

Sexual selection in harems: male competition plays a larger role than female choice in an amphipod

Vikram K. Iyengar^a and Bianca D. Starks^b

^aDepartment of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA and

^bDepartment of Biology, Paine College, 1235 Fifteenth Street, Augusta, GA 30901, USA

Spatial distribution can be affected by sexual selection, particularly in mating systems where males have exaggerated traits used to compete for access to females. Although it is rare to be able to disentangle selection arising from male competition versus female choice in such mating systems, we here report experiments in which we manipulated group size and sex ratio to determine the relative roles of males and females in a harem polygyny. *Megalorchestia californiana* is an amphipod (family Talitridae) that is sexually dimorphic—males are not only larger than females but also possess enlarged red antennae and gnathopods that are used to hold and guard females prior to mating inside their burrows. We conducted 2 main types of experiments: 1) we varied the mobility of 3 amphipods (2M/1F) to determine the relative roles of male competition and female choice and 2) we monitored groups of 9 or more individuals to determine how intersexual and intrasexual interactions affect overall spatial distribution. In our 3-amphipod tests, we found that male competition was more important than female choice in explaining burrow preferences. Our large group experiments, however, indicated that females also play an active role in mate selection, as females settled in random locations in single-sex groups, whereas females clustered around larger males in mixed-sex groups. Finally, we found that male body mass was correlated with the length and redness of the antennae, which suggests that males may signal their quality through visual communication. *Key words*: honest signaling, intrasexual competition, mate choice, *Megalorchestia californiana*, polygyny, sexual dimorphism. [*Behav Ecol* 19:642–649 (2008)]

Exaggerated male traits are seen throughout the animal kingdom and have been the subject of an increasing number of studies in sexual selection (Shuster and Wade 2003; Kokko et al. 2006; Roulin and Bize 2007). In polygynous mating systems, this type of sexual dimorphism can be the result of female choice, where females mate preferentially based on the male's expression of these traits (e.g., Clutton-Brock et al. 1977; Loison et al. 1999), male competition, where males use armaments (sensu Berglund et al. 1996) in intrasexual battles for access to females (e.g., Forsyth and Alcock 1990; Gwynne and Jamieson 1998; Bateman 2000; Kelly 2005), or a combination of both (Andersson 1994; Berglund et al. 1996; Arnqvist and Rowe 2005). In harem polygyny mating systems, males usually compete with each other for groups of females in contests usually determined by differences in body size or weaponry, which dictate fighting ability (e.g., Huntingford and Turner 1987; Riechert 1998; Kelly 2006c). Males may compete directly for access to females or may instead control resources essential for female survival and reproduction (Darwin 1871; Emlen and Oring 1977; Davies 1991).

Even in a harem polygyny mating system, both intra- and intersexual selection may occur because both sexes can benefit from this type of mating system. Males benefit by having access to multiple females because male reproductive success is limited by the number of mates (Trivers 1972; Arnold and Duvall 1994). Females, by allowing males to compete, may also benefit by joining the harem of (and mating with) a male of high genetic quality (Arnold 1994; Wade and Shuster 2004).

Females are by no means passive in a harem polygyny mating system, however, as exaggerated male characters can be used by both sexes to assess male quality: males that use such characters to accurately assess a rival's quality before engaging in a potentially costly fight are favored by selection (e.g., Hack 1997; Neat et al. 1998; Briffa and Elwood 2004; Kelly 2006c) and females often choose which harem to join based on assessing both phenotypic and genetic benefits (e.g., McMahon and Bradshaw 2004; Sanchez-Prieto et al. 2004). Although food distribution and antipredator behavior can have a profound effect on spacing among individuals (e.g., Wrangham and Rubenstein 1986; Campbell et al. 2006), both antagonistic male interactions and female preferences in harem polygyny mating systems can also lead to sex differences in spatial distribution (e.g., Moehlman et al. 1998; Prohl and Berke 2001). Thus, monitoring how the spatial distribution varies according to relative size and population sex ratio can provide insight into sexual selection. By observing the spatial distribution of amphipods in controlled environments, we here provide experimental and observational results that contribute to understanding sexual selection in harem-holding species. Furthermore, to our knowledge, this represents the first study of harem polygyny where male competition or female choice was eliminated to determine the primary mechanism responsible for the mating system.

Megalorchestia californiana, also known as the California Beach Flea or California Beach Hopper, is an amphipod found on flat, exposed beaches of medium to fine sand from Vancouver Island, British Columbia, Canada, to southern California (Bousfield 1982). Whereas most amphipods are flattened mediolaterally and limited to an entirely aquatic lifestyle swimming on their "side," *M. californiana*, like other crustaceans of the family Talitridae, walk upright and achieve great terrestrial mobility by using powerful extensor muscles

Address correspondence to V.K. Iyengar. E-mail: vikram.iyengar@villanova.edu.

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and terminal uropods to jump (Bowers 1964). *Megalorchestia californiana* is usually found in the intertidal zone above the high tide line under or near the washed-up seaweed (Bousfield 1982). Both sexes occupy burrows during the day to avoid predators and desiccation, and, like many amphipods, they are nocturnal foragers on dead or decaying plants and animals (Craig 1973; Pennings et al. 2000; Cardoso 2002). Typically longer than 2 cm, these amphipods are one of the largest beach hoppers, and they emerge conspicuously by the thousands from their burrows at dusk (Bowers 1964; Bousfield 1982).

Although some amphipods are either sexually monomorphic or have larger females (presumably due to a fecundity advantage; e.g., Hatcher and Dunn 1997; Glazier 1999), males are larger than females in many amphipod species (Birkhead and Clarkson 1980; Bousfield 1982; Wen 1993; Zeidler 2004). In *M. californiana*, males are not only larger than females (15% on average; Bousfield 1982) but also differ from females in 2 other striking ways: 1) they possess elongated antennae with a thickened basal peduncle that is orange to red in color and 2) they have an enlarged second pair of gnathopods, appendages normally used for walking that look like pink boxing gloves with a terminal hook. Both of these traits play an important role in the reproductive behavior of these amphipods.

Megalorchestia californiana has a harem polygyny mating system, and males are often seen during the early morning hours using their enlarged gnathopods and antennae to fight for possession of burrows that may contain multiple females (Bowers 1964). Males are able to monopolize access to multiple females because females reproduce asynchronously and breed only once per year with 1 male (Bousfield 1982). Because most individuals only survive for 1 year (Bowers 1964), females usually mate only once in their lifetime, whereas males are capable of mating several times. Female amphipods are usually available for fertilization for less than an hour after molting, as this is the only time before ovulation that the cuticle is flexible enough to allow eggs to be released through the genital pores into the brood pouch (Conlan 1991). Just prior to fertilization, males use their antennae to position females and their enlarged gnathopods to clasp females in a condition known as amplexus (Williamson 1951). This type of mate guarding is common among amphipods (e.g., Dunham et al. 1986; Iribarne et al. 1995; Hume et al. 2005). Although some aspects of sexual selection have been studied in other amphipods (e.g., Birkhead and Clarkson 1980; Hatcher and Dunn 1997; Wellborn 2005), the relative roles that males and females play in the mating decisions of *M. californiana* were previously unknown.

We investigated the mating system of *M. californiana* by monitoring inter- and intrasexual interactions under conditions where we could manipulate the group size, sex ratio, body mass, and potential burrowing sites. Specifically, the goals of the present study were 1) to determine whether sexually dimorphic characters in *M. californiana* are correlated with each other, thereby allowing both sexes to assess overall male quality based on one trait; 2) to verify empirically the field observation that multiple males are less likely to cohabit than multiple females; 3) to assess the relative importance of male competition and female choice by varying the mobility of 3 amphipods (2M/1F) and observing their burrow preferences; and 4) to examine spatial distribution within larger groups to determine how same-sex and mixed-sex interactions affect overall dispersion patterns in a more natural setting. Given the extreme sexual dimorphism, extensive male weaponry, and high densities that allow for monopolizing females, we expected male competition to play a larger role than female choice in shaping the mating system of *M. cali-*

formiana. Additionally, we hypothesized that male body mass would correlate positively with antennal size and color, thus enabling males to repel rivals by communicating their fighting ability and to attract females by advertising their material resources (i.e., location and size of burrow) and/or genetic quality.

MATERIALS AND METHODS

Collection and care of study organism

All experimental *M. californiana* were sexually mature adults collected on Hobuck Beach in Clallum County, WA. Individuals were found beneath the washed-up bull kelp (the brown alga *Nereocystis luetkeana*) and caught by hand before being transported in buckets full of sand to our laboratory in Friday Harbor, WA. We also collected extra sand from the same beach for use in all experiments. Individuals were sexed based on the presence of an enlarged second pair of gnathopods and enlarged orange/red antennae that only males possess. Females usually have only 1 h between molting and ovulation when eggs can be fertilized by males before they develop within the brood pouch over a period of 2–3 weeks (Conlan 1991). As a result, females with eggs in their brood pouch were assumed to have already mated and were not used. Prior to use in experiments, males and females were housed separately in large 38-l glass aquaria that contained sand and food (strips of bull kelp) that were replaced daily. Because amphipods are most active at night (Bowers 1964; Cardoso 2002), all individuals being used in experiments were released into their experimental enclosures before dusk (ca., 7 PM) and their positions were assessed the following morning after dawn (ca., 7 AM).

Marking and Measurements

We weighed each individual (± 0.05 mg) and measured the length of its antennae (the mean of the left and right antennae) and thorax (the first 7 segments behind the head; ± 0.05 mm for both measurements). Each amphipod was then marked by gluing a bee tag with a unique color-number combination to its thorax. For all these experiments, individuals were judged to be “size matched” if they differed by less than 5% in body mass and judged to be “different sized” if they differed by more than 10% in body mass. Once amphipods were used in an experiment, they were maintained in a separate tank and not used again. Experimental individuals were chosen randomly from the captive population, except for cases that required paired individuals of certain sizes.

For a subset of males ($n = 24$), we obtained quantitative hue scores on the antennae by taking 2 digital photographs of each individual with a red color standard, followed by analysis with Adobe® Photoshop® (Adobe Systems, Inc., San Jose, CA). Photographs were taken under standardized lighting conditions (in a dark room on a white background at a distance of 0.25 m) using an Olympus C-750 Ultra Zoom digital camera. Hue was measured using the program’s Color Picker function in Photoshop, which assigns numerical values around a 360° color wheel where lower hue scores correspond to redder colors (Dale 2000). The average of 5 pixels was taken in the center of the basal (P1) and distal (P2) parts of the peduncle of the left antenna. We then calculated the overall antennal hue for the individual by taking the average of these 2 values. We confirmed that the red color standard was constant in each photograph to ensure standardization among all the images. Furthermore, the repeatability of the entire process was high, as there was a strong correlation

between the hue scores of the 2 photographs taken of each individual ($r^2 = 0.97$, $F_{1,22} = 618.92$, $P < 0.0001$).

Experimental enclosures

We used 2 types of enclosures that differed greatly in size. For all experiments involving 3 or fewer amphipods, we used 1-l Gladware® plastic containers (henceforth called containers) with 2 holes drilled into the bottom. Cylindrical plastic vials (diameter = 2.5 cm, length = 10 cm) were then filled with sand and attached to the bottom of the containers by twisting them into threaded polyvinyl chloride connectors that were previously glued around each hole. More sand was added to the top of the artificial burrow to make it level with the bottom of the container. We then made a small hole (ca., 3 cm deep) in each vial of sand to facilitate burrowing because the amphipods have difficulty in creating new burrows in these small vials. Furthermore, we always had at least as many artificial pre-dug burrows as males because, under conditions where suitable habitat is limited, males are much more likely to fight for a pre-existing burrow than create their own (Bowers 1964). When we needed to inhibit the movements of certain individuals, we created a deeper hole in the sand-filled vial (ca., 6 cm deep) and isolated that individual below a piece of wire mesh (with 1 mm² holes) located 3 cm below the surface (similar methodology to Kelly 2006b). As a result, we assumed that any amphipod inspecting that artificial burrow could sense the presence of the isolated individual below the mesh.

For all experiments involving 9 or more amphipods, we constructed large (60 × 60 cm) Plexiglas® arenas (henceforth called arenas) filled approximately 6 cm deep with sand. The arenas were divided into 9 equal sections with string that amphipods could easily crawl over so that we could examine the distribution of individuals among the sections. Additionally, we placed a small piece of bull kelp in each section to control for biases in activity based on hunger while maintaining relative consistent habitat quality among the sections. As a result, spatial distributions could be attributed to interactions with other individuals rather than habitat quality. Because suitable burrowing habitat was not limited in this larger enclosure, there were no pre-dug burrows (the sand was smoothed over before each trial) and individuals were free to burrow in any location within the arena. Because olfactory cues are important in mate choice in some amphipods (e.g., Krang and Baden 2004), the sand was also rinsed and mixed prior to each trial to eliminate chemical cues from previous trials.

Individual burrow fidelity

Amphipods (47 males and 39 females) were individually placed in containers overnight with 2 artificially pre-dug burrows to determine if they returned to the same burrow on consecutive mornings. Because we were monitoring their location over multiple days, we allowed the amphipod to remain in the artificial burrow all day after we had noted its location in the morning. If individuals returned to the same burrow 2 mornings in a row, they were allowed to remain in the container and monitored for an additional 24 h.

Two-amphipod interactions

We released different combinations of 2 amphipods in containers to determine whether amphipods are likely to share the same burrow the following morning based on sex and relative size. To this end, we conducted 5 separate experiments in which we used the following pairs: different-sized males ($n = 37$), size-matched males ($n = 40$), different-sized females

($n = 41$), size-matched females ($n = 35$), and a male and a female ($n = 42$).

Female choice and male competition: 3-amphipod interactions

We conducted 4 experiments, each of which involved 3 individuals. The first involved the simultaneous release of 2 different-sized females and a male ($n = 38$), whereas the second involved releasing 2 different-sized males and a female ($n = 36$). Based on the results of the second experiment, we conducted 2 more experiments using 2 different-sized males and a female. To eliminate male competition, we isolated the 2 males beneath the mesh to prohibit movement and allowed the free-moving female to choose with whom to burrow ($n = 41$). In the last trial, we eliminated female choice by isolating the female in one artificial burrow and allowing the free-moving males to compete for access to her burrow ($n = 42$).

Arena experiments: 9 or more amphipods

To determine the effects of inter- and intrasexual selection under more natural population densities, we conducted 3 experiments in larger arenas where we observed the distribution of 9 males, 18 females, and 9 males with 18 females, respectively ($n = 10$ trials for each). The third experiment in this group was representative of amphipod sex ratios and size ranges found in nature at the peak of breeding season (e.g., Bowers 1964; Koch 1990; Morritt and Stevenson 1993). For each of these experiments, all individuals were released simultaneously in the evening and their location was recorded the following morning.

Data analysis

All statistical analyses were performed using the statistical program JMP® 5.1 (SAS Institute 2004). We used linear regression analyses to determine the relationship between female body mass and thorax length and the relationship between male body mass and thorax length, antennal length, and antennal hue. We conducted chi-square goodness-of-fit tests to analyze the distribution resulting from each container experiment and chi-square tests of independence to compare the results from different experiments. All random expected distributions were even for the 2-amphipod interactions (50% for each of the 2 burrows) and 3-amphipod interactions with 2 males and 1 female because males chose separate burrow in every trial (50% probability that the female would burrow with each male). In 3-amphipod interactions where there were 2 females and 1 male, the expected random distribution in 2 burrows was 25% for all 3 together, 50% for a lone female and male–female cohabitation, and 25% for a lone male and cohabitation among the females. For the arena experiments with larger groups, we determined the distribution of amphipods using 2 types of analyses. First, we compared our results with a Poisson distribution to see if the amphipods dispersed randomly or not; second, if the distribution was not random, then we calculated the index of dispersion (where $I_d = s^2(n - 1)/\text{mean}$) and compared this with the chi-square distribution to look for evidence of a clumped distribution (hypodispersion) or uniform distribution (hyperdispersion). Additionally, using chi-square analyses, we compared the distribution of males with and without females and the distribution of females with and without males. Finally, after testing for (and confirming) normality (Shapiro–Wilk W -test) and equal variances (Bartlett's test), we used 2-sample t -tests to determine if there was a size difference between males found with females versus males found alone.

RESULTS

Measurements

For both sexes, there was a positive relationship between body mass and thorax length (males: $r^2 = 0.82$, $F_{1,148} = 682.91$, $P < 0.0001$; females: $r^2 = 0.77$, $F_{1,193} = 636.37$, $P < 0.0001$). Male body mass was also positively correlated with antennal length (Figure 1) and negatively correlated with the hue of the peduncle, which demonstrates that larger males have redder antennae (lower hue scores correspond to red, whereas larger hue scores correspond with orange; Figure 2).

Individual burrow fidelity

Males demonstrated burrow fidelity, as 34 out of 47 individuals used the same burrow on the first 2 nights ($\chi^2 = 9.72$, degrees of freedom [df] = 1, $P < 0.005$) and 29 of those 34 returned to the same burrow the third night ($\chi^2 = 18.74$, df = 1, $P < 0.0001$). Conversely, the burrows chosen by females on the second night did not differ from random, as 18 out of 39 individuals returned to the same burrow ($\chi^2 = 0.23$, df = 1, $P = 0.63$). Furthermore, only 10 of those 18 females returned to the same burrow the third night ($\chi^2 = 2.32$, df = 1, $P = 0.13$). There was a significant difference between males and females in burrow fidelity based on the first 2 nights ($\chi^2 = 6.16$, df = 1, $P < 0.05$).

Two-amphipod interactions

Males preferred to be alone rather than burrowing together, regardless of their relative sizes (84% on average; Table 1). Different-sized and size-matched females, on the other hand, did not avoid burrowing together, as they burrowed as often together as they did apart (45% vs. 55%, on average; Table 1). When interacting with members of their own sex, males were more likely to occupy separate burrows than females for both different-sized and size-matched pairs (different sized: $\chi^2 = 6.79$, df = 1, $P < 0.01$; same sized: $\chi^2 = 9.04$, df = 1, $P < 0.005$).

When a male and a female were placed together, they shared the same burrow in 81% of the trials (Table 1). When comparing these intersexual interactions with the intrasexual interactions of different-sized males, we found that males behave differently toward others based on sex, as males are less likely to cohabitate with other males than with females ($\chi^2 = 32.61$, df = 1, $P < 0.0001$). We also found a significant difference in how females interact with different sexes, as a female paired with another individual is more likely to cohabitate with that other individual if it is male ($\chi^2 = 11.09$, df = 1, $P < 0.001$).

Female choice and male competition: 3-amphipod interactions

When 2 different-sized females and 1 male were released simultaneously and were free to move, all 3 ended up in the same burrow in 76% of the trials (29 out of 38 trials; $\chi^2 = 49.04$, df = 2, $P < 0.0001$). When 2 different-sized males and 1 female were released simultaneously, however, males ended up in separate burrows in every trial, with females burrowing with the larger males over 80% of the time (Table 2). To determine whether this result was due to female choice or male competition, we conducted 2 more experiments with 2 males and 1 female. In trials where 2 different-sized males were isolated in separate burrows and the female was free to choose, females were equally likely to burrow with either male (Table 2). This distributional pattern, with female choice in the absence of male competition, was different from that observed when all 3

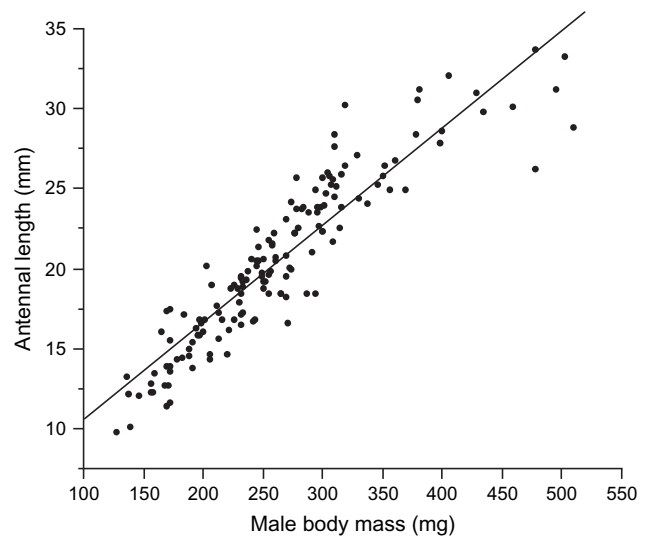


Figure 1
Male antennal length increases as a function of his body mass ($r^2 = 0.85$, $F_{1,148} = 810.08$, $P < 0.0001$).

individuals were released simultaneously ($\chi^2 = 11.27$, df = 1, $P < 0.001$). However, in trials where different-sized males were free to compete and the female was isolated in a burrow, larger males shared the burrow with the female over 70% of the time (Table 2). This distributional pattern was consistent with that observed under more natural conditions in which all 3 individuals were free to move ($\chi^2 = 0.89$, df = 1, $P = 0.35$).

Arena experiments: 9 or more amphipods

In single-sex trials, males distributed themselves in a pattern significantly different from random ($\chi^2 = 31.30$, df = 4, $P < 0.0001$) with an index of dispersion value consistent with a uniform distribution ($I_d = 56.10$, df = 89, $P > 0.975$). Females, on the other hand, were randomly distributed in single-sex trials ($\chi^2 = 5.92$, df = 6, $P = 0.43$).

In the trials where 9 males and 18 females were placed simultaneously in an arena, males were again distributed in a pattern significantly different from random ($\chi^2 = 98.41$, df = 5,

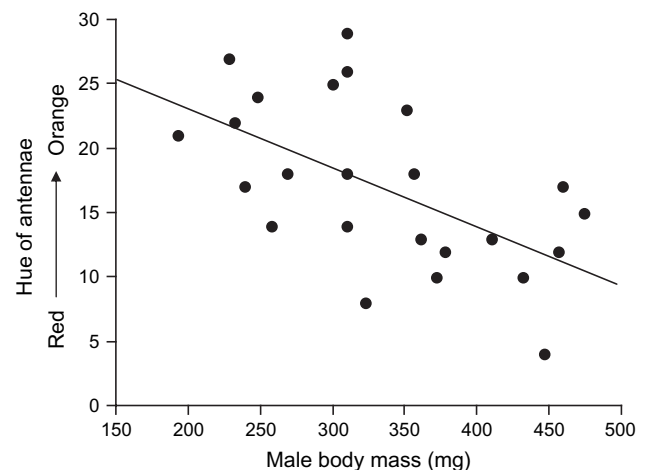


Figure 2
The hue of the male's antennae decreases (redness increases) as a function of his body mass ($r^2 = 0.33$, $F_{1,22} = 10.67$, $P < 0.005$).

Table 1
Locations of 2 amphipods when placed in a container with 2 potential burrowing sites

Experimental individuals	Number of trials	Burrow location (same/different)	χ^2 (df = 1)	<i>P</i> value
Different-sized males	37	7/30	15.40	<0.0001
Size-matched males	40	5/35	25.31	<0.0001
Different-sized females	41	19/22	0.22	0.64
Size-matched females	35	15/20	0.72	0.40
1 male and 1 female	42	34/8	17.32	<0.0001

$P < 0.0001$), but the index of dispersion value indicated a clumped distribution ($I_d = 147.12$, $df = 89$, $P < 0.025$). The distribution of males with and without females present was significantly different ($\chi^2 = 107.61$, $df = 5$, $P < 0.0001$). In these same trials, females were also distributed in a pattern significantly different from random ($\chi^2 = 70.16$, $df = 6$, $P < 0.0001$) with an index of dispersion indicating a clumped distribution ($I_d = 134.91$, $df = 89$, $P < 0.025$). The distribution of females with and without males present was significantly different ($\chi^2 = 120.72$, $df = 6$, $P < 0.0001$). These females were primarily found near larger males, as males found in burrows containing females were 17% larger than males found alone (Figure 3).

DISCUSSION

Sexually dimorphic characters are often indicative of sexual selection (Darwin 1871; Andersson 1994). This is particularly true in harem polygyny mating systems where males often have exaggerated traits that can be used to attract females (intersexual selection) or compete with other males for access to groups of females (intrasexual selection). Although males are larger than females in many amphipods, there are relatively few studies on sexual selection within this taxonomic group (e.g., Birkhead and Clarkson 1980; Wen 1993; Hatcher and Dunn 1997; Wellborn 2005). The California Beach Flea, *M. californiana*, is particularly remarkable among amphipods in its sexual dimorphism—males are not only significantly larger than females but also possess enlarged gnathopods and red antennae that may be used in both mate choice and intrasexual competition.

Across many taxa, male body mass is associated with the ability to secure and defend a harem (Huntingford and Turner 1987; Shuster and Wade 2003). In many polygynous amphipods, body mass is also positively correlated with other char-

Table 2
Locations of 3 amphipods (2 different-sized males, 1 female) when placed in a container with 2 potential burrowing sites

Experimental individuals	Number of trials	Female burrow location (# with large male/# with small male)	χ^2 (df = 1)	<i>P</i> value
Simultaneous release	36	29/7	14.44	<0.0001
Female choice only (males isolated)	41	18/23	0.61	0.43
Male competition only (females isolated)	42	30/12	7.97	<0.005

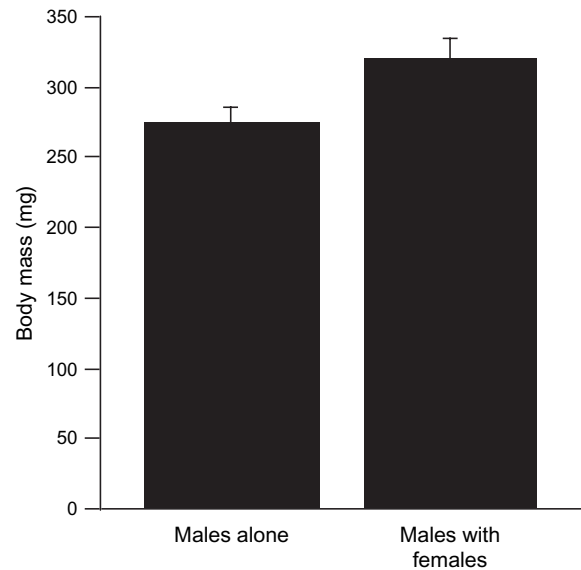


Figure 3
Males in burrows with females were significantly larger in body mass (Mean \pm standard error) than those found alone ($t = 2.46$, $df = 88$, $P < 0.05$).

acters, including weaponry (e.g., Bertin and Cezilly 2003; Hume et al. 2005; Wellborn 2005). In *M. californiana*, larger males were indeed more successful in securing females. Furthermore, we found that the male body mass was correlated with the length and redness of the antennae, 2 parameters potentially responsible for reproductive success. Based on our observations, antennal length is an important component of fighting ability, as larger males often use their long antennae not only to pry smaller male occupants out of a burrow but also to lift their opponents while jabbing them with their gnathopods. Larger males also have redder antennae, which means that male antennal color could be used by males to gauge an opponent's fighting ability and by females to judge male quality. Such coloration is often an honest signal of quality (e.g., Hill 1991; Wolfenbarger 1999; but see Dale 2000), and, because many crustaceans can see red (Cronin and Jinks 2001; Porter et al. 2007), there is the potential for visual communication based on male antennal color in *M. californiana*. Many arthropods, including crustaceans, can also see UV (Cronin and Jinks 2001). Although we did not measure UV reflectance in this study, we plan to measure it in the future, as these amphipods may also use this parameter to assess quality. Given the high population densities and close proximity of burrows in the field (Bowers 1964), it is likely that, similar to other systems in which males occupy established territories, there may be a selective advantage for individuals to recognize their neighbors and assess their quality without risking injury due to fighting (dear enemy effect: Fisher 1954; Shuster and Wade 2003).

As we predicted, male *M. californiana* exhibited stronger intrasexual aggression tendencies than females, a pattern typically observed in harem polygyny mating systems (e.g., Modig 1996; Kelly 2006a). In our container experiments, males preferred to occupy separate burrows regardless of their relative sizes, whereas females were not averse to cohabitation. When a male and a female were placed together with 2 potential burrowing sites, however, the pair usually occupied the same burrow. Thus, males were not averse to sharing their burrow per se—they simply kept potential rivals away while accepting potential partners. The sex differences in aggression were

particularly evident in our 3-amphipod experiments, as all 3 amphipods were found in the same burrow only when 2 of the participants were female. When 2 different-sized males and a female were placed together simultaneously, males always occupied separate burrows, with the female usually in the larger male's burrow. When males were confined within burrows to prevent male competition, females were equally likely to be found with either male. However, if the female was restricted such that female choice was precluded but male competition could occur, the larger male outcompeted his smaller rival for the female's burrow in a pattern consistent with the (more natural) situation where all participants could freely move. Given our observations on how the males use their enlarged antennae and gnathopods in intrasexual combat, it was not surprising to find that male competition played a relatively larger role than female choice regarding cohabitation in *M. californiana*.

Although these experiments revealed the relative importance of male competition and female choice, they occurred under highly controlled conditions with a restricted number of pre-dug burrow sites. Our second set of experiments involved observing distributional patterns in larger arenas where, in the absence of artificial burrowing sites, all individuals were free to move at a density and sex ratio observed at the peak of breeding season (Bowers 1964). As expected, females settled in random locations in single-sex groups but clustered around larger males in mixed-sex groups. Because we controlled for nonsexual factors that can influence distributional patterns (such as predator avoidance and food location; e.g., Wrangham and Rubenstein 1986), the differences in female distribution based on the presence of males must be due to interactions among the amphipods. Given the high density of females and their ability to crawl or hop quickly, it is likely that females chose to associate with particular males rather than being confined by a dominant male. Furthermore, these arena experiments only took place over 1 night with a 2:1 ratio of females to males, and it would be difficult for a male to monopolize multiple females in a single evening. Thus, under more natural conditions with unrestricted movement and unlimited burrowing sites, there is evidence that female choice does indeed play a role in the mating system of *M. californiana*.

Based on our observations of male intrasexual aggression, we were not surprised to find that males in large single-sex groups were spaced in a uniform pattern often seen in animals that exhibit territorial behavior (Huntingford and Turner 1987; Riechert 1998; Shuster and Wade 2003). Interestingly, in mixed-sex groups, males—similar to the females—had a clumped distribution. This pattern may be the result of smaller, less competitive males employing an alternative mating strategy. By settling near the larger, higher quality males, these “satellite” males may be hoping to take advantage of opportunities to mate with the numerous females in the vicinity of the larger male (e.g., Brockmann 1996; Martin and Taborsky 1997; Arakaki et al. 2004).

Our results indicate that, in the absence of environmental variation, females cluster around larger males; however, under natural conditions, there are external factors that may influence female distribution. For example, various aspects of male burrows may affect female recruitment due to the potentially profound effect on her fitness. Deeper burrows may provide cooler, more constant temperatures that are metabolically favorable for reproduction, and burrows located more centrally underneath certain types of seaweed may allow for greater access to higher quality food. Perhaps, rather than choosing mates based solely on intrinsic male characteristics, females may instead be choosing settlement locations based on the male's ability to control resources valuable to females (resource-holding potential; Parker 1974). Our container experiments

show that female settlement is biased even in the absence of variation in burrow phenotype, as pre-dug burrows were standardized and never modified by males during the experiments. Furthermore, our arena experiments showed that females clumped around larger males, even when resources were evenly distributed. Thus, the spatial distributions we observed in the laboratory cannot be attributed to environmental factors, and the tendency of both sexes in *M. californiana* to aggregate is likely driven, in part, by sexual selection. Nevertheless, because there are some harem polygynies based on access to resources (e.g., Modig 1996; Sanchez-Prieto et al. 2004; Kelly 2006b), it will be important in future experiments to disentangle the effects of male characteristics and burrow phenotype on female distribution.

The degree of plasticity in the behaviors of *M. californiana* over the course of the breeding season remains unknown. Although our large arena experiments with a natural population sex ratio more accurately mimicked field conditions than did our small container experiments, we only examined spatial distributions at a fixed population density and sex ratio. The female-biased sex ratio that we used is consistent with the peak of the breeding season in many amphipods (e.g., Koch 1990; Forbes et al. 1996); however, some amphipods, including *M. californiana*, have a long breeding season during which population densities and sex ratios vary over time (Williamson 1951; Bowers 1964). Variation in these population parameters have been shown to affect reproductive behavior in amphipods (e.g., Lewbel 1978; Wen 1993; Iribarne et al. 1996; Forbes et al. 2006). Although our current study indicates that males exhibit more burrow fidelity than females in *M. californiana*, these experiments were done in the absence of other individuals. We suspect that, in nature, a male's burrow fidelity is dependent on his harem size and the density of rivals, whereas a female's burrow fidelity is determined by the quality of her mate relative to other potential suitors in the population. We are currently conducting studies to examine individual burrow fidelity and overall spatial distribution based on the natural variation in relative sizes, densities, and sex ratios in field populations.

This study provides the first empirical data regarding sexual selection in *M. californiana*, and our results demonstrate that male competition is more important than female choice in shaping this harem polygyny mating system. Although we have not yet disentangled the relative roles that male quality and resource value play in this mating system, we predict that the distribution of amphipods is the result of a sequential process. First, the highest quality males compete for burrows in the best locations with respect to food and shelter; second, the females cluster near these large males where they have access to a high-quality mate and his resources; and finally, smaller males settle nearby to exploit potential extra-harem mating opportunities. Although sexual selection has been studied in other amphipods, there are a few aspects of this mating system that are particularly noteworthy. For example, in the amphipod *Corophium volutator*, all females reproduce synchronously during 2 short breeding seasons where males visit multiple burrows that contain individual females (Forbes et al. 1996; McCurdy et al. 2000). In *M. californiana*, on the other hand, there is a longer breeding season in which females, who mate only once, breed asynchronously in burrows controlled by males. These life-history traits lend themselves to a high potential for monopolization of females by certain males (Emlen and Oring 1977), which probably led to the extreme sexual dimorphism seen in *M. californiana*. Future studies regarding the plasticity of male and female reproductive strategies through field observations and experimental manipulation of environmental factors will provide further insight into sexual selection in this amphipod.

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