Influential Interactions: Group Dynamics of the Maritime Earwig, *Anisolabis maritima*

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Blinks/NSF REU/BEACON 2015
Summer 2015

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Keywords: *Anisolabis maritima,* maritime earwig, dispersion, distribution, sexual selection

Abstract

Dispersion patterns of individuals within a group can reveal important aspects about social interactions and the mating system of the species. Our study examined the distribution patterns of the maritime earwig, *Anisolabis maritima*, to determine the influence of sexual selection on the mating system. Male and female *Anisolabis maritima* both possess weaponry – however, females are very aggressive whereas males are tolerant of cohabitation, which led us to hypothesize that leks might be forming, or that aggressive females would maintain territories that would control the group environment. We examined single-sex and mixed-sex groups of 18 earwigs in a large enclosure throughout their active period to determine whether they were distributing themselves randomly, uniformly, or in clumps. We found that, in single-sex groups, males form clumps and females form uniform territories. Mixed-sex groups are uniform at first and become clumped, where females controlled uniformity and males changed their behavior in response to females. We also conducted a series of trials between three individuals, either single-sex groups or mixed-sex groups with two different-sized individuals of one sex and one individual of the other, to examine sexual selection and cohabitation preferences. Among single-sex groups, we found that females were unwilling to cohabitate, and small females were more likely to be excluded from shelters than large females – in single-sex male groups, however, males were willing to cohabitate, with small and medium-sized males equally likely to be excluded. Among mixed-sex groups we found a preference for smaller opposite sex partners, but the patterns suggest assortative mating.

Introduction

Populations structure themselves in the space of their habitat by the complex interaction of several biotic factors, including intraspecific competition, resource availability, and mate choice. Thus, dispersion patterns can provide insight into important behavioral and ecological factors that govern intraspecific interactions. If individuals in a population are found in a random distribution, then it is likely that individuals are seeking randomly distributed resources such as food or shelter. A uniform, or hyperdispersed, distribution indicates territoriality, and individuals are probably holding and defending spaces from conspecifics within the territory. Clumped, or hypodispersed, distribution indicates aggregations of individuals, and might represent groups of females with a dominant male as a harem, or groups of males advertising to females as a lek. Harems are a type of polygynous mating system where males compete for access to a group of females. This type of polygynous mating system has been observed in another species of beach arthropod, the California beach flea (*Megalorchestia californiana*), where males use their large front gnathopods to hold females within their burrows and maintain groups of females (Iyengar & Starks 2008). There is an alternate form of sexual selection and competition-based structure called lekking. This behavior is seen most frequently in birds, but has also been observed in mammals and several orders of insects (Wickman & Rutowski 1999). Lekking involves a group of males that group together and pose or compete for the attention of visiting females.

Harems and leks, as well as other group dispersion patterns structured around a mating system, illustrate the connection between dispersion patterns and sexual selection. For example, intersexual selection, or having one sex choose a partner, can not only affect physical traits but also influence the types of interactions that occur among individuals. Males will often develop traits, such as ornaments, to make themselves more attractive to females and thus be chosen as a mate. This type of competition leads to the elaborate plumage seen on male individuals of many species of birds. Intrasexual selection is between organisms of the same sex and usually takes the form of direct confrontation over mates. Rather than ornamentation, this type of competition generally leads to the development of weaponry, such as the antlers of a deer or the notable and sometimes alarming appendages of the rhinoceros beetles (McCullough et al. 2014). Both kinds of competition, however, can lead to sexual dimorphism: a difference in form between individuals of different sex of the same species. The dimorphisms resulting from competition can affect which individuals can best compete for food, or hold a harem or territory, and are therefore important factors in determining group structure and dynamics.

In this study, we examined the behavior and group dynamics of the maritime earwig, *Anisolabis maritima* (Dermaptera: Anisolabididae). *A. maritima* is commonly found under driftwood on beaches all over the world. It is sexually dimorphic in that, while both sexes possess weaponry, they differ in form and function. As in all earwigs, females have straight forceps and males have curved forceps – however, this species is unique among earwigs in that the forceps of male *A. maritima* are asymmetrically curved (Bennett 1904). Both males and females use these forceps in prey capture, but the sexes differ in how their forceps are used in combat. Females have been found to be much more aggressive than males, and will use their forceps to seriously injure other individuals, especially in cases of maternal care, as females protect their nests against predators and conspecific egg cannibalism (Miller et al. 2011). Males participate in competitions where they pinch each other's abdomens with their forceps in order to determine dominance, but, unlike conflicts with or between females, these competitions are seldom fatal (Munoz & Zink 2012). Previous work has found that competition and choice influence earwig cohabitation and mate choice. These studies found that males are more likely to cohabitate than females (Hack & Iyengar 2013). Larger mates are both preferred and competitively dominant, but more asymmetric forceps lend a competitive advantage in size-matched males (Munoz & Zink 2012, Kendall-Bar & Iyengar 2014). This study seeks to determine how these behaviors and previous observations of competition and choice combine to form population distributions in earwig habitats.

To observe the dispersion patterns of earwig groups, we placed groups in environments with shelters resembling their natural driftwood habitat, such that they could space themselves within the environment. We used groups of all males, all females, and mixed sexes earwigs to determine the effect of inter- and intrasexual dynamics on dispersion patterns. We also held a series of smaller scale trials. Building on previous experiments (Kendall-Bar 2014), we released three earwigs of single or mixed sexes simultaneously in an arena with two shelters, to see with whom they would cohabitate. The patterns within these small-scale trials will help determine the underlying patterns and potentially explain how individual interactions may affect broad-scale patterns at the population level. Within the larger arenas, we hypothesized that groups of females would be regularly distributed due to their aggressive behaviors and tendency to hold nest territories, whereas males would be more likely to be clumped or randomly distributed due to their tolerance of cohabitation and non-fatal competition interactions. Like *M.*

californiana, earwig populations tend to have more females than males – however, due to the aggressive and territorial nature of females, we considered it unlikely that mixed groups will form harems as *M. californiana* does. Due to the willingness of males to cohabitate and the territorial nature of females, lekking behavior seems a reasonable possibility in maritime earwigs. Males have been seen in the periphery of female nest territories in the wild (personal observation), suggesting that such aggregations may be forming. It is possible that males may be competing using their size and asymmetrical forceps to compete for better places in the lek. Within mixed-sex groups, we hypothesizes that females would remain uniformly dispersed, whereas males would likely be clumped, either to avoid aggressive females of to form a lek to advertise to females.

Materials and Methods

Collection and Care of Study Organism

Sexually mature individuals were collected from under driftwood above the high tide line at False Bay, Cattle Point, and the Friday Harbor Lab Beach on San Juan Island, WA. Upon being brought back to the lab, each individual was sexed and then marked with a unique color and number bee tag glued to its pronotum. Individuals were maintained in containers containing substrate and a piece of wet sponge until use in an experimental trial, which always occurred within 48 hours of collection. We knew that differences in hunger levels of the field-collected individuals would not affect behavior, as it has been found in male competition studies that food is not a motivating factor for aggression until at least 9 days of starvation (Munoz & Zink 2012).

Arena Trials

Each arena was comprised of a 58-quart clear plastic tub (76.2cm L x 50.8cm W x 16.5cm D) with a divider placed in the middle to divide it into two 45.7cm x 45.7cm arenas. The arena divider and walls were covered with red plastic reading sheets to maintain a consistent and dark environment. Each arena was covered by a thin layer of damp sand, upon which shelters were placed. Shelters were 13x13cm squares of clear plexiglas covered with 14x14cm red plastic reading sheets, raised 1cm off the ground and spaced evenly to form 9 sections with avenues in between. This was meant to resemble the shelter provided by driftwood, which is shallow and dark. 18 individuals of varying sizes were chosen haphazardly for each trial. Single-sex trials were composed of 18 males or females, and mixed-sex trials were composed of 9 males and 9 females. Individuals were added to the arenas simultaneously. Because these earwigs are nocturnal, experiments were set up in the late afternoon, between 4 and 6pm, and checked at 6 hours and 12 hours such that the 6 hour check was late at night during their peak activity hours, and 12 hour checks were early the next morning, when earwigs would be settled into positions that they were likely to maintain throughout the entire following day. At each check, the location of each bug within the arena was recorded, as well as any moving or deceased individuals.

Tub Trials

Each small-scale "tub" arena was comprised of a white plastic 11.4-quart tub (34.3cm L x 31.75cm W x 14.2cm D) with a thin layer of damp sand in the bottom. Shelters in these arenas were red tinted boxes (5 x 5 x 1cm) with one side cut open for entry and covered by a matching lid, filled with sand to match the arena. Shelters were placed facing each other in the arena about 20cm apart. We ran 4 types of trials, each consisting of 3 haphazardly-chosen earwigs: three males (of varying size), three females (of varying size), two different-sized males and a female, or two different-sized females and a male. Earwigs that differed by at least 10% in body size (judged by the width of the 6th abdominal segment) were considered to be "different-sized". Experiments were set up in the late afternoon and checked after 6 and 12 hours. At each check, the location and activity of each individual was recorded, taking special note of any cohabitation, movement, or deaths.

Measurements

After each trial, individuals were removed from their arena or tub and frozen in Eppendorf tubes marked with their trial number and bee tag designation. Images were taken from a CCD camera (Lumenera Infinity 2-5C model) with dissection scope (Nikon SMZ800 model), and measurements were taken using ImageJ. The width of the 6th abdominal segment to determine relative size, and the length and width of the forceps were measured to determine degree of asymmetry (Munoz & Zink 2012). Although many studies use the pronotum width as an index (Simmons & Tomkins 1996, Tomkins & Simmons 1996, Munoz & Zink 2012), we used the sixth abdominal segment as an index for body size (DiGennaro et al. unpublished) because the bee tags used for individual marking often obstructed the view of the pronotum. The length of each forcep was measured as the distance from the tip of the forcep perpendicularly to the base of the last abdominal segment. The width of each forcep was taken as the distance between the line defining length and the outer edge of each forcep. Forceps curvature (width over length) was used to determine forceps asymmetry (right curvature divided by left curvature; Munoz & Zink 2012).

Statistical Analyses

In the arena trials, distributions in arena trials were compared to a Poisson distribution, a model distribution generated by a random process (and thus resembling a random distribution). Distributions that differed significantly from the Poisson distribution were then analyzed with an index of dispersion to determine whether the pattern they showed was uniform or clumped. Distributions between different trials were compared using chi-squared tests-of-independence. The number of individuals moving at 6 hours was compared between single-sex trials and single sexes within mixed trials using a paired t-test, the number of individuals moving at 6 hours was compared between both single-sex types and the mixed-sex trials as a whole using an ANOVA. In the tub trials, cohabitations were compared with chi-squared tests of independence. The sizes of individuals cohabitating were compared using paired t-tests.

Results

Arena Trials

The distribution of male-only groups at 6 hours was not significantly different from a Poisson distribution (χ^2=10.8, df=6, p=0.094), indicating they were randomly dispersed at 6 hours after introduction in the arena. The distribution of single-sex male groups at 12 hours was significantly different from a Poisson distribution (χ^2=28.6, df=8, p=0.00037) and an index of dispersion indicated these groups were clumped (I_d=111.0, df=107, p<0.025). The distribution of female-only groups differed from the Poisson distribution at 6 hours (χ^2=105.6, df=3, p<0.00001) and the index of dispersion indicated these groups were uniformly distributed (I_d=20.0, df=116, p<0.025). However, the distribution of female-only groups at 12 hours was not significantly different from the Poisson distribution, indicating that they were randomly distributed (χ^2=0.84, df=5, p=0.974).

The distribution of individuals in mixed-sex groups was significantly different from the Poisson distribution at both 6 hours (χ^2=21.8, df=4, p<0.0005) and 12 hours (χ^2=24, df=8, p=0.002). At 6 hours, these groups were uniformly distributed (I_d=49.0, df=116, p<0.025) whereas at 12 hours these groups were clumped (I_d=159.5, df=116, p<0.025).

Within the mixed-sex trials, males were randomly distributed at both 6 hours (χ^2=0.28, df=4, p=0.991) and 12 hours (χ^2=2.21, df=5, p=0.819). The distribution of females within mixed sex groups was significantly different from the Poisson distribution at 6 hours (χ^2=32.5, df=3, p<0.00001) and an index of dispersion indicated that they were uniformly distributed (I_d=54.3, df=116, p<0.025). However, females within mixed-sex groups were randomly distributed at 12 hours (χ^2=0.66, df=4, p=0.956).

Most distributions between trials were different from each other, including those with dispersion patterns of similar types. For example, even though females in single-sex and mixed-sex groups were both uniformly distributed, the females were more uniformly distributed in single-sex groups (Table 1). Distribution of single-sex male groups and mixed-sex groups at 12 hours were not different, distribution of groups of single-sex female groups and mixed-sex groups at 12 hours were not different (but male and female single-sex groups at 12 hours were significantly different), males within mixed-sex groups at 6 and 12 hours were not different, and males and females within mixed-sex groups were not different (Table 1).

Movement, defined as the number of individuals moving at 6 hours, was not significantly different between male single-sex trials, female single-sex trials, and mixed-sex trials (F=0.603, df=2, p=0.553). Movement in single-sex male trials and movement of males within mixed-sex trials was not significantly different (t=-0.925, df=21.0, p=0.366). Females in single-sex trials moved more than female in mixed-sex trials (t=2.425, df=21.8, p=0.012).

Tub Trials

In trials of single-sex trials, males were equally likely to cohabitate as they were to be found alone, as multiple males were found sharing a shelter in 40% of the trials (17 out of 42). In trials where there was only 1 male in each shelter, medium and small males were equally likely to be excluded (Table 2). Among the 13 cases where 2 males shared a shelter, there were 3 large-medium cohabitations, 3 large-small cohabitations, and 7 medium-small cohabitations. Males were significantly more likely to cohabitate than females (χ^2=9.61, df=1, p=0.002). Females preferred to be alone in shelters, two shared a shelter only very rarely (less than 12% of the time) and all three never shared a shelter. Overall, when one female was found in each shelter, the smallest female was more likely to be excluded from the shelter (68% of the time; Table 2).

In mixed-sex tub trials with two males and one female, the female was more likely to be found with the smaller male, and in trials with two females the male was more likely to be found with the smaller female (Table 3). In trials with 2 different-sized males and a female, females found with large males were smaller than females found with small males (3.96 mm ± 0.12 SEM vs. 4.55 mm ± 0.06 SEM; Figure 1). In trials with 2 different-sized females and a male, males found with large females were larger than males found small males (5.23 mm ± 0.09 SEM vs. 4.73 mm ± 0.06 SEM; Figure 1).

Table 1. Chi-squared test-of-independence comparisons of distribution patterns in large arena trials. All distributions were found to be significantly different from each other, except for the distributions of male groups and mixed groups at 12 hours, the distribution of female groups and mixed groups at 12 hours, males within mixed groups at 6 and 12 hours, and males and females within mixed groups at 12 hours.

Comparison	Significant?	Statistics
18 Males 6h vs 18 Males 12h	Yes	χ^2=25.90, df=8, p=0.00109
18 Males 6h vs 9 Males 6h	Yes	χ^2=52.19, df=6, p<0.00001
18 Males 12h vs 9 Males 12h	Yes	χ^2=37.15, df=8, p=1.1E-05
18 Females 6h vs 18 Females 12h	Yes	χ^2=107.68, df=5 p<0.00001
18 Females 6h vs 9 Females 6h	Yes	χ^2=495.49, df=3 p<0.00001
18 Females 12h vs 9 Females 12h	Yes	χ^2=71.21. df=5, p<0.00001
18 Males 6h vs 18 Females 6h	Yes	χ^2=276.39, df=6 p<0.00001
18 Males 12h vs 18 Females 12h	Yes	χ^2=24.42, df=8, p=0.00195
18 Males 6h vs 18 Mixed 6h	Yes	χ^2=69.90, df=6, p<0.00001
18 Males 12h vs 18 Mixed 12h	No	χ^2=10.07, df=8, p=0.26015
18 Females 6h vs 18 Mixed 6h	Yes	χ^2=55.42, df=4, p<0.00001
18 Females 12h vs 18 Mixed 12h	No	χ^2=11.06, df=8, p=0.19832
18 Mixed 6h vs 18 Mixed 12h	Yes	χ^2=47.86, df=8, p<0.00001
9 Males 6h vs 9 Males 12h	No	χ^2=1.58, df=5, p=0.90366
9 Females 6h vs 9 Females 12h	Yes	χ^2=31.75, df=4, p<0.00001
9 Males 6h vs 9 Females 6h	Yes	χ^2=35.06, df=4, p<0.00001
9 Males 12h vs 9 Females 12h	No	χ^2=2.75, df=5, p=0.73846

Table 2. Single-sex trials in which three individuals were placed together simultaneously in a container with two available shelters, and positions were recorded after 12h (overnight). Across all trials, males were equally likely to cohabitate as to be found alone in shelters (χ^2=1.53; df=1; p=0.22). In trials where there were no more than 1 male per shelter, medium and small males were equally likely to be excluded from shelters (χ^2=1.99; df=1; p=0.16). Females preferred to be alone in shelters (χ^2=28.70; df=1; p<0.0001), and the smallest female was most likely to be excluded from shelters (χ^2=5.28; df=1; p=0.02).

Trial Type	**N**	**All 3 in one shelter**	**2 in one shelter, 1 in the other**	**1 per shelter, 1 left out**		
Three Males	42	4 (9.5%)	13 (31.0%)	25 (59.5%)		
				Large left out	Medium left out	Small left out
				0	16	9
Three Females	43	0 (0%)	5 (11.6%)	38 (88.4%)		
				Large left out	Medium left out	Small left out
				0	12	26

Table 3. Mixed-sex trials in which three individuals (two different-sized individuals of the same sex) were placed together simultaneously in a container with two available shelters, and positions were recorded after 12h (overnight). In trials with two males and one female, the different-sized males occasionally cohabitated; among the trials where they did not, the female was more likely to be found with the smaller male (χ^2=12.66; df=1; p=0.0004). In trials with two females and one male, the different-sized females never cohabitated; overall, the male was more likely to be found with the smaller female (χ^2=5.95; df=1; p=0.01).

Trial Type	**N**	**All 3 in one shelter**	**Same-sex cohabitation**	**Larger of pair with an opposite sex partner**	**Smaller of pair with an opposite sex partner**
2 Females + 1 Male	43	0 (0%)	0 (0%)	14 (31.8%)	30 (61.2%)
2 Males + 1 Female	43	0 (0%)	6 (14.0%)	8 (18.6%)	29 (67.4%)

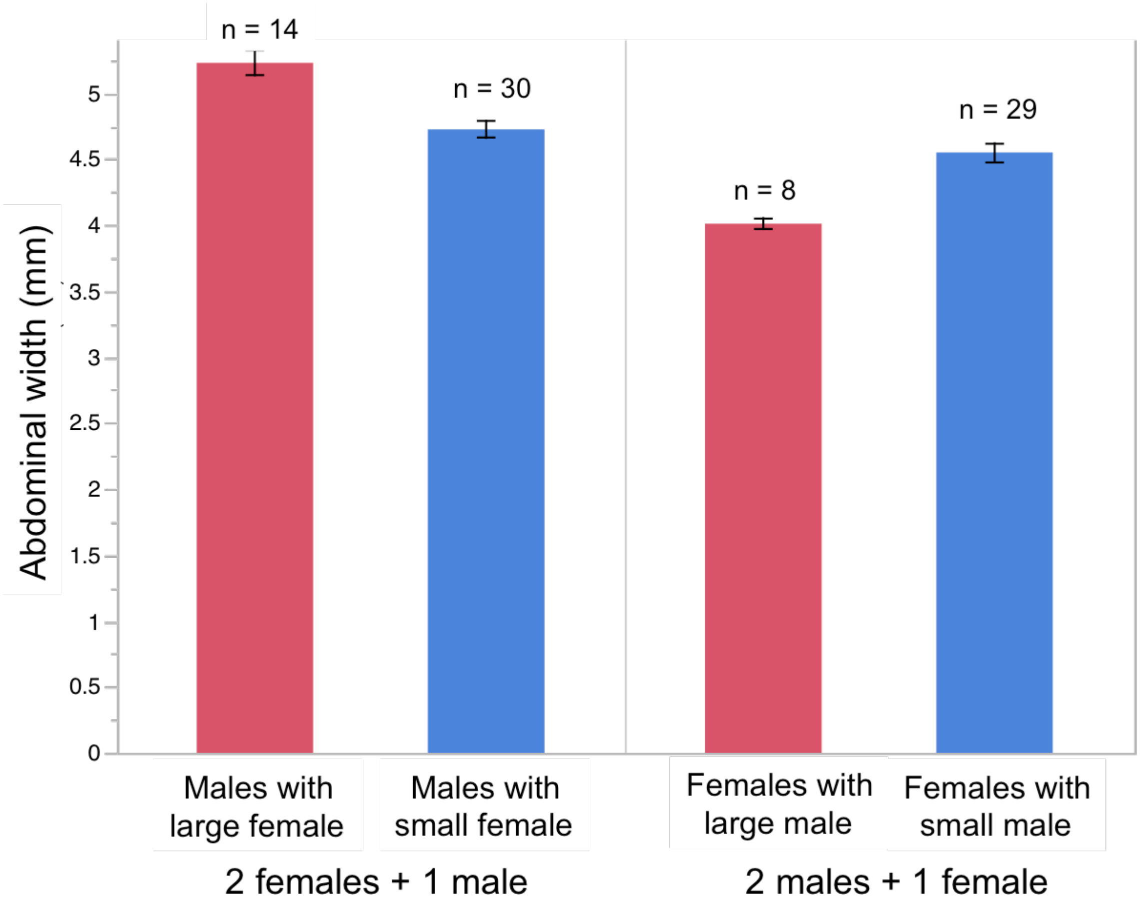

Figure 1. Size-based cohabitation with the opposite sex. In trials with 2 different-sized females and one male (2F+1M), the males that were found with large females were significantly larger than those found with small females (t=4.31; df=35; p=0.001). Conversely, in trials with 2 different-sized males and one female (2M+1F), the females that were found with large males were significantly smaller than those found with small females (t=4.44; df=42; p<0.0001).

Discussion

When examining the arena dispersion trials, it is important to consider that maritime earwigs are nocturnal, so 6 hour trial checks were late at night, during peak activity hours, and 12 hour checks were early the next morning when earwigs had settled into positions they would likely maintain for the entire day. In the arena trials, males in single-sex groups were randomly distributed at 6 hours, at peak activity hours, but formed aggregations at 12 hours, when they were likely settling in for the day. This suggests that males wander at first but aggregate over time, which fits with our knowledge of the lack of lethal intrasexual interactions (Munoz & Zink 2012) and their willingness to cohabitate in small shelters (Kendall-Bar 2014). Our distributional patterns suggest that males are tolerant of cohabitation, which might be because in the field, aggressively territorial females limit male roaming area, and males who are willing to clump with other males in limited territory or around resources increase availability of both space and resources to themselves.

Female earwigs are more territorial than males and aggressively protect and maintain their nests in the field (Miller et al. 2011), which lead us to predict that would be uniformly distributed. As predicted, at 6 hours they were uniformly distributed suggesting that they space themselves out via aggressive confrontations. However, they are randomly distributed at 12 hours, which suggests these aggressive interactions wane over time as females in the arena become more familiar with each other. Females might initially seek to aggressively establish territory in a new environment, leading to uniform distribution. However, since they do not have a nest or other resource to protect, it is likely that as the environment and the other individuals become familiar, expending the energy to aggressively defend a territory that does not benefit a female becomes unnecessary.

Mixed-sex groups were uniformly distributed at 6 hours and clumped at 12 hours, and within the mixed-sex groups, females are uniform and males are random at 6 hours, but both females and males are randomly distributed at 12 hours. This suggests that female aggression is controlling the uniform pattern for the whole arena at 6 hours, as they aggressively defend their surroundings from both females and males. However, as in the single-sex arena, they do not continue to maintain aggression as time passes, showing that they do not change their behavior in response to the presence of males. Males, on the other hand, change their behavior in response to female presence: they do not form aggregations by the time 12 hours have passed as they would on their own. This pattern could arise because they are pursuing females and choose not to aggregate, or it could be because female aggression is causing them to disperse more widely. Either way, it shows that female presence and aggression alters and controls distribution patterns in mixed-sex environments throughout the night.

The mixed-sex group as a whole, however, has a clumped distribution at 12 hours, despite the two random patterns within it. This could be due to several factors. It may be that a reduced density of females leads to fewer aggressive interactions, which causes females to be more tolerant of other individuals, either males of females, to be near them, and allows for aggregations to form. The theory that lower density of females reduces conflict is supported by the fact that the number of female individuals moving at 6 hours, during peak activity, is lower in mixed-sex trials than in single-sex trials, which suggests that there is less disturbance due to conflict in mixed-sex trials, or less reason for females to be fleeing between shelters. Furthermore, it may be the case that that males are in fact grouping in a formation similar to a lek, but the pattern can’t be seen in the data due to low density in a large space. A traditional lek is comprised of individual females visiting an aggregation of posing or competing males; since female maritime earwigs are aggressive and territorial, this type of females visiting behavior seems more unlikely than we initially thought. However, it may be the case that a different type of mating system involving male groups, perhaps males grouping around an established female territory, could be found. Due to the male tendency to clump in the field and our lab studies, lekking or lek-like behaviors might still be a feasible possibility and should be examined more closely, perhaps with larger numbers of males and a smaller number of females in the same type of arena.

In the tub trials, males were equally likely to cohabitate as to be found alone, which matches the distributional patterns seen in the larger arena, and matches predictions made about male behavior based on previous studies showing a willingness to cohabitate (Kendall-Bar 2014) and a lack of mortality in dominance interactions (Munoz & Zink 2012). Large males were never left out of shelters, likely because are intimidating and can defeat smaller males, but we found no difference in whether medium-sized or smaller males were excluded from shelters. This confirms earlier research that larger males are more competitively dominant (Munoz & Zink 2012) and shows that in addition to competing for food, larger males are better able to compete for and hold shelters. Regarding females, they rarely cohabitate (less than 12% of the time), and there were never 3 females in a shelter. The smallest female is most likely to be excluded, indicating size-based aggression not seen between the medium and small size classes of males. For both sexes, however, the largest individual always secured a shelter. This confirms that, for both males and females, the deciding factor in competition for resources (in this case space) is the size of the individual. Larger females, like larger males, are more aggressive and more physically intimidating, and are likely better able to defend and maintain their shelter spaces. Furthermore, the fact that the smallest females were the most likely to be excluded, whereas small and medium-sized males were equally likely to be excluded, suggests that there is more size-based aggression for females vs. males. This suggests that female aggression is a more important factor in determining habitat distribution than male dominance competitions, as it occurs more intensely and between more individuals.

In the two female one male tub trials, males were found with the smaller female 68% of the time. This could be male preference for small female but, given that encounters with large, aggressive females can be fatal, it may be more that males are intimidated. In fact, males found with large females are, on average, 11% larger than those found with the smaller female. Since the two females in these trials were never found together, this means that it’s likely that the male was roaming around, and they generally settled with the smaller, less intimidating female. Only if the male was extremely large could it defend itself against the large female and cohabitate with her. Previous research has shown a preference for larger female mates (Kendall-Bar 2014), which may be the case as larger individuals are better nest protectors and likely to have more offspring. However, in those experiments the large female was confined within the shelter and could not reach a male cohabitation partner to hurt him, whereas in this case a large female could easily attack an undesirable male. Only males of a certain size can defend themselves against the large, aggressive females, which might be the more desirable mates. Male earwigs tend to be the same size as or smaller than female individuals, with a few very large male morphs (personal observation). This may have come about because females prefer smaller males, but very large males can defend themselves against and mate with the most successful females, producing rarer large offspring. Large males exclusively being able to cohabitate and copulate with desirable large females presents the possibility of assortative mating between large individuals, which could be examined further in trials of three unconstrained individuals of distinct size classes.

Regarding the two male, one female tub trial results, females tend to cohabitate with the smaller males. Although the pattern could be determined via male-male competition, this is not necessarily so because sometimes males will cohabitate rather than choose to compete over a space with a female. Therefore, this pattern is likely to be a female preference for smaller males. However, in the relatively few cases (22% of the time) when females were found with large males, they were, on average, 15% smaller than those found with the small male. This suggests that although most females would rather be with a smaller male, small females may be unable to get away or defend themselves from large males, especially in our small arenas where they can be easily cornered. This combative size advantage allows larger males to forcibly cohabitate with smaller females, despite what their personal mating preference might be.

Earwigs are an unusual species in that both males and females have weaponry. The presence of weaponry on both sexes, rather than just one as might be seen in a more typical system, is naturally going to affect both the group dynamic of the species in general and how their mating system is structured. While initially lekking seemed like a potential mating system for this species due to males forming clumped distributions, female aggression and territoriality make a traditional lekking system seem unlikely. However, distributional patterns in this study have provided some insight into the mating system of the maritime earwig. First of all, we have seen that female individuals, rather than male individuals, aggressively defend their surroundings, maintaining an area around them that might be considered a “territory”. Males, while competitive, are willing to cohabitate and form aggregations, which might mean that a non-traditional lekking-like system where males form groups could be an interesting possibility to examine as a mating structure for this species. This possibility could be further examined with more arena trials, perhaps with mixed-sex groups where one sex has a higher density than the other to see whether groupings occur. We have seen that female aggression controls mixed-sex environments as a whole, so detailed examinations of large mixed-sex environments and specific interactions between both sexes, perhaps with a time-lapse camera, might give us a clearer idea of what interactions are occurring and how individual interactions influence overall distributional patterns, including the mating system.

On the smaller scale, in tub trials with 3 individuals, we have seen an overall preference for smaller mates, but a pattern of large males being able to defend themselves against and pair up with desirable large females, suggesting a patterns of size-based assortative mating. This may have lead to the pattern of mostly small males in the field with a few large male morphs. The assortative pattern of large males cohabitating and mating with large females while smaller males end up with more average females might have implications for the larger mating system, where we might see smaller males approaching smaller females and larger approaching larger. This possibility could be examined more closely with a three-individual trial, like the one we constructed here, with free roaming earwigs of different sexes and distinct size classes.

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