Cumulative observational data collected over 3 years suggest that the main breeding season for this species is October–January. Both mate attraction and navigation may be facilitated by the olfactory capabilities of amblypygids, while their giant interneurons may be involved in their foraging behavior.

Résumé : Bien que le système sensoriel et la neuroanatomie très particuliers des amblypyges laissent croire que l'olfaction joue un rôle important dans leur vie, il n'existe pas à ce jour de données comportementales qui appuient cette hypothèse. Une étude de marquage et de recapture de l'amblypyge, *Phrynus parvulus*, du Costa Rica nous à permis d'en connaître plus sur l'écologie et le comportement des amblypyges. La répartition et les mouvements d'individus ont pu être notés pendant plus de 2 mois dans deux enceintes de 50 par 25 m. En tout, 88 adultes ont été marqués (60 mâles et 28 femelles) et en moyenne 51 % d'entre eux ont été revus, les femelles (75 %) plus fréquemment que les mâles (40 %). Il n'y a pas de différence sexuelle dans la fréquence ou la distance des déplacements, mais, dans le temps, les femelles tendent à être plus susceptibles d'être revues sur le même arbre. Alors que les individus des deux sexes sont probablement à la recherche de partenaires, les femelles cherchent peut-être aussi une bonne crevasse ou un refuge pour la journée. Une fois qu'une femelle s'est accouplée et qu'elle a pondu, elle reste probablement stationnaire. Les patterns de déplacement et le choix d'arbres semblent être dictés par la présence d'autres individus de la même espèce, mais aussi par des facteurs de l'environnement, tels que l'importance de la surface de l'arbre, la couverture de mousses et la présence de contreorts. Nos données, accumulées pendant 3 années, indiquent que la période principale de reproduction pour cette espèce se situe d'octobre à janvier. Tant l'attraction des partenaires que la navigation peuvent être facilitées par les capacités olfactives des amblypyges, alors que leurs interneurones géants jouent sans doute un rôle dans les comportements de quête de nourriture.

[Traduit par la Rédaction]

Introduction

Because of their bizarre appearance and nocturnal lifestyle, whip spiders (order Amblypygi) constitute an arachnid order about which very little is known. Members of this order are characterized by having a dorsoventrally flattened body, heavily spined pedipalps that are used in prey capture, and

modified first legs. Unlike most arachnids, amblypygids do not walk on eight legs but instead use only six for locomotion. Their first pair of legs are extremely thin, elongate, and very mobile. As these legs are held out in front of their bodies, probing the environment, they greatly resemble insect antennae, which is how they earned the name antenniform legs. A closer look at the tips of these antenniform legs reveals up to 10 different sensory organs encompassing a variety of functions (for review see Foelix and Hebets 2001). While all axons of these sensory organs proceed to the central nervous system, some of the sensory fibers synapse with giant interneurons located in the antenniform legs (Foelix and Hebets 2001). Although the presence of the giant interneurons has been known for over 20 years (Foelix and

Troyer 1980), their function is still a mystery. Typically, the giant-fiber system of invertebrates is involved in fast escape responses but it seems clear that this is not their role in amblypygids (Igelmund and Wendler 1991). Other possible functions of the giant interneurons of amblypygids include intraspecific signaling, navigation, and foraging.

Not only do amblypygids have a unique sensory system, owing to their antenniform legs and giant interneurons, but they also possess extremely large mushroom bodies (Strausfeld et al. 1998). Neuroanatomists recognize mushroom bodies as neuropils of the central nervous system that are generally associated with olfactory pathways. Although past dogma has been that the mushroom bodies play a large role in animal learning and memory, a more recent hypothesis is that they integrate information about multiple sensory stimuli (Strausfeld et al. 1998). Amblypygids stand out among arthropods in that their mushroom bodies are so large and convoluted that "they appear to have miniaturized other brain neuropils" (Strausfeld et al. 1998). While olfaction does not play a large role in the lives of most arachnids, electrophysiological studies have recently revealed that amblypygids do indeed have a well-developed olfactory capability (Hebets and Chapman 2000). However, since we know so little about their natural behaviors, we have no insight into the use of this olfactory capability in the daily lives of amblypygids.

The visual system of amblypygids is extremely poor. Like most spiders they possess 8 eyes, but unlike those of many of the nocturnal spiders, these eyes do not have a light-reflecting layer, or tapetum. Typically nocturnal animals have specialized visual systems that allow them to navigate through the darkness. Since amblypygids do not have a specialized visual system, they probably rely heavily on other sensory inputs such as olfaction, contact chemoreception, and mechanoreception. How well amblypygids are able to use these sensory systems and how reliant they are on them remain unknown, since we do not even know if amblypygids move, and if they do, how far they are likely to move, etc.

While the unique nature of the amblypygid sensory system and neuroanatomy has drawn the attention of many neurobiologists, few behavioral studies exist that can shed light on the function of either the giant interneurons or the enlarged mushroom bodies of this group. Of the 120 described amblypygid species, only about 10% have been observed with respect to their behavior. All of these observations were studies of reproductive behavior conducted in the laboratory (Alexander 1962; Weygoldt 1970; Weygoldt and Hoffmann 1995). The few field studies of amblypygids have provided some information on individual activity patterns as well as some suggestive observations regarding mating behavior (Beck and Pabst 1969; Beck 1972); however, no long-term field study has been conducted on any amblypygid species.

This study provides a foundation of information on the ecology and behavior of amblypygids upon which we can build hypotheses relating to the function of their specialized sensory system. One of the commonest uses of olfaction in animal systems involves intersexual signaling, such as the use of pheromones in many different insect groups. Olfactory signals are also used in territory marking and intrasexual interactions. Knowledge of the spatial distribution and movement patterns of males and females should lend insight into potential inter- and intra-sexual interactions. By individually marking animals and following their movement patterns for months, this study addressed questions relating to sex differences in spatial distribution and movement patterns of an amblypygid commonly found in Costa Rica, *Phrynus parvulus*. Field observations collected over 3 years contribute other general information about this poorly known arachnid group, such as seasonality and feeding behavior.

Materials and methods

Plot study

The mark–recapture portion of this study was conducted at La Selva Biological Station, Sarapiqui Province, Costa Rica, from May through August of 1999. Two 50 by 25 m plots were randomly chosen from a subset of potential locations in primary forest using the Global Information System. The plots were more than 400 m apart and both were more than 50 m off trail. Within each plot, all trees with a diameter at breast height of 15 cm or greater were numbered, labeled with flagging tape, and included in the study. The circumference of marked trees at a vertical height of 0.75 m was estimated by using a tape measure to follow the tree's surface in and out of buttresses. A few marked trees within each plot were chosen as focal trees, and distances and angles to other marked trees were measured in order to construct a map of tree locations. A colleague (Corine Vriesendorp) identified marked trees to the lowest taxonomic level possible. The degree of vine cover as well as degree of moss cover on the lower trunks (~2 m and below) of marked trees were scored in the following way: 1 = 0% cover, 2 = <50% cover, and 3 = >50% cover. Trees were also scored as positive or negative when buttressing was present or absent, respectively.

Trees were surveyed in plot 1 on 16 nights over approximately 2 months and in plot 2 on 13 nights over a month and a half. A survey was conducted approximately every 4 nights. Heavy downpours and high winds sometimes delayed a survey until the 5th night. Generally surveys were conducted between 20:00 and 24:00, although three surveys in plot 1 were conducted from 02:00 to 05:00. The three early-morning survey results did not differ from the night survey results and thus, all data were analyzed together. During a survey, the trunk of every marked tree within each plot was scanned from ~2 m down to the ground for the presence of *P. parvulus*. The light used for observations was white light from a headlamp. Trees were generally circled at least 2 times. Any unmarked individuals were captured, marked, measured, sexed, and returned to the location where they were captured. Some unmarked individuals were not captured, owing to their rapid escape response. If a capture attempt was not successful, the location, approximate size, and sex of the unmarked individual were recorded. Although the shape of the genital operculum is often used to determine sex, there are general gestalt differences between the sexes that were used to sex uncaptured individuals. Representative specimens of *P. parvulus* are deposited in the "Arthropods of La Selva" collection at La Selva Biological Station.

DecoColor opaque paint markers were used to individually mark the captured animals with a two-digit number, using a different color for each digit (red = 0, orange = 1, yellow = 2, etc.). Once the individual was marked, digital calipers were used to measure cephalothorax length (CL)

and cephalothorax width (CW). CL was measured between the two narrowest points of the cephalothorax (in the center) and CW was measured at the widest point of the cephalothorax. The sex of each individual was determined on the basis of general gestalt as well as the shape of the genital operculum and notes were taken regarding the general state of the animal (missing legs, presence of eggs, etc.). If an individual that was already marked was resighted, records were taken regarding its location upon resighting. The positions of previously marked individuals were recorded without disturbing them.

The total number of individuals marked from each plot was calculated and a χ^2 test was conducted to determine whether recapture rates or movement rates differed between the sexes. A movement index (number of nights when an individual was found on a different tree / number of trees in the plot / number of surveys carried out between first capture and the end of the study) and a residency index (number of nights when an individual was found on the same tree / number of trees in the plot / number of surveys carried out between first capture and the end of the study) were also calculated for males and females.

General observations

Less systematic observations were also made periodically during January of 1998 and 1999, May through August of 1999, and January of 2000 and 2001. These observations were made during general survey walks along trails at night. The individual's vertical distance from the ground (height on the tree) was measured and recorded along with its sex. Sometimes animals were collected and their CL and CW were recorded. Any information regarding feeding or other activity was also recorded.

Results

A total of 38 trees in plot 1 and 37 trees in plot 2 were marked, measured, and included in this study.

Resighting frequencies

In plot 1, 132 different *P. parvulus* were sighted, 55 of which were collected, marked, and released (31 males, 16 females, 8 immatures). In plot 2, 111 different individuals were sighted, 45 of which were collected, marked, and released (29 males, 12 females, 4 immatures). The number of males marked during the course of the study was double the number of females marked (Table 1). Females were resighted significantly more frequently than males ($\chi^2 = 8.87$, $P < 0.003$; Table 1). Of the individuals that were resighted, only 33% of the females moved to a different tree, while 50% of the males moved, but this difference is not significant ($\chi^2 = 1.29$, $P = 0.26$; Table 1). Among the individuals that were resighted, there was no difference between the sexes in terms of the number of times they were seen ($t_{[43]} = 1.062$, $P = 0.29$).

Movement patterns and residency indices

There was no difference in movement indices between the sexes (mean = 0.037 for males, mean = 0.02 for females; $t_{[84]} = 0.64$, $P = 0.53$), but females had a significantly higher residency index (mean = 0.07 for males, mean = 0.11 for fe-

males; $t_{[84]} = 3.45$, $P = 0.0009$). The higher female residency index indicates that females have higher site fidelity than males and are more likely to be found in the same place over time. The residency index did not depend on body size for males or females (all: $F_{[1,83]} = 2.06$, $P = 0.09$; males only: $F_{[1,56]} = 2.06$, $P = 0.16$; females only: $F_{[1,25]} = 2.28$, $P = 0.14$). The residency index also did not depend on tree size ($F_{[1,80]} = 3.45$, $P = 0.56$).

When individuals moved, the two sexes tended to move similar distances (mean = 11.12 m for 12 males over 16 movements; mean = 11.48 m for 6 females over 11 movements). The greatest known distance a female traveled was 36 m and the greatest known distance a male traveled was 30 m. Eleven individuals moved from the original tree without returning on a survey night. Seven individuals moved away from the original tree and subsequently returned to a closer, but different tree (three males, four females). Five individuals left their original tree and returned on a later date (two males, three females).

Sex-based encounter frequencies

The number of different males and females that each individual had the potential to encounter during the survey was determined by calculating the number of different males and females with which an individual shared a tree at any given time. Potential encounter frequencies of males and females did not differ between the sexes (number of males encountered: $t_{[86]} = -0.11$, $P = 0.91$; number of females encountered: $t_{[86]} = 0.72$, $P = 0.47$; Table 2). On any given night, the male/female potential encounter frequencies also did not differ between the sexes (encounters with males: $t_{[86]} = -1.5$, $P = 0.13$; encounters with females: $t_{[86]} = 0.18$, $P = 0.86$; Table 2). However, within a sex, males had the potential to encounter significantly more different males than different females during the survey period ($t_{[59]} = 2.0$, $P < 0.03$), while females showed no difference in their potential to encounter individuals of either sex ($t_{[27]} = 0.32$, $P = 0.38$).

Individual-based movement decisions

Trees were separated into size categories based upon circumferences of <50, 50–99, 100–149, 150–200, and >200 cm. When the sexes were compared, an individual's decision to move was not associated with the size of the tree to which it subsequently moved relative to the size of its original tree (i.e., whether the tree was greater, smaller, or similar in size to the original tree) ($\chi^2 = 1.4$, $P = 0.51$). Sixty percent of the females and 67% of the males moved to a tree of equal size, 16% of females and 19% of males moved to a larger tree, and 25% of females and 15% of males moved to a smaller tree. Body size was not a predictor of movement either. There was no difference in body size between the individuals that moved and those that did not (did not move: $N = 68$, CL = 9.6 ± 0.3 mm (mean ± SD); moved: $N = 17$, CL = 10.5 ± 0.61 mm; $t_{[83]} = -1.3$, $P = 0.18$).

Factors influencing choice of tree

When the results of surveys of all trees across nights were combined ($N = 1086$), 82% of the time a tree had no marked individuals present. Only one sex was present 14% of the time and both sexes were present 4% of the time. Across trees, male density was correlated with female density, suggesting

Table 1. Summary of marked adult *Phrynus parvulus* from the two plots combined.

	Males	Females
Total no. of adults marked	60	28
Proportion of individuals resighted (%)	40a	75b
Proportion of resighted individuals that moved (%)	50	33

Note: Values followed by a different letter are significantly different at $P < 0.003$.

Table 2. Potential encounter rates of males and females.

	Avg. no. of different males	Avg. no. of different females	Avg. no. of males encountered/night	Avg. no. of females encountered/night
Females	0.84 ± 0.20	0.79 ± 0.16	0.43 ± 0.15	0.42 ± 0.09
Males	0.88 ± 0.14a	0.65 ± 0.11b	0.72 ± 0.1	0.40 ± 0.60

Note: Values followed by a different letter are significantly different at $P < 0.03$.

that tree choice is not sex-specific or non-independent ($r^2 = 0.168$; Fig. 1). Using sightings of a total of 62 different males (60 marked males + 2 unmarked males over 93 sightings) and 32 different females (28 marked females + 4 unmarked females over 76 sightings), I calculated the likelihood of finding either sex in the presence of the same sex or the opposite sex or alone on a given night. Who an individual is likely to be found on the same tree with on a given night depends significantly upon the sex of the individual in question ($\chi^2 = 15.04$, $P = 0.0005$). Females were most likely to be found near males and males were most likely to be found near females (Table 3).

Amblypygids were found on a total of 31 tree genera in 20 different families (Appendix A). When data from all trees were combined, a stepwise regression model showed tree circumference to relate most strongly to the number of individuals observed on a tree on more than one occasion ($r^2 = 0.46$, $F_{[1,72]} = 35.5$, $P < 0.00001$; Fig. 2, Table 4), while the amount of moss cover also played a role ($F_{[1,72]} = 8.67$, $P = 0.004$; Table 4). However, tree circumference was the only tree characteristic to be correlated with the total number of different individuals seen on a tree over the course of the survey ($r^2 = 0.54$, $F_{[1,72]} = 66.12$, $P < 0.00001$; Table 4). The amount of moss cover is associated with tree circumference, with trees with >50% moss cover being significantly smaller than those in the other two categories ($F_{[2,72]} = 4.9$, $P = 0.01$). Vine cover had no effect on either the number of individuals visiting a tree or the number of individuals remaining on a tree (Table 4). Trees with buttressing were more likely to have individuals remain on them ($F_{[1,1]} = 7.15$, $P = 0.009$), but buttressing did not significantly affect the total number of individuals visiting a tree ($F_{[1,1]} = 0.31$, $P = 0.58$; Table 4). There was no correlation between female size (CW) and tree size ($F_{[1,34]} = 1.7$, $P = 0.2$) or between male size and tree size ($F_{[1,69]} = 0.77$, $P = 0.38$).

Predators and prey

Only one predation event was witnessed in the field. A scorpion was seen feeding on an amblypygid (Eben Gering, personal communication). No other data exist on natural predators. Two females were collected with more than 50 dipteran puparia attached to their abdomens, but these have yet to be identified (E.A. Hebets, unpublished data). Individuals were seen feeding on numerous crickets and katydids (Ortho-

ptera), harvestmen (Opiliones), spiders (Araneae), millipedes, roaches (Blattoidea), and moths (Lepidoptera). On two different occasions, individuals were witnessed catching moths out of the air.

Seasonality and vertical stratification

There was no difference in the overall proportions of males and females across the 5 months of the surveys ($\chi^2 = 2.3$, $P = 0.53$); however, there was a difference in the proportions of females with eggs versus those without ($\chi^2 = 15.9$, $P = 0.003$; Fig. 3). When all of the data from January observations were combined, 38% of the females had eggs, while during May–August only 9–11% had eggs. Both males and females were larger in June than in January and May, a pattern that can be seen in both CW and CL (females: CW, $F_{[4,105]} = 3.38$, $P = 0.01$; CL, $F_{[4,105]} = 4.06$, $P = 0.004$; males: CW, $F_{[4,156]} = 4.42$, $P = 0.002$; CL, $F_{[4,156]} = 3.77$, $P = 0.005$; Fig. 4). Males were larger, on average, than females (CW: $t_{[306]} = -2.74$, $P = 0.007$; CL: $t_{[306]} = -3.39$, $P = 0.0008$).

When data from all of the months were combined, there was no difference in the tree height at which females ($N = 95$, 80.22 ± 6.45 cm (mean ± SD)), females with eggs ($N = 35$, 83.64 ± 10.63 cm), or males ($N = 179$, 84.23 ± 4.7 cm) were found ($F_{[2,305]} = 0.13$, $P = 0.88$). But, on average, all individuals were found significantly higher up the tree in January than in May ($F_{[4,287]} = 5.84$, $P = 0.0002$) (January: 97.98 ± 4.96 cm (mean ± SD); May: 55.79 ± 7.99 cm; June: 76.67 ± 11.20 cm; July: 63.66 ± 13.39 cm; August: 77.59 ± 11.39 cm). This difference between January and May is explained by males alone, but the trend is seen in females as well (males: $F_{[1,287]} = 3.45$, $P < 0.0001$; females: $F_{[1,287]} = 2.3$, $P = 0.06$; Fig. 5).

Discussion

While the giant interneurons of the antenniform legs and the enlarged mushroom bodies of amblypygids make their sensory system and neuroanatomy unique, the behavioral correlates and functions of these structures have to this point remained a mystery. The enlarged diameter of giant fibers allows for extremely rapid conduction of nerve impulses, which is typically involved in predator evasion. The amblypygid giant-fiber system, however, does not seem to work in

Fig. 1. Average density (number per tree) of male *Phrynus parvulus* versus the average density of females over time ($r^2 = 0.168$, *t* test comparing densities, $P = 0.42$). For each tree in each survey, densities of males and females were calculated and then averaged; 31 trees with values of zero for densities of both males and females were excluded.
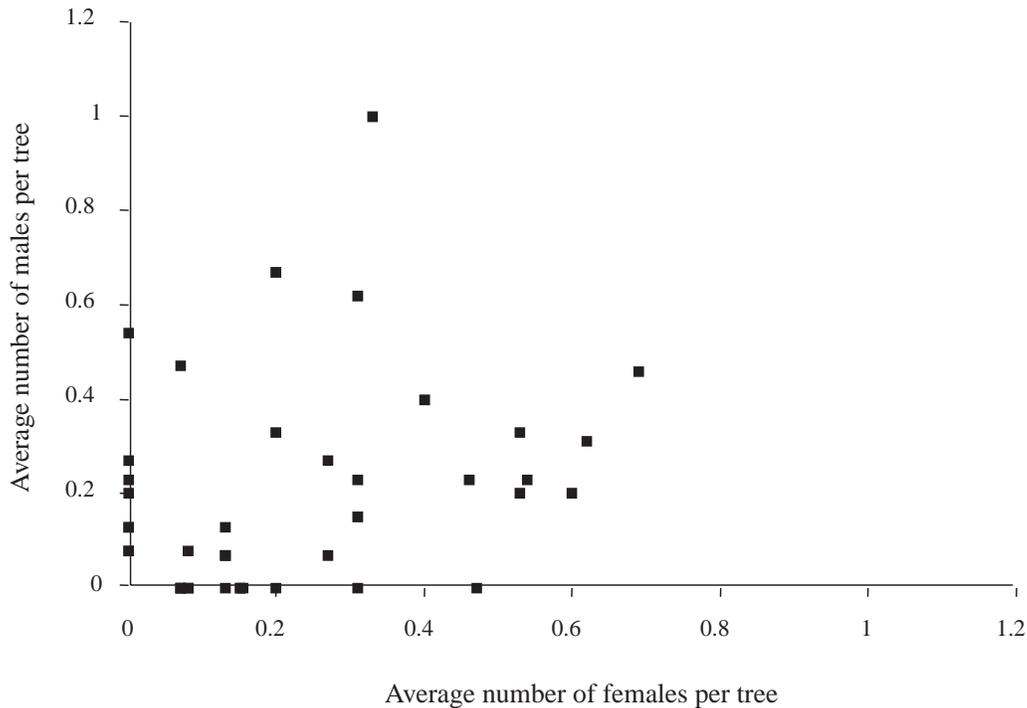
Table 3. Percentage of individual associations on a given night.

	Male (N = 62; 93 sightings)	Female (N = 32; 76 sightings)
Male	30	50
Female	41	14
Alone	29	36

Note: A 3×2 contingency test indicates that individual associations are sex-dependent ($P = 0.0005$).

an escape response (Igelmund and Wendler 1991), leaving functional roles in inter- or intra-sexual interactions and foraging as possibilities. While I did not observe any natural interactions during the course of this study, I did witness predation events. The speed and accuracy with which I observed amblypygids capture moths out of the air was incredibly impressive and suggests to me an extremely rapid transfer of sensory information. Since the visual system of amblypygids is not well developed, they must rely on other sensory inputs such as mechnoreception, olfaction, and contact chemoreception to identify and locate prey. Sensory hairs on the tip of the antenniform leg serve all of these sensory functions and at this stage, a likely hypothesis as to the function of the giant-fiber system of amblypygids relates to their sit-and-wait foraging strategy.

Since the occurrence of intersexual interactions is often dictated by the mating system of a particular group, which is in turn influenced by dispersal and spatial distributions (Emlen and Oring 1977), understanding the natural spatial distribution and movement patterns of males and females potentially lends insight into their intersexual interactions. Spatial distributions are influenced, for example, by whether or not males aggregate in leks, females congregate according to an

environmental resource, or one sex releases a pheromone as a long-range sex attractant. In this long-term individual mark–recapture study, I found that males and females tend to be distributed equally through space, with no obvious sex-specific aggregations. Neither males nor females seem to aggregate in same-sex associations to attract members of the opposite sex. Instead, both males and females are most frequently found in association with each other, a pattern that can be explained in a variety of ways.

It is possible that one sex releases a long-range sex attractant, drawing the attention of a member of the opposite sex. Males, for example, may be attracted to females via olfactory signals, resulting in the same-sex association seen in Fig. 1. The presence of a member of the opposite sex may also affect an individual's likelihood of remaining in a particular location. For example, if males are wandering randomly, they may arrest their movement once they come into contact with a female. Lastly, both sexes may choose trees not because of the presence of conspecifics at all, but according to the quality of the same resource, such as crevices or other djurnal hideouts, and using the same choice criteria.

If members of one sex signal their presence in order to attract members of the opposite sex, I should have seen differences in movement patterns between males and females. However, both males and females seemed to move similar distances with similar frequencies. While movement indices did not differ between males and females, recapture rates did differ. Based upon the number of marked males in this study (twice that of females) and the similar movement indices, the resighting frequency for males should have been much higher than was observed. This low resighting frequency for males can be explained in several ways. Males may be more difficult to see in the field than females, thus biasing the ob-

Fig. 2. Correlation between tree surface area (calculated from the circumference at a vertical height of 0.75 m) and the total number of different *P. parvulus* seen over time ($r^2 = 0.54$, $P < 0.00001$).
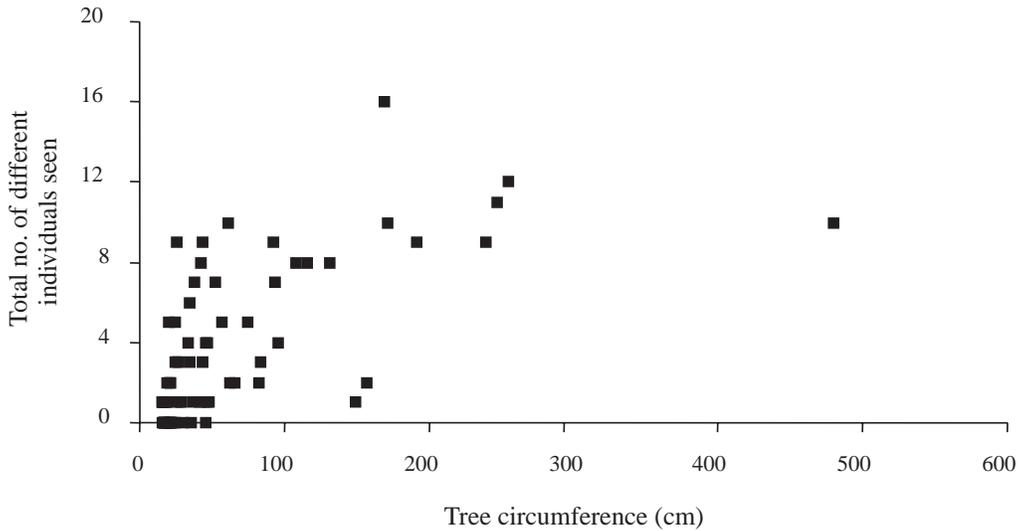
Table 4. Tree characteristics that affected or did not affect the number of individuals visiting and remaining on a tree.

	Surface area?	Buttressing?	Moss cover?	Vine cover?
No. of different individuals seen over time	Yes	No	No	No
No. of individuals seen more than once	Yes	Yes	Yes	No

servations. There may be differential predation rates, with males suffering higher predation than females. Or males may actually move more frequently than females but my study design may not have allowed me to detect this higher male movement index. Addressing the first explanation, it is unlikely that males are more difficult to observe than females, since they are larger, on average, and show similar color patterns. Predation rates are not known and thus the second hypothesis of higher predation rates cannot be ruled out. The third hypothesis of a higher than observed movement index for males seems the most plausible. Because of the limited size of the plot, males could easily have exited it during the study and thus would not have been resighted. The fact that females are more likely to be found in the same location over time than males also suggests that male movement rates are higher, which could be the result of mate searching.

Females showed higher site fidelity than males; they were more likely to be found in the same crevice night after night. Although males and female moved with similar frequencies, the pattern of high female site fidelity could be explained if there was a subset of females remaining stationary while the rest were moving. When females are separated into those that moved and those that remained stationary, there is no difference in size, and therefore in age. However, although the sample size in the surveys was low, none of the six females with eggs ever moved. It is possible that the difference in movement patterns within females may reflect differences in mating history. The subset of females that remained loyal to their crevice may have been mated females waiting to lay eggs and hatch young, while the subset that moved may have been unmated and potentially searching for mates or high-

quality crevices. Since it can take from several weeks to several months for a female amblypygid to lay eggs after mating, followed by another 3 months for egg development (Weygoldt 2000), it may be beneficial for a female to remain stationary during this period.

Females may also move in search of resources only (i.e., good trees or crevices) and stay put once they find them. Given that there is loyalty to crevices and assuming that there is variation in crevice/tree quality, there should be some competition over homes. If this is the case, I would expect that older (i.e., larger) females would occupy the "best" crevices/trees. Following this argument, there should be a detectable size difference between females that moved and those that did not (i.e., females that moved would be smaller, on average, than those that remained stationary). Again this pattern was not found, as there was no size difference between the two groups of females. Nevertheless, this possibility cannot be completely ruled out, since crevice or tree quality could change with changing environmental conditions.

During the day, individuals were found deep in buttresses of large trees, in crevices of tree trunks, underneath loose pieces of bark, or in holes or burrows at the base of trees. Although there were no sex-specific aggregations, certain tree characteristics were strongly associated with the presence of amblypygids (Table 4). The strongest predictor of the number of individuals on a tree was its circumference. The more surface area a tree provides, the more individuals it tends to house. The presence of buttressing on a tree affects the likelihood of an individual remaining on the tree, but is not associated with the total number of individuals that will visit the tree over time. Thus, large trees may sim-

Fig. 3. Distribution of males, females, and females with eggs through time. Females with eggs were more prevalent in January than in any other month ($\chi^2 = 15.9$, $P = 0.003$).
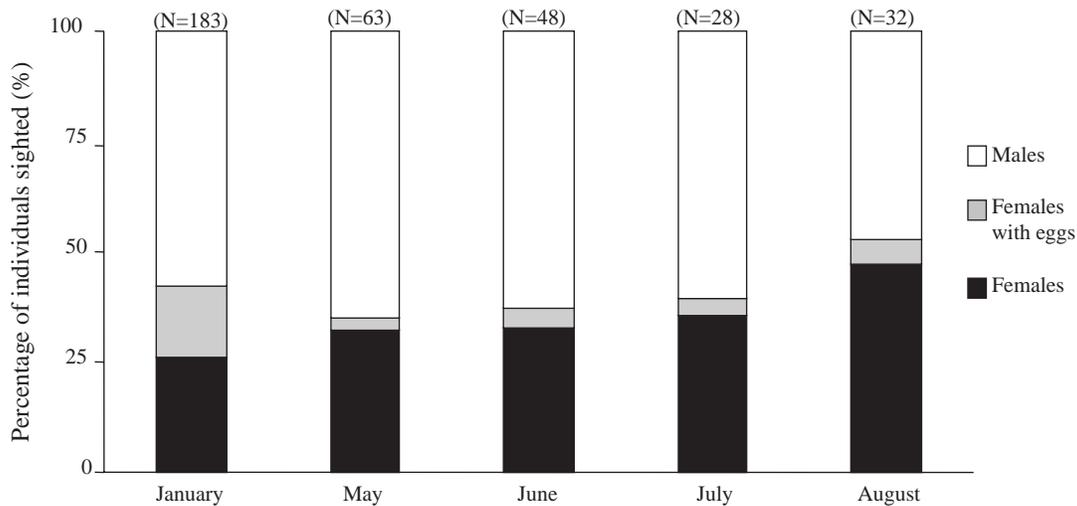
Fig. 4. Comparison of sizes (cephalothorax width) of individuals across time. Both males and females were smaller, on average, in January and May than in June ($P = 0.01$ for females, $P = 0.002$ for males). The same letter above the bars indicates that males and females did not differ, while different letters indicate that they were significantly different.
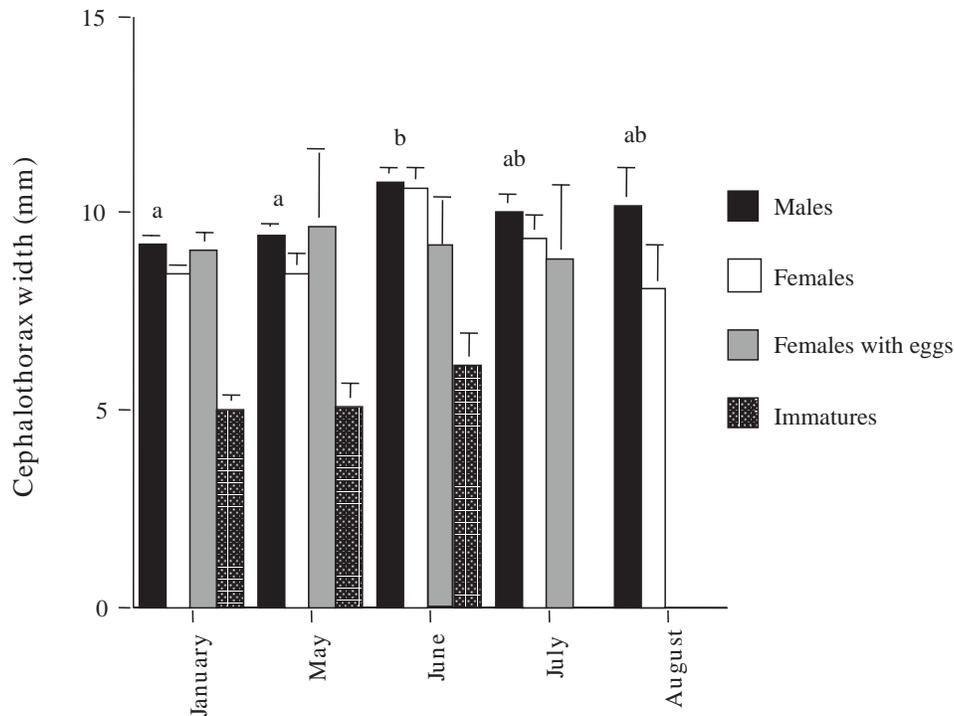
ply be more likely to be found than small trees, and (or) some tree characteristics may be important in "attracting" individuals, while others may influence their decision to remain (Table 4).

Seasonality and stratification

Surveys were carried out during only 5 months of the year: one in the dry season (January) and the remaining four in the wet season (May–August). The overall sex ratios of amblypygids at La Selva Biological Station did not differ in the two seasons, but the proportions of females with eggs did differ. The proportion of egg-carrying females was higher

in January than in any other month. As discussed previously, amblypygids are thought to take from a few weeks to a few months after mating to lay eggs (Weygoldt 2000), which suggests that the mating season for this species is from October to January. However, a small proportion of females with eggs were present during the remaining 4 months of the surveys, suggesting that some females mate throughout the year. I have seen one or two females with live young on their abdomens in June, July, and January, further confirming that levels of breeding are low year-round.

The vertical stratification of individuals was considered in light of documented distribution patterns in tropical roaches

Fig. 5. Comparison of the vertical heights of individuals on trees across time. Both males and females were found to be significantly higher in January than in May ($P = 0.0002$). The same letter above the bars indicates that males and females did not differ, while different letters indicate that they were significantly different. Only males and females were included in this analysis.
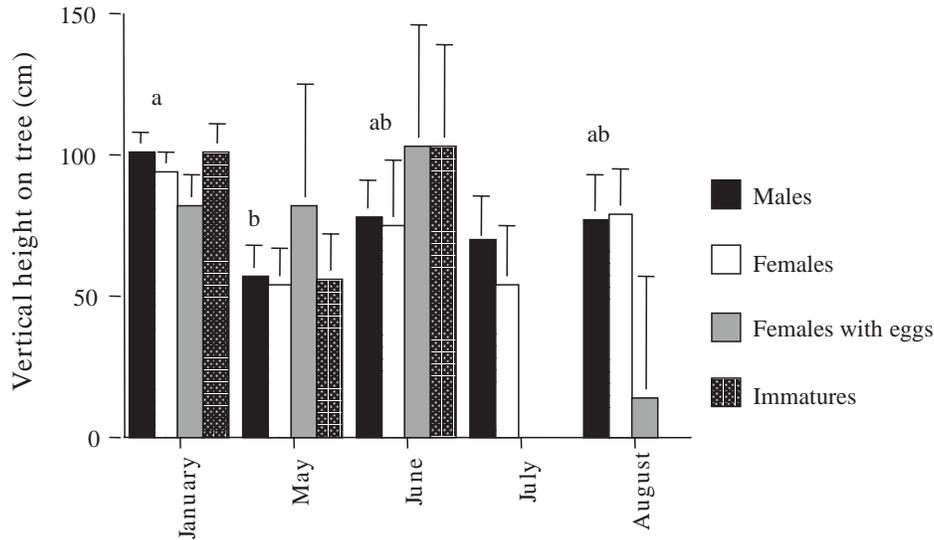
from another study conducted at La Selva Biological Station (Schal 1982, 1986). Male and female roaches are vertically stratified on tree trunks, with males placing themselves higher, on average, than females (Schal 1982). As air slowly rises in the understory of the forest, males that are higher up are better able to detect pheromones released by females below. With the idea that amblypygids may use pheromones for mate attraction, I looked for a similar pattern. When all data were combined, there was no difference in the heights of females, females with eggs, and males. However, there was a seasonal pattern of all individuals being located significantly higher on the tree in January than in May. But since there was no difference between the sexes in vertical stratification across months, it seems unlikely that mating strategies can explain this seasonal pattern; it is more likely explained by differences in habitat between wet and dry seasons.

Conclusion

The results from this study provide the first solid foundation of information that can begin to shape our picture of the basic ecology and natural history of the amblypygid *P. parvulus*. For a nonvisual animal, this species exhibits behavioral patterns that are complex, with individuals frequently moving through a heterogeneous environment for distances over 30 m. Males and females of this species most likely wander in search of mates. While males and females are often found in association with each other, the putative use of olfactory signaling in mate attraction is still unresolved. Controlled laboratory wind tunnel experiments are necessary to assess the potential use of pheromones in mate attraction. Resources, however, do seem to be important in the spatial distribution of individuals. Since the visual system of amblypygids is not well developed, it is likely that olfaction plays a role in resource assessment and navigation. Both males and females move great distances and often return to the same tree. A well-developed olfactory capacity in conjunction with an enlarged mushroom body could facilitate complex odor-based spatial learning and navigation in this group.

Acknowledgements

References

Alexander, A.J. 1962. Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pockock of Trinidad. W. I. (Arachnida, Peipalpi). Zoologica (N.Y.), **47**: 23–37.

Beck, L. 1972. Zur Tagesperiodik der Laufaktivität von *Admetus pumilio* C. Koch (Arach., Amblypygi) aus dem neotropischen Regenwald II. Oecologia, **9**: 65–102.

Beck, L., and Pabst, H. 1969. Zur Tagesperiodik der Laufaktivität von *Admetus pumilio* C. Koch (Arach., Amblypygi) aus dem neotropischen Regenwald. Verh. Dtsch. Zool. Ges. **33**: 178–184.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science (Washington, D.C.), **197**: 215–223.

Foelix, R., and Hebets, E.A. 2001. Sensory biology of whip spiders (Arachnida, Amblypygi). Andrias, **15**: 129–140.

Foelix, R., and Troyer, D. 1980. Giant neurons and associated synapses in the peripheral nervous system of whip spiders. J. Neurocytol. **9**: 517–535.

Hebets, E.A., and Chapman, R.F. 2000. Electrophysiological studies of olfaction in the whip spider *Phrynus parvulus* (Arachnida, Amblypygi). J. Insect Physiol. **46**: 1441–1448.

Igelmund, P., and Wendler, G. 1991. The giant fiber system in the fore legs (whips) of the whip spider *Heterophrynus elasphus* Pocock (Arachnida: Amblypygi). J. Comp. Physiol. A, **168**: 75–83.

Schal, C. 1982. Intraspecific vertical stratification as a mate-finding mechanism in tropical cockroaches. Science (Washington, D.C.), **215**: 1405–1407.

Schal, C. 1986. Vertical community structure and resource utilization in Neotropical forest cockroaches. Ecol. Entomol. **11**: 411–423.

Strausfeld, N.J., Hansen, L., Li, Y., Gomez, R.S., and Ito, K. 1998. Evolution, discovery, and interpretations of arthropod mushroom bodies. Learn. Mem. **5**: 11–37.

Weygoldt, P. 1970. Lebenszyklus und postembryonale Entwicklung der GeiBelspinne *Tarantula marginemaculata* C.L. Koch (Chelicerata, Amblypygi) in Laboratorium. Z. Morphol. Tiere, **67**: 58–85.

Weygoldt, P. 2000. Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics. Apollo Books, Stenstrup, Denmark.

Weygoldt, P., and Hoffmann, P. 1995. Reproductive behavior, spermatophores, and female genitalia in the whip spiders *Damon diademai* (Simon, 1876), *Phrynichus* cf. *ceylonicus* (C.L. Koch, 1843) and *Euphrynichus alluaudi* (Sikon, 1936) (Chelicerata: Amblypygi). Zool. Anz. **234**: 1–18.

Appendix A

Table A1. Tree species, characteristics, and total number of different *Phrynus parvulus* seen.

Family	Genus	Species	Total no. of *P. parvulus*	Surface area (cm)	Bark aroma	Bark latex present?
Annonaceae	*Guatteria*	*diospyroides*	1	15.8	Oils	No
	Unonopsis	*pittieri*	0	22.5	Oils	No
Araliaceae	*Dendropanax*	*arboreus*	0	17.5	Medicinal	No
			1	17	Medicinal	No
			0	16.7	Medicinal	No
Arecaceae	*Iriartea*	*deltoidea*	1	20.6	None	No
			0	18.2	None	No
	Socratea	*exorrhiza*	6	20	None	No
			0	16.8	None	No
	Welfia	*regia*	0	21.7	None	No
			1	15.4	None	No
			0	24.5	None	No
			0	20.2	None	No
			0	16.8	None	No
Boraginaceae	*Cordia*	*bicolor*	1	44.8	None	No
Burseraceae	*Protium*	*panamense*	3	27.2	Turpentine	Yes
			9	92	Turpentine	Yes
Combretaceae	*Terminalia*	*oblonga*	2	157	None	No
			5	70	None	No
Dead tree			0	16.4	None	No
			4	33	None	No
			8	115.7	None	No
			3	24.2	None	No
			0	36	None	No
Fabaceae	*Dussia*	*macroprophyllata*	1	48.3	Bean	No
Fabaceae	Indet.	Indet.	2	82.5	Bean	No
			3	82.5	None	No
Fabaceae	*Pterocarpus*	*officinalis*	9	239	Bean	No
Hernandiaceae	*Hernandia*	*stenura*	5	25	Rank	No
Indet.			8	42.4	None	No
Lauraceae	*Ocotea*	*hartshorniana*	1	139.5	Oils	No
Meliaceae	*Carapa*	*nicaraguensis*	10	232.3	None	No
	Guarea	*guidonia*	4	82.3	Sweet	No
		bullata	1	29.2	Sweet	No
		sp. 1	1	25.2	Sweet	No
			1	19	Sweet	No
			1	28	Sweet	No
	Trichillia	*septentrionalis*	0	22.5	None	No
		septentrionalis	2	20.9	None	No
Mimosaceae	*Bungsdorfia*	*elegans*	9	192	None	No

Table A1. (*concluded*).

Family	Genus	Species	Total no. of *P. parvulus*	Surface area (cm)	Bark aroma	Bark latex present?
	Inga	sp. 1	4	46	None	No
		sp. 2	9	93.5	None	No
		alba	2	62.1	None	No
	Pentaclethra	*macroloba*	11	247	None	No
			9	43.5	None	No
			13	25.8	None	No
			3	34.9	None	No
			10	61.5	None	No
			4	46.5	None	No
			16	114	None	No
			1	15.3	None	No
			8	76.4	None	No
			10	103.4	None	No
			5	57.3	None	No
			7	52.7	None	No
			7	38.4	None	No
			12	180	None	No
Moraceae	*Brosimum*	*alicastrum*	3	43.3	None	Yes
	Naucleopsis	*naga*	0	45.5	None	Yes
			0	20.5	None	Yes
	Perebea	*hispidula*	1	18.1	None	Yes
			0	29.7	None	Yes
			0	21	None	Yes
Myristicaceae	*Otoba*	*novogranatensis*	1	16.8	Oils	Yes
	Virola	*sebifera*	2	19.1	Oils	Yes
			1	41.5	Oils	Yes
			1	36.4	Oils	Yes
Rhizophoraceae	*Cassipourea*	*elliptica*	1	17.3	None	No
Rubiaceae	Indet.		1	15.4	None	No
Sapotaceae	*Pouteria*	*durlandii*	1	47	None	Yes
Sapotaceae	*Pouteria*	*reticulata*	0	15.8	None	Yes
Tiliaceae	*Goethalsia*	*meiantha*	8	131	None	No
			6	34.8	None	No
			2	65.5	None	No