

Original Article

Intersexual conflict during mate guarding in an androdioecious crustacean

Chiara Benvenuto^{a,b} and Stephen C. Weeks^a

^aIntegrated Bioscience Program, Department of Biology, The University of Akron, Akron, OH 44325-3908, USA and ^bDepartment of Biological Sciences, Kent State University, 256 Cunningham Hall, Kent, OH 44242-0001, USA

Traditional interpretations of mating behaviors assume cooperation between the sexes. The field of sexual conflict provides a contrasting view: The sexes are commonly in conflict because they diverge in benefits/costs of reproduction. Precopulatory mate guarding, wherein males attempt to monopolize mates by physically pairing before fertilization, is one expected case of conflict. Initial guarding models focused mainly on male reproductive success, considering mate guarding as a pure male mating strategy. Intersexual conflict models instead consider costs and benefits for both sexes. We provide new insights exploiting a promising study system for intersexual conflict: the androdioecious crustacean *Eulimnadia texana*. Androdioecy (coexistence of males and hermaphrodites) provides unique opportunities to test sexual conflict hypotheses because hermaphrodites can facultatively self-fertilize. The ability to self-fertilize is expected to decrease the benefits of mating with males, whereas it is less likely to affect guarding costs.

This asymmetry can thus intensify conflicts, which can be easily detected, if present. We show that hermaphrodites suffer higher costs than males during a guarding event and thus prefer shorter guarding times, whereas males, seeking to avoid loss of mating opportunities, prefer longer guarding times. Moreover, larger male size (relative to hermaphrodite size) confers greater control over hermaphrodites, leading to increased guarding durations. As sexual conflict theory predicts, guarded mates are not “passive” interactors but struggle to maximize their own fitness. The result of the conflict is a compromised guarding time that differs from the optimal strategy of either single sex. *Key words*: androdioecy, *Eulimnadia texana*, intersexual conflicts, mate guarding. [*Behav Ecol* 23:218–224 (2012)]

INTRODUCTION

Recent research reveals that widespread conflicts occur between the sexes, especially during reproduction (Partridge and Hurst 1998; Arnqvist and Rowe 2002, 2005; Martin and Hosken 2003; Parker 2006; Tregenza et al. 2006). One such “sexual conflict” involves the amount of time spent pairing before or after a male fertilizes a female (“mate guarding”). This behavior applies to a broad variety of taxa from invertebrates (including rotifers, spiders, crustaceans, and insects) to vertebrates (including reptiles, birds, amphibians, and primates) and can be performed before mating in order to ensure a mate (precopulatory mate guarding; Ridley 1983; Jormalainen 1998) or after mating (postcopulatory mate guarding) in order to prevent the female from re-mating (Birkhead and Møller 1998) or as a form of ejaculate protection (e.g., in crickets; Loher and Rence 1978; Simmons 1991).

Precopulatory mate guarding is extremely common in crustaceans, spiders, and amphibians, in which female receptivity is restricted in time (Ridley 1983; Jormalainen 1998). Guarding males stay close (or attached) to their mate, waiting for the moment when fertilization can occur (Jormalainen 1998). In crustaceans, this usually occurs when the female molts. The initiation of guarding is an active behavior of males, and for

this reason, initial mate guarding models focused on the parameters males would use to optimize their time, deciding how long to guard a female instead of searching for another (Parker 1974; Grafen and Ridley 1983). Indeed, mate guarding has been historically considered a male mating strategy (but see also Eens and Pinxten 1995): Males attempt to maximize their fitness by monopolizing females (Parker 1974).

There has been a change in perspectives and methodological approaches to the study of mate guarding as an optimal male mating strategy. Instead of focusing on optimality and conflict within a sex (male–male competition), intersexual conflict models analyze costs and optimal strategies in both sexes (Jormalainen, Tuomi, and Yamamura 1994; Yamamura and Jormalainen 1996; Jormalainen 1998). In species where female receptivity is brief, both males and females need the guarding phase to mate successfully. Because female receptivity is so short, mate guarding will assure the presence of both sexes at the right time. According to theory (Jormalainen, Tuomi, and Yamamura 1994; Yamamura and Jormalainen 1996; Jormalainen 1998), if females are receptive (or very close to receptivity), they will not resist guarding because both sexes cooperate during pairing, and thus no conflict arises. If females are far from receptivity, males should not be interested in pairing, and again, there will be no conflict because the lack of interest in mating coincides between the sexes. Traditional models should yield to sexual conflict models when males choose to guard females that are close to but not yet receptive, manifested by males attempting to enforce guarding while females resist (Jormalainen 1998). In fact, as time before molting increases, the costs to females of being

Address correspondence to C. Benvenuto, who is now at UCD School of Biology & Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland. E-mail: cbenvenu@kent.edu.

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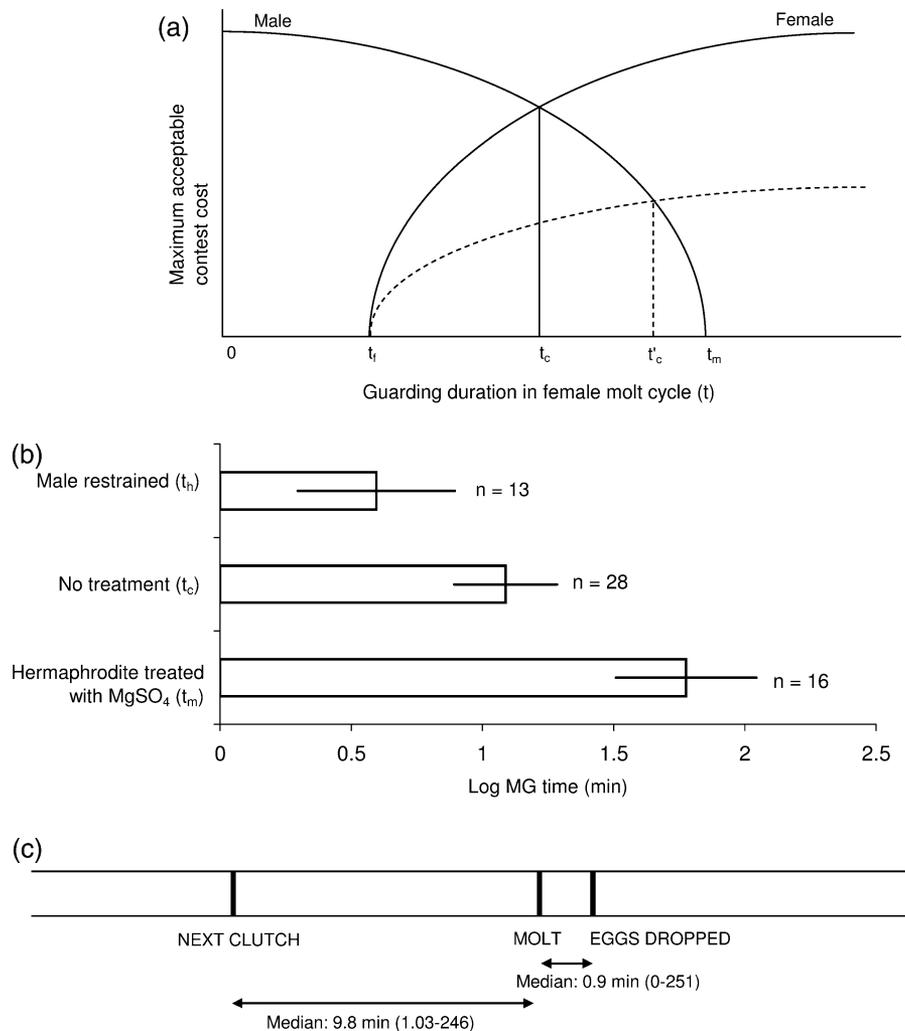


Figure 1

(a) Graphical model of the variation of conflict costs (“maximum acceptable contest cost”) for males and females over a female’s molt cycle; t_f : optimal guarding time for females; t_m : optimal guarding time for males. A compromised guarding time is derived by superimposing the function describing the male’s willingness to persist in guarding onto the female’s willingness to resist guarding. The intersecting point represents the compromised mate-guarding duration (t_c); t'_c : new compromised guarding time when one sex (e.g., males) can exert more power over the other (e.g., due to size difference) and thus can skew the guarding duration toward the optimum of the more powerful sex (t_m) [from figure 2 page 294 in Jormalainen (1998); used with permission of the publisher]. (b) Mean mate guarding (MG) time (\log_{10} transformed) for each treatment. No treatment: represents the compromised guarding time (compare with t_c from [a]); male restrained: represents the optimal guarding time for hermaphrodites (compare with t_f from [a]); hermaphrodites treated with MgSO_4 : represents the optimal guarding time for males (compare with t_m from [a]); see MATERIALS AND METHODS for detailed explanations. Error bars represent two standard errors of the mean. (c) Schematic reproductive cycle of hermaphrodites, modified from figure 1 page 68 in Weeks and Benvenuto (2008); used with permission of the publisher. Please note that the cycle is reported in inverse chronological order, with fertilization of eggs (next clutch) on the left in order to reflect the same order of the x axis in the graphical model (a). The length of the bars in (b) can give an idea of the moment when males start guarding, if compared with the reproductive cycle of the hermaphrodites (c): when males are in charge of the guarding decision (t_m), the guarding phase starts early in the hermaphroditic reproductive cycle, even before the hermaphrodite molts; when hermaphrodites are in charge of the guarding decision (t_f), the guarding phase starts later in the hermaphroditic reproductive cycle.

mate-guarded increase (see the extreme case of juvenile females guarded by adult males; Jones et al. 2010 and references therein). Females “close” to receptivity might experience prolonged energetic costs during mate guarding because they carry guarding males, are limited in their feeding behavior, or are susceptible to higher predation. Thus, such females might be willing to expend energy to avoid being guarded because prolonged guarding is costly to them (see below). Long guarding durations can be so costly to produce detrimental long-term fitness effects (i.e., reduced growth and fertility; Takeshita et al. 2011).

The male’s “optimal guarding criterion” (i.e., the length of the guarding with reduced costs, in terms of losing other mating

opportunities) can be quite long (Jormalainen 1998; Figure 1a) because it assures a mating event. However, females should prefer short guarding times to minimize the costs of being guarded. A compromise in mate guarding duration is predicted with an intermediate “compromised” guarding time (t_c) between male and female optima (Jormalainen 1998; Figure 1a). This compromised time is influenced by the relative “power” of the two sexes (Parker and Partridge 1998): When one sex is stronger than the other, it can shift the compromised guarding time toward its own optimum (Jormalainen 1998; t'_c ; dotted line in Figure 1a).

Sexual conflict models predict intersexual conflicts to be widespread, and yet such conflicts have been difficult to detect

and assess (Arnqvist and Rowe 2002; Chapman et al. 2003). Evolutionary conflicts arise when specific behaviors generate unequal costs/benefits for two individuals. When studying mating behaviors, it is often straightforward to assess and quantify direct mating costs while assuming the benefit of the behavior as a general “mating success.” We pursued a new approach to the study of intersexual conflicts by analyzing mate guarding behavior in a mixed mating system. In such a system, where both selfing and outcrossing are common, not only the costs but also the benefits of mating behavior differ between the sexes. We used the clam shrimp *Eulimnadia texana* (Packard, 1871) as our study organism. In this species, males do not guard females, but rather hermaphrodites, because the genus *Eulimnadia* is androdioecious (Sassaman and Weeks 1993). Males and hermaphrodites coexist in populations, and true females do not exist, a rare condition among animals (Weeks, Benvenuto, and Reed 2006).

The life cycle of these branchiopods is quite short, being adapted to the ephemeral environment they inhabit (such as temporary pools in the deserts of southwestern United States). Upon hydration, nauplii hatch in 24 h from encysted eggs; shrimp reach sexual maturity in a week and they live for an additional 1–3 weeks, depending on the duration of the hydrated pool (Weeks et al. 1997). Hermaphrodites are self-compatible but outcrossing with males does occur. Males usually make up 5–30% of the population in androdioecious clam shrimp (Weeks et al. 2008). Male *E. texana* guard their mates using a pair of their thoracic appendages that are modified into “claspers.” Hermaphrodites lack claspers and thus can either outcross with males or self-fertilize their own eggs. Males clasp the hermaphrodite’s carapace thereby attaining the physical contact necessary to gather information on the receptive state of the hermaphrodite (Weeks and Benvenuto 2008). If a guarding event starts, males can remain attached to their mate for up to 2 h. Males can finally transfer sperm at the end of precopula, after the hermaphrodite has molted (Knoll 1995; Weeks et al. 2004; Weeks and Benvenuto 2008). Sperm cannot be stored to fertilize successive clutches of eggs (Weeks, Crosser, Gray et al. 2000). Fertilized eggs are moved to a brood chamber located at the back of the hermaphrodite. Eggs are then deposited while, or directly before, molting. After molting, hermaphrodites are receptive until the next clutch is moved to the brood chamber and the eggs are again fertilized (Weeks and Benvenuto 2008; Figure 1c). Hermaphrodites produce one or two clutches of eggs a day, from sexual maturity to senescence (Weeks et al. 1997).

Eulimnadia texana is a promising system for studies of mate guarding behaviors and intersexual conflicts in particular because of the copresence of males and hermaphrodites. The main benefit of precopulatory mate guarding is relatively similar for males and females in dioecious species with no sperm competition: Both sexes seek to acquire a mate during the window of receptivity in the female’s reproductive cycle. In androdioecious species, however, the benefit is likely higher for males, who would not reproduce at all if the window of opportunity is missed, than for hermaphrodites, who have the option to self-fertilize. Selfing does incur a cost of inbreeding depression (which is quite high in this species, ranging from 0.5 to 0.7; Weeks and Zucker 1999; Weeks, Crosser, Bennett et al. 2000), proportionally increasing the benefits of outcrossing for hermaphrodites. Nonetheless, males should always have a higher benefit to mate guarding than hermaphrodites in androdioecious species.

To test the intersexual conflict mate guarding model (Jormalainen 1998; Figure 1a), we assessed 1) the incidence of unequal feeding costs to male and hermaphroditic *E. texana* during mate guarding, 2) the optimal mate guarding time for each sex (manipulating the other sex to reduce its

influence on mate guarding duration) and the compromised guarding time (Figure 1a), and 3) the “power asymmetry” (Jormalainen 1998) between the sexes, using individuals of differing sizes (Figure 1a), to test the prediction that such a power difference skews the compromised mate guarding time toward the larger and more powerful interactor (Jormalainen 1998).

MATERIALS AND METHODS

Guarding costs

A variety of possible intrinsic costs can be involved with mate guarding, including survival costs (e.g., different predation on couples vs. individuals; Cothran 2004), energetic costs (Plaistow et al. 2003), and reduced feeding (Robinson and Doyle 1985). In the low-predation environments common to these shrimp (Dumont and Negrea 2002), the last of these costs is likely most important. We analyzed the level of variation in the “fullness of the gut” as a measure of food intake in mate guarding couples. We used individuals from three different *E. texana* populations from the Jornada Experimental Range, Las Cruces, NM, USA. Animals were raised in semi-natural conditions (sediment containing encysted eggs was moved to plastic pools and hydrated on site during July 2005). Newly formed couples were gently removed from the rearing pool using a plastic pipette, whose tip had been cut to enlarge the aperture. Each couple was released into a Petri dish with water from the same pool. Handling was thus minimal. We photographed 69 guarding couples at the beginning and end of the guarding phase. The digestive tract is a clear tube (when empty), slightly curved at the head and near the telson, lacking an enlarged stomach, and fully visible through the transparent carapace. Images were analyzed using GIMP 2.4.7 (GNU Image Manipulation Program). We measured the length of the filled portion of the gut at the beginning and end of the observation to calculate the variation in gut fullness (the length of the filled gut at the end of guarding minus the length of the filled gut at the beginning of guarding). Because these lengths were not normally distributed, we compared the reduction in gut fullness on mate guarding time in the sexes using a nonparametric Spearman’s ρ correlation.

Compromised and optimal guarding times

Encysted eggs were obtained from a dried pond near Portal, AZ, USA. We raised clam shrimp in the laboratory and used similarly sized animals to be individually video recorded for 24 h (using a Panasonic CCD video camera connected to a Samsung SSC-1280 time-lapse video recorder) in 50-ml glass beakers. Hermaphrodites were chosen with eggs visible in their brood chamber at the beginning of the recording (receptivity changes with time and hermaphrodites will molt and drop eggs at a certain point in time during the experiment). Both individuals in each pair were measured with a caliper (maximum carapace length).

Hermaphrodite optimal guarding criterion

Hermaphrodite optimal guarding criterion was assessed by restricting the movement of males. To tether the males, shrimp were placed on a Petri dish and the outer carapace was dried with Kimwipes. One end of a fine cotton thread, dipped in a small dot of non-toxic superglue, was positioned on the carapace. The glue was allowed to dry and the shrimp was quickly returned to the water. The other end of the thread was fixed to the rim of the beaker with a paper clip, leaving

just enough length for the male to swim up and down in the water column. The procedure was fast and harmless but effective in limiting male mobility. Males were given a 5-min acclimation period before introducing two hermaphrodites into the beaker. Males are the more active sex when searching for mates, and thus, when they are constrained, the probability of mate guarding decreases. Therefore, in order to increase the chances of recording a mate-guarding event, we used two hermaphrodites for each male. If more than one hermaphrodite was guarded, only data obtained from the first guarding event were used.

Male optimal guarding criterion

Male optimal guarding criterion was assessed by treating hermaphrodites for 75 min with a 10 mg/ml solution of magnesium sulfate, MgSO_4 (concentration previously used in amphipods; Sutherland et al. 2007). This solution acts as a muscular relaxant: At the end of the treatment, hermaphrodites were lying on the bottom of the beaker, beating their pleopods, but unable to swim. Hermaphrodites were then moved to clean water for 5 min to wash away any residual of MgSO_4 . They were then individually moved to the beaker for recording, where they were paired with a male. The action of the muscular relaxant is temporary and the hermaphrodites recover slowly after some hours. To make sure that the treatment did not alter the normal reproductive physiology of the hermaphrodites, we compared the interval between molting and dropping the eggs in a reduced data set obtained from the treatments (male restrained: $n = 9$; hermaphrodite treated with MgSO_4 : $n = 9$; compromised time: $n = 26$) and also using instances when the hermaphrodites selfed ($n = 70$).

Compromised guarding time

Compromised guarding time was assessed when neither sex was manipulated. We used a one-way analysis of covariance (ANCOVA) to assess variation in mate guarding time in the three treatments: male restrained, female MgSO_4 treated, and compromised (unmodified) guarding time. Our covariate, the size difference between the sexes (male size minus hermaphrodite size), was not significantly associated with mate guarding time ($F_{1,51} = 1.2034$, $P = 0.2778$). Because we also did not detect a significant interaction between treatment and covariate ($F_{2,51} = 0.0508$, $P = 0.9505$), this potential covariate was not considered in the final analysis. Tukey's honestly significant differences test was used to detect significant pairwise differences between the three treatment groups. Sample videos of the experimental treatments are available in the electronic Supplementary Material.

All reported means were calculated by back transformations of the log-transformed analyses, unless otherwise specified.

Effect of size

Immature clam shrimp were raised at low and high densities to obtain mature individuals of different size but the same age. It is commonly observed in the laboratory and field that populations with higher density have smaller individuals (Weeks and Bernhardt 2004). We prepared similarly sized (males and hermaphrodites of comparable size) and differently sized (large males paired with small hermaphrodites and vice versa) pairs. Forty-three couples were video recorded for 24 h. We performed a linear regression on the size difference in each couple (male length minus hermaphrodite length) relative to mate guarding duration. In all analyses, in order to meet the assumptions of normality, mate-guarding time was \log_{10} transformed.

RESULTS

Guarding costs

Hermaphrodites suffered from reduced feeding during mate guarding (Figure 2). The level of gut fullness decreased with increasing guarding duration: Longer times spent in precopula reduced food intake for the hermaphrodites (Spearman's $\rho = -0.41$, $P = 0.0005$; Figure 2) but not the males (Spearman's $\rho = -0.06$, $P = 0.6160$; Figure 2).

Compromised and optimal guarding time

The muscular relaxant did not significantly alter the hermaphrodites' reproductive physiology (no change in the time from dropping the eggs to molting was noted among treatments: Wilcoxon/Kruskal-Wallis test; $\chi^2 = 0.3748$, $P = 0.8291$, $n = 44$, degrees of freedom [df] = 2; including selfing; $\chi^2 = 0.8720$, $P = 0.8322$, $n = 114$, df = 3). Mate-guarding time differed significantly across the three treatments ($F_{2,54} = 17.2242$, $P < 0.0001$, Figure 1b). The optimal guarding time for males (i.e., hermaphrodites treated with MgSO_4 ; mean guarding time = 59.70 min, 95% confidence interval [CI] = 43.54–81.86) was significantly longer than the compromised guarding time (i.e., neither sex treated; mean guarding time = 12.24 min, 95% CI = 9.64–15.54), and the compromised guarding time was longer than the optimal guarding time for hermaphrodites (i.e., males restrained; mean guarding time = 3.94 min, 95% CI = 2.77–5.59).

We also considered the reproductive state of the hermaphrodites (with and without eggs in the brood chamber) at the beginning of mate guarding for each treatment, finding an overall difference in mate guarding time (ANCOVA: $F_{5,50} = 25.2477$, $P < 0.0001$; Figure 3). In each treatment, mate-guarding time was significantly shorter when the hermaphrodites were closer to receptivity (i.e., no eggs in the brood chamber) than when the hermaphrodites had not yet dropped their eggs at the beginning of the guarding phase (Figure 3). We did not detect a significant interaction between size and treatment (ANCOVA: $F_{5,45} = 0.5390$, $P > 0.7$) nor a significant effect of size difference on mate-guarding duration (ANCOVA: $F_{1,50} = 2.9098$, $P = 0.0942$).

Effect of size

The linear regression indicated a shorter guarding duration when hermaphrodites were larger than males ($M-H < 0$) and a longer guarding duration when males were larger than hermaphrodites ($M-H > 0$; $y = 0.228x + 1.049$, $P = 0.002$, $n = 43$, $r^2 = 0.211$, best fit = dotted line in Figure 4), thus detecting a general increase in mate-guarding time as the difference between males and hermaphrodites increased (Figure 4).

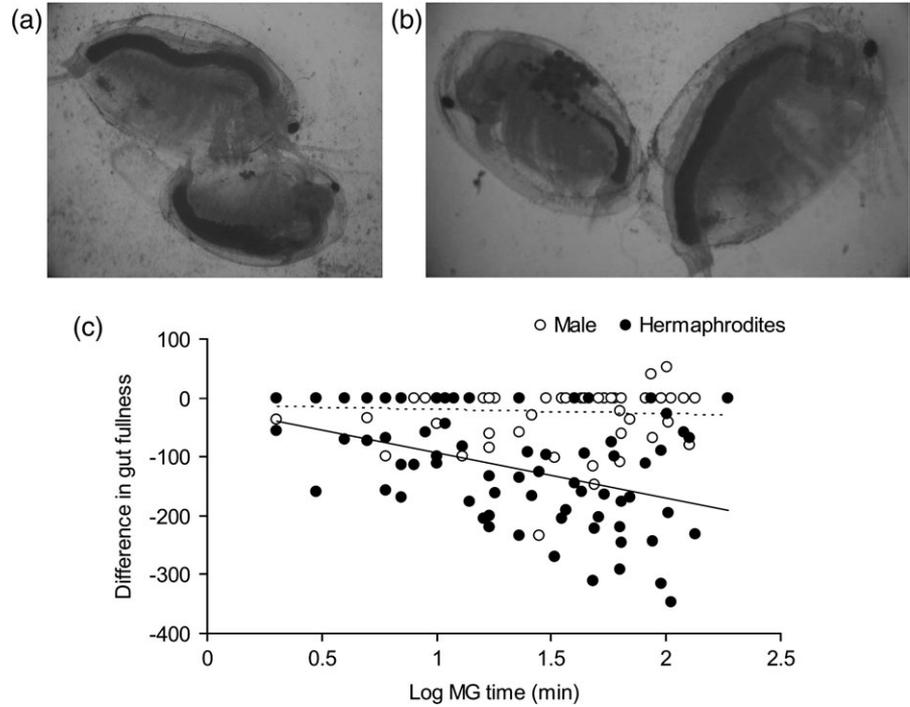
DISCUSSION

Guarding costs

Only hermaphrodites experienced reduced feeding during mate guarding. The higher reduction in food intake for the hermaphrodites corresponded to the longer time they spent being guarded. Clam shrimp are filter feeders, and while engaged in mate guarding, hermaphrodites will close their carapace (which limits filter feeding) as a response to the act of being guarded. Males instead continue to actively swim and filter feed. We have visually assessed the amount of food in the gut as an estimate of ingestion rate. This is a quantitative assay of diet, and even though we did not assess the assimilation efficiency, we expect that a reduction in food intake will likely result in energetic costs. In other crustacean species, males

Figure 2

(a) Representative picture taken at the beginning of the mate-guarding bout (12:05 PM). The male (top) holds the hermaphrodite (bottom) with his claspers. The digestive tract (dark tube on dorsal side of both shrimp) of both the male and the hermaphrodite is nearly full. (b) Representative picture taken at the end of the guarding phase (1:08 PM). Eggs (spheres on the dorsal side of the hermaphrodite—left side of photo) were fertilized and moved to the brood chamber (dorsal side of hermaphrodite) and the male (right side of photo) released the hermaphrodite. Note the decrease of gut fullness in the hermaphrodite during the 63 min of the guarding phase while there is no change in male gut fullness. (c) Reduction in gut fullness from the beginning to the end of the observational period as a function of mate guarding (MG) duration (\log_{10} transformed). Best fit trend line: continuous line (hermaphrodite) and dotted line (male).



suffer higher costs than females: In the amphipod *Gammarus lawrencianus*, males cannot feed while guarding (Robinson and Doyle 1985). In *E. texana*, however, hermaphrodites appear to suffer a higher guarding cost than do males.

Compromised and optimal guarding time

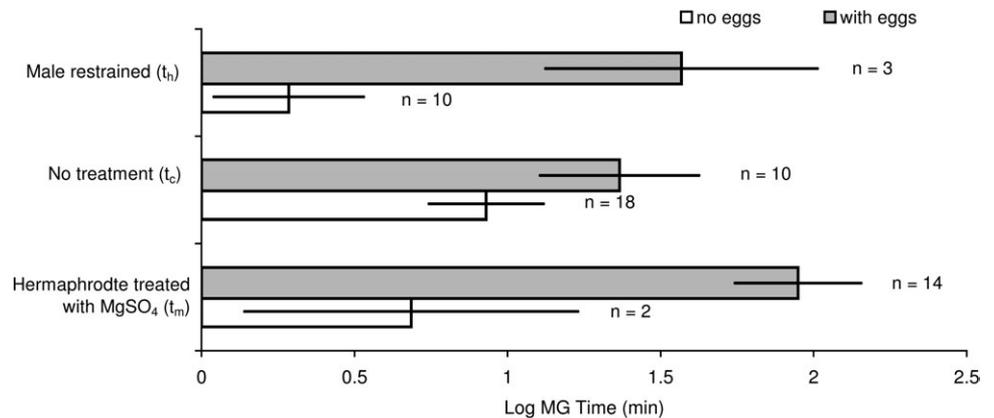
We assessed differences in optimal guarding times (“optimal guarding criteria”; Jormalainen 1998) between the two sexes when we allowed each sex to control the guarding decision (by reducing the ability of the other sex to respond). Additionally, we recorded compromised guarding times when neither of the sexes was manipulated. Mate-guarding duration was longest when hermaphrodites were treated with a muscular relaxant, and thus, their ability to resist mate guarding was inhibited. Mate guarding was shortest when males were restrained in their

movement, and thus, they could not actively seek mates but were rather forced to wait for hermaphrodites to approach them. Hermaphrodites are capable of assessing male presence (Medland et al. 2000) and thus can decide to swim within reach of males when they are ready to be fertilized. An intermediate “compromised” mate-guarding duration was measured when both participants could respond to the other.

These results are consistent with the sexual conflict mate-guarding model (Jormalainen 1998; compare Figure 1a with Figure 1b). We cannot exclude that the manipulations also altered the capability of each sex to provide mutually beneficial signals to the potential mate. Restrained males could not actively seek mates, but because hermaphrodites are able to recognize the presence of males and approach them, the lack of initiative by the males could have been quickly overcome. The muscular relaxant might inhibit hermaphroditic

Figure 3

Mean mate-guarding (MG) time (\log_{10} transformed) for each type of experiment accounting for the receptivity state of the hermaphrodite. Error bars represent two times the standard error.



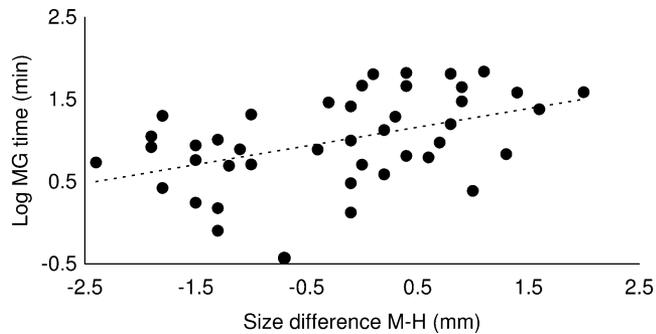


Figure 4
Correlation of size difference between the sexes in mate-guarding couples (male size minus hermaphrodite size) with mate guarding (MG) time (log₁₀ transformed).

behavior(s) that could be important signals to males; nevertheless, the treatment does not affect the hermaphrodite's reproductive cycle and therefore males should still be able to obtain physiological information, such as changes in hormone concentrations, used to assess hermaphrodite's receptivity (Benvenuto 2008). The most parsimonious explanation for these results is that length of guarding is determined via intersexual conflict, in which males and hermaphrodites struggle to shift guarding time to their own optima, rather than a cooperative pairing between the sexes in which the pair follows the male's optimal strategy. In this sexual conflict, males guard longer to assure a successful mating (t_m in Figure 1a,b), whereas females (or hermaphrodites in this case) prefer to shorten guarding duration as much as possible (t_f and t_h in Figure 1a,b) because guarding is costly. A resolution to the conflict is reached between the sexes, with actual guarding duration being a compromise between the two optimal guarding times (t_c in Figure 1a,b). In particular, the closer the hermaphrodites are to receptivity (hermaphrodites with no visible eggs in the brood chamber), the shorter should be the compromised guarding time, with both sexes benefiting. Thus, mate-guarding duration is best explained as a resolution of a conflict rather than the traditional prediction that guarding duration follows the optimal male mating strategy.

Inhibition of female resistance has been used in other mate-guarding studies (Jormalainen and Merilaita 1995; Jormalainen and Shuster 1999; Cothran 2008). As found herein, anesthetized females were guarded longer than unmanipulated controls. Male persistence has traditionally been more difficult to manipulate (i.e., via osmotic stress or clipping of nails or dactyls; Jormalainen and Merilaita 1995; Jormalainen and Shuster 1999). In the current study, we were able to reduce hermaphrodite's resistance and male's persistence independently, which allowed a more complete test of the sexual conflict model than has been possible in other systems.

Effect of size

When a male encounters a possible mate, he can decide if it is favorable to start a guarding phase or not. Once the male starts guarding, the chosen mate can accept or resist the guarding attempt. Persistence and resistance are predicted to be proportional to the balance of costs and benefits determined by the duration of the mate guarding phase as well as the relative power of one interactor to control the other (Jormalainen 1998). We assessed this latter prediction by matching individuals of different size in mate-guarding couples. Larger size of one sex is predicted to alter the compromised guarding duration by shifting the power to the larger interactor, allowing that sex to partially overcome the alternate's persistence

(male) or resistance (female/hermaphrodite). This should result in a skewing of the compromised guarding time toward the optimal guarding time of the larger sex (t_c ; dotted line in Figure 1a). *Eulimnadia texana* hermaphrodites are often seen "kicking" (bending of the abdomen rapidly) when clasped by a male. This can be considered as a possible form of physical resistance to being guarded. The larger the hermaphrodite compared with the male, the more effective will be the resistance. Similarly, the larger the male compared with the hermaphrodite, the easier it will be to overcome the hermaphrodite's resistance. We observed, as predicted, a significant decrease of guarding time when hermaphrodites were larger than males (and thus hermaphrodite resistance was more effective than male persistence) and a significant increase in mate guarding time when males were larger than hermaphrodites (and thus male persistence was more effective than hermaphrodite resistance). Similar results have been reported for the isopod *Idotea baltica* (Jormalainen and Merilaita 1993; Jormalainen, Tuomi, and Merilaita 1994; Jormalainen and Merilaita 1995) and indicate that size represents an important form of differential power between the sexes that modifies the resolution of mate-guarding conflicts, as predicted by theory (Jormalainen 1998).

Although *E. texana* presents comparable sizes for males and hermaphrodites, a sexual size dimorphism has been reported for clam shrimp species belonging to the genera *Limnadia* and *Limnadopsis* (Weeks, Zofkova, and Knott 2006). In the two dioecious genera, males are larger than females and the mate guarding time is significantly longer than in *E. texana* (Benvenuto 2008; Benvenuto and Weeks 2011). Moreover, both *Limnadia* and *Limnadopsis* experience the 50:50 sex ratios typical of dioecious species, while in androdioecious species, the overall sex ratio is highly skewed toward hermaphrodites (Pannell 2002; Weeks, Benvenuto, and Reed 2006; Weeks et al. 2008). An increase in male size might be selected to better control the guarding process and skew the compromised guarding time toward male optima (intersexual conflict) or it might be selected in response to higher male-male encounter rates in dioecious versus androdioecious species (intrasexual conflict).

Eberhard (2005) proposed the use of facultative hermaphrodites as a conceptual example that could increase our understanding of sexual selection. Indeed, in this study, androdioecy revealed what sexual conflict theory predicts to be commonplace: Rather than cooperation during mating, differential mating costs/benefits for the sexes can lead to conflicts that can be resolved by compromise or may end in domination of the more powerful sex over the less powerful. The current study suggests that intersexual behavioral conflicts are indeed more common than traditional behavioral models assume, and thus, studies of precopulatory mating behavior should consider "negotiations" (Martin and Hosken 2003) and compromises between the sexes rather than assume that one sex dominates these interactions.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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