

Sexual selection by the seashore: the roles of body size and weaponry in mate choice and competition in the maritime earwig (*Anisolabis maritima*)

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Received: 26 July 2016 / Revised: 5 September 2016 / Accepted: 2 October 2016 / Published online: 1 December 2016
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Abstract

The spatial distribution of organisms can provide insight into their mating systems, either revealing mating preferences (intersexual selection for ornaments), competition for mates (intrasexual selection for armaments), or both. Teasing apart the relative contributions of these selective forces is a critical step in understanding mating systems, particularly given the potential combinations and complexities that arise when both sexes possess weaponry. We examined the mating system of the maritime earwig *Anisolabis maritima*, an insect well suited for studies of sexual selection because males differ markedly from females in body size (males are more variable in size, and sometimes substantially larger, than females) and weaponry (males possess asymmetrical, curved forceps, whereas females have straight forceps). We varied sex, body size, and forceps asymmetry among trios of earwigs and examined their spatial distribution under conditions where movement was restricted to promote either intersexual choice or intrasexual competition. Our results indicate strong sexual selection for larger sizes through both competition and choice in both sexes. However, females had no preference for males based on forceps asymmetry. We discuss how the competition and cohabitation patterns provide insight into the mating system, including how the possession of weaponry by both sexes

could operate in intrasexual competitive battles as well as serve as a basis for assessing the quality of a potential mate.

Significance statement

Sexually dimorphic traits are often the result of either intersexual selection, where one sex chooses the other based on phenotypic qualities, or intrasexual selection, where members of one sex compete with each other for mating opportunities. Although many mating systems lie squarely on one end of this spectrum, it is often less clear which selection forces shape mating systems when both sexes possess weaponry. We monitored cohabitation patterns to examine the relative roles of mate choice and competition in *Anisolabis maritima*, an earwig in which males have asymmetrical, curved pincers, whereas females have symmetrical, straight pincers. By restricting the movement of certain individuals within trios, we found that large size but not forceps asymmetry was important in both mate choice and competition. Our results indicate that weaponry and aggression may significantly affect both sexes and contribute to the complexity of the mating system.

Keywords Cohabitation · Sexual selection · Mate choice · Competition

Communicated by J. C. Choe

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Introduction

Sexual selection, in the form of intersexual choice or intrasexual competition, is often responsible for morphological differences between sexes (Darwin 1871; Andersson 1994). Sexual dimorphism, as a consequence, is traditionally viewed as the result of female choice for male ornaments (Clutton-Brock et al. 1977; Shuster and Wade 2003), male-male competition where females mate with dominant males

(Huntingford and Turner 1987; Emlen 2008), or a combination of both (Berglund et al. 1996; Arnqvist and Rowe 2005). In many species, body mass and weaponry, usually possessed by males, are used in contests to defend resources (e.g., territories, food, nesting sites or females) that directly result in reproductive success (e.g., Forsyth and Alcock 1990; Gwynne and Jamieson 1998; Bateman 2000; Kelly 2005; Iyengar and Starks 2008). Although large females often achieve increased reproductive success due to increased fecundity (Shuster and Wade 2003), females of nesting species may also use size and weaponry to secure resources and defend their offspring (Clutton-Brock 2009; Watson and Simmons 2010). Although body and/or weapon size may affect fight outcomes, prolonged physical confrontations can be costly due to high energetic demands and the risk of injury or even mortality, either from opponents (Sneddon et al. 1999; Briffa and Elwood 2004) or from predators (Jakobsson et al. 1995; Kelly and Godin 2001). As a result, the ability for individuals to quickly and accurately assess a rival's fighting ability before engaging in potentially costly combat should be favored by natural selection (Maynard Smith and Parker 1976; Hack 1997; Neat et al. 1998; Kelly 2006). This ability is particularly important within large groups, where there is often a selective advantage for individuals to recognize their neighbors and assess their quality without risking injury from fighting (dear enemy effect: Fisher 1954; Shuster and Wade 2003). Thus, when both males and females possess weaponry and live in close proximity, there is the potential for both intersexual choice and intrasexual competition between both sexes to co-occur in interesting and complex ways to shape the mating system (Davies 1991; Shuster and Wade 2003; Kokko et al. 2006).

Insights into the selective forces shaping mating systems can arise through monitoring the spatial distribution and proximity of individuals (Emlen and Oring 1977). Although sensitivity to the locations of food and predators can affect spacing patterns that can, in turn, affect mating systems (e.g., Wrangham and Rubenstein 1986; Davies 1991; Campbell et al. 2006), mate choice and competition can also lead to sex differences in spatial distribution (e.g., Moehlman et al. 1998; Prohl and Berke 2001; Iyengar and Starks 2008). Thus, investigating how individuals distribute themselves relative to others on the basis of sex and body size can reveal information about both intersexual and intrasexual selection. In most species with high levels of intrasexual aggression, sexual dimorphism manifests itself with males being armed with weaponry that females lack (reviewed in Emlen 2008). Earwigs are a very interesting group in which to study reproductive behavior because they possess sexually dimorphic weaponry (males have curved posterior forceps, whereas females have straight forceps), which is a strong indicator that there are different selection pressures on males and females linked to the mating system (Tomkins and Simmons 1996). By monitoring the

spatial distribution of earwigs in controlled environments, we here provide experimental and observational results that contribute to understanding sexual selection in a species where both sexes have morphological characteristics that could support various combinations of intersexual and intrasexual selection.

Anisolabis maritima, also known as the maritime or seaside earwig (Family Anisolabididae), is an insect found in groups under driftwood and seaweed at or above the high-tide line (Bennett 1904; Langston 1974). Although their likely origin is the Mediterranean region, the maritime earwig is now widely distributed throughout the world from temperate to tropical coastal habitats due to dispersal from freighter transit (Scudder 1876; Hincks 1947). Maritime earwigs, however, are relatively inconspicuous on most beaches because they spend most of their time under beach debris to avoid desiccation and escape predators, emerging only at night to forage on small arthropods (Langston and Powell 1975). Beneath these shelters, females construct nests in which they lay an average of 42 eggs that they defend from predators, including conspecifics (Miller et al. 2011). While retaining many common earwig characteristics, *A. maritima* differs in two important ways: (1) male forceps are curved, as is typical, but they are markedly asymmetrical, which is unusual in a weapon that may also play a role in female choice (Munoz and Zink 2012; Callander et al. 2013); and (2) there is a huge size variation among males (while many males are smaller than females, there are a substantial number of "giant" males that are 50% larger than the average female; *pers. obs.*).

Sex, body size, and forceps have been shown to play important roles in interactions among earwigs (e.g., Moore and Wilson 1993; Forslund 2000; van Lieshout and Elgar 2009). As in many earwig species (Vancassel 1984; Sauphanor and Sureau 1993; Kölliker 2007), *A. maritima* males and females differ fundamentally in their aggression during agonistic encounters with conspecifics. Males usually resolve their disputes non-lethally by squeezing each other's abdomens, perhaps a means to assess size, strength and fighting ability (Munoz and Zink 2012). Females, on the other hand, often kill conspecifics while vigorously guarding their nests, and larger females defend their eggs or juveniles against conspecific cannibalism more effectively due to their increased size and resulting dominance in intraspecific competition (Miller et al. 2011). Similarly, greater size confers a competitive advantage for both sexes in intrasexual battles for food and shelter (Munoz and Zink 2012; Hack and Iyengar *in review*). While asymmetrical traits have been demonstrated to aid in male-male combat among arthropods (e.g., Oliveira and Custódio 1998; Miller and Wheeler 2005) and ungulates (Alvarez 1995) and female choice in many crustaceans (reviewed in Marriapan et al. 2000), the functionality of the asymmetry in male *A. maritima* forceps is not completely understood. However, we do know that, in the absence of size

differences, the male maritime earwig's unique forceps asymmetry is an advantage among size-matched small male combatants but not among large males (Munoz and Zink 2012). Thus, although fluctuating asymmetry does not affect competition or mate choice in primarily symmetrical European earwigs (Walker and Fell 2001), there was evidence that both male forceps asymmetry and size could affect competition in *A. maritima*. Overall, these results highlight the importance of examining the roles of these male characteristics when examining intersexual and intrasexual interactions in this species.

Mating systems are often characterized by the relative degree of intrasexual selection (competition between same-sex individuals, usually males) and intersexual selection (mating preferences for the opposite sex, usually females; Shuster and Wade 2003). However, it is often challenging to disentangle the relative contributions of intersexual and intrasexual selection when the traits under selection are important for contests for territories (e.g., nests), food, and mates (Bonduriansky and Rowe 2003; Wong and Candolin 2005). Our experiments used cohabitation patterns among different combinations of individuals to infer how sex, size, and forceps asymmetry may affect mate choice and competition in *A. maritima*. Specifically, we conducted four types of experiments: (1) female choice, where a female chose between two males that differed in body size or in forceps asymmetry; (2) male choice, where a male chose between two females differing in body size; (3) male competition, where two males, differing in either body size or forceps asymmetry, competed for a female; and (4) female competition, where two females differing in body size competed for a male. Although we restricted the movement of individuals in these experiments, we felt that cohabitation outcomes were reasonable indications of competition or mating preferences given the high levels of aggression observed among individuals both in nature and in captivity. Overall, we posited that size would play an important role in governing interactions—we expected size-based aggression to result in larger individuals outcompeting smaller ones for access to a potential partner, and we expected individuals to preferentially interact with larger, presumably higher quality individuals (larger females often have greater fecundity and larger males are often of higher genetic quality; Ghiselin 1974; Andersson 1994). We hypothesized that both intrasexual and intersexual selections were likely to play important roles because both males and females possess weaponry and exhibit elevated levels of aggression.

Materials and methods

Collection and care of earwigs

We collected sexually mature adults found under driftwood above the high-tide line on beaches at Friday Harbor

Laboratories, Cattle Point, and False Bay on San Juan Island, WA. We avoided collection of females guarding nests, assuming that recent mating success would make them less likely to engage in courtship and copulatory behavior. Earwigs were housed individually in plastic tubs or glass jars (0.5 L) with moistened sand (from False Bay) and used within 48 h of collection. We assumed that the animals' hunger during experiments was negligible and would not affect behavior, because, in male competition studies, they need to be starved for at least 9 days to ensure that they would fight over food (Munoz and Zink 2012).

Marking and measurements

To track individuals during trials without disturbing them, we marked each experimental earwig by gluing a colored and numbered bee tag to its pronotum. After use in only one trial, each earwig was frozen for subsequent morphological measurements using ImageJ 1.48v. Using pictures taken from a digital camera (SONY CCR-DC374) attached to a dissecting scope (Nikon SMZ800), we measured the head width and abdominal width (using widest point of 6th abdominal segment as an index of body size; Munoz and Zink 2012). "Size-matched" individuals were defined as having sixth abdominal segment widths within 5% of each other, whereas "different-sized" individuals differed by more than 10%.

We also measured the forceps length for all earwigs, as well as forceps width to calculate the degree of asymmetry for males. The length of each forceps was defined as the distance from the tip of the forceps perpendicularly until the base of the final abdominal segment, and the width of each forceps was defined as the distance between the line defining length and the outer edge of each forceps (Munoz and Zink 2012). For males, we used the curvature (width over length) of each forceps to determine overall forceps asymmetry (right curvature over left curvature). Quantifying male forceps asymmetry is potentially important in this earwig, because male competition for food was a function of differing asymmetry in small males but not in large males (Munoz and Zink 2012). Because of the differential importance of forceps asymmetry in competition trials, we treated small and large males as belonging to distinctive groups in our experimental design. This classification was based on measured size differences and field observations of two male size classes ("small" ones that are smaller than or equal to the size of females, and "large" ones that are significantly larger than females and comprise most of the upper quartile of the population); we treated small and large males as belonging to distinctive groups in our experimental design. In cases where we used size-matched males differing in forceps asymmetry ("high" vs. "low"), we used males that differed by at least 10% in this parameter. Because there was no correlation between male body size and forceps asymmetry

($r^2 = 0.01$; $F_{1,108} = 1.21$; $P = 0.27$), we treated these as separate variables in our experiments.

Experimental enclosures

The experimental arenas were white plastic tubs ($15 \times 21 \times 10$ cm) filled 0.5 cm deep with moistened sand and contained two shelters ($5 \times 5 \times 1$ cm) placed 15 cm apart (Fig. 1). The shelters were created by removing one lateral side of a transparent red plastic box to facilitate entry into this enclosed area, which simulated their natural dark habitat underneath driftwood, while allowing us to monitor the position of the earwig. We also restricted the movement of certain individuals by confining them to one half of the shelter using wire mesh (3 mm) to allow antennation without body and forceps contact (Fig. 1). To account for the fact that antennation (and therefore assessment) was likely to be more difficult for confined earwigs, we allowed some initial assessments prior to introduction of earwigs into the arena. Specifically, we first placed all three experimental earwigs together in small paper cups (diameter 3.5 in. where they could freely antennate each other for approximately 30 s (based on preliminary experiments, this maximized the time for assessment while minimizing the risk of pre-trial injury). Then, based on the experiment, certain earwigs were confined in the shelters and placed in the arena, followed by the release of the free-moving individual(s).

For all experiments, earwigs were released in the late morning, and the positions of the earwigs were recorded at 12 and 24 h to determine any differences between periods of peak (nighttime) activity and subsequent establishment of stable (daytime) positions. All observations were made under red light to minimize disturbance. Containers and shelters were rinsed and new sand was placed in the arena and shelters following each trial to remove potential chemical traces of previous participants. To minimize observer bias, blinded

methods were used when all behavioral data were recorded and/or analyzed.

Experiment 1: female choice

We released one female earwig in containers with two shelters, each of which contained a restricted male, to determine whether females exhibit cohabitation preferences based on male body size or forceps asymmetry. We conducted three sets of experiments in which we used the following pairs of restricted males: different-sized males with the same forceps asymmetry (expt. 1A; paired $t = 1.32$; $df = 40$; $P = 0.19$), size-matched small males with differing forceps asymmetry (expt. 1B), and size-matched large males with differing forceps asymmetry (expt. 1C).

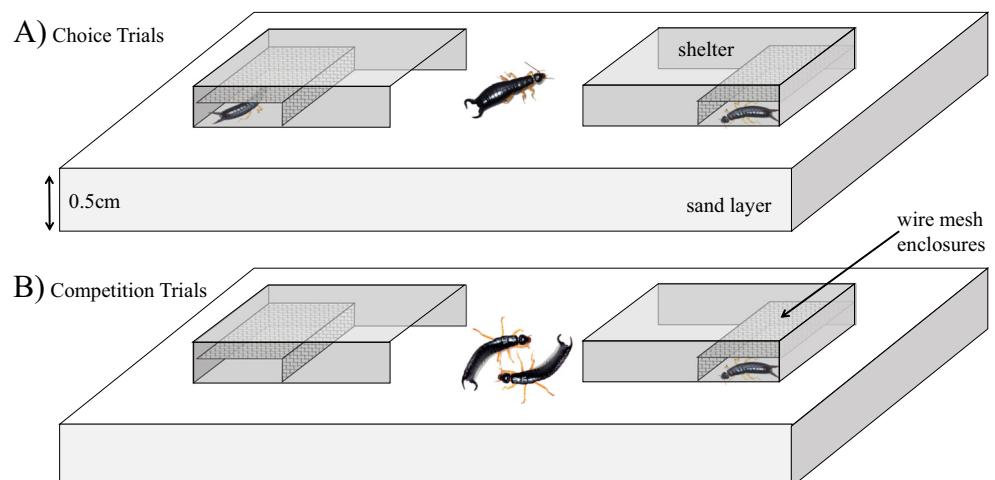
Experiment 2: male choice

We released one male earwig in containers with two shelters, each of which contained a restricted female, to determine whether males exhibit cohabitation preferences based on female body size. We conducted two sets of experiments, one in which we allowed small males to choose between different-sized females (expt. 2A), and another in which large males chose between different-sized females (expt. 2B).

Experiment 3: male competition

We released two male earwigs in containers with two shelters, one of which contained a restricted female, to determine whether males were more likely to cohabitate with females based on their own body size or forceps asymmetry. We conducted three sets of experiments in which we used the following pairs of males: different-sized males with the same forceps asymmetry (expt. 3A; paired $t = 0.85$; $df = 42$; $P = 0.40$), size-matched small males with differing forceps asymmetry (expt.

Fig. 1 Arenas for two types of experiments: **a** Choice trials (expts 1 and 2), where two same-sex individuals were restricted in shelters and one opposite-sex individual was free to choose, and **b** competition trials (expts 3 and 4), where the two same-sex individuals were free to compete for access to a shelter containing one opposite-sex individual



3B), and size-matched large males with differing forceps asymmetry (expt. 3C).

Experiment 4: female competition

We released two female earwigs in containers with two shelters, one of which contained a restricted male, to determine whether females were more likely to cohabitate with males based on their own body size. We conducted two sets of experiments, one in which the shelter contained a small male (expt. 4A), and another in which the shelter contained a large male (expt. 4B).

Data analysis

All trials were used except those in which individuals died (<5% of the trials). We conducted chi-squared goodness-of-fit tests to analyze the distribution resulting from each set of trials and chi-square tests-of-independence to compare the results at different times within an experiment and for comparisons between different experiments. When comparing distributions and different times within an experiment (12 vs. 24 h), we used a generalized linear mixed model (GLMM) with a binomial error distribution and trial number as a random effect. We performed all statistical analyses in JMP Pro 11.

Results

Experiment 1: female choice

Females preferred to cohabitate with larger males at 12 h but not at 24 h (Table 1), and this represents a significant change in behavior between the two times (GLMM $\chi^2 = 7.17$, $df = 1$, $P = 0.007$). Females did not exhibit cohabitation preferences based on forceps asymmetry for small males or large males at either 12 or 24 h (Table 2) nor were there differences in behavior between these two times (size-matched small males GLMM $\chi^2 = 2.21$, $df = 1$, $P = 0.14$; size-matched large males GLMM $\chi^2 = 0.25$, $df = 1$, $P = 0.62$). Females also did not exhibit different cohabitation preferences between the two size-classes of males differing in forceps asymmetry at 12 h ($\chi^2 = 0.14$, $df = 1$, $P = 0.71$) or 24 h ($\chi^2 = 0.37$, $df = 1$, $P = 0.54$).

Experiment 2: male choice

Small males did not exhibit any preference for cohabitation with small vs. large females at 12 or 24 h, (Table 2), and there were no differences in behavior between these two times (GLMM $\chi^2 = 0.00$, $df = 1$, $P = 1.00$). Large males did not exhibit any cohabitation based on female size at 12 h but preferred larger females at 24 h (Table 2), and this represents a significant change in behavior between the two times

(GLMM $\chi^2 = 6.01$, $df = 1$, $P = 0.014$). Large and small males demonstrated a similar lack of cohabitation preferences based on female size at 12 h ($\chi^2 = 0.08$, $df = 1$, $P = 0.78$), but large males did prefer to cohabitate with larger females more than small males did at 24 h ($\chi^2 = 6.58$, $df = 1$, $P = 0.010$).

Experiment 3: male competition

Larger males cohabitated with females more often than smaller males at both 12 and 24 h (Table 3), and there was no difference in behavior between the two times ($\chi^2 = 0.06$, $df = 1$, $P = 0.80$). Size-matched males of differing forceps asymmetry did not differ in cohabitating with the female at 12 or 24 h (Table 3), and there were no differences in behavior between these two times for either small or large males (size-matched small males GLMM $\chi^2 = 0.58$, $df = 1$, $P = 0.45$; size-matched large males GLMM $\chi^2 = 0.55$, $df = 1$, $P = 0.46$). Additionally, males showed no difference in the cohabitation frequency with females based on the male's forceps asymmetry among large males vs. small males at 12 h ($\chi^2 = 0.02$, $df = 1$, $P = 0.90$) and at 24 h ($\chi^2 = 2.64$, $df = 1$, $P = 0.10$).

Experiment 4: female competition

Larger females cohabitated with small males more often than smaller females at both 12 and 24 h (Table 4), and there was no difference in behavior between the two times (GLMM $\chi^2 = 0.47$, $df = 1$, $P = 0.49$). However, large and small females did not differ in cohabitating with large males at 12 or 24 h (Table 4), and there were no differences in behavior between these two times (GLMM $\chi^2 = 1.58$, $df = 1$, $P = 0.21$). Finally, outcomes were significantly different depending on whether different-sized females were competing for large or small males; large females were significantly more likely to cohabitate with small vs. large males both at 12 h ($\chi^2 = 18.90$, $df = 1$, $P < 0.0001$) and at 24 h ($\chi^2 = 6.26$, $df = 1$, $P = 0.012$).

Discussion

In this study, we examined cohabitation patterns to determine the relative roles of size, sex, and forceps asymmetry on intersexual choice and intrasexual competition in the maritime earwig, an insect where males and females possess sexually dimorphic weaponry. Overall, our results show that size appears to play a stronger role in intrasexual competition rather than intersexual choice, as competitions for access to mates were consistently dominated by larger individuals. Differences in male forceps asymmetry, on the other hand, did not translate to intraspecific competitive inequalities, nor did they affect female mate choice. This result was surprising given that this trait affected competition for food among small maritime earwigs

Table 1 Female choice trials (expt 1): cohabitation preferences of females placed in a container with two shelters, each containing a restricted male

Experiment	Male A	Male B	Number	Cohabitation at 12 h (A/B)	χ^2 (df = 1)	<i>P</i> value	Cohabitation at 24 h (A/B)	χ^2 (df = 1)	<i>P</i> value
1A: different-sized males	Large	Small	41	28/13	5.62	<i>0.02</i>	16/25	1.99	0.16
1B: size-matched small males	High asym	Low asym	33	15/18	0.27	0.60	21/12	2.49	0.11
1C: size-matched large males	High asym	Low asym	32	16/16	0.00	1.00	18/14	0.50	0.48

*Significant *P* values are in *italics*

(Munoz and Zink 2012) and that differences in forceps size had been shown to confer competitive and mating advantages in the European earwig (Radesater and Halldorsdottir 1993; Tomkins and Simmons 1998). There were only two experiments where we observed differences in cohabitation preferences between 12 h (night) and 24 h (day), which indicate that there are similar motivations regarding cohabitation at both these time periods of peak activity and quiescence, respectively. The fact that we have observed courtship and copulation both at night and in the daytime (pers. obs.) also suggests that qualities desirable in courtship and cohabitation generally do not vary between the two time periods that we examined.

One notable exception occurred in our experiments where females chose between different-sized males, as females preferred to cohabitate with larger males at 12 h but showed no such preference at 24 h. Given that large males dominate in intraspecific competition (perhaps representing higher quality and reproductive fitness; Munoz and Zink 2012), this difference in female behavior suggests that many females initially interested in the larger male ultimately cohabitated with the smaller male. In fact, we found that 44% of females (18 out of 41) switched from cohabitating with large males at 12 h to cohabitating with small males at 24 h. We hypothesize that these females initially took advantage of having a means to safely assess larger, more aggressive males without risking injury (the males were restricted) but then eventually decided to cohabitate with generally less threatening smaller males. Avoiding larger, more aggressive winners of intrasexual combat in favor of subordinate males has been observed in closely related blattodeans (cockroaches; Moore et al. 2001), as well as a variety of taxa including birds, fish and other arthropods (reviewed in Qvarnström and Forsgren 1998). We are currently performing experiments in *A. maritima* to determine whether relative size and/or circadian variations in motivation are responsible for the

differences in intersexual cohabitation preferences between these two time periods.

Differing forceps asymmetry did not affect female preferences, regardless of male size. Even though male weapons evolved for intrasexual conflict can be co-opted by females to judge male quality (Fitzpatrick et al. 1995), there is strong evidence that male size and forceps length affect competition but have no bearing on female choice across many earwig species (Moore and Wilson 1993; Walker and Fell 2001; Forslund 2003; van Lieshout and Elgar 2009). Thus, although male forceps asymmetry had been found to be important in determining dominance in size-matched intrasexual competition for food (Munoz and Zink 2012), it is understandable that, when removed from a competitive context, the difference in forceps asymmetry might not manifest itself in altered female preference.

Given that larger females are likely to be more fecund across taxa (Ghiselin 1974) and thus a more desirable mate (Andersson 1994), we were surprised that only large males (at 24 h) demonstrated a preference to cohabitate with the larger female. We postulate that large males were likely assessing the females during the initial period (12 h) before ultimately cohabitating with the larger female. The lack of cohabitation preferences based on female size for small but not large males suggests that the relative sizes of males and females affect pairings. In this experiment, small males may have been intimidated by larger, aggressive females, whereas large males benefited from equivalent or greater body size and weaponry that enabled them to cohabitate with a larger, more fecund female.

Our male competition experiments yielded results consistent with a previous study on males competing for food (Munoz and Zink 2012) in that large males were dominant in obtaining access to a resource (in this case, females). Large males were more likely to cohabitate with the female at both time periods,

Table 2 Male choice trials (expt 2): cohabitation preferences of males placed in a container with two shelters, each containing a restricted female

Experiment	Female A	Female B	Number	Cohabitation at 12 h (A/B)	χ^2 (df = 1)	<i>P</i> value	Cohabitation at 24 h (A/B)	χ^2 (df = 1)	<i>P</i> value
2A: small male choice	Large	Small	45	19/26	1.09	0.30	20/25	0.56	0.46
2B: large male choice	Large	Small	42	19/23	0.38	0.54	30/12	7.97	<i>0.0048</i>

*Significant *P* values are in *italics*

Table 3 Male competition trials (expt 3): cohabitation when two males were placed in a container with two shelters, one of which contained a restricted female

Experiment	Male A	Male B	Number	Cohabitation at 12 h (A/B)	χ^2 (df = 1)	<i>P</i> value	Cohabitation at 24 h (A/B)	χ^2 (df = 1)	<i>P</i> value
3A: different-sized males	Large	Small	43	34/9	15.49	<0.0001	33/10	12.97	0.0003
3B: size-matched small males	High asym	Low asym	32	17/15	0.13	0.72	20/12	2.02	0.16
3C: size-matched large males	High asym	Low asym	33	17/16	0.03	0.86	14/19	0.76	0.38

*Significant *P* values are in *italics*

whereas discrepancies in forceps asymmetry among size-matched males (both small and large) did not affect cohabitation/competitive outcomes. This last result was unexpected given that increased forceps asymmetry among small males had been shown to be advantageous when competing for food (Munoz and Zink 2012). The differential competitive ability may not have manifested itself because of the less dire circumstances in our experiment; the urge to find a mate (when the male may have had recent access to females in the wild) may not create the same urgency as finding food in response to prolonged starvation. Regarding competitive size advantages, however, the combination of male intrasexual size-based aggression with evidence that large (but not small) males prefer large females suggests that assortative mating may occur in *A. maritima*.

Our female competition experiments demonstrated that the cohabitation outcomes differ with respect to whether different-sized females are released in an arena with a small vs. large male. These cohabitation outcomes were originally designed to investigate the role of competition among females. However, given the fact that larger individuals dominate smaller ones when competing for resources in both the lab (Munoz and Zink 2012) and the field (pers. obs.), these experiments reflect preferences by larger (and more aggressive) females rather than the results of intrasexual selection. When a small male was restricted within one of the shelters, larger females cohabitated with the small male more often than they occupied the empty shelter, which suggests that larger female's interest in mating with the smaller, less-intimidating male. Interestingly, large females, when faced with a large male in one of the shelters, chose to occupy the empty shelter as often as they cohabitated with the large male. In other words, since

larger females have advantages in aggressive encounters, they were equally likely to outcompete the smaller female for the empty shelter as opposed to the one with the potential mate. Although this could indicate a lack of interest in mating, the differences between female competitions for large vs. small males suggest that some females may be intimidated by the large (and more aggressive) male. We are currently conducting follow-up experiments to determine whether females are changing their tactics based on their relative size compared to the potential mate, and whether this could lead to assortative mating in the population where individuals only mate with size-matched or smaller individuals.

Our results indicate an undeniably complex mating system, in which intrasexual and intersexual forces combine to create some unexpected effects that do not necessarily align with the results of either of these contributions in isolation. For example, the competitive advantage of forceps asymmetry was not mirrored in the context of sexual selection in our study; however, the extreme curvature of the right forceps in males of this species still warrants further investigation regarding its function (Simmons and Tomkins 1996; Bateman 2000). It should also be noted that, even though we observed that large males were more successful in intrasexual contests against smaller males (Munoz and Zink 2012), female choice must also play a role because females cannot be coerced into mating due to the positioning required for interlocking genitalia (Briceño and Eberhard 1995). We also have evidence for assortative mating, although the roles that weaponry and aggression play in the underlying mechanism and its consequences remain unknown (Crespi 1989). Continuous monitoring of groups composed of unrestricted individuals of different sexes and

Table 4 Female competition trials (expt 4): cohabitation when two females were placed in a container with two shelters, one of which contained a restricted male

Experiment	Female A	Female B	Number	Cohabitation at 12 h (A/B)	χ^2 (df = 1)	<i>P</i> value	Cohabitation at 24 h (A/B)	χ^2 (df = 1)	<i>P</i> value
4A: for small male	Large	Small	33	29/4	21.37	<0.0001	27/6	14.45	0.0001
4B: for large male	Large	Small	32	12/20	2.02	0.15	17/15	0.13	0.72

*Significant *P* values are in *italics*

sizes will help us to better understand how interactions among individuals combine to shape group dynamics and the mating system.

Acknowledgments We thank A. Summers, B. Swalla, and the staff at Friday Harbor Laboratories for promoting this research and for access to lab facilities and field sites. We also thank E. Iyengar for assistance in collecting earwigs and A.G. Zink, A.L. Bezzerides, and two anonymous reviewers for providing insightful comments on this manuscript. This research was supported by a grant from the National Science Foundation (DBI 1262239).

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