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Asymmetric forceps increase fighting success among males of similar size in the maritime earwig

Nicole E. Munoz^{1,2} and Andrew G. Zink¹

¹Department of Biology, San Francisco State University, CA 94132, USA

Abstract

Extreme asymmetric morphologies are hypothesized to serve an adaptive function that counteracts sexual selection for symmetry. However direct tests of function for asymmetries are lacking, particularly in the context of animal weapons. The weapon of the maritime earwig, *Anisolabis maritima*, exhibits sizeable variation in the extent of directional asymmetry within and across body sizes, making it an ideal candidate for investigating the function of asymmetry. In this study, we characterized the extent of weapon asymmetry, characterized the manner in which asymmetric weapons are used in contests, staged dyadic contests between males of different size classes and analyzed the correlates of fighting success. In contests between large males, larger individuals won more fights and emerged as the dominant male. In contests between small males, however, weapon asymmetry was more influential in predicting overall fighting success than body size. This result reveals an advantage of asymmetric weaponry among males that are below the mean size in the population. A forceps manipulation experiment suggests that asymmetry may be an indirect, correlate of a morphologically independent factor that affects fighting ability.

Introduction

Asymmetric structures are common in bilateral animals. A potential to gain insight into the interplay between developmental and evolutionary mechanisms has motivated investigations into the adaptive significance of asymmetric morphologies (Palmer 1996; Palmer 2009). Many studies indicate that sexual selection discriminates against asymmetry (reviews in Møller & Pomiankowski 1993; Møller & Swaddle 1997). Thus, an advantage conferred by asymmetry is necessary to offset the disadvantage posed by discrimination against asymmetry (Huber et al. 2007). Asymmetric morphologies have been found adaptive in feeding (crustaceans: reviewed in Mariappan et al. 2000; insects: Inoda et al. 2003; snakes: Hosoi et al. 2007), mating positions (insects and spiders: reviewed in Huber et al. 2007) and courtship displays (crustaceans: Oliveira & Custódio 1998; insect: Dageron et al. 2011).

Perhaps due to a rare occurrence of asymmetric weaponry, the function of asymmetric structures when used in animal contests has received little attention. Asymmetry is well known in the chelae of crustaceans, and these structures are important in many contexts. Often times, the smaller chela is used for capturing prey and grooming while the larger chela is used in agonistic interactions (reviewed in Mariappan et al. 2000). Female fiddler crabs (*Uca tangeri*) prefer males with greater asymmetry, possibly because a larger chela captures the attention of females (Oliveira & Custódio 1998). An experimental reversal of the side (left vs. right) having the larger chela in green crabs (*Carcinus maenas*) indicates the importance of asymmetry in this species (Juanes et al. 2008). We refer readers to the following review for a thorough treatment of asymmetry in crustacean chelae (Mariappan et

²Present address: Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA

al. 2000). Note, that in the remainder of this article, we restrict use of the term "asymmetric weapon" to refer to a structure that forms a single, functional unit as opposed to asymmetry in structures on either side of the body that can act independently, such as in the chelae of many crustaceans where one chela is larger than the other (e.g. Oliveira & Custódio 1998; Juanes et al. 2008; Claverie & Smith 2010).

Animal weapons can serve as a means for females to assess potential mates or to defend resources through contests (reviewed in Emlen 2008). When used in animal contests, weapons may inflict injury or provide a means to assess a rival's fighting ability either as a visual signal or through direct combat (Panhuis & Wilkinson 1999). The asymmetry in the horns of fallow deer (*Dama dama*) is thought to facilitate interlocking between males, enabling rivals to assess the strength or endurance of one another (Alvarez 1995). The horns of the beetle *Agathidium* Panzar are asymmetric, emanating from only the left mandible (Miller & Wheeler 2005). Males with horns are better at displacing rivals than males without horns. The stag beetle (*Prosopocoilus inclinatus*) exhibits morph-dependent asymmetry in mandibles where smaller males are asymmetrical and larger males are symmetrical (Okada et al. 2008). However, to our knowledge, the degree to which weapon asymmetry is beneficial when males compete has never been characterized.

In this study we examine the function of an asymmetric weapon used in animal contests. Both body size Review by (Andersson 1994) and weapon size (e.g. prawn chelae: Barki et al. 1997; crab chelae: Sneddon et al. 1997; head armour in chameleons: Stuart-Fox & Whiting 2005) are known indices of fighting ability. The weapons of male maritime earwigs (*Anisolabis maritima*) consist of a pair of hook-like structure located at posterior end and are commonly known as forceps (Fig. 1). Many species of earwigs use forceps to fight over access to females and food (Moore & Wilson 1993; Forslund 2000), and female *A. maritima* use forceps to defend nests (Miller et al. 2011; Miller & Zink 2012). In the forceps of male maritime earwigs, the right side is more curved than the left side (see Results, Fig. 1), and agonistic interactions consist of forceps strikes identified by a rapid twisting of the abdomen such that the forceps forcefully contact the opponent (Fig 2.; further illustrations can be found in Briceño & Eberhard 1995, Fig. 57, p. 34). Briceño & Eberhard did not observe earwigs to injure conspecifics (1995). Thus, we suspected that asymmetry facilitates rivals to assess one another, perhaps through the force exerted when clasping a rival between forceps.

Appearing structurally similar to the forceps of maritime earwigs, the larval stage of a beetle (*Cabomba caroliniana*) exhibits asymmetry in the hook-like structures of its mandibles. Larvae were found to be more efficient at feeding on right-handed snails (i.e. having shells that spiral in one direction) compared to left-handed snails (i.e. having shells that spiral the opposite direction) (Inoda et al. 2003). When feeding on right-handed snails, larvae of *C. caroliniana* place the straighter, left mandible on the outside of the shell. The larvae crush the central axis of the shell using the right mandible, which is more curved than the left (Inoda et al. 2003). This stereotyped feeding behavior was not observed and larvae were not as efficient when feeding on left-handed snails. Thus, it appears that asymmetry enables efficient feeding, which may result in specializing on right-handed snails (Inoda et al. 2003).

Based on the way in which the mandibles of the larvae in *C. caroliniana* are used to feed on snails (Inoda et al. 2003), we hypothesized that male maritime earwigs may use their forceps in a similar way such that the curvier, right side is used to clasp the opponent against the straighter, left side. Though injury may not be inflicted, male earwigs may be able to assess the strength of rivals based on the pressure exerted by forceps. If forceps asymmetry facilitates grasping rivals, then earwigs should exhibit stereotyped fighting behavior, possibly through consistent twisting of the body in one direction. We also posited that

asymmetry may facilitate interlocking of forceps in order to assess a rival's strength, as in the asymmetric antlers of fallow deer (Alvarez 1995), in which case we should observe earwigs to interlocking forceps during contests. To test these non-mutually exclusive hypotheses, in the first part of this study we (1) characterized forceps asymmetry, (2) characterized the manner in which forceps are used in contests, and (3) staged dyadic contests between males of different size classes and analyzed the degree to which asymmetry determined contest outcome. In the last part of this study, we staged contests between males where we modified forceps in order to determine if forceps asymmetry *per se* was responsible for contest outcome.

Methods

General methods

Male *A. maritima* for staged contests were collected from three sites along the San Francisco Bay, CA (Keller Beach, Richmond, CA: 12/22/09; 1/16/10; Richardson Bay, Tiburon, CA: 2/7/10; Pt. Pinole, Richmond, CA: 2/7/2012; 3/1/2012). Males for experiments with manipulated forceps were collected from Keller Beach, Richmond, CA: 4/8/10 and Richardson Bay, Tiburon, CA: 4/16/10. Earwigs were housed at 24° C, in ambient humidity and on a 12:12 h light:dark photoperiod. Individuals were housed solitarily from the time of collection. Earwigs were first held in plastic containers 2.5 cm in diameter and 9.5 cm tall with moistened cat food for 24 h to standardize background satiation levels and then subsequently moved to glass jars 9 cm in diameter and 9.5 cm tall filled to a height of 3 cm with moistened potting soil with no food supplements. Individual males only participated in one contest before they were frozen and measured.

Morphological measurements were made from pictures taken with a digital camera (Leica FireCam) attached to a dissecting microscope (model ES2, Leica Microsystems) using ImageJ v 1.43r. Following previous studies on the European earwig (*F. auricularia*), we measured pronotum width as an index of body size (Simmons & Tomkins 1996; Tomkins & Simmons 1996; Tomkins 1999; Tomkins & Simmons 1999; Forslund 2003). We defined the length of each side of forceps as the distance of the line perpendicular from the final abdominal segment to the tip (Fig. 1a). The length of the line perpendicular to forceps length at the widest point defined forceps width. We calculated forceps curvature as the ratio of width to length. We quantified asymmetry in forceps curvature as the ratio of right to left curvature (Fig. 1a). We performed a paired *t* test to test the consistency of the direction of forceps asymmetry (Palmer 1994).

Based on preliminary observations, we divided contests into three separate categories based on the differences in pronotum width. Contests were either between (1) different-sized, (2) same-sized large, or (3) same-sized small males. If an individual had a 10 % or greater size advantage, the contest was said to be between males of different body size. We defined size-matched contests as those in which the size advantage was less than 10 %. Size-matched contests where the mean pronotum width of the contestants was less than 2.7 mm (mean of all earwigs in this study) were categorized as "small vs. small". Size-matched dyads with mean pronotum width greater than or equal to 2.7 mm were categorized as "large vs. large". In an effort to generate variation in pairings of body size and weapon metrics across contests, earwigs were matched at random. Contests were always between earwigs from the same collection date and site and between earwigs that had been food deprived for the same amount of time. Duration of starvation across contests ranged from 9–28 days.

A small piece of hard cat food was glued to the center of a 9.5 × 11.5 × 4 cm (l × w × h) plastic arena in order to isolate the effects of fighting over a resource from differences in ability in handling a food item. We marked the pronotum of earwigs with paint for

identification. Marked earwigs were placed on the arena within an open-bottom clear cylinder (2.5 cm diameter, 0.5 cm tall) on opposite sides of the arena and were allowed to acclimate for 3 min. The cylinders were simultaneously lifted and a video camera (Samsung SMX-F34) suspended 21 cm above the arena recorded contests for 30 min.

Rivals exchanged strikes until one individual retreated away from the food resource to a distance of at least 1 cm, giving the other earwig an opportunity to feed. Here, we define "agonistic interactions" as an exchange of strikes, beginning with the first strike and ending when one earwig retreated. After approximately 4 min, one earwig, by initiating the majority of interactions and forcing the opponent to retreat, appeared to monopolize the food item (see results). Thus, we concluded that 30 min was sufficient time to identify a 'winner' and 'loser' in contests. We defined the 'winner' as the opponent that had access to the food source for more time over the 30-minute contest. While the time spent feeding could be interpreted as the individual's hunger levels and confound our results (Maynard Smith 1982; Hansen 1986; Houston & McNamara 1988), this effect is likely negligible because we standardized satiation levels by feeding earwigs ad libitum and then starving each pair of contestants for an equal amount of time. Each video was scored to record the proportion of time spent feeding, the proportion of agonistic interactions initiated, and the total number of forceps strikes.

Staged contest experiments

Pair-wise contests were staged between 1000–1900 h. We analyzed the number of times males twisted their bodies towards the left and towards the right when delivering strikes. Based on results of our manipulation experiment, this was done for five small-small and five large-large contests selected at random. One male was selected randomly from each contest as the focal male. For each contest category, the number of left vs. right strikes were compared using a paired *t* test.

Relations among pronotum width, abdomen width, forceps length (left side) and asymmetry in forceps curvature were tested using Spearman's ρ correlation coefficients. We checked for biases in collection site and starvation time among contest categories using a χ^2 contingency test. The time spent feeding by winners and losers was compared using a paired *t* test.

In analyzing the influence of morphological measurements on contest outcome, one male was randomly selected from each contest as the focal male. Winners were coded as 1 and losers were coded as 0. Differences in pronotum width, forceps asymmetry, forceps length, and all two-way interactions were entered into a logistic regression model as independent variables with contest outcome as the dependent variable. Assuming $\alpha = 0.05$, all data were analyzed using JMP V 9.0.

Forceps manipulation experiment

Based upon results from the staged contests, we performed a manipulation experiment that disrupted asymmetry to investigate if asymmetry per se is advantageous for winning small vs. small contests. In small-small contests, if having more asymmetric forceps is indeed advantageous then manipulated forceps should affect contest outcome, with more asymmetric males winning more contests. On the other hand, if there is no effect of forceps asymmetry after manipulation it is likely that a correlate of asymmetry that we did not measure is also important for winning contests. In the latter case the original forceps morphology, which we measured prior to contests, should be a significant predictor of fighting success. As a control we also staged contests between large males, in which forceps are not a significant predictor of fighting success. If our manipulations did not adversely

affect contest outcome then body size should still be the only predictor of fighting success in contests between large males.

We staged size-matched contests where we randomly shortened forceps on the left side of one individual and right side of the other individual by approximately 15 % of the total length in order to manipulate forceps asymmetry. This resulted in some pairings where the more asymmetric pre-manipulated individual was still more asymmetric after manipulation. In the other pairings, the more asymmetric pre-manipulated individual was the least asymmetric male after manipulations. We assumed that having either the left or right side of forceps manipulated imposed equal physiological burden on the male, such that the resulting fighting success could be determined by the newly manipulated forceps asymmetries. We attempted to modify forceps such that forceps tips terminated at a point so as not to influence the area which applies pressure (Fig. 3).

The same procedure described above was used for staging contests with the additional steps of imaging and measuring forceps prior to manipulation. Pronotum width and forceps measurements were repeated from sacrificed earwigs, and forceps were re-measured to verify the measurements from live earwigs and if matches actually corresponded to our definition of size-matched dyads. All earwigs competed only once.

Data were analyzed following the methods from the first part of our study by entering the difference in pronotum width and difference in forceps asymmetry into a logistic regression model. Two logistic regression models were made with either forceps asymmetry as measured either before or after manipulations.

Results

Forceps asymmetry

Right forceps of male maritime earwigs had significantly greater curvature than left forceps ($t_{165} = 12.89$, $p < 0.0001$), indicating that the forceps of maritime earwigs in this study exhibit directional asymmetry. Table 1 shows the correlations among male size (pronotum width) and forceps morphology for all earwigs in this study ($n = 180$). Pronotum width was correlated with forceps length, forceps asymmetry and abdomen width. Abdomen width was correlated with forceps length and forceps asymmetry. Forceps asymmetry was not significantly correlated with forceps length.

Characteristics of contests in maritime earwigs

While maritime earwigs generally clasped opponents between forceps during strikes, strikes never inflicted physical harm in this study. During combat, earwigs aligned themselves side by side while facing in opposite directions (Fig. 2a). When delivering strikes, earwigs twisted their bodies to the left significantly more than to the right (paired t tests: small vs. small: $t_4 = 4.97$, $p = 0.008$; large vs. large: $t_4 = 4.917$, $p = 0.008$). When twisting to the left, the straighter, left side of forceps was placed beneath the abdomen of the opponent while the curvier, right side clasped the top part of the dorsal side of the abdomen as illustrated in Fig. 2b (and vice versa when the abdomen was twisted to the right during strikes) (see Briceño & Eberhard 1995 Fig. 57, p. 34 for further illustrations). These strikes were very rapid and we were only able to resolve the details of this action by playing back videos at a reduced speed. Occasionally, upon clasping an opponent between forceps, the aggressor was able to move the opponent by forcefully swinging its abdomen. However, forceps were rarely used in this manner (once in 5 of 90 contests), so we did not include these data in analyses. The only types of interactions that we observed appeared to be agonistic. We did not observe earwigs to interlock forceps.

Of the 90 contests that we staged, 14 ended in ties, two of which contained no agonistic interactions. Overall, winning individuals produced more strikes using forceps (paired t test: $t_4 = 4.64$, $p < 0.0001$). The proportion of strikes initiated changed over time. There was no difference in the number of fights initiated within the first (one-sample t test: $t_{50} = 0.32$, $p = 0.75$) and second (one-sample t test: $t_{48} = 1.252$, $p = 0.217$) 2-min time bin. After 4 min the overall contest winner initiated the majority of fights across all subsequent 2-min time intervals (Fig. 4a). Duration of fights in the first 4 minutes of overall contests, during establishment of the dominant earwig, were longer compared to the last 26 min of contests (Student's t test: $t_{84.1} = 3.36$, $p = 0.0013$; Fig. 4b) suggesting that the subordinate was not resisting as much after dominance had been established. The overall winner of 30-minute contests produced more strikes than the contest loser after dominance was established (one-sample t test: $t_4 = 4.64$, $p < 0.0001$), but not during the first 4 min of contests (one-sample t test: $t_{70} = 1.72$, $p = 0.090$).

Determinants of fighting success

Difference in pronotum width ($\chi^2 = 9.78$, SE = 2.45, $p = 0.0018$) and the interaction between difference in pronotum width and difference in forceps asymmetry ($\chi^2 = 4.11$, SE = 6.40, $p = 0.043$) were significant predictors of contest outcome ($n = 76$ overall model pseudo $r^2 = 0.61$, $p < 0.0001$). We performed a post-hoc analysis by entering difference in pronotum width and difference in forceps asymmetry as independent variables into a logistic regression model for each contest category (Table 2). Morphological predictors of fighting success varied with contest category (Fig. 5). In small-small contests ($n = 25$), forceps asymmetry ($\chi^2 = 8.10$, SE = 3.73, $p = 0.0004$) was a significant determinant of contest winner, with more asymmetric males winning more contests. Difference in forceps asymmetry was also significant in small-large contests ($n = 36$, $\chi^2 = 4.19$, SE = 8.76, $p = 0.041$), but difference in pronotum width ($\chi^2 = 28.50$, SE = 4.12, $p < 0.0001$) had a much greater influence on contest outcome in this category. Difference in pronotum width was the only significant predictor in large-large contests ($n = 15$, $\chi^2 = 5.54$, SE = 7.30, $p = 0.019$).

Manipulation experiment

Manipulating the asymmetry of forceps did not appear to influence the way in which earwigs used their forceps during contests. Nor did the manipulation appear to influence the extent to which earwigs responded to strikes from opponents. When difference in asymmetry and difference in pronotum width were entered into a logistic regression model, difference in asymmetry as measured from post-manipulated forceps was not a determinant of contest outcome. Instead, there was a trend for difference in asymmetry, as measured from earwigs before contest manipulations, to predict contest outcome in small vs. small dyads (Table 3). Although not significant, we found a trend among small males for more asymmetric males, as measured before manipulations, to win more contests ($n = 9$, $\chi^2 = 3.02$, SE = 12.27, $p = 0.082$). In large-large contests ($n = 13$), larger males won contests both when pre-manipulated ($\chi^2 = 5.15$, SE = 7.11, $p = 0.023$) or manipulated ($\chi^2 = 5.34$, SE = 9.63, $p = 0.033$) weapon asymmetry was entered into either model. As we found in large vs. large staged contest trials, asymmetry was not a significant predictor in the manipulation experiment when entered into either model (Table 3).

Discussion

We found that the determinants of fighting success in maritime earwigs depended on the size of individuals that competed. Greater weapon asymmetry favored winning in contests between small males, but greater body size favored winning in contests between large males (Table 2). Aside from systems where distinct morphotypes are associated with alternative reproductive tactics (e.g. Shuster 1989; Gross 1996; Barki et al. 1997), size-dependent

determinants of fighting success have been found in only a few systems (e.g. Pavey & Fielder 1996; Lailvaux et al. 2004; Pomfret & Knell 2006). In the dung beetle (*Euoniticellus intermedius*), both body size and weapon size determined contest outcome between small males, but weapon size became increasingly important as body size increased (Pomfret & Knell 2006). Before discussing this main result, we discuss the measures we took to isolate factors other than body and weapon morphology that are known to influence animal contests, which is followed by a discussion of the possible functions of asymmetric forceps.

Non-morphological factors affecting fighting ability that we controlled

Prior fighting success is known to influence future fighting success where successful combatants tend to continue winning, a phenomenon known as the winner-loser effect (e.g. McDonald et al. 1968; Moore et al. 1988; Whitehouse 1997). Male maritime earwigs likely encountered rivals of a range of sizes and asymmetries in the field prior to collection. Given that small males lose to large males (Table 2), males are likely to have a history of both winning and losing. Thus, prior experience likely did not confound our results. Furthermore, winner-loser status may not be retained indefinitely and could decay over time (Chase et al. 1994; Dugatkin 1997; Hsu & Wolf 1999). We assumed that we minimized any residual winner-loser status by isolating earwigs for a minimum of 9 d prior to contests. Motivation can also affect fighting success such that individuals that have been without food for longer periods may be more motivated to fight for a food item (Maynard Smith 1982; Hansen 1986; Houston & McNamara 1988). Difference in satiation levels likely had a minimal effect on our results, because we standardized satiation by feeding earwigs ad libitum for 24 h, after which paired contestants were deprived of food for an equal amount of time. Given that we adequately controlled for these potentially confounding factors, we conclude that our results were due to morphological differences that generated a difference in an ability to defend a food resource (i.e. resource holding potential).

The function of asymmetric forceps

We found that the forceps of *A. maritima* exhibit directional asymmetry where the right side is more curved than the left side. We found that both small and large males used their forceps the same way; both favor twisting to the left when delivering strikes. When clasping opponents with forceps, the straighter, left side of forceps was placed under the abdomen of the opponent while the more curved, right side contacted the dorsal side of the abdomen (Briceño & Eberhard 1995 (Fig. 57, p. 34). This stereotyped fighting behavior may be a way for male earwigs to assess rivals. Asymmetric mandibles of the larvae of a water beetle are thought to enhance an ability to grasp and crush snail shells coiled in a particular direction (Inoda et al. 2003). In a similar manner, the asymmetric forceps of male maritime earwigs may enhance an ability to clasp and apply pressure to rivals. Clasping an opponent's abdomen between forceps may be a means to gauge the size of the opponent. In addition, the force at which a male clasps its opponent may provide an indication of the aggressor's fighting ability. Thus, asymmetry may facilitate rival assessment among males.

The hypothesis that males are assessing each other during direct combat is supported by the progression of agonistic encounters. An individual's willingness to engage in agonistic interactions should reflect the likelihood of the individual out-competing a given rival (Parker 1974; Maynard Smith 1982). Without any information about a rival's fighting ability prior to contests, an individual's best strategy is to assume it has an equal likelihood of winning and losing. Thus, if earwigs were able to assess a rival's fighting ability based on non-contact cues, one would expect the initiation of agonistic interactions to be disproportionate between opponents at the beginning of contests with winning males initiating the majority of interactions at the start of contests (Barrette & Vandal 1986; Ladich 1998; Bergman & Moore 2005). However, we found that during the early stages of

contests, each opponent initiated agonistic interactions equally. The losing male initiated fewer interactions as the contest progressed (Fig. 4a), which indicates earwigs may be assessing an opponent's fighting ability through fighting itself

Upon gaining information about the fighting ability of an opponent through combat, males less capable of defending the food source are expected to refrain from engaging in further combat because engaging in combat would be a waste of energy (Enquist & Leimar 1983). Indeed, given that multiple exchanges of forceps strikes may be necessary for an individual to determine the likelihood of winning, we also found that early interactions lasted significantly longer than those at the end of contests (Fig. 4b) (but see Mesterton-Gibbons et al. 1996). Successive encounters between size-matched male crayfish also decrease in duration, and chemical signals likely maintain dominance hierarchies over the course of several days (Breithaupt 2011). Given that earwigs reside in loosely maintained groups (Briceño & Eberhard 1995), which makes repeated encounters with conspecifics highly likely, maritime earwigs may also be able to recognize opponents after initial contests. However, more work should be done in this area.

It is worth noting that while we did not observe earwigs to inflict injury during contests, it is possible that contests may not have escalated to the highest intensity if food deprivation resulted in a relatively low motivation to compete for food. Furthermore, contests over other resources, such as mates, could result in contests of higher intensity where injury may be inflicted.

Weapon asymmetry is beneficial for winning contests in small but not large males

Although asymmetry may facilitate assessment of rivals in male maritime earwigs, this explanation alone does not explain why greater asymmetry benefits small males competing against small males, and why asymmetry does not benefit large males competing against large males. Though only applying to contests between small males, to our knowledge, the present study is the first to describe a system where greater weapon asymmetry [in terms of "object symmetry" as opposed to two separate structures on either side of the body (Klingenberg et al. 2002)] is associated with successful resource defense. Given that asymmetry may enhance grasping of objects (Inoda et al. 2003), small, male maritime earwigs with more symmetric forceps may be less able to assess a rival due to a diminished capacity to grasp a rival's abdomen, thereby preventing the aggressor from effectively applying pressure with forceps. Such an effect was found in a squat lobster (*Munida rugosa*) where chelae with greater curvature were better suited than straighter chelae for applying pressure (Claverie & Smith 2007).

However, in our manipulation experiment we found a marginally non-significant trend where asymmetry as measured prior to manipulation determined contest success in small males; manipulated asymmetry was not significant (Table 3). It is worth noting that our manipulations likely did not influence contest outcome, because neither asymmetry as measured prior to nor after manipulation determined the outcome of contests between large males. Instead, pronotum width was important for winning contests between large males with manipulated forceps. This is the same result we found in large-large contests in the first part of our study where forceps were not manipulated, which emphasizes the importance of body size and not forceps asymmetry in winning contests between large males.

One interpretation of the results from the manipulation experiment is that a correlate of asymmetry, and not asymmetry *per se*, may be responsible for establishing dominance between small males. While we never observed damage inflicted on rivals, the right side of forceps may be beneficial for piercing and capturing prey. Maritime earwigs are common predators of amphipods of the family Orchestiidae (Behbehani & Croker 1982), which have

softer bodies and were abundant at collection sites (personal observation). Thus, compared to small males with less asymmetric forceps, small males with more asymmetric forceps may have had greater success in capturing prey in the field. Even though we attempted to standardize satiation, the energetic effects in the form of increased glucose or glycogen levels afforded by an enhanced diet (Yuval et al. 1998) possibly carried over into our contests. Indeed, a morphological-independent index of energetic availability determined residency in the bot fly (*Cuterebra austeni*) (Kemp & Alcock 2003). Consequently, asymmetry may be an incidental correlate of fighting ability among small males. Support for this hypothesis could be garnered by repeating the experiment with earwigs raised in the lab that were provided with food ad libitum throughout development, which would give all males the same energetic history. If contest outcome was due to an enhanced diet in nature afforded by weapon asymmetry, then asymmetry should not determine contests between males that were raised in the lab. Other factors that may covary with asymmetry and influence contest outcome may be maneuverability.

Another possibility is that small earwigs did not have experience using modified forceps, and thus did not utilize the novel asymmetry to their advantage. This may indeed be the case since we modified forceps immediately prior to competition. By modifying the left side of one male and the right side of the other, our manipulation may have placed both males at a disadvantage. In the absence of an advantage due to forceps morphology, some other factor should determine contest outcome in small males. Analysis of post-manipulation morphology found that the larger contestant won, which makes sense since body size was found to determine contest outcome between large males. When we repeated the analysis using pronotum width and pre-manipulation morphology, we found that pre-manipulation asymmetry determined contest outcome, supporting our previous hypothesis that asymmetry may have conferred a size-independent physiological advantage for winning contests due to an enhanced ability to capture prey. However, pre-manipulation asymmetry may have been significant because of a correlation between asymmetry and body size (Table 1).

In large males, asymmetric forceps were not important in determining contest outcome. Forceps in large males may be large enough to subdue prey without a need for asymmetry to improve prey capture, as may be the case in small males. Another reason may be because large males settle contests differently than small males, though large and small males appeared to use forceps in the same way. More studies on the effect of asymmetry on other aspects of life history, such as female mate selection and prey capture, may provide a more conclusive explanation for the difference in the importance of weapon asymmetry between large and small males.

Conclusion

Asymmetric weapons in maritime earwigs may be a means for males to assess rivals. While not necessarily important for larger males, based on our results, weapons asymmetry confers an advantage when small males compete. This advantage may be due to asymmetry itself improving the transmission of force applied to an opponent's abdomen, or due to an advantage conferred by asymmetry outside of male-male contests that would also generate an advantage in contests, such as improved prey capture. Given the potential for increased asymmetry to translate into a fitness benefit, maritime earwigs may be experiencing selection for more asymmetric forceps due to competition for food among small males.

Overall, this study provides insight into the function of an asymmetric weapon. The study of functional asymmetry has been recognized as a promising area of research with the potential to give insight into the interplay between developmental and evolutionary mechanisms (Palmer 1996; Palmer 2009). Continued study of function in weapon asymmetry among male maritime earwigs *A. maritima* may continue to be a productive avenue of research. In

addition, understanding the role of female assessment of male weapons and male body size in *A. maritima* will be important in future research.

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Fig. 1.

Examples of forceps from male *A. maritima*. (a) Definition of forceps width (w) and length (l). Dashed line is a reference marker perpendicular to the anterior-posterior axis and tangent to the last abdominal segment. We defined curvature as w/l . (b)–(f) show the diversity in asymmetry in weaponry among the males.

Fig. 2.
An agonistic encounter between two male maritime earwigs. (a) The two males align bodies, facing in opposite directions. (b) The attacking male (on right) uses right (curved) forcep to grab the dorsal region of an opponent's abdomen. Illustrations by Christopher Quock.

Fig. 3.
Example of forceps that were modified on the (a) right or (b) left side.

Fig. 4.

(a) Fraction of agonistic interactions initiated by the contest winner over time during 30-minute contests. Numbers within bars are P values comparing the mean to 0.50. Dominance was achieved after four minutes when the overall contest winner initiated greater than half of the interactions. (b) Mean duration of each fight before (first 4 min) and after (last 26 min) dominance was established. Fights were significantly shorter after dominance was established. Figures show the mean $\pm$ 1 SE. Numbers above each bar indicate the contests with agonistic interactions for that time bin.

Fig. 5. The relation between (a) the difference in pronotum width and (b) the difference in forceps asymmetry with the probability of winning a contest for each of three contest categories. The lines are the fitted probability of winning from the models in Table 2 with either difference in forceps asymmetry, in (a), or difference in pronotum width, in (b), set to zero.

Table 1

Spearman's ρ correlation values (above diagonal) and significance values (below diagonal) among pronotum width and forceps curvature, curvature asymmetry and length.

	Pronotum width (mm)	abdomen width (mm)	Forceps length (mm)	Asymmetry in forceps curvature
Pronotum width (mm)	-	0.94	0.63	0.56
Abdomen width (mm)	< 0.0001	-	0.58	0.61
Forceps length (mm)	< 0.0001	< 0.0001	-	0.027
Asymmetry in forceps curvature	< 0.0001	< 0.0001	0.71	-

Table 2

Results of fitting a logistic regression model to each category separately with contest outcome as the dependent variable and the difference in pronotum width (P) and difference in forceps asymmetry (A) as independent variables.

Contest category	n	Variable	Estimated coefficient	SE	df	χ^2	p	pseudo r^2
Small vs. large	36	P	10.12	4.12	1	28.50	<0.0001	0.83
		A	-14.16	8.76	1	4.19	0.041	
Small vs. small	25	P	0.87	5.09	1	0.029	0.86	0.46
		A	8.52	3.73	1	8.10	0.0044	
Large vs. large	15	P	12.75	7.30	1	5.54	0.019	0.48
		A	2.89	5.38	1	0.30	0.58	

Table 3

Results of a forceps manipulation experiment. For each contest category, two logistic regression models were fitted the difference in pronotum width (P) and either the difference in pre-manipulated asymmetry or manipulated asymmetry geometry (A) as independent variables. Contest outcome was the dependent variable.

Contest category	n	Variable	Estimated coefficient	SE	df	χ^2	p	psuedo r^2
Small vs. small	9							
pre-manipulated forceps		P	-10.27	9.55	1	1.62	0.20	0.66
		A	14.14	12.27	1	3.02	0.082	
manipulated forceps		P	-15.35	9.81	1	4.52	0.034	0.53
		A	-1.03	0.98	1	1.47	0.22	
Large vs. large	13							
pre-manipulated forceps		P	13.04	7.11	1	5.15	0.023	0.44
		A	2.08	5.71	1	0.13	0.72	
manipulated forceps		P	19.85	9.63	1	5.34	0.033	0.53
		A	0.77	0.60	1	1.03	0.22	