

Weaponry, size, and sex ratio affect spatial distribution within small and large groups of the maritime earwig (*Anisolabis maritima*)

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Abstract

Dispersion patterns within a group can reveal important aspects about social interactions and sexual selection within a species. We examined the distribution patterns of the maritime earwig (*Anisolabis maritima*), an insect well suited for studies of aggression, sociality, and sexual selection since both sexes live in close proximity and possess weaponry in the form of sexually dimorphic pincers. To examine intra- and intersexual interactions within small groups, we conducted trials with three earwigs with limited access to shelters. In single-sex trios, we found that both males and females exhibited strong size-based intrasexual aggression, as larger individuals were less likely to be excluded from shelters; however, males were more likely to cohabit than females. In mixed-sex trios, we found that both males and females preferred smaller opposite-sex partners, and cohabitation patterns indicate that both sex- and size-based differences in aggression can influence overall spatial distribution. We also examined larger single-sex and mixed-sex groups of 18 earwigs to determine whether they had random, uniform, or clumped distributions. Similar to previous field observations, males tended to form aggregations, whereas females were distributed uniformly, a pattern indicative of territoriality. Mixed-sex groups, on the other hand, were uniform during nocturnal periods of high activity but then become clumped after settling into more stable daytime positions. Overall, our results suggest that females have high levels of aggression regardless of the social context, whereas males alter their aggressive behavior in the presence of females.

KEYWORDS

aggregation, Dermaptera, dispersion, insect, shelter sharing, social behavior

1 | INTRODUCTION

Animals aggregate for reasons that may directly involve interactions among conspecifics, such as access to mates, kinship, or anti-predator benefits (Höglund & Robertson, 1990; Kaseda & Khalil, 1996; Raveh, Vogt, Montavon, & Kolliker, 2014; Torney, Berdahl, & Couzin, 2011), or indirectly involve environmental factors including use of common resources or habitat limitation (Campbell, Akbar, Adnan, &

Kunz, 2006; Cornulier & Bretagnolle, 2006; Nekola & Kraft, 2002; Wiens, 1976). The spatial distribution of organisms within these aggregations, however, often reflects interactions among individuals, where levels of aggression, courtship, or tolerance vary based on the sex, relative body size, and density of the participants (Iyengar & Starks, 2008; Osbourne, Umbers, & Keogh, 2013; Quinn, Adkison, & Ward, 1996; Thiel & Lovrich, 2011). As the density increases within these aggregations, there may be more opportunities for selection

based on interactions within social networks (Fisher & McAdams, 2017; Wolf, Brodie, & Moore, 1999). In such cases, individual behavior and social position may affect copulation success (Formica et al., 2012; Oh & Badyaev, 2010; Wey & Blumstein, 2012), but often effects on copulation success are dependent on density and interactions with others (social selection: Bercé, Kramer, Bernhauerová, & Drake, 2018; Formica et al., 2011; Heuck, Herrmann, Schabo, Brandl, & Albrecht, 2017; Marvin, 1998). For example, in forked fungus beetles, large males always have higher fitness than small males in low-density groups (positive individual selection); however, large males do not have a size-based fitness advantage if they interact with many individuals in a high-density group (negative social selection; Formica et al., 2011).

Monitoring the spatial distribution of both small and large groups can provide insight into sexual selection, where variation in traits affects reproductive success, as well as social selection, where variation in interactions influence selection on phenotypes. In small groups, cohabitation in a potential nesting site may indicate either social gregariousness or sexual competition that can involve either intrasexual rivalry or intersexual mate choice. Competitive interactions and mating preferences may also influence the distribution of individuals in large groups (Arnold & Duvall, 1994; Eurich, McCormick, & Jones, 2018; Sutherland, 1996; Taff, Freeman-Gallent, Dunn, & Whittingham, 2013). For example, if individuals in an area are found in a random distribution, then it is likely that individuals are seeking randomly distributed resources such as food or shelter without concern about the relative location of conspecifics (Brown & Gordon, 1970; Frost & Bergmann, 2012; Hui & Williams, 2017). A uniform, or hyperdispersed, distribution indicates territoriality, where individuals are likely holding and defending spaces from conspecifics within the area (Cooper & Randall, 2007; Jaeger, Wicknick, Griffis, & Anthony, 1995; Pielou, 1960). A clumped, or hypodispersed, distribution reflects aggregations of individuals, which indicates grouping based on the presence of others for anti-predatory, social, or sexual benefits (Höglund & Alatalo, 1995; Kullmann, Thunken, Baldauf, Bakker, & Frommen, 2008; Stamps, 1988). Thus, dispersion patterns can provide insight into the biotic and social drivers that influence the mating and social system.

The maritime earwig, *Anisolabis maritima* (Family Anisolabidae), is an insect found in aggregations under beach debris on temperate and tropical beaches throughout the world (Hincks, 1947; Scudder, 1876). Maritime earwigs are found in groups that vary in both size (up to 2.75 per 100 cm²; Hack & Iyengar, 2017) and composition (small groups may be single-sex, whereas larger groups are typically mixed-sex; personal observation). Unlike other earwigs (Lordan, Alegre, Blanco, Sarasua, & Alins, 2014; Sauphenor & Sureau, 1993), high-density aggregations of *A. maritima* occur only beneath shelters within narrow habitat conditions, as they are restricted to dwelling under driftwood within 3 m of the high-tide line (Hack & Iyengar, 2017; Langston & Powell, 1975). Despite their abundance, maritime earwigs are relatively inconspicuous because they spend most of their time beneath driftwood and only emerge at night to scavenge for small arthropods (Langston & Powell, 1975). The most distinctive

features of earwigs are the posterior forceps (pincers) that are used in aggressive strikes to capture prey and deter conspecifics (Bennett, 1904). In *A. maritima*, the size of this weaponry is positively correlated with body size for both sexes (Miller, Rudolph, & Zink, 2011; Munoz & Zink, 2012), but its shape is sexually dimorphic, as females have straight forceps where males have asymmetrical, curved forceps. Body size and weaponry often determine the outcome of agonistic encounters among earwigs (Forslund, 2000; Tomkins & Simmons, 1998; van Lieshout & Elgar, 2009). Larger individuals with larger forceps usually win intrasexual battles for resources including food and access to mates (Kendall-Bar & Iyengar, 2017; Moore & Wilson, 1993; Munoz & Zink, 2012). Males and females differ in their aggression toward conspecifics. Females, who lay eggs and care for their offspring through hatching, vigorously guard their nests from predators, often killing other earwigs to prevent intraspecific cannibalism (Miller et al., 2011). Males, on the other hand, typically resolve their disputes through pinching of each other's abdomens in non-lethal rituals that allow the assessment of size, strength and fighting ability (Munoz & Zink, 2012; Suzuki, 2010).

In this study, we examined how group size and composition affect spatial distribution in the maritime earwig. Previous work in *A. maritima* revealed cohabitation preferences among pairs of earwigs were sex-dependent, with females being more aggressive and less likely to share shelters than males (Hack & Iyengar, 2017). Prior experiments with three earwigs, where some individuals were restricted in movement, also showed that larger individuals of both sexes outcompeted smaller same-sex rivals to cohabitate with a potential partner in competition trials, but only females chose to cohabitate with a larger partner in choice trials (Kendall-Bar & Iyengar, 2017). We here examined the cohabitation and dispersion patterns among freely moving maritime earwigs to determine whether spatial distribution is affected by the sex, size, and composition (sex ratio) of the group. First, we followed up directly on previous work by observing small groups of three earwigs in different sex ratios (three different-sized males, three different-sized females, two different-sized males with a female, or two different-sized females with a male) to determine if cohabitation patterns remain the same under more natural conditions of unrestricted movement. For our same-sex trials, we expected larger individuals to outcompete smaller ones for limited shelters (Hack & Iyengar, 2017). In our mixed-sex trials, we posited that such intrasexual size-based aggression would lead larger individuals to dominate same-sex rivals and ultimately cohabitate with the opposite-sex individual, as seen in previous competition experiments with restricted individuals (Kendall-Bar & Iyengar, 2017).

Second, we examined dispersion patterns within large groups of 18 earwigs in different sex ratios (single-sex female, single-sex male, and mixed-sex) under a large, subdivided sheltered area to provide insight into their social interactions at more natural aggregation densities. We measured spatial distributions at two time points in these large groups because we expected to observe more random or uniform distributions (hyperdispersion) at the height of activity (6 hr, nighttime) when they may be assessing each other and more clumped distributions (hypodispersion) when they had settled into stable daytime positions

(12 hr, morning). Since females show higher levels of aggression, then we expected to find all-female groups with uniform distribution due to increased hostility among their members (Kendall-Bar & Iyengar, 2017; Miller et al., 2011). In contrast, given that males are generally less aggressive toward conspecifics, then they should be found in closer proximity (i.e., more clumped distribution) due to higher cohabitation tolerance (Hack & Iyengar, 2017). We also hypothesized that mixed-sex groups would display a clumped pattern due to the advantage of being near many conspecifics when seeking mating opportunities (Iyengar & Starks, 2008; Kendall-Bar & Iyengar, 2017). Finally, we tested whether size played a role shaping distribution patterns, as we predicted that larger individuals, especially females, would be less likely to be found in close proximity to others due to their increased aggression and intimidation of others (Hack & Iyengar, 2017).

2 | METHODS

2.1 | Study organism

Sexually mature *A. maritima* individuals were collected under driftwood on beaches at Friday Harbor Laboratories and False Bay on San Juan Island, WA, with permission of the University of Washington in June and July 2015. We did not use females guarding nests because parental care affects their behavior (Miller et al., 2011). Non-guarding females, on the other hand, may still be seeking opportunities for additional matings since the breeding season lasts May through August. Earwigs were housed individually in glass jars (0.5 L) with moistened sand and used within 48 hr of collection. Each earwig was used only in one trial. We assumed that hunger in the field-collected individuals was negligible and would not affect behavior, as previous male competition studies found that food is not a motivating factor for aggression until after at least 9 days of starvation (Munoz & Zink, 2012).

2.2 | Marking and measurements

To track individuals during all trials, we marked each earwig with a unique color/number bee tag glued onto its pronotum. After every trial, each earwig was frozen for subsequent morphological measurements using ImageJ 1.48v. Using pictures taken from a digital camera (Lumenera Infinity 2-5C) attached to a dissecting microscope (Nikon SMZ800), we measured abdominal width (using the widest point of the 6th abdominal segment as an index of body size; Munoz & Zink, 2012). We defined “size-matched” earwigs as having sixth abdominal segment widths within 5% of each other, whereas “different-sized” earwigs differed by at least 10%.

2.3 | Small group experiments: three earwigs

Small group trials took place in white plastic tubs (34.3 × 31.75 × 14.2 cm), filled 0.5 cm deep with moistened sand, that contained two transparent red plastic shelters (5 × 5 × 1 cm) placed 20 cm apart. To test whether sex affects distribution within

a shelter, we observed single-sex groups of males (MMM) and females (FFF), whose sizes varied by more than 10% and defined as “small,” “medium,” and “large” ($n > 40$ for each). For comparison, we also observed two different-sized males with a female (MMF) or two different-sized females with a male (FFM; $n > 40$ for each). For each trial, three earwigs were released into the experimental arena in the late afternoon, and their positions were recorded at 12 hr to examine their morning location following the period of nighttime activity. Between trials, containers and shelters were rinsed with warm water, allowed to dry for at least 12 hr, and then replenished with new sand to remove potential traces of previous participants.

2.4 | Large group experiments: eighteen earwigs

Large group trials took place in large clear plastic tubs (45.7 × 45.7 × 16.5 cm) where walls were covered with red cellophane to maintain a relatively dark environment. Each arena was filled 0.5 cm deep with moistened sand and contained 9 plexiglas squares (13 × 13 cm each) arranged in a 3 × 3 arrangement to cover most of the sandy area. In effect, the arena was a large square shelter subdivided into nine equal sections each separated by approximately 1 cm. Each square was raised 1 cm off the sand (using a small rock at each corner) to facilitate movement within and between these nine sections, and each clear plexiglas square was covered with a red-tinted plastic sheet to provide darkness for the earwigs while allowing us to view and record their position under red light. We conducted three types of experiments in which we observed the distribution of 18 males (single-sex male = SSM), 18 females (single-sex female = SSF), or 9 males and 9 females (mixed-sex = MS; $n = 9$ trials for each group composition), which approximates the average density of earwigs found in the field (Hack & Iyengar, 2017; personal observation). The earwigs for each large group trial were released in the late afternoon, and the position of each individual (i.e., the section in which each was found) was recorded at 6 and 12 hr to determine any differences between peak (nighttime) activity and the subsequent establishment of resting (daytime) positions. Between trials, containers and shelters were rinsed with warm water, allowed to dry for at least 12 hr, and then replenished with new sand to remove potential traces of previous participants.

2.5 | Statistical analyses

To analyze cohabitation in small group (3-earwig) trials, we ran linear mixed-effects models in which we coded whether an individual was cohabitating within a shelter at 12 hr as binomial (0 for no, 1 for yes). All models included a random effect of group to account for lack of independence of responses of individuals within the same trial. We then divided these trials based on whether they were same-sex or mixed-sex, and modeled each group separately. For the same-sex trials, we also coded individuals based on their relative size within the trio (small, medium or large). We first ran a model using all relevant parameters as a fixed effects (main effects only). All possible interactions where full crossing of variables could be achieved were

then added to the model and removed in a stepwise fashion. The best model was chosen by lowest AIC. Post hoc comparisons using Tukey's HSD were used where necessary. All models and appropriate post hoc tests were conducted in R v3.4.0 using RStudio v1.1.383.

For the large group (18-earwig) trials, we determined the distribution of earwigs using two types of analyses. First, we compared our results with a Poisson distribution to determine whether earwigs were dispersed randomly or not; second, whether the distribution was not random, and then, we calculated the index of dispersion (where $I_d = s^2 (n-1) / \bar{x}$) and compared this value with the chi-square distribution to look for evidence of a clumped (hypodispersion) or uniform distribution (hyperdispersion; Lutz & Kehr, 2017; Marcelino & Barbosa, 2016).

Additionally, we wanted to examine whether body size had an impact on whether an individual was likely to be found in a group. To this end, we conducted a general linear model (GLM) for the large group (18-earwig) trials in which we determined whether an individual was alone or cohabitating within a section of the sheltered area at 12 hr as binomial (0 for solitary, 1 for group). We analyzed these data in a manner similar to that described above for the small group trials.

3 | RESULTS

3.1 | Small group experiments: three earwigs

We found cohabitation differences across our small group (3-earwig) trials (Table 1). All-female (FFF) trials were less likely to have cohabitating individuals than two-female-one-male (FFM) trials (estimate = -3.11, $z = -6.03$, $p < 0.001$). All-female (FFF) trials were also less likely to have cohabitating individuals than two-male-one-female (MMF) trials (estimate = -3.08, $z = -5.44$, $p < 0.001$). Likewise, all-male (MMM) trials were less likely to have cohabitating individuals than two-female-one-male (FFM) trials (estimate = 2.27, $z = 5.85$,

$p < 0.001$), and all-male (MMM) trials were also less likely to have cohabitating individuals than two-male-one-female (MMF) trials (estimate = 2.24, $z = 6.09$, $p < 0.001$). There was no difference between all-male (MMM) and all-female (FFF) trials, and there was no difference between two-male-one-female (MMF) and two-female-one-male (FFM) trials.

Larger individuals in FFF trials were significantly less likely to be cohabitating than larger individuals in FFM trials (estimate = -3.12, $z = -6.03$, $p < 0.001$). Larger individuals were significantly less likely to be cohabitating in FFF trials than larger individuals in MMF trials (estimate = -3.08, $z = -5.44$, $p < 0.001$). Larger individuals were significantly more likely to be cohabitating in FFM trials than in MMM trials (estimate = 2.27, $z = 5.85$, $p < 0.001$). Individuals were significantly more likely to be cohabitating in MMF trials than in MMM trials (estimate = 2.24, $z = 6.09$, $p < 0.001$).

In the same-sex trials main effects model, there was no overall difference in cohabitation between MMM and FFF trials, nor between the differing size classes (Table 2 and Supporting Information Table S1). When a size by sex interaction is introduced in the full model, which accounts for the difference in size between males and females, males were significantly more likely to cohabitate with same-sex individuals than females. Post hoc comparisons revealed that the large individual was significantly less likely to cohabitate than medium-sized (estimate = -3.10, $z = -2.85$, $p = 0.012$) and small individuals (estimate = -3.66, $z = -3.06$, $p = 0.006$). Overall, the largest individual was always likely to have its own shelter, but there was no difference between the cohabitation status of small and medium individuals (estimate = -0.56, $z = -0.63$, $p = 0.804$). We also found that large females were significantly less likely to cohabitate than small males (estimate = -7.14, $z = -3.01$, $p = 0.031$) and medium males (estimate = -7.14, $z = -3.01$, $p = 0.031$).

In the mixed-sex trials, there was a significantly higher likelihood of cohabitation in MMF trials than in FFM trials (Table 3 and Supporting Information Table S2). Larger individuals were significantly less likely

Variables	Estimate	SE	Z value	p Value
Full Model (AIC = 524.10)				
Sex ratio (MMM vs. FFF vs. MMF vs. FFM)	14.10	5.17	2.73	0.006
Size (6th abdominal segment width)	-1.13	0.80	-1.42	0.157
Sex (Male vs. Female)	-6.69	3.99	-1.68	0.094
Size*Sex ratio	-2.35	1.14	-2.05	0.040
Size*Sex	1.67	0.84	2.00	0.045
Random effect of group: Variance = 0, SD = 0				
Main effects only (AIC = 537.50)				
Sex ratio (MMM vs. FFF vs. MMF vs. FFM)	3.22	0.40	8.13	4.42 e-16
Size (6th abdominal segment width)	-1.02	0.20	-5.14	2.72e-07
Sex (Male vs. Female)	0.95	0.31	3.09	0.002
Random effect of group: Variance = 1.5e-19, SD = 3.87e-10				

TABLE 1 Linear mixed-effects models with binomial error distribution (0 for not cohabitating, 1 for cohabitating) for all small group (3-earwig) trials. Categorical fixed effects were sex ratio (all male = MMM vs. all female = FFF vs. two males and one female = MMF vs. two females and one male = FFM), size (based on 6th abdominal segment width), and sex (male vs. female). Model selection was performed using Akaike information criteria (AIC), and only significant interactions were used

TABLE 2 Linear mixed-effects models with binomial error distribution (0 for not cohabitating, 1 for cohabitating) for same-sex small group (3-earwig) trials only. Categorical fixed effects were sex ratio (two males and one female = MMF vs. two females and one male = FFM), size (based on 6th abdominal segment width), and sex (male vs. female). Model selection was performed using Akaike information criteria (AIC), and only significant interactions were used

Variables	Estimate	SE	Z value	p Value
Main effects only (AIC = 176.70)				
Sex (Male vs. Female)	2.16	1.52	1.42	0.155
Size Class (Small vs. Medium vs. Large)	-1.58	0.28	-5.62	1.94e-08
Random effect of group: Variance = 69.26, SD = 8.322				
Interaction model (AIC = 176.80)				
Sex (Male vs. Female)	5.58	2.40	2.33	0.02
Size Class (Small vs. Medium vs. Large)	4.63	1.90	2.43	0.015
Sex * Size Class (Male vs. Female)	-4.19	2.27	-1.85	0.064
Random effect of group: Variance = 82.62, SD = 9.09				

TABLE 3 Linear mixed-effects models with binomial error distribution (0 for not cohabitating, 1 for cohabitating) for mixed-sex small group (3-earwig) trials only. Categorical fixed effects were sex ratio (two males and one female = MMF vs. two females and one male = FFM), size (based on 6th abdominal segment width), and sex (male vs. female). Model selection was performed using Akaike information criteria (AIC), and only significant interactions were used

Variables	Estimate	Standard Error	Z value	p Value
Full model (AIC = 295.50)				
Sex Ratio (MMF vs. FFM)	10.80	3.78	2.86	0.004
Size (6th abdominal segment width)	-1.17	0.47	-2.50	0.012
Sex (Male vs. Female)	-6.69	3.99	-1.68	0.094
Size*Sex Ratio	-2.30	0.79	-2.91	0.004
Size*Sex	1.67	0.84	2.00	0.045
Random effect of group: Variance = 0, SD = 0				
Main effects only (AIC = 302.10)				
Sex Ratio (MMF vs. FFM)	-0.17	0.30	-0.57	0.57
Size (6th abdominal segment width)	-1.58	0.28	-5.62	1.94e-08
Sex (Male vs. Female)	1.25	0.34	3.66	0.0003
Random effect of group: Variance = 1.87e-16, SD = 1.37e-08				

to be cohabitating. While there was no overall difference in cohabitation between males and females, there was a significant interaction between size and sex, larger individuals were significantly less likely to be cohabitating, but larger males were significantly more likely to cohabitate than larger females.

In MMF trials, different-sized males occasionally cohabitated; when they did not, the female was more likely to be found with the smaller male (78.4% vs. 21.6%; $\chi^2 = 12.66$, $df = 1$, $p = 0.0004$; Supporting Information Table S2). In FFM trials, different-sized females never cohabitated, and the male was more likely to be found with the smaller female (68.2% vs. 31.8%; $\chi^2 = 5.95$, $df = 1$, $p = 0.01$; Supporting Information Table S2). To determine the mechanism driving this pattern, we analyzed size differences based on cohabitation partners in both mixed-sex experiments. In MMF trials, the females that were found with large males were 12.3% smaller than those found with small males ($t = 4.44$, $df = 42$, $p < 0.0001$; Figure 1). Conversely, in FFM trials, the males that were found with

large females were 10.6% larger than those found with small females ($t = 4.31$, $df = 35$, $p = 0.001$; Figure 1).

3.2 | Large group experiments: Eighteen earwigs

The distribution within single-sex female groups (SSF) differed from the Poisson distribution at 6 hr ($\chi^2 = 105.61$, $df = 3$, $p < 0.00001$) with an index of dispersion indicating a uniform distribution ($I_d = 20.00$, $df = 116$, $p < 0.025$; Table 4). The distribution within single-sex female groups at 12 hr, however, was not significantly different from the Poisson distribution, indicating that females were randomly distributed at this time ($\chi^2 = 0.84$, $df = 5$, $p = 0.974$). The distribution within single-sex male groups (SSM) at 6 hr was not significantly different from a Poisson distribution ($\chi^2 = 10.80$, $df = 6$, $p = 0.095$), indicating that males were randomly dispersed at this time (Table 4). The distribution within single-sex male groups at 12 hr, conversely, was significantly different from a Poisson distribution ($\chi^2 = 28.62$,

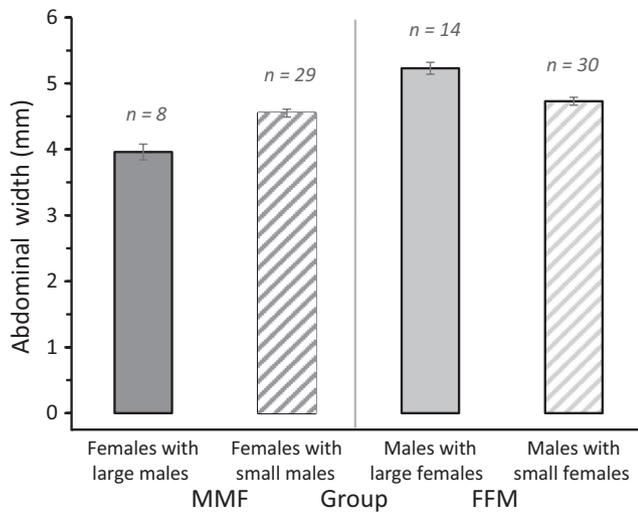


FIGURE 1 Size (\pm SEM) of maritime earwigs based on the relative size of their opposite-sex cohabitant in small group, mixed-sex trials. Group compositions are as follows: MMF = two different-sized males and a female; FFM = two different-sized females and a male

TABLE 4 Spatial distribution of individuals in large groups at 6 hr (nighttime, peak activity) and 12 hr (morning, quiescence), and comparisons of the differences in distribution between the two time periods

Group composition	6 hr	12 hr	6 hr vs. 12 hr Significant differences?
Single-sex, Males (SSM)	Random	Clumped	Different
Single-sex, Females (SSF)	Uniform	Random	Different
Mixed-sex (MS, all individuals)	Uniform	Clumped	Different
Mixed-sex, females only	Uniform	Random	Different
Mixed-sex, males only	Random	Random	Same

Note. This analysis is based on 27 large group trials (nine each of three group compositions).

Bold words indicate $p < 0.05$.

$df = 8$, $p = 0.00037$), and the index of dispersion indicated a clumped distribution ($I_d = 111.01$, $df = 107$, $p < 0.025$).

The distribution of all individuals in mixed-sex groups (MS) was significantly different from the Poisson distribution at both 6 hr ($\chi^2 = 22.66$, $df = 4$, $p = 0.00015$) and 12 hr ($\chi^2 = 24.03$, $df = 8$, $p = 0.0023$; Table 3). At 6 hr, these groups were uniformly distributed ($I_d = 49.00$, $df = 116$, $p < 0.025$), whereas at 12 hr these groups were clumped ($I_d = 159.48$, $df = 116$, $p < 0.025$).

Separating the distribution of each sex within these mixed-sex trials, we found that males were randomly distributed at both 6 hr ($\chi^2 = 0.28$, $df = 4$, $p = 0.991$) and 12 hr ($\chi^2 = 2.21$, $df = 5$, $p = 0.819$). The distribution of females within mixed-sex groups was significantly

different from the Poisson distribution at 6 hr ($\chi^2 = 32.49$, $df = 3$, $p < 0.00001$), and the index of dispersion indicated a uniform distribution ($I_d = 54.32$, $df = 116$, $p < 0.025$). At 12 hr, however, females within mixed-sex groups were randomly distributed ($\chi^2 = 0.66$, $df = 4$, $p = 0.956$).

There was no significant difference in whether individuals were more likely to be solitary within a section of the sheltered area based on the individual's size, sex, or the overall group composition (Table 5). However, the significant interaction between size and sex indicates that larger females were significantly more likely to be solitary than larger males.

4 | DISCUSSION

Spatial distribution within groups can provide insights into social interactions including aggression and sexual selection (Emlen & Oring, 1977; Riechert, 1998; Shuster & Wade, 2003). In this study, we examined the roles of sex, group composition, and group size on cohabitation and spatial distribution to better understand group dynamics in the maritime earwig. As predicted, cohabitation patterns within small groups of three same-sex earwigs reflected sex-based differences in aggression similar to previous experiments on pairs of earwigs (Hack & Iyengar, 2017). Specifically, when shelters were limited, males were almost four times more likely to cohabitate with each other than females, which reflects the males' tolerance of close proximity and ritualized aggression that rarely results in mortality (Kendall-Bar & Iyengar, 2017; Munoz & Zink, 2012). Females, on the other hand, rarely cohabitated, a pattern indicative of their elevated levels of aggression (Hack & Iyengar, 2017). For both sexes, the largest individual was never excluded from a shelter, further supporting size-based advantages in competition within same-sex groups (Hack & Iyengar, 2017; Munoz & Zink, 2012). Size clearly determines the winner in intrasexual competition for resources, as larger individuals appear more able to dominate their rivals to control access to shelters.

Our mixed-sex experiments with three freely moving earwigs followed up similar previous experiments where certain individuals were restricted to determine the presence of intrasexual competition and intersexual choice in isolation (Kendall-Bar & Iyengar, 2017). Among small groups of three earwigs with two different-sized same-sex individuals, we expected to observe patterns concomitant with previous results in which an earwig cohabitated with the larger of the two caged opposite-sex individuals. Surprisingly, within the context of unrestricted movement among all three participants, we found cohabitation with the smaller potential partner for both female and males: females preferred to cohabitate with the smaller of two males over three-quarters of the time, and males preferred to cohabitate with the smaller of two females over two-thirds of the time. Despite the similarity in these patterns, the relative sizes of individuals found with larger vs. smaller different-sex individuals suggest that there are different size-related interactions involved. The rare females found with larger males were significantly smaller

TABLE 5 Generalized linear models with binomial error distribution (0 for solitary, 1 for group). Categorical fixed effects were group composition (single-sex male = SSM vs. single-sex female = SSF vs. mixed-sex = MS), size (based on 6th abdominal segment width), and sex (male vs. female). Model selection was performed using Akaike information criteria (AIC), and only significant interactions were used

Variables	Estimate	SE	Z value	p Value
Full GLM (AIC = 496.94)				
Group composition (SSM vs. SSF vs. MS)	-0.95	0.52	-1.82	0.069
Size (6th abdominal segment width)	-5.41	3.53	-1.53	0.126
Sex (Male vs. Female)	-3.21	2.06	-1.56	0.120
Size * Sex	8.88	4.38	2.03	0.043
Main effects only (AIC = 499.14)				
Group composition (SSM vs. SSF vs. MS)	-0.86	0.52	-1.65	0.100
Size (6th abdominal segment width)	0.389	2.03	0.19	0.848
Sex (Male vs. Female)	0.87	0.44	1.97	0.049

than those females cohabitating with smaller males, which suggests that these (small) females were coerced by larger, aggressive males into cohabitating within a shelter. On the other hand, the rare males found with larger females were significantly larger than those males found with smaller females, which—given that females are generally more aggressive than males—indicates that only large males were able to tolerate the aggression from large females and cohabitate with them. In most organisms that are sexually dimorphic, only one sex possesses weaponry and individuals prefer a larger partner since they are usually of higher genetic quality and/or may provide access to more resources (Andersson, 1994; Emlen, 2014). Our mixed-sex small group experiments, however, show that size-based aggression and weaponry between both sexes may lead to cohabitation patterns that are mediated not by intrasexual competition, but instead by intimidation from potential partners. Our results also demonstrate that, while intrasexual competition appeared to be a stronger selective force in small groups when individuals were restricted in movement (Kendall-Bar & Iyengar, 2017), intersexual interactions played a much larger role when all individuals were free to move. Although we do not know whether cohabitation preferences directly correlate to mating preferences, this difference in group dynamics in these different contexts highlights the importance of testing organisms under circumstances that mimic more natural conditions.

Our results from these small groups also demonstrate that interactions among mixed-sex groups differ significantly from those in same-sex groups. For example, we found that large individuals of both sexes were much more likely to cohabitate in presence of opposite-sex individuals, which suggests that body size and aggression are used competitively to repel same-sex rivals and to secure potential partners. Although this pattern was expected based on how organisms across taxa use body size and weaponry (Arnqvist & Rowe, 2005), our experiments also revealed how sex-specific aggression can affect interactions and spatial distribution within small groups based on sex ratios. We found more cohabitation in trials with two males and a female vs. two females and a male, which likely is a reflection of the fact that male maritime earwigs are typically less aggressive and more tolerant of cohabitation with either sex.

Furthermore, while large individuals were generally less likely to cohabitate than small ones, large males were more likely to cohabitate than large females. These results demonstrate the importance of such sex differences in aggressive and competitive behaviors, which suggests that, in addition to group size, the group composition (i.e., sex ratio) is likely to have a profound effect on observed spatial distributions.

We also examined dispersion patterns in arenas with large groups (of differing sex ratios) at a density that resembles what is found in nature (Hack & Iyengar, 2017). Within each of these trials, we additionally looked at temporal dynamics by determining spatial distributions at 6 hr, at night when peak activity occurs, and at 12 hr, in the morning when their quiescent period starts and positions are relatively stable (personal observation). In single-sex trials with females, we found that females were uniform at 6 hr but randomly distributed at 12 hr, which suggests they were initially aggressive with strangers, perhaps sorting out dominance relationships before settling anywhere in the arena (Huntingford & Turner, 1987). It is unlikely the females are establishing any type of territories within a few hours of being placed in the experimental arena—instead, the high levels of nocturnal activity likely lead to an increased number of encounters that result in increased hostility and aggression, particularly among females. 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 (dear enemy effect: Fisher, 1954; Shuster & Wade, 2003). Males, on the other hand, were randomly distributed at 6 hr and then clumped at 12 hr. Since males are generally more tolerant of close proximity (particularly to other males; Hack & Iyengar, 2017), this result suggests that males initially may be exploring the arena in a random fashion initially before eventually settling down close to each other. Given that shelter space was not limited within these trials (indeed the entire arena was essentially a subdivided sheltered area), males were not clustering due to habitat limitation. Indeed, in species with sex-based differences in weaponry, armed males often establish territories and distribute themselves uniformly as the result

of aggressive interactions, whereas females may be distributed randomly or clumped around males (Iyengar & Starks, 2008; Shuster & Wade, 2003; Stamps, 1988). In *A. maritima*, both sexes possess weaponry, so it appears that the sex-based differences in aggression (likely rooted in the evolution of vigorous maternal care of nests in close proximity; Miller et al., 2011) may be responsible for the sex differences in dispersion patterns.

Earwigs in large, mixed-sex groups showed dispersion patterns that were different than the same-sex trials. Overall, individuals from mixed-sex trials were uniformly distributed at 6 hr and clumped at 12 hr, but the mechanism driving these patterns can be ascertained through examining the spatial distributions of each sex. For the earlier time period of peak activity (6 hr), females appear to be driving the overall uniform spatial distribution through aggression since females were uniformly distributed, whereas the males were randomly distributed. When they settled into resting daytime positions (12 hr), all individuals were clumped even though both females and males each showed a random distribution when analyzed separately. We suspect that, given their aggression and general dominance over the opposite sex, females are not altering their behavior since they are randomly distributed in both single-sex all-female trials and in mixed-sex trials at 12 hr. Males, on the other hand, alter their behavior based on context, as demonstrated by their clumped distribution in the single-sex all-male trials but random distribution in the presence of females. Indeed, the male's random distribution is not different at 12 hr from the female's random distribution in mixed-sex trials. Thus, the males are distributing themselves in a manner similar (and in close proximity) to the females present, which in turn leads to an overall clumped distribution among all individuals in mixed-sex groups. These results support the idea that males are more gregarious than females in *A. maritima* because males prefer to cohabitate in same-sex clusters when only males are present and prefer to cohabitate near females (but not other males) when females are available. Female interactions are mediated by aggressive tendencies, as they ultimately distribute themselves randomly after a period of establishing dominance through hostile interactions through forcep strikes. In other words, while female aggression mediates most interactions initially in mixed-sex groups to create a uniform distribution, eventually it is the males who adjust their behavior in the presence of females to create observed clumped spatial distribution once overall group dynamics stabilize.

Our results show that spatial distribution is a function of sex and group composition in both small and large groups in *A. maritima*. Earwigs are unusual in that both sexes have weaponry (Emlen, 2014; Huntingford & Turner, 1987), and this equality between males and females means that all individuals must consider risk of injury regardless of whom they encounter. This potential for intimidation while seeking partners was particularly evident in the mixed-sex three-earwig trials, where both males and females preferred to cohabitate with a smaller, and therefore less dangerous, opposite-sex partner. Intersexual choice and aggression were absent from previous experiments in which certain individuals were restricted and prevented from fighting; this surprising reversal of cohabitation

patterns not only reflects the importance of observing behavior under natural conditions, but also warrants further investigation regarding the mechanism responsible. There are currently experiments underway to continuously monitor all the behaviors in these small groups by quantifying and classifying all interactions including hostile strikes, courtship acts, antennation, and incidental contacts. Such direct observations may help determine if larger individuals dominate through bullying (i.e., directed aggressive behavior toward smaller individuals) or intimidation (i.e., smaller individuals avoiding larger ones). Regardless of the specific mechanism, the selection of smaller partners when given a size-based choice provides evidence of an interesting trade-off: While large size provides benefits during intrasexual confrontations (Munoz & Zink, 2012), such aggressive, intimidating traits may be selected against regarding intersexual mate choice (Arnqvist & Rowe, 2005; Eldakar, Dlugos, Wilcox, & Wilson, 2009; Thornhill & Alcock, 1983).

The large group experiments demonstrated that the sex ratio determines the overall spatial distribution, which is not surprising given documented sex-based differences in aggression (Goldsmith, Stewart, Adams, & Trimble, 1996; Hack & Iyengar, 2017; Miller et al., 2011). Although we monitored distributions at periods of peak activity and quiescent stability, we only recorded positions within the first 12 hr. We do not know how the interactions (and the spatial distributions) may change over time. For example, we do not know the degree to which individuals show site fidelity, but increased site fidelity is often correlated with group stability, which in turn often leads to reduced hostility (Fisher, 1954; Shuster & Wade, 2003). It is also unknown whether spatial distributions change over the course of the year between the breeding and non-breeding seasons; however, we have some preliminary evidence that densities change within the breeding season, as aggregations are more dense in the first half (when more individuals may be seeking mates) than in the second half (when more females are likely to be aggressively guarding eggs; Coonfield & Iyengar, 2017). Although these experiments establish the important effects of sex and size on spatial distribution in the maritime earwig, it will be important to continuously monitor group dynamics and use social network analyses to determine the mechanisms responsible for the patterns we observed.

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