

Sexual selection by the seashore: mate choice and competition in the maritime earwig, *Anisolabis maritima*

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Blinks-NSF REU-BEACON 2014
Summer 2014

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Keywords: *Anisolabis maritima*, maritime earwig, cohabitation,
sexual selection, mate choice, competition

Abstract

Sexual selection involves a complex interplay between intrasexual selection and intersexual selection in which choice and competition converge to maximize reproductive fitness. Our study examines these selective forces in the maritime earwig, *Anisolabis maritima*, an earwig species in which both females and males possess weaponry. Forceps asymmetry has been noted as a competitive advantage in size-matched small male maritime earwigs and was examined as a factor determining sexual selection along with body size. We examined the roles of these two factors, body size and forceps asymmetry, as it relates to four types of sexual selection; female choice, male choice, male competition, and female competition. We limited the movement of certain earwigs while allowing others to move freely within artificial arenas to examine choice and competition. Our results revealed strong sexual selection for larger sizes through both competition and choice, but there was no preference based on forceps asymmetry. We found significant results in all four trial types, including not only the more traditional male competition and female choice, but also female competition and male choice. However, competition trials yielded our most compelling results. This complex, multidimensional mating system is likely driven by competitive forces and highly influenced by factors determining dominance in intraspecific competition.

Introduction

Sexual selection, in the form of intersexual choice or intrasexual competition, is often responsible for morphological differences between sexes. Sexual dimorphism is traditionally the result of female choice for male ornaments or male competition where females mate with dominant males (Darwin 1872). For example, male amphipods possess weaponry with which they fight against other males to gain control of harems (Iyengar & Starks 2008). Female choice is evident in certain organisms whose exaggerated features are not useful for confrontation between males, such as pheasants and birds of paradise (Orians 1969). Occasionally, both male competition and

female choice are important, such as in the Bluefin killifish, where females will spawn with dominant males much more readily (McGhee, Fuller & Travis 2007). However, there are significant deviations from this classical trend. Sex role reversals may result from increased male investment leading to male instead of female mate choice, as in katydids (Bonduriansky 2001). In harem polyandry, another type of role reversal, selection pressures may also lead to large females which use weaponry to guard groups of males, such as in jacanas (Emlen, Wrege & Webster 1998). It is important to note that, in all mating systems, intersexual choice and intrasexual competition are not mutually exclusive, and often come together to create complex mating systems (Andersson 1994).

In most of the animals that follow the classical trend of female choice paired with male competition (e.g., amphipods, red deer), the males are armed with weaponry that the females lack. Earwigs (Order Dermaptera) are unusual in that both females and males possess weaponry used in both intra and intersexual competition. Sexual dimorphism is still evident, however, in the straight female forceps relative to the more curved male forceps. In the earwig *Euborellia brunneri*, male forceps length and body weight are sexually selected through intrasexual competition, but have no bearing on female preference (Van Lieshout & Elgar 2009). In most earwigs, the male forceps are curved and symmetrical. The maritime earwig, *Anisolabis maritima*, is unique within earwigs, because the sexually-dimorphic male curved forceps are

Figure 1: This photo shows a small male maritime earwig (left) next to a larger female maritime earwig (right).



naturally asymmetrical (Figure 1).

Anisolabis maritima is an invasive species first described in the Mediterranean and thought to have originated there (Scudder 1876). It is now found worldwide (Langston 1974). They are predatory scavengers which feed on amphipods, crickets, and smaller earwigs (Bennett 1904). Females exhibit

maternal care and are often aggressive in defending nests containing eggs or juveniles. Larger female maritime earwigs guard their nests against conspecific cannibalism more effectively due to their increased size and resulting dominance in intraspecific competition (Miller et al. 2011). The same trend is present in males, for which greater size confers a noticeable competitive advantage. However, where size difference is negligible, the male maritime earwig's unique forceps asymmetry occasionally becomes an advantage. For example, among similarly-sized small males, a greater degree of forceps asymmetry is associated with dominance (Munoz & Zink 2012). Although fluctuating asymmetry in largely symmetrical European earwigs was found to have no effect on sexual selection, we sought to determine the role of forcep curvature in this primarily asymmetrical species. However, there is evidence that the female maritime earwig chooses her mate based on size and not asymmetry (DiGennaro et al. unpublished). In the same study, smaller females were more sexually active and primarily chose size-matched mates. We build on these studies by investigating the relative roles of size, sex and forcep curvature on intersexual choice and on intrasexual competition in the maritime earwig. Specifically, we conducted 4 types of experiments: (1) female choice, where a female chose between two males either differing in body size or in forceps asymmetry; (2) male choice, where a male chose between two females differing in body size; (3) female competition, where two females differing in body size competed for a male; and (4) male competition, where two males, differing in either body size or forceps asymmetry, competed for a female.

We hypothesize that female preference for size-matched or smaller males will hold. We posit that it is unlikely that large males, although dominant in contests against smaller males (Munoz & Zink 2012), can coerce females into mating, mostly due to the females' higher level of aggression overall. This may be an adaptation resulting from the responsibility to defend their nest. Given the aggressive behavior of female maritime earwigs, female choice and possibly female competition may be more important than male choice or competition in determining mating. We examined who the earwigs cohabitate with, assuming that their choice to cohabitate is

indicative of mate choice. Hack and Iyengar (2013) examined cohabitation between various sexes and sizes and found that the aggressive female maritime earwig is more likely to cohabitate with males, possibly indicating their inclination to mate.

Materials and Methods

Collection and care of study organism

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 their recent mating success would make them less likely to engage in copulatory behavior again. The insects were collected by hand haphazardly, occasionally focusing on particular sexes or sizes based on our experimental needs. The animals were sexed and individually placed in vials with moist substrate and brought back to the lab for use in experiments within twenty four hours. We also collected extra sand from False Bay for use in experiments. We assumed that the animals' hunger during experiments was negligible and would not affect behavior, because in male competition studies, they would not fight over food until 9 to 28 days of starvation (Munoz & Zink 2012).

Measurement

After use in only one trial, each earwig was frozen and measured. Using a SONY camcorder (model CCR-DC374) attached to a dissecting scope and image analysis program ImageJ, we measured the head width, pronotum width, abdominal width (using widest point of 6th abdominal segment), and forceps length for all earwigs, as well as forceps width to calculate the degree of asymmetry for males (Munoz & Zink 2012). The width of the sixth abdominal segment was used as an index for body size (DiGennaro et al. unpublished). Many studies have used pronotum width as an index for body size (Simmons & Tomkins 1996; Tomkins & Simmons 1996; Munoz & Zink 2012), but in our size-matched trials, we used bee tags which obstructed the view of the

pronotum. We decided that the unobstructed abdominal measurement would be more reliable. “Size-matched” individuals were defined as having sixth abdominal segment widths within 5% of each other, while “different-sized” individuals differed by more than 10%. The length of each forcep was defined as the distance from the tip of the forcep perpendicularly until the base of the final abdominal segment. The width of each forcep was defined as the distance between the line defining length and the outer edge of each forcep. We used forceps curvature (width over length) to determine forceps asymmetry (right curvature over left curvature). Quantifying male forceps asymmetry is important in this earwig, because asymmetry occasionally determines dominance, especially when we assess the competitive ability of small males (Munoz & Zink 2012).

Marking

Marking was not necessary for most trials, because visual assessment was adequate for tracking both males and females differing by at least 10% difference in body size. For male competition trials where we used two size-matched males (not necessary in female choice trials, where size-matched individuals were in separate enclosures), we labeled both individuals with bee tags on the pronotum.

Experimental enclosures

Two different enclosures were used over the course of each trial. First, the earwigs were put together in small paper cups (diameter 3.5 in) where they could freely antennate each other or, in the case of the competition trials, fight. Then, the earwigs were placed in plastic containers (15 x 21 x 10 cm). In each

Figure 2: This wire-mesh enclosure enables earwigs on the outside to antennate the captive earwig while preventing the earwig inside from escaping.



trial, two additional enclosures were taped flush against the bottom of the plastic container. These enclosures consisted of a red plastic box (5 x 5 x 1cm) with the top and one side removed to facilitate movement into the enclosed area. Wire mesh (1/8 inch) was hot-glued to the sides of the container (Figure 2) to allow antennation while preventing escape or entry, and these shelters were taped to the bottom of the arena with double-sided tape to prevent earwigs from getting underneath them (Figure 3). The lids of the small red boxes (i.e. the roofs) were placed on top after it was evident that the free earwig(s) had assessed the earwig(s) in mesh cages. These shelters mimic the shallow and complete shelter provided in their natural habitat by driftwood. Moist sand was placed in the cage and just outside of it, but nowhere else in the enclosure, to encourage the earwig to pick between artificially limited options. Fresh sand, free of potential pheromones, was used each time. The position of the earwigs was recorded over a twenty four hour period where their positions were monitored at 6h, 12h, and 24h. We only used the results from 12h and 24h into the experiment, at 23:00 and 8:00 the next morning, because based on their positions, it seemed as though they needed the twelve hours to settle down and stay in a position with more consistency. Their positions were recorded using a code which designated any animal under a shelter as either a 1 or 4 (depending on which side) and any animal out of a shelter as a 2 or 3, respectively (Figure 3).

In the trials below, we separated trials with size-matched large males and with size-matched small males. We thought it important to make this distinction because a previous study showed that winning battles over food is determined by differing asymmetry in small males but not in large males (Munoz & Zink 2012).

Figure 3: In a choice trial, a female chooses a shelter (in position 4).



Choice trials

These trials involved providing a free-moving individual with the opportunity to choose between two shelters each containing one individual of the opposite sex. First, a male-female pair was placed in the paper cup enclosure for one minute to ensure that both parties had assessed each other prior to the trial. The order in which the two suitors were exposed to the opposite sexed individual was randomized. Those two opposite sexed individuals were then each enclosed in the wire mesh area of a shelter. The red lids to the shelters were placed on top after the choosing individual was released into the enclosure and had visited both wire mesh enclosures. We recorded the number of times each choice was made and the number of times no choice was made. We employed the statistical program JMP to make comparisons with these values.

Experiment 1A: Female choice based on male body size

For these experiments, the choosing female was released and her position monitored with respect to two different-sized males each trapped in an artificial wire mesh enclosures, placed on opposite sides of the plastic container.

Experiment 1B & 1C: Female choice based on forceps asymmetry

For these experiments, the choosing female was released and her position monitored with respect to two size-matched males differing in forceps asymmetry each trapped in an artificial wire mesh enclosure, placed on opposite sides of the plastic container. In the trials for Experiment 1B, we used size-matched small males and in 1C we used size-matched large males.

Experiment 2A & 2B: Male choice based on female body size

For these experiments, the choosing male was released and his position monitored with respect to two different-sized females each trapped in an artificial wire mesh enclosure, placed on opposite sides of the plastic container. Experiment 2A used a small male and 2B a large male, each choosing between one large and one small female.

Competition trials

These trials involved providing two free-moving same-sex individuals with the opportunity to compete for a shelter containing an opposite-sex individual. The same-sex competitors were placed in a paper cup enclosure together for 4 minutes while their encounters were recorded. For each earwig, the number of forcep strikes, threats, and retreats were recorded to obtain an initial assessment of dominance. Unlike the choice trials, one shelter was empty whereas the other contained an individual of the opposite sex. The same assessment with the wire mesh enclosures took place, although this time, one of the enclosures was empty. The red lids to the shelters were placed on top after both of the competing individuals had visited the wire mesh enclosure containing the opposite sex individual. We counted the number of times each competitor was found in the shelter, in the empty shelter, and outside of either shelter. Again, we used JMP to compare values and obtain our results.

Expt 3A: Male competition based on body size

For these experiments, two different-sized males were released and their positions monitored with respect to the female trapped in an artificial wire mesh enclosure.

Expt 3B & 3C: Male competition based on forceps asymmetry

For these experiments, two size-matched males differing in forceps asymmetry were released and their positions monitored with respect to the female trapped in an artificial wire mesh enclosure. The trials involve two size-matched small males in Experiment 3B and two size-matched large males in 3C.

Expt 4A & 4B: Female competition based on body size

For these experiments, two different-sized females were released and their positions monitored with respect to the male trapped in an artificial wire mesh enclosure. In Experiment 4A, different-sized females compete over a small male and in Experiment 4B, they compete over a large male.

Results

Choice Experiments

After noting the positions of all individuals making choices, we counted the choosing individuals in shelters making each choice and those not making a choice. Within the individuals who were under a shelter, we counted and compared those in each shelter to determine which earwig the choosing individual chose to cohabitate with, using it as an indication of their mating preference. All trials in which individuals died were not used.

Experiment 1: Female Choice

Expt 1A: Females choose between Different-Sized males

Females preferred large males at night, but not in the morning (Table 1). However, the difference between these two values was not significant ($\chi^2=2.431$; $df=1$; $P=0.1189$) and a preference for large males persisted. At night, large females preferred to be inside shelters as opposed to outside. The difference was not significant in the morning, but the difference between times, again, was not significant ($\chi^2=0.077$; $df=1$; $P=0.7813$), so a preference for being under shelters persisted. Large males were, on average, 27.16% larger than small males (paired $t=14.327$; $df=29$; $P<0.0001$).

Expt 1B: Females choose between Size-Matched Small Males

Females did not have a preference for high or low asymmetry males at night or in the morning. The differences between asymmetry preference at night and in the morning was not significant ($\chi^2=0.382$; $df=1$; $P=0.5363$). Females also did not have a preference for staying inside shelters at night or in the morning. The difference in shelter preference at night and in the morning was, again, not significant ($\chi^2=0.102$; $df=1$; $P=0.749$). On average, these size-matched small males differed in asymmetry by 14.40% (paired $t=5.1711$; $df=19$; $P<0.0001$) while fulfilling our criteria of not being different in body size (on average differing by only 0.19% in body size; paired $t=0.111$; $df=19$; $P=0.9129$).

Expt 1C: Females choose between Size-Matched Large Males

As with size-matched small males, with large males, females did not exhibit a preference based on male forceps asymmetry. When comparing night to morning, there was no difference ($\chi^2=1.213$; $df=1$; $P=0.2707$). When it comes to shelter preference, females preferred to be in shelters in the morning but not significantly at night. This difference, between shelter preference at night and in the morning, was significant ($\chi^2=4.723$; $df=1$; $P=0.0298$). Also, females had a higher preference for staying in shelters in the morning with size-matched large males than with size-matched small males ($\chi^2=9.521$; $df=1$; $P=0.0020$). On average, these size-matched large males differ in asymmetry by 16.38% (paired $t=5.1734$; $df=19$; $P<0.0001$) while fulfilling our criteria of not being different in body size (on average differing by only 1.97% in body size; paired $t=1.041$; $df=19$; $P=0.3109$).

Table 1: Experiment 1: Female Choice Trials:									
Data for female choice experiments, where "High" represents the high asymmetry male and the "Low" represents the low asymmetry male.									
Trial Type	Male Choice A	Male Choice B	Time elapsed	Cohabitation incidence (C) (Choice A / Choice B)	χ^2 (C)	<i>p</i> value (C)	Shelter incidence (S) (in/out)	χ^2 (S)	<i>p</i> value (S)
IA: Different sized males	Large	Small	12	18 / 3	11.8873	0.0006*	21 / 9	4.9370	0.0263*
			24	13 / 7	1.8280	0.1764	20 / 10	3.3980	0.0653
IB: Size-matched Small males	High	Low	12	7 / 5	0.3349	0.5628	12 / 8	0.8054	0.3695
			24	5 / 6	0.0910	0.7629	11 / 9	0.2003	0.6545
IC: Size-matched Large males	High	Low	12	10 / 4	2.6566	0.1031	14 / 6	3.2913	0.0696
			24	10 / 9	0.0527	0.8185	19 / 1	19.7853	<0.0001*

Experiment 2: Male Choice

Expt 2A: Small males choose between Different-Sized Females

Although there was a slight preference for large females, this difference was neither significant at night nor in the morning. Cohabitation preference did not differ between times ($\chi^2=0.249$; $df=1$; $P=0.6179$). These small males chose to be under shelter at night and in the morning and did not change their preference for shelter between those times ($\chi^2=0.582$; $df=1$; $P=0.4454$). Large females, on average, differed in size from small females by 25.94% (paired $t=11.556$; $df=29$; $P<0.0001$).

Expt 2B: Large males choose between Different-Sized Females

A significant preference for large females existed in the morning, but not at night, and the difference between times was not significant ($\chi^2=2.088$; $df=1$; $P=0.1485$). These large males, unlike the small males, did not choose to be under shelter until the morning, with the large female they chose. The difference in shelter preference between times was not significant ($\chi^2=0.536$; $df=1$; $P=0.464$). Large females, on average, differed in size from small females by 17.86% (paired $t=6.898$; $df=19$; $P<0.0001$).

Table 2: Experiment 2: Male Choice Trials:

Data for female choice experiments displaying cohabitation and shelter incidence for small and large male choice.

Trial Type	Female Choice A	Female Choice B	Time elapsed	Cohabitation incidence (C) (Choice A / Choice B)	χ^2 (C)	<i>p</i> value (C)	Shelter incidence (S) (in/out)	χ^2 (S)	<i>p</i> value (S)
2A: Small Male Choice	Large	Small	12	18 / 9	3.0582	0.0803	27 / 3	22.0839	<0.0001*
			24	15 / 10	1.0068	0.3157	25 / 5	14.5552	0.0001*
2B: Large Male Choice	Large	Small	12	8 / 6	0.2867	0.5923	14 / 6	3.2913	0.0696
			24	13 / 3	6.7382	0.0094*	16 / 4	7.7098	0.0055*

Competition Trials

We documented the positions of competing individuals as well, noting also any instances where the competitors kill each other (Figure 4). We compared the number of competitors in the shelter with the female, killed earwigs not included, to each other to determine which competitor had more “success”. Because the dominant large males and females preferred these inhabited shelters as opposed to the empty shelter on the other side, we

can assume that residing in the shelter with the third earwig was a sign of success. When splitting by both time and competitor, we compared the amount of time spent in and out of shelters by the same type of competitor in the same time period. Competitors who were killed in or outside a shelter were considered out of a shelter, because the dominant competitors were more likely to be in shelters than out of shelters, proving it desirable protection. We did not include all values for comparisons of earwigs residing in the shelter with the female to earwigs residing in the empty shelter, but we generally found that the dominant earwigs largely preferred the shelter with a mate to an empty shelter. For example, large females were in shelters with males much more often than in shelters without males (Female competition over Small males: 12h: $\chi^2=17.229$; $df=1$; $P<0.0001$; 24h: $\chi^2=12.203$; $df=1$; $P=0.0005$; Female competition over Large males: 12h: $\chi^2=10.124$; $df=1$; $P=0.0015$; 24h: $\chi^2=6.738$; $df=1$; $P=0.0094$).

Figure 4: This shows the difference between an earwig that has died of natural causes (left) and one that has been killed by a competitor (right).



Experiment 3: Male Competition

Expt 3A: Different-sized males compete over one female

Large males were more likely to end up in the same shelter as the female both at night and in the morning (Table 3). Their success at night and in the morning was not significantly different

($\chi^2=0.149$; $df=1$; $P=0.6999$). These large males were also more likely to be in shelters at both times, while the small males were not. In fact, there were more small males outside of their shelters in the morning than there were inside shelters, though not significantly. These small males were more likely to be outside of their shelters in the morning than at night ($\chi^2=4.000$; $df=1$; $P=0.0455$), while the difference in shelter preference between times was not significant for large males ($\chi^2=2.128$; $df=1$; $P=0.1447$). Large males were more likely to be in shelters than small males at both times (12h: $\chi^2=7.399$; $df=1$; $P=0.0065$; 24h: $\chi^2=10.772$; $df=1$; $P=0.0010$). Large males, on average, differed in size from small males by 25.23% (paired $t=15.899$; $df=24$; $P<0.0001$).

Expt 3B: Size-matched small males compete

High and low asymmetry males were equally as likely to end up in the same shelter with the female at night and in the morning. High asymmetry males were more likely to be in shelters in the morning, but all other competitors and times showed no shelter preference. These high asymmetry males were slightly more likely than low asymmetry males to be inside shelters at night and in the morning, but not significantly (12h: $\chi^2=1.257$; $df=1$; $P=0.2623$; 24h: $\chi^2=0.564$; $df=1$; $P=0.4527$). High and low asymmetry males were only slightly more likely to be inside shelters in the morning (High: $\chi^2=3.059$; $df=1$; $P=0.0803$ & Low: $\chi^2=3.673$; $df=1$; $P=0.0553$). On average, these size-matched small males differed in asymmetry by 16.95% (paired $t=4.608$; $df=16$; $P=0.0003$) but fulfilled our criterion of not being different in body size (on average differing by only 1.96% in body size; paired $t=1.023$; $df=16$; $P=0.3214$).

Expt 3C: Size-matched large males compete

Competition between size-matched large males revealed no competitive advantage to forceps asymmetry and no difference in success of males between night and morning ($\chi^2=0.144$; $df=1$; $P=0.7046$). Although at night high asymmetry males were not more likely to be inside shelters, low asymmetry males were and both high and low were more likely to be inside shelters in the morning. High asymmetry males were thus much more likely to be in shelters in the morning than

at night ($\chi^2=7.991$; $df=1$; $P=0.0047$) and low asymmetry males were not ($\chi^2=0.183$; $df=1$; $P=0.6685$). When comparing the two, low asymmetry males were more likely to be in shelters at night than high asymmetry males ($\chi^2=4.154$; $df=1$; $P=0.0415$), but the difference was not significant in the morning ($\chi^2=1.834$; $df=1$; $P=0.1757$). Overall, size-matched large males had a higher shelter preference than size-matched small males ($\chi^2=7.627$; $df=1$; $P=0.0057$). On average, these size-matched large males differed in asymmetry by 21.45% (paired $t=5.394$; $df=15$; $P<0.0001$) but fulfilled out criterion of not being different in body size (on average differing by only 1.45% in body size; paired $t=0.768$; $df=15$; $P=0.4546$).

Table 3: Experiment 3: Male Competition Trials:
 Data for male competition experiments, where "High" represents the high asymmetry male and the "Low" represents the low asymmetry male.

Trial Type	Time elapsed	Competitor	Resides with female	χ^2 (S)	p value (S)	Shelter incidence (S) (in/out)	χ^2 (C)	p value (C)
3A: Different sized males	12	Large	21	7.3255	0.0068*	24 / 1	26.2602	<0.0001*
		Small	7			17 / 8	3.3139	0.0687
	24	Large	19	4.4815	0.0317*	21 / 4	12.6739	0.0004*
		Small	8			10 / 15	1.0068	0.3157
3B: Size-matched Small males	12	High	4	0.0000	1	9 / 8	0.0589	0.8083
		Low	4			8 / 10	1.6990	0.1924
	24	High	8	0.0000	1	13 / 3	6.7382	0.0094*
		Low	8			9 / 4	1.9735	0.1601
3C: Size-matched Large males	12	High	7	0.0000	1	7 / 8	0.0667	0.7962
		Low	7			13 / 3	6.7382	0.0094*
	24	High	8	0.2867	0.5923	13 / 1	12.2032	0.0408*
		Low	6			12 / 4	4.1860	0.0047*

Experiment 4: Female Competition

Expt 4A: Different-sized females compete over Small male

Large females were more likely to end up in the same shelter as the male for both time periods (Table 4). The difference in their success was not significant between morning and night ($\chi^2=1.464$; $df=1$; $P=0.2263$). These large females were also more likely to be in shelters as opposed to outside shelters at both times. The difference in large female shelter preference with respect to time (higher at night) was almost significant ($\chi^2=3.412$; $df=1$; $P=0.0647$). Small females were not more likely to be in shelters at night or in the morning and the difference between these was not significant ($\chi^2=0.951$; $df=1$; $P=0.3294$). Large females were more likely to be in shelters than small females were at night ($\chi^2=13.699$; $df=1$; $P=0.0002$), but not in the morning ($\chi^2=1.059$; $df=1$; $P=0.3033$). Large females, on average, differed in size from small females by 20.21% (paired $t=7.675$; $df=18$; $P<0.0001$).

Expt 4B: Different-sized females compete over Large male

Unlike competition over a small male, large females only won significantly at night, not in the morning, but this difference was not significant ($\chi^2=1.771$; $df=1$; $P=0.1833$). Large females, as with competition over small males, were more likely to be inside shelters at both time periods. Small females, unlike with competition over small males, were significantly more likely to be outside their shelters in the morning (still not significant at night). The difference between night and morning was almost significant ($\chi^2=2.980$; $df=1$; $P=0.0843$). Large females had exactly the same shelter preference at night and in the morning. As with in competition for small males, large females were more likely to be in shelters than small females were at night ($\chi^2=4.537$; $df=1$; $P=0.0332$), but the difference was not significant in the morning ($\chi^2=0.176$; $df=1$; $P=0.6752$). None of the differences between competition over small males and over large males were significant. Large females, on average, differed in size from small females by 23.24% (paired $t=8.700$; $df=18$; $P<0.0001$).

Table 4: Experiment 4: Female Competition Trials:

Data for female choice experiments showing number of males who succeeded at finding shelter with the female and finding shelter in general (both with and without female)

Trial Type	Time elapsed	Competitor	Resides with female	χ^2 (S)	<i>p</i> value (S)	Shelter incidence (S) (in/out)	χ^2 (C)	<i>p</i> value (C)
4A: Compete for Small male	12	Large	17	17.2292	<0.0001*	18 / 1	18.5043	<0.0001*
		Small	1			8 / 11	0.4757	0.4904
	24	Large	13	6.7382	0.0094*	14 / 5	4.4389	0.0351*
		Small	3			11 / 8	0.4757	0.4904
4B: Compete for Large male	12	Large	14	10.1241	0.0015*	16 / 3	9.7654	0.0018*
		Small	2			10 / 9	0.0527	0.8185
	24	Large	13	2.6407	0.1042	16 / 3	9.7654	0.0018*
		Small	6			15 / 4	6.7828	0.0092*

Discussion

In these experiments, cohabitation was used as an indication of mating preference. This is a reasonable connection to draw when we consider the earwigs' elevated level of aggression. A sign of tolerance for members of the opposite sex in such close quarters is likely indicative of an individual's willingness to tolerate a sexual advance or copulatory attempt. Also, the competition trials showed dominant earwigs greatly preferred shelters with mates to shelters without mates, suggesting there is a connection between cohabitation and mate choice.

Female Choice

Female preference for large males can be explained by their dominance in intraspecific competition, representing higher quality and reproductive fitness. The difference between morning and night, resulting in significance at night that does not persist until the morning, may be explained by the earwigs' nocturnal behavior. These nocturnal creatures may be more likely to pursue a mate at night, when they are in less danger from predation. However, this explanation

does not hold when considering their preference for shelter. The fact that there is no preference for shelters in the morning suggests that the earwigs are more likely to seek shelter (and possibly protection) at night. However, seeing as the females are very aggressive overall, it is possible that they are pursuing shelter primarily for the male inside and not the protection it may provide.

Differing forceps asymmetry did not affect female preference. This is understandable when we consider the female earwig's ability to assess such a discrete character remotely, across the wire mesh barrier. Although they may be able to assess asymmetry during the one minute, unrestrained paper cup encounter, they may not be able to connect that asymmetry assessment to the earwig once it is placed in a wire mesh container. Because asymmetry had been found to be important in determining dominance in size-matched intrasexual competition for food (Munoz & Zink 2012), when removed from a competitive context, it is doubtful that the difference in asymmetry would manifest itself in altered female preference. The females' shelter preference shows the indecision the cohabitation incidence suggests. They are not decisively in shelters any of the times except for once in size-matched large male trials. This in itself suggests an interesting trend. In the morning, when choosing between two size-matched small males, the females do not prefer to be inside as opposed to outside shelters, but they do prefer to be inside shelters when choosing between two size-matched large males. This could suggest that females who end up with one of the large males (either one) may be more satisfied with their choice than females forced to choose between two small males. This reinforces our discoveries within the female choice between two different-sized male trials, where large males represented a better mate choice due to higher quality and dominance.

Male Choice

When comparing small male choice to large male choice, we noticed another interesting pattern. Small males tended to seek shelter early, and were inside shelters more than outside both at night and in the morning. Large males took their time entering shelters and were not decisively inside

shelters until the morning. In the morning, these large males made the choice for the dominant, large female. Small males may have been too eager to find protection, and this may have hindered their ability find the shelter in which the more desirable, more dominant, large female resided. Also, some small males may have recognized the higher quality of the larger female, while others were intimidated by her, because of that same higher quality and dominance.

Male Competition

In these experiments, the dominance associated with larger sizes was evident. Large males had more success cohabitating with the females at both time periods. They also were able to crowd out small males from the shelters, one time even reversing the typical trend for shelters (more inside shelters than out). By the morning, large males had crowded out the small males to the extent when there were more small males outside of shelters than in (though not significantly more). This experiment clearly exhibits the greater competitive ability of larger males.

In size-matched trials, there was no apparent competitive advantage to increased forceps asymmetry. In the morning, when the dominance of a large male resulted in higher shelter occupation relative to small males, we saw high asymmetry males mirror this higher shelter occupancy (but at this time the difference between them and low asymmetry males was not significant). However, this trend suggests that high asymmetry males were slightly more dominant than low asymmetry males, if analyzed analogously to trends seen in different-sized male competition trials. The occurrence of this trend in size-matched small males, but not in size-matched large males, supports the idea that asymmetry is important only when determining dominance between small males (Munoz & Zink 2012). Size-matched small males had lower preference for shelter than size-matched large males, the opposite of the trend we observed in small and large male choice trials. This might be explained by differing priorities in the presence of a competitor. For example, in the absence of a competitor, large males may have considered it essential to assess mates while small males seek shelters, but if a competitor is present, their

priorities may change. The size-matched small males could focus on fighting while the size-matched large males sought shelter from their competitor. These hypotheses are speculative due to the small sample size and slightly contradictory results we obtained for this experiment – however, we are hopeful that, with a larger sample size, we can better resolve these unclear results.

Female Competition

As in the male competition trials, the size advantage for large females was evident. When competing over small males, large females “won” the male and shelters each time. The large females not only had a competitive advantage when the prize was a mate, but also when it was protection. When competing over a large male, large females had the same high success rate, but it was not significant in the morning. When competing over large males, large females won over the shelters significantly more than small females at night, but not in the morning, again following the trend above. This could relate back to the trend we observed in the female choice experiments, where females had a significant choice for large males at night but not in the morning, and support the hypothesis that at night, when the nocturnal females were more active, their choices were more representative of their natural behavior. Perhaps the large females dominated the small females more during this period of nocturnal activity, and therefore may have tolerated more shelter occupancy by small females in the morning.

Conclusions and Future Directions

Our results did not support all of our original hypotheses. For example, we did not see a female preference for males that match or are smaller than the female’s size, as a previous study had suggested (DiGennaro et al. unpublished). Instead, for both males and females, large sizes were both desirable and indicative of dominance. This resulted in greater choice and competitive advantage associated with large earwigs. These large sizes likely represent higher quality,

fertility/fecundity, and overall reproductive success, all of which are qualities that make a desirable mate. These large sizes have a competitive ability that matched this hypothesized reproductive ability and allowed them access to mates and protection in the presence of a competitor.

Varying asymmetry does not seem to affect choice or be indicative of a competitive advantage, although there is some evidence to support high forceps asymmetry as a competitive advantage, but not necessarily as a desirable mate characteristic. Likewise, there is little evidence to support that asymmetry produces a significant difference in access to shelters.

Overall, contrary to our hypotheses, female choice and competition were not the only important factors we observed in this mating system. Instead, we observed significance in all aspects of sexual selection. We observed not only intrasexual selection or intersexual selection, but a combination of the two. Furthermore, we have observed the less traditional forms of the two (female competition and male choice) as well as the more traditional male competition and female choice. It seems as though all of these factors influence sexual selection in the maritime earwig, perhaps because both sexes possess weaponry that could operate in intrasexual competitive battles as well as serve as a basis for assessing quality of a potential mate. The more resolute results we obtained for competition trials suggest that competition is more instrumental in sexual selection processes than choice, which is understandable considering the high level of competitive and aggressive conspecific interactions.

Our separation of measurements at night and in the morning revealed interesting results, especially in male choice experiments. Preferences in the morning and at night may have revealed interesting nuances in earwig behavior. These trends should be analyzed to determine whether measurements taken during the nocturnal earwig's natural period of activity (night) or inactivity (day/morning) are more indicative of natural behavior. Also, although occasionally our separation of large and small males yielded interesting results, it seems unlikely that the behavior (especially in our competition trials) differed greatly. In our comparisons of the data, we rarely found

significant differences in data from trials with large and small males. The similar data obtained for small and large males suggests these data could be pooled in future studies.

Future studies should comparatively assess the contribution each factor (female/male choice and male/female competition). This may be achieved by observing intrasexual and intersexual interactions simultaneously where all three earwigs are able to freely interact. Obviously, this would have the added advantage in that copulation could be observed and recorded, as opposed to these experiments where for the most part there was a physical barrier between individuals of opposite sex preventing more intimate contact. Also, a follow-up study in which the sample size were much larger and/or the trials much longer could reveal significance where we found none or rule out false positives in our study.

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