DISPERAL PATTERNS OF THE CELLAR SPIDER IN RESPONSE TO MANIPULATED SEX RATIOS AND DENSITY

by Jonathan D. Edwards

The cellar spider, *Pholcus manueli* (Araneae, Pholcidae), has recently expanded its range and is now abundant throughout the Midwest. However, little is known about its biology and especially factors that might influence its dispersal. Studying *P. manueli* dispersal patterns should shed light on whether an individual can assess its environment and what factors might be important in the decision to disperse from an area. In a laboratory experiment, I observed both males and females dispersing from an environment perceived to be male dominant. In a field study, I observed that neither sex ratios nor density had a significant effect on the likelihood of dispersal. However, when comparing the amount of dispersal in the male and female biased populations, there again tended to be more dispersal in male dominated enclosures. Therefore, movement of these spiders between patches is caused, at least in part, by the demography of the population.
DISPERAL PATTERNS OF THE CELLAR SPIDER IN RESPONSE TO
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TABLE OF CONTENTS

List of Tables ........................................................................................................................................ iii

List of Figures ........................................................................................................................................ iv

Acknowledgements ................................................................................................................................... v

Introduction .............................................................................................................................................. 1-3

Methods
   Animal Care and Rearing ....................................................................................................................... 4
   Laboratory Experiment
      Experimental Arena ................................................................................................................................. 4-5
      Handling of animals ................................................................................................................................. 5
      Experimental Procedure ........................................................................................................................... 5-6
      Statistics .................................................................................................................................................. 6
   Field Experiment
      Experimental Arena ................................................................................................................................. 6-7
      Handling of animals ................................................................................................................................. 7
      Experimental Procedure ........................................................................................................................... 7
      Statistics .................................................................................................................................................. 7-8

Results
   Laboratory Experiment ............................................................................................................................... 9
   Field Experiment ........................................................................................................................................ 9-10

Discussion .................................................................................................................................................... 11-13

Future Directions/Research Questions ....................................................................................................... 14

Literature Cited ......................................................................................................................................... 15-18

Tables/Figures ........................................................................................................................................... 19-24

Appendix A ................................................................................................................................................ 25
LIST OF TABLES

Table 1 .......................................................................................................................... 19
LIST OF FIGURES

Figure Legends .................................................................................................................. 20

Figure

1 ........................................................................................................................................ 21
2 ........................................................................................................................................ 22
3 ........................................................................................................................................ 23
4 ........................................................................................................................................ 24
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INTRODUCTION

Theoretical and empirical work has explored the benefits of dispersal and its importance for the long-term persistence of species. Both theory and experimental data show dispersal can work to mitigate the effects of genetic drift in small populations or decrease the mutation load, and also increase a species range over time (see review in Ronce 2007). For example, models have shown dispersal can arise as a result of benefits to fitness if individuals reside in a landscape with variable habitat quality and respond appropriately to their own patch before deciding to disperse (McPeek & Holt 1992).

Since for most species males benefit from extra matings more than females (Orians 1969), dispersal could help males discover additional populations and, thus, allow males access to a greater number of mates (Greenwood 1980). On the other hand, dispersal could leave males with missed mating opportunities due to being solitary while in transit (Alberts & Altmann 1995) or with no mate because of increased risk of predation (Yoder et al. 2004). Other forces driving the evolution of dispersal include inbreeding avoidance (Ruf et al. 2011), escaping intraspecific competition (van Valen 1971), and avoidance of kin competition (Moore et al. 2006). Dispersal has also been observed to change in response to both high population density (Lena et al. 1998) and low resources (Kennedy & Ward 2003) showing that it is a plastic behavior. If density of a population and scarcity of resources are driving individuals to colonize new patches at the edge of a species boundary, it could lead to range expansion of that species (Travis & Dythan 2002).

The sex ratio and density of local populations are particularly important to the dispersal of adults by increasing competition, which might be different for males and females. Variation in sex ratios can place females under stronger sexual selection (Emlen & Oring 1977) and they may need to disperse to find appropriate mates. Density is another factor that can have an impact on dispersal patterns (Lena et al. 1998). Animals are able to track and assemble in high densities as they move around areas of plentiful resources (Cartar 2009), and, even when there are many resources, density may constrain a population by limiting the space available and increasing competition (Matlack & Harper 1986). There is some expectation that there could be sex-specific differences in dispersal patterns. Under the traditional sex roles, males primarily evaluate sex ratios to
successfully find a mate, but females are more likely to consider density as an indicator of resource competition (Hirota 2007). This sex-specific difference in response to density was recently shown in the sheetweb spider, *Erigone atra*, in which females changed their behavior in response to different intraspecific densities while the male change in behavior was specific to high density of males/low density of females (De Meester & Bonte 2010). In web-building spiders, males are often smaller than females, and it has been suggested that the smaller size make males more mobile and better able to disperse (Bowler & Benton 2009). While there appears to be different reasons explaining why both sexes disperse from high density, it is clear that both sexes can respond to density and sex ratios.

Understanding the impacts invasive species have on their community is an important area of future research. A species is defined as invasive if it is first introduced and naturalized in an area, and then spreads to an area distant from the original site of introduction (Richardson et al. 2000). Many systems hosting invasive species have been under investigation to tease out the potential ecological and social threats imposed by invasions (Pimentel et al. 2000, Simberloff 2000). The African honey bee invasion in North America has given us an opportunity to observe how an invasive can negatively impact the biodiversity of native competitors (Roubik & Wolda 2001) and what factors contribute to successful invasions (Schneider et al. 2004). It is also possible for the invasive to have a positive impact on members of its community by facilitating population growth in native species through a number of mechanisms such as competitive release and habitat modification (Rodriguez 2006). While there can be many criteria that contribute to the success of an invasive (see Schneider et al. 2004 for the Africanized bee example), dispersal ability is a key factor for whether any species is able to be spread.

In recent years, barns, sheds, and basements in southwestern Ohio that were once occupied by *Pholcus phalangioides* (Araneae, Pholcidae; Fuesslin 1775) have had the spider disappear. In their place, *P. manueli* (Araneae, Pholcidae; Gertsch 1937) have started to populate these habitats (Personal observation). Both species can be defined as invasive, and this pattern of one invasive, *P. manueli*, increasing while the other invasive species, *P. phalangioides*, is declining has occurred in several areas throughout the Midwest, but the reason this is happening is unclear. To this day, there is a lot of
information concerning *P. phalangioides* ecology and behavior (Uhl 1998; Schäfer & Uhl 2002; Uhl et al. 2004; Hoefler et al. 2010), but published studies on the ecology or behavior of *P. manueli* appear to be absent. The two species have been known to cohabitate in the same location (B. Cutler, Personal communication) and have similar morphology, so it is reasonable to assume that the two species have similar ecological roles. These spiders are not known to disperse over long distances by ballooning, but are suspected to do so by phoresy or move short distances by walking. Since the range of a species is highly dependent on their ability to disperse (Neubert & Caswell 2000), understanding what factors go into the dispersal decision of *P. manueli* is an important first step in understanding the reasons for this spider’s widening range and its replacing of a once abundant congener.

The studies reported here examine the separate and combined effects of sex ratio and density on the dispersal of adults of a newly dominant synanthropic species, *P. manueli*. I hypothesized that sex ratios and density both play roles in a spider’s decision to disperse or remain in its current environment. In the laboratory I examined dispersal of adult male and females in environments dominated by each sex. I predicted that individuals would be more likely to disperse when placed in an environment containing webs built by individuals of the same sex. In another study, I monitored the reaction of individuals in established populations that differed in sex ratio and density. Here I predicted that the more biased sex ratio would encourage individuals of the majority sex to leave the population and higher density in the patch would produce higher rates of dispersal relative to larger, less dense spaces.
METHODS

Animal care and rearing- To generate a diverse laboratory population, animals used in the laboratory study were collected at various juvenile stages from webs located in ten different barns from six different sites that were within 13km of Miami University in Butler County, OH, USA (see Appendix A). I also collected adults from these same sites to be used in the field study. At least 40 spiders were collected from each location to insure that experimental animals came from different clutches. Voucher specimens of *P. manueli* are stored at the Florida State Collection of Arthropods in Gainsville, FL, USA. Juveniles were reared to adults in an environmental room at 25°C, 50% relative humidity, and a 13:11 light/dark cycle at Miami University. Juveniles were housed individually in transparent plastic cups (7.5cm tall x 11cm diameter) with lids. I fed juvenile spiders twice a week; in the first feeding I gave them 2 crickets (*Acheta domesticus*), each about the size of the spider’s body and two to three days later I gave them 2-6 fruit flies (*Drosophila melanogaster*). After the spiders reached adulthood, I shifted them to one feeding per week alternating between 2 crickets and 2-6 fruit flies to ensure the diverse diet. All spiders were adults for a minimum of four weeks before they are used in an experiment. For the laboratory experiment, I only used animals between 4 and 10 weeks after their final molt; I did not control for spider age or sexual history in the field trials.

Laboratory Experiment-

Experimental arena- In the laboratory, I tested the dispersal response of single adult male or single adult female spiders to six different treatments. I established the environments in rectangular glass-side terraria, each measuring 30cm tall and 30 x 75cm at the base. Each terrarium contained empty *P. manueli* webs in the center that had been constructed within cylinders (8.75±0.25cm diameter and 10.5±0.25cm tall) made of 0.64cm hardware cloth (Fig. 1). Each cylinder in the arena was placed on its end. Either all males or all females had produced the webs in each arena. One empty cylinder was placed in each of the four corners of the terrarium to provide focal animals with potential web sites and to remove right angles from the arena. I documented the dispersal of *P. manueli* using the following four treatments: male response to female webs, male response to male webs, female response to female webs, and female response to male
webs. One replicate of each treatment was conducted simultaneously. Between trials, I wiped the inside of the arenas with 70% ethanol and allowed them to air dry in order to cleanse them of any chemical cues left by experimental animals.

Handling of animals- I established a pool of 40 virgin males and 40 virgin females to build the webs that would be used in the center of the arena (Fig. 1). These animals were placed in cups lined with a removable cylinder made of hardware cloth (8.75±0.25cm diameter and 10.5±0.25cm tall). They were left for a minimum of two weeks so that they could build complete webs inside these cups. Webs were selected at random out of those that had reached the minimum building time. To attain an empty web, I would first take the hardware cloth cylinder out of the cup and then either blow on or gently prod the spider with a blunt object until it left the web. Care was taken to not damage the web. Then, cylinders with empty webs were placed in the arenas. Once removed from the web, the spider was placed in the same cup with a clean hardware cloth cylinder to begin building a new web. Web-builders that died during trials were replaced with another virgin spider in a clean cylinder to keep the pool size at 40 animals.

I selected the focal animals that I would monitor in experiments from a separate pool of virgin males and females. These animals were housed individually in cups (7cm tall x 11cm diameter) with no hardware cloth. These focal animals were fed two days before they participated in an experiment. From this point, these animals will be referred to as focal-animals. None of these animals were reused.

Experimental procedure- At the commencement of an experimental run, I removed the focal animal from its home container and placed it in the center of the arena under a plexiglass cylindrical vial (11.8cm tall x 5cm diameter) lined with Rain-X® Super™ (Unelko Corporation, Scottsdale, Arizona, USA) on the inside. Rain-X® Super™ was used to prevent the spider from climbing or attaching web to the vial. I held the focal spider under the vial while I set up the arena with hardware cloth cylinders containing empty webs placed in a circular pattern around the focal spider and an empty hardware cloth cylinder in each corner (Fig. 1). After the focal animal had five minutes to acclimate, the vial was lifted and it was released so that it could explore and respond to its surroundings.
The spider was allowed to explore the arena over night before sampling so it had sufficient time to select a preferred location and lay down webbing. The spiders would have their own web started by the first observation if they were located outside of an already made web. The focal animals were introduced in the arena between 10:00 h and 15:00 h the day before data collection began. The position of the spider inside the terrarium was recorded three times a day for four consecutive days with observations at 08:00 h, 12:00 h, and 16:00 h. Animals were classified as dispersed if they were located outside, and not touching, the ring of empty webs; they were classified as remaining if they were observed in or attached their web to the ring of webs. There appears to be a clear preference for spiders in the defined dispersing area to leave the terrarium because 81% of total dispersing data had the spider located in one of the upper corners (at least 5 cm from the corner) of the arena. Spiders that remained were inside an already built web 96% of the “remaining” observations. I ran 15 replicates of each treatment but one female in an environment with female webs escaped and had to be removed from the dataset.

Statistics- Logistic regression was used to test for an effect of the sex of the focal animal, sex of the webs in the environment and the time the focal animal was in the arena on the dispersal of the focal spider. Time was analyzed using 08:00 h observations from the first and the fourth day of the trials. These times were chosen so I could keep the time of day consistent while being able to analyze any difference between the first and fourth day. During the course of the experiment, I noticed that some animals moved in and out of the cluster of webs and, thus, dispersed and then returned. I tested the frequency with which this occurred using Fisher exact tests.

Field Experiment-

Experimental arena- In the field I established small populations that differed in sex ratio and density and examined dispersal frequency within enclosures. Field enclosures consisted of Ozark Trail® (Northpole US, LLC, Washington, Missouri, USA) two person dome tents (213 cm x 213 cm x 107 cm high from center) that were set-up two miles north of Oxford, Ohio, USA at Miami University’s Ecology Research Center underneath a canopy of trees. I first established populations of spiders with different sex ratios and densities in glass sided terraria with plexiglass lids that were placed in the
center of the floor of each tent. While all populations consisted of six adult spiders, I varied density by placing them in either large (30cm x 30cm x 75cm) or small (31cm x 25.5cm x 51cm) glass terraria. Before I placed the lid on the terrarium, I sprayed it with Pam® (ConAgra Foods, Inc., Omaha, Nebraska, USA) cooking spray to prevent the spiders from attaching webs that would be damaged when the lid was removed. The populations were given two days to establish themselves in the terraria before I removed the barrier to allow dispersal. Between trials, I wiped the inside of the tents and terraria with 70% ethanol, then allowed them to air out for two days before the next round of trials.

Handling of animals- Populations consisted of six adult spiders: five males and one female, five females and one male, or three males and three females, all replicated at both a high (established in a small terrarium) and low (established in a large terrarium) densities. While all spiders had been on the standard adult feeding regime for a minimum of four weeks, I fed them an extra meal of two crickets two days prior to the commencement of the experiment to standardize hunger levels and to reduce the likelihood of cannibalism. As a result, only one spider was cannibalized out of the 180 individuals during trials. At the same time, spiders were marked with a different color of water-based paint on the abdomen to identify each individual spider during trials.

Experimental procedure- On the third day after population establishment, the barrier for dispersal was removed at 08:00 h. At that time, the number and sex of the individuals that survived the establishment period was recorded. Also on the third day after establishment, data were recorded at 13:00 h and 18:00 h; on the four subsequent days of the trial, I recorded data at 08:00 h, 13:00 h, and 18:00 h. Each time I checked the tent, I recorded the sex and location of each spider. Specifically, I categorized each spider as disperser (more than 10cm away from their home terrarium) or non-disperser (either inside or within 10cm of their home terrarium). I ran these experiments between July and September 2010 and gathered a total sample size of five for each treatment.

Statistics- First, I used a multivariate logistic regression to determine the effects of density and all three sex ratio treatments had on the dispersal over the five days of the experiment. Because I wanted a more specific comparison to my laboratory experiment, I ran another logistic regression testing the effects of density and sex ratio including only
the biased sex ratio treatments. To setup these logistic regressions, I added the number of dispersers and non-dispersers from each category: sex ratio, density, and sex of the disperser. I also examined if the density or sex ratio of the population affected the timing of dispersal. The average time of dispersal was calculated for all the spiders in each tent and compared in an ANOVA with density, sex ratio, and sex of the focal animal as factors. Animals that were not dispersed by the last observation period were not used in this analysis. Because I was curious as to the timing of dispersal relative to daylight, I compared the frequency of dispersal by the end of the first day (10 hours after barriers lifted) with the frequency of dispersal that occurred between then and the first morning observation of the second day (24 hours after barriers lifted) using the Cochran Mantel Haenszel Test. This is a chi-squared test that allowed me to control for the replicate tents. In an effort to determine if there was a difference in the sex of the first disperser, I documented the sex of the first disperser in each tent if it could be determined who that individual was.
RESULTS

Laboratory Experiment-

Focal spiders of both sexes were more likely to disperse when surrounded by male webs and were more likely to remain associated with female webs (Table 1; Fig. 2). There were no differences between the reactions of male and female spiders and there was no difference in the number of animals dispersing between days one and four (Table 1).

The overall frequency of movement did not differ by sex of the animals moving (Fisher exact p=0.456) or the sex that built the webs (Fisher exact p=0.165). However, the direction that the animals moved was affected by the time of day (Fisher exact p<0.0001; Fig. 3); all of the animals that moved during the night moved away from the cluster to a dispersed position (n=16) and all of the animals that moved during the day returned to the cluster (n=16).

Field Experiment-

Neither the density nor the sex ratio of the populations I established in field enclosures had a significant effect on dispersal (Table 1; Fig. 4). However, in an analysis that just considered the biased treatments, there is an indication (i.e. p<0.1) that dispersal might be higher in male biased treatments (Table 1). There was no effect of sex ratio or density on the timing of dispersal (F=1.2612, p=0.3127, df=5).

There were no effects of sex ratio ($\chi^2=1.88$, p=0.930) or density ($\chi^2=0.15$, p=0.985) on the frequency of dispersal, so I combined all the treatments to determine if the time of day affected the dispersal. By the end of the first day I only observed dispersal in 6 of the 30 trials, but by the next morning dispersal had occurred in all of the tents. Thus, the likelihood of dispersal was significantly higher at night than during the day ($\chi^2=28.29$, p<0.0001). This data corroborates with the laboratory data, which indicate there are different behaviors during dark and light hours in the environmental chamber (Fig. 3).

The most prevalent difference found in the sex of the first disperser here was the difference between sex ratio treatments. The first disperser could not be determined in eight out of the ten equal ratio tents because at least one member of each sex dispersed in the same time interval. In male biased treatments, males were the first disperser eight out
of ten times, and females were the first disperser seven out of ten times in the female biased tents.
DISCUSSION

These studies were conducted to investigate the impact of sex ratios and density on the propensity of an invasive web spider to disperse. My results strongly suggest that the sex ratio affected the dispersal decision of adult spiders. Specifically, spiders of both sexes were more likely to disperse in populations dominated by males than in those dominated by females in both the laboratory and the field. Surprisingly, I was unable to uncover an effect of spider density on dispersal in my field study.

Males from the laboratory project were more likely to disperse in response to male built webs which corroborates well with data from the field study, where there tended to be more dispersal in male biased populations. Males used in the laboratory experiment were virgin, so it is reasonable to see why these animals would exhibit risky behavior (i.e. dispersal) when there are no signs of a female present. Sexual history can affect the behavior of *Pholcus* (Uhl 1998), so the unmated status of these males should induce a high propensity to disperse away from perceived intense male-male competition environments in search of females. On the other hand, settling in a population dominated by the presence of conspecific females is beneficial to males because it provides them with many mating opportunities, which can be a limiting factor to their fitness (see Kokko et al. 2006).

Females were more likely to disperse in the presence of opposite sex webs in the laboratory, and the selecting forces on the females for this behavior are not obvious. With *Pholcus*, females indiscriminately accept their first mate (Schäfer & Uhl 2002), so I expected to see these virgin females gravitate toward the male webs. If the females perceive that they are in a female biased population then they could be voluntarily placing themselves under high levels of sexual selection (Emlen & Oring 1977). Whatever is communicated through the female webs is more attractive to the females than the signal received from the male webs. The higher affinity for female dominated populations may be explained in terms of resource gathering. Some spiders are able to sense prey availability through chemical cues within webs (Johnson et al. 2011), and since the females used as web-builders in this experiment were well fed, there may have been information within the webs regarding the condition of the web-builders. For young
virgin females of this species, it may be more important to secure resources for egg production than it is to find a mate.

In the laboratory, spiders were introduced to the arena as naïve, so they needed to assess the demographics of the environment through chemical cues in the webs. Males of many spider species are already known to detect and adjust their behavior in response to cues from silk (Suter & Renkes 1982), and are also able to assess the receptivity of a female (Xiao et al. 2009). However, it is not well established if female spiders use chemical cues or pheromones as a receiver of information. Results here indicate that both sexes are able to detect cues from the webs and it is likely that these spiders use chemical communication to discriminate between the sexes in the field.

This study lacks statistical evidence in support of the hypothesis that density affects the likelihood of dispersal (Table 1). I avoided extremely high densities and fed the spiders well to avoid high levels of cannibalism. In doing this, I not only reduced cannibalism, but I may have reduced the chances of seeing an impact of density on dispersal. When resources are high, web-building spiders experience less competition for resources with conspecifics and will tolerate their presence to a greater extent (Rypstra 1986). In fact, web-building spiders are able to tolerate conspecifics enough in high prey densities that they choose their web sites and establish colonies based on prey availability (Mestre & Lubin 2011). When spiders aggregate in these areas, they also have the potential to benefit from having neighbors by catching more prey as a result of the ricochet effect (Rypstra 1989, Uetz 1989). Pholcus phalangioides is considered quasi-social spider because they tolerate conspecifics and live at high densities (see Hoefler et al. 2010). Thus the fact that well-fed *P. manueli* did not alter their dispersal rate in response to density suggests they may be quasi-social as well.

It has been noted previously that *Pholcus* is mainly diurnal (Netwig 1985), but data from these studies indicate that these spiders disperse at night. Since dispersal can be a risky behavior (Yoder et al. 2004), it is likely that these spiders move at night to avoid visual predators. *Pholcus manueli* does not appear to be completely nocturnal because during collection and maintenance of these animals, I observed behaviors such as web-building and prey-capture during the day. Other animals are able to function without a preference for day or night for most (Mendina-Vogel et al. 2007) or just one
behavior (Bruch & Binkowski 2002), but it is still unclear how nocturnal *P. manueli* actually is. More research is needed to ascertain if there is a nocturnal preference for other behaviors in this spider.

The treatment in the laboratory experiment showing the highest proportion of spiders remaining was the male focal animal/female webs, and this is also the most variable treatment (Fig. 2). The spiders in the laboratory experiment were tested in isolation, which would be uncommon in the field if *P. manueli* has a tendency to congregate. These spiders may be experiencing conflicting cues, which could explain the large variance seen in that treatment.

Information from these studies is likely to be applied to the field of invasion ecology. In this study system, one invasive predator, *P. manueli*, is replacing another, *P. phalangioïdes*, in certain areas throughout the Midwest. Invasive spiders can negatively affect the number of native spiders in its community (Hogg & Daane 2011), but more research is needed here to determine the effects of this new invasive species on its community.

In the laboratory, I was able to see a difference in how spiders reacted to the silk of males compared to females. There was more dispersal in the presence of male webs which agrees with the results found in the field, where there tended to be more overall dispersal in male dominated environments. These dispersal patterns were likely driven by males searching for a mate, while there is not a clear explanation for the females’ movements. What is more clear is that *P. manueli* uses chemical communication in identification of conspecifics and also prefers to move at night, a behavior which likely provides cover from predators.
FUTURE DIRECTIONS/RESEARCH QUESTIONS

• Are males or females more likely to eat a prey item within a given week? Would a difference here explain a difference in condition between the sexes and be a reason why females would choose a location based on resource availability information in the webs? Male spiders often forgo prey capture in favor of mate searching. If this is happening with P. manueli then there might be a difference in condition being communicated through the webs.

• How much more do P. manueli move at night than in the day? Is there a preference for prey capture at any time of the day? Explore other behaviors and if there is a preference at any time of the day for these.

• Why is there a recent trend of P. manueli dominating where P. phalangioides used to be abundant? Is P. manueli able to outcompete P. phalangioides for resources? Are there environmental factors favoring P. manueli?

• What is being communicated through web-based chemical cues? How long to these pheromones last? Can spiders detect diet quality from webs?

• How social is P. manueli? The lack of affect of density in the field study could be explained by social behaviors.

• Why do females disperse from male dominated environments?

• Is there an interaction between density and prey capture?

• Is there any evidence of benefits of female association (ricochet effects)? There was a lack of affect of density on dispersal in these studies. Aggregating could be a selected behavior if there are benefits to these individuals.

• Is cannibalism more prevalent in either sex? I suspect that there might be a higher level of aggression in a male P. manueli defending its web from intruders because there was more dispersal away from male dominated environments by both sexes.
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Table 1: Z-scores and p-values from multiple logistic regressions from the laboratory and field data. In the laboratory, effects of sex of the spider *Pholcus manueli* (focal animal sex), sex of the web-builders (Webs in the arena), and observations on day 1 and day 4 (Time) on the dispersal frequency of the focal animal were analyzed. From the field data, effects of density and different sex ratios on the number of dispersal kernels were analyzed.

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<thead>
<tr>
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<th>Z-score</th>
<th>P</th>
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<tbody>
<tr>
<td><strong>Laboratory</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Focal animal sex</td>
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<td>0.39827</td>
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<td>Webs in the arena</td>
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<td>0.00537*</td>
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<td>Time</td>
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<td><strong>Field – all sex ratio treatments</strong></td>
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<td></td>
</tr>
<tr>
<td>Even ratio v. female bias</td>
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<td>0.267</td>
</tr>
<tr>
<td>Even ratio v. male bias</td>
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<td>0.457</td>
</tr>
<tr>
<td>Density</td>
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<td>0.584</td>
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<tr>
<td><strong>Field – biased sex ratio treatments</strong></td>
<td></td>
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<tr>
<td>Male bias v. female bias</td>
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<td>0.07441</td>
</tr>
<tr>
<td>Density</td>
<td>-1.018</td>
<td>0.30873</td>
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</table>
FIGURE LEGENDS

**Figure 1:** Arena set-up for the laboratory experiment in glass terraria (30cm x 75cm x 30cm tall): (R) where the spider, *Pholcus manueli*, was released, (W) where the cylinders with webs already constructed were placed in a circular pattern in the center of the terrarium, and (B) is where blank cylinders without webs were provided for structure.

**Figure 2:** Proportion of the spider *Pholcus manueli* observed to be dispersed in each treatment at 24 hours and 96 hours after release. Each column represents the proportion dispersed; error bar on each column represents the binomial distribution. Sample size for each treatment equals 15 except for the female focal animal/female built webs treatment where n=14. Logistic regression was performed on data and revealed that web-builders’ sex is a reliable predictor of dispersal behavior and is indicated by the asterisk.

**Figure 3:** Mean proportion of the spider *Pholcus manueli* dispersed during each observation across all treatments in the laboratory experiment. Black lines in the figure are treatments with a male focal animal (m animal) and grey lines are treatments with a female focal animal (f animal). Data points marked by squares are treatments with male-built webs (m webs) and data points marked by triangles are treatments with female-built webs (f webs). The grey background is when there were dark periods in the environmental chamber and white background is when the lights in the environmental chamber were on.

**Figure 4:** The mean proportion of the spider *Pholcus manueli* dispersers in each treatment by the end of the trials. Each column represents the proportion dispersed for a given treatment; error bar on each column represents the standard error. Sample size for each treatment equals five.
Figure 1
Figure 2

The figure shows a bar chart comparing the proportion of dispersing male and female focal animals over 24 hours and 96 hours. The chart includes error bars indicating variability or standard error.
Figure 3
Figure 4

The graph shows the mean proportion dispersing across different density and sex ratio conditions. The x-axis represents the density levels (Low, High) and sex ratio conditions (Equal, Male, Female), while the y-axis represents the proportion dispersing, ranging from 0 to 1. The error bars indicate the variability in the data.
APPENDIX A

Collection sites for the spider *Pholcus manueli* in Butler County, Ohio, USA.

<table>
<thead>
<tr>
<th>Name</th>
<th>Contact Information</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Christine Kelly</td>
<td>email: <a href="mailto:christine@cekelly.com">christine@cekelly.com</a></td>
<td>39.5328 N. Latitude 84.7508 W. Longitude</td>
</tr>
<tr>
<td>Bob Sherman</td>
<td>phone: 513-523-5715</td>
<td>39.5049 N. Latitude 84.7114 W. Longitude</td>
</tr>
<tr>
<td>ERC</td>
<td>phone: 513-529-5634</td>
<td>39.5309 N. Latitude 84.7229 W. Longitude</td>
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<td>Pearson Hall</td>
<td>phone: 513-529-3100</td>
<td>39.5109 N. Latitude 84.7314 W. Longitude</td>
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<tr>
<td>Julie Bath</td>
<td>phone: 513-497-5644</td>
<td>39.4063 N. Latitude 84.6567 W. Longitude</td>
</tr>
<tr>
<td>Honey Tree Stables</td>
<td>phone: 513-868-0783</td>
<td>39.4700 N. Latitude 84.6826 W. Longitude</td>
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