

# Mate guarding behavior in clam shrimp: the influence of mating system on intersexual conflict

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**Abstract** Mate guarding is a male strategy to gain access to receptive females but often results in antagonistic interactions between the sexes because of different costs/benefits of guarding. In addition to social, morphological, and physiological parameters, the type of mating system should also affect the strength of the conflict and thus the guarding duration. Specifically, when compared to females, self-compatible hermaphrodites might have reduced benefits of outcrossing. We investigated mate guarding in dioecious (co-presence of females and males) and androdioecious (co-presence of hermaphrodites and males) branchiopod crustaceans. Both sexes in androdioecious systems should shift their guarding times to lower values relative to dioecious systems because (1) androdioecious males are present in lower percentages than dioecious males and thus encounter rates with receptive mates are relatively greater for them; and (2) hermaphrodites should have low incentive to incur high costs of mate guarding, having the alternative of self-fertilization, and thus should be highly eager to resist. While females preferred short guarding

times, when allowed to control the guarding duration (males tethered), dioecious males did not increase their guarding duration when females (treated with muscular relaxant) could not resist, in contrast to what has previously been found for androdioecious males. This indicates that hermaphrodites are more willing to resist mate guarding than females. The among-species comparisons supported our hypotheses: compromised guarding times were significantly lower in androdioecious than in dioecious species. The introduction of a parameter (mating system) not previously investigated in mate guarding models resulted in a powerful test of mate guarding theory, adding a valuable contribution to our understanding of intersexual conflict.

**Keywords** *Eulimnadia texana* · *Eulimnadia dahli* · *Limnadia badia* · *Limnadopsis tatei* · Androdioecy · Intersexual conflicts · Mate guarding

## Introduction

Precopulatory mate guarding is a behavioral strategy used by males to gain access to receptive females. It is commonly found in species in which female receptivity is limited to a brief period of time, or when the breeding season is particularly short (Ridley 1983; Jormalainen 1998). This behavior has been described in a variety of taxa, from invertebrates (e.g., crustaceans, rotifers, and insects; Rowe 1994; Jormalainen 1998; Schröder 2003) to vertebrates (e.g., anurans, birds, and reptiles; Ridley 1983; Cuadrado 2001; Sinervo and Zamudio 2001; Komdeur et al. 2007). Mate guarding duration can be influenced by several factors such as physiology (e.g., female molting in arthropods; Bauer 1996), morphology (relative size

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between the sexes and variation in male size; Cuadrado 1998; Hume et al. 2002), population structure (e.g., sex ratio and density, which primarily determine mate encounter rate; Jivoff and Hines 1998; Rondeau and Sainte-Marie 2001), and mating history (Sparkes et al. 2002; Ortigosa and Rowe 2003). Many of these factors can also vary temporally in a single mating event (e.g., time to molt) or locally in a single population (e.g., encounter rates in different microhabitats). As a result, the guarding duration is predicted to be quite variable: variability has been documented across species (Jormalainen and Merilaita 1995) and across populations of the same species (Jormalainen et al. 2000).

Intersexual interactions during mate guarding can initiate a conflict if males and females experience different costs and benefits (Jormalainen et al. 1994b; Yamamura and Jormalainen 1996; Jormalainen 1998). The main benefit of guarding is to assure copulation when there is only a brief window of receptivity in females. Costs include an increased risk of predation (couples are more conspicuous than individuals to predators; Cothran 2004), the reduced ability to feed (Robinson and Doyle 1985), and energetic costs (Plaistow et al. 2003). Since costs affect each sex differently, males should prefer long guarding times (optimal male guarding time) to avoid the cost of losing other mating opportunities, while females should prefer short guarding times (optimal female guarding time) to minimize the intrinsic costs of being guarded (Jormalainen 1998). A “compromised guarding time” should result from the relative levels of male persistence to guard and female resistance to being guarded (Jormalainen 1998), and should be somewhere between the optimal guarding times of the two sexes.

The mating system of a group of animals should also influence the strength of the conflict and thus the guarding duration. Emlen and Oring (1977) defined mating system as “...the general behavioral strategy employed in obtaining mates. It encompasses such features as (i) the number of mates acquired, (ii) the manner of mate acquisition, (iii) the presence and characteristics of any pair bonds, and (iv) the patterns of parental care provided by each sex.” Instead of using this ecological framework, Shuster and Wade (2003) analyzed the role of females’ spatial and temporal distribution to determine the mating system. Here, we will refer to another group of mating (or sexual) systems that categorizes organisms on the basis of the presence of sexual types: hermaphroditism (sequential or simultaneous hermaphrodites), dioecy (co-presence of males and females), androdioecy (co-presence of males and hermaphrodites), and gynodioecy (co-presence of females and hermaphrodites). The last two groups are mixed mating systems (mixtures of outcrossing and selfing) and are particularly informative for the study of mating behaviors.

Intersexual antagonistic selection is theorized to be stronger in sexual organisms with internal fertilization and a promiscuous mating system because of the direct interaction of proteins and seminal fluid between females and males and possibly between multiple mates of the same female (Rice 1998). Thus, intersexual conflicts have been analyzed mainly in dioecious and polygamous species. Hermaphrodites represent a unique situation because they can combine, in a single individual, male and female evolutionary interests. In most cases, hermaphrodites are not self-compatible and thus still need mates: costs and benefits related to reproduction will vary depending upon whether the animal acts as sperm donor or sperm recipient. When a specific role is preferred, conflicts can arise (Michiels 1998). Eberhard (2005) suggested using facultative hermaphrodites (organisms where the “female’s strict need of males to reproduce” is removed) as a possible test to investigate sexually antagonistic coevolution. Because self-compatible hermaphrodites do not need males to reproduce (and therefore are less constrained by male counter-adaptations), female traits under antagonistic selection should evolve more freely. Facultative, self-compatible hermaphrodites can avoid “male-imposed costs,” if they are too high, completely avoiding any interactions with males without reducing their fitness to zero (which would happen in females under similar circumstances).

To our knowledge, mate guarding has never been investigated via comparisons of a dioecious system with a mixed mating system. Androdioecy is a rare mating system in animals (see Weeks et al. 2006a and references therein). A comparison of mating behavior in closely related dioecious and androdioecious species allows for the assessment of different strategies used by the different sexes. Clam shrimp (branchiopod crustaceans) are an excellent model system to test the predictions of theoretical models of mate guarding because they present a variety of mating systems (unisexual and bisexual) including parthenogenesis, cyclic parthenogenesis, hermaphroditism, androdioecy, and dioecy (Sassaman 1995; Weeks et al. 2008). Androdioecious and dioecious clam shrimp mate guard in a similar way: males have the first two pairs of thoracic appendages modified into “claspers” which allow them to gain and maintain physical contact with their mate. In androdioecious species, males are the only means of outcrossing: hermaphrodites, lacking claspers, cannot mate with other hermaphrodites (Knoll and Zucker 1995). Thus, hermaphrodites can self-fertilize or outcross with males while females can only outcross. Moreover, the sex ratio is different between the two mating systems: in androdioecious species, males are a smaller portion of the population (15–25%), whereas the dioecious species usually have a 50:50 sex ratio (Weeks et al. 2008).

The first goal of this study was to describe the mate guarding behavior in the dioecious species *Limnadia badia* (Wolf 1911) to assess whether this dioecious clam shrimp is experiencing mate guarding as a form of intersexual conflict (conflicts have been shown to occur during mate guarding in androdioecious clam shrimp; Knoll and Zucker 1995; Weeks and Benvenuto 2008; Benvenuto and Weeks 2011). The second goal of this study was to compare mate guarding duration in four species of clam shrimp, two dioecious and two androdioecious, to note whether the mating system is influencing the strength of intersexual conflict during mate guarding.

The expectations derived from Jormalainen's (1998) model are that each sex in the dioecious species should sustain longer mate guarding times than in androdioecious species, but for different reasons: males should have longer mate guarding because they experience greater male–male competition (due to the sex ratio being less favorable than in androdioecious populations) and females should accept longer mate guarding because they must mate to produce offspring (unlike hermaphrodites that can self-fertilize). Thus, the benefit of being guarded should be higher for females than hermaphrodites. As a result of differences in optimal mate guarding times, the overall compromised time should be longer in the dioecious than in the androdioecious species. A difference in mate guarding duration between two mating systems can represent a measure of the different strength (or resolution) of the conflict involved during precopula. This new approach represents a unique method to explore the ideas of conflict over mate guarding.

## Materials and methods

### Clam shrimp species

We analyzed mate guarding times of four species, all belonging to the family Limnadiidae: two dioecious—*Limnadia badia* and *Limnadopsis tatei* (Spencer and Hall 1896)—and two androdioecious—*Eulimnadia dahli* (Sars 1896) and *Eulimnadia texana* (Packard 1871). These species differ in a number of ways in addition to their mating systems and the sex ratios. Dioecious species live longer (personal observation), present a longer female receptive cycle (i.e., time from molt to the moment eggs are moved into the brood chamber), and have larger individuals of both sexes than androdioecious species (Table 1). Also, a size dimorphism has been reported for *L. badia* and *L. tatei*, with males significantly larger than females, but such a dimorphism has not been reported for clam shrimp in the genus *Eulimnadia* (Weeks et al. 2006c).

### Rearing in the laboratory

Clam shrimp were obtained from encysted eggs contained in sediment collected from various locations: *E. texana*—Portal (31°57.387'N; 109°08.998'W; Wallace Tank), Arizona, USA (this collection site has been referred as WAL in other studies, e.g., Sassaman and Weeks 1993; Weeks et al. 1999, 2000, 2008); *E. dahli*—The Humps (Shire of Kondinin, 32°0.558'S; 118°36.321'E), Western Australia; *L. badia*—Dingo Rock (Shire of Lake Grace, 33°19.009'S; 118°57.534'E) and Puntapin Rock (Shire of Wagin, 33°19.495'S; 117°23.941'E) both in Western Australia; *L. tatei*—Kadji-Kadji (Shire of Morawa, 29°8.233'S; 116°24.833'E), Western Australia.

For all species, ~500 ml of sediment was added to 37-l aquaria which were then filled with de-ionized water. Aquaria were aerated via air stones and illuminated with Durotest sunlight-simulating fluorescent lights. Water temperature was maintained at a constant 27°C. Sexual maturity was reached earlier in androdioecious species (approximately 5–7 days after hydration) than in dioecious species (approximately 10–12 days after hydration for *L. badia* and 15 days for *L. tatei*). Clam shrimp were allowed to feed and mate in the rearing aquaria; animals were randomly selected for the experiments using a plastic pipette, whose tip had been cut to enlarge the aperture.

### Video recordings

Mate guarding time was assessed by video recording individual couples in 50-ml glass beakers with a Panasonic CCD video camera connected to a Samsung SSC-1280 time-lapse video recorder. Tapes were recorded for 72 h (dioecious species) or 30 h (androdioecious species) to document a complete guarding cycle per pair. Clam shrimp were fed at the beginning of the experiment and again every 24 h (a couple of drops of a solution of yeast and ground fish flake food). Since size can affect the guarding duration, the majority of animals were measured with calipers after the trial (maximum carapace length, in millimeters). They were returned to separate aquaria (not to use the same individuals more than once). Tapes were scored for mate guarding time, recording the start of clasping time, the end of clasping, the time at which the eggs were dropped, and the time at which the hermaphrodites/females molted (these last two measures were used to calculate the receptive cycle of hermaphrodites and females).

#### 1. Mate guarding in *Limnadia badia*

We investigated mate guarding duration in the dioecious *L. badia*, following the theoretical framework proposed by Jormalainen (1998): we assessed the optimal mate guarding time for each sex and we

**Table 1** Comparison among the four species for type of mating system; percentage of males in the population; mean ( $\pm$  standard deviation) male and female/hermaphrodite size (in millimeters); reproductive cycle(time from molt to the moment eggs are moved to the brood chamber, mean  $\pm$  standard deviation in minutes)

Species	Mating system	% Males	Mean ♂ size (mm)	Mean ♀ size (mm)	♀ Receptive cycle (min)
<i>Eulimnadia dahli</i>	Androdioecious	26.9 <sup>b</sup>	3.1 $\pm$ 2.5	3.1 $\pm$ 2.6	18.47 $\pm$ 30.40
<i>Eulimnadia texana</i>	Androdioecious	17.9 <sup>a</sup>	4.6 $\pm$ 1.7	4.5 $\pm$ 1.6	10.91 $\pm$ 21.01
<i>Limnadia badia</i>	Dioecious	44.7 <sup>b</sup>	7.1 $\pm$ 0.4	6.4 $\pm$ 0.3	223.57 $\pm$ 272.89
<i>Limnadopsis tatei</i>	Dioecious	52.1 <sup>b</sup>	10.5 $\pm$ 0.5	9.7 $\pm$ 0.6	74.89 $\pm$ 154.06

♂ males, ♀ females or hermaphrodites depending on mating system

<sup>a</sup>Weeks et al. 2006b<sup>b</sup>Weeks et al. 2008

compared it to the compromised guarding time of couples. The optimal guarding time for each sex was measured by restricting the possibility of the other sex to respond (see also Benvenuto and Weeks 2011). Female optimal guarding time was assessed by restricting the movement of males with a cotton thread glued to the carapace. Individual males were removed from the water and placed on a Petri dish. The outer carapace was dried with Kimwipes<sup>®</sup> and one end of a fine cotton thread, dipped in a small dot of non-toxic superglue, was positioned on the carapace. As soon as the glue was dry, the shrimp was 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 on the water column, but not far from the point where it was tied. This procedure is fast and harmless to the shrimp, but effective in limiting mobility. Other than restricting the male movements, and thus reducing the opportunity to actively search for receptive females, the treatment does not affect other male mating behaviors. Males were given a 5-min acclimation period before introducing a female into the beaker. Eight pairings were recorded using animals from Dingo ( $n=3$ ) and Puntapin ( $n=5$ ) populations. Male optimal guarding time was assessed treating females with a 10 mg/ml solution of magnesium sulfate ( $MgSO_4$ ). This solution had been successfully used as a muscular relaxant to assess mating behavior in the freshwater amphipod *Paracalliope fluviatilis* (Sutherland et al. 2007). Females were moved to a beaker full of  $MgSO_4$  solution for 75 min. At the end of this period, females were lying on the bottom of the beaker, beating their pleopods, but unable to swim. Treated females were moved to clean water for 5 min to wash away any residual of  $MgSO_4$  and then individually placed in beakers for recording, where they were paired with a male. Ten pairings were recorded, using Dingo ( $n=2$ ) and Puntapin ( $n=8$ ) populations. In order to obtain data on compromised guarding time, one male and one female were placed in a

beaker to be recorded. None of the individuals were subject to any kind of treatment. A total of 17 pairings were recorded (Dingo rock population).

## 2. Compromised mate guarding across species

Compromised guarding time was also measured for the other three species: the androdioecious species (*E. texana* and *E. dahli*), and the dioecious *L. tatei*. We analyzed a total of 74 couples (19 for *E. dahli*, 31 for *E. texana*, 17 for *L. badia*, and seven for *L. tatei*).

## Statistical analyses

We analyzed the *L. badia* dataset using a blocked, 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. Treatment was considered a fixed effect and outcrop a random effect. Difference in size between sexes (male size minus female size) was assessed as a covariate. The addition of the random effect did not significantly improved the model ( $P=0.34$ ). Both the covariate and the interaction between the covariate and the main effect were not statistically significant ( $P=0.15$  and  $P=0.25$ , respectively), and thus the simpler, one-way ANOVA was used in the final analysis. Tukey's HSD test was used to detect significant pairwise differences between the treatments.

We analyzed variation in mate guarding time between mating systems, nesting species (treated as fixed effect following Gotelli and Ellison 2004) in mating systems. To account for variation in male size, female/hermaphrodite size, and length of receptive cycle of females/hermaphrodites, we used these factors as covariates in a reduced dataset (where we had all measurements of size). The nested, one-way ANCOVA did not find any influence of size (male size,  $P=0.83$ ; female or hermaphrodite size,  $P=0.96$ ) or length of receptive cycle ( $P=0.77$ ) on mate guarding duration. In all cases, the interactions of the possible covariates with the main effects were not significant. We considered the size difference between the sexes as

another possible covariate, which was also not significant ( $P=0.16$ ) nor was its interaction with mating system ( $P=0.54$ ). All analyses were performed using JMP 6.0 (SAS Institute 2003). To meet criteria of normality, mate guarding time was  $\log_{10}$ -transformed.

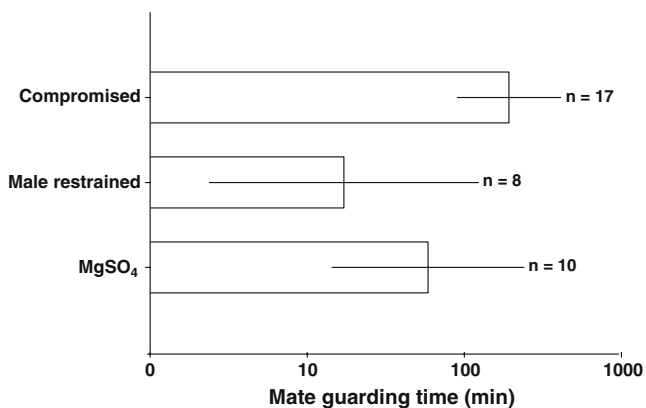
## Results

**Mate guarding in *L. badia*** Treatment (male constrained, female treated with  $\text{MgSO}_4$ , and unmanipulated pair) had a significant effect on mate guarding duration ( $F_{2,32}=4.25$ ,  $P=0.02$ , Fig. 1). The optimal mate guarding time for females, obtained when males were restrained (ranging from 0.98 to 1,382.25 min; median=18.94 min), was significantly lower than the compromised guarding time (from 7.75 to 1,385.25 min; median=229.33 min). On the other hand, Tukey's HSD test did not find any significant difference among the optimal male guarding time (from 1.45 to 577.93 min; median=147.55 min) and the optimal female guarding time or compromised time.

**Compromised mate guarding across species** The statistical analysis revealed a significant difference in mate guarding time among species nested within mating system: dioecious species guarded significantly longer than androdioecious species (Table 2; Fig. 2). Male size, hermaphrodite/female size, size dimorphism, or females/hermaphrodites' reproductive cycle did not influence the effect of the mating system on mate guarding duration.

## Discussion

Enough information has been accumulated on the mate guarding behavior of the androdioecious clam shrimp *E.*



**Fig. 1** Mean guarding time ( $\log_{10}$ -transformed) for each type of treatment in *Limnadia badia* (see text for details). Error bars represent two times the standard error. Mate guarding time is expressed on a logarithmic scale

**Table 2** Nested ANOVA on mate guarding time ( $\log_{10}$ -transformed) among species (nested within mating system)

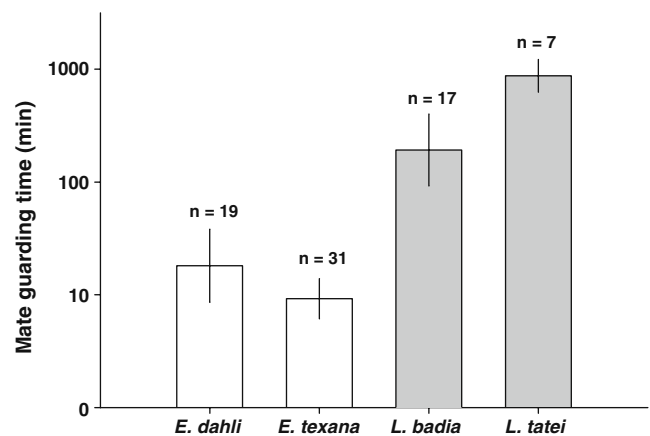
Source	SS	df	F ratio	Prob>F
Species (mating system)	3.14	2	4.70	0.0121
Mating system	31.47	1	94.21	<0.0001
Error	23.38	70		

SS sum of squares

*texana* to consider it a case of intersexual conflict (Knoll 1995; Knoll and Zucker 1995; Weeks and Benvenuto 2008; Benvenuto and Weeks 2011). Given the different costs/benefits of guarding for males and hermaphrodites, the optimal guarding times of the two sexes do not coincide. This leads to a conflict that can be resolved by a compromise (the “compromised guarding time”), subject to the influence of the more powerful sex (e.g., in terms of size). We thus moved onto the analysis of the same behavior in a dioecious species of clam shrimp and in the subsequent comparison in mate guarding strategies between dioecious and androdioecious species.

### Mate guarding in *L. badia*

Female *L. badia* “prefer” to be guarded for a shorter guarding time than the compromised guarding time typical of the species. This is in agreement with the general theory that shorter guarding time is optimal in females (relative to males) because being guarded is costly to females (Jormalainen 1998). Contrary to expectations, and to what was found in *E. texana*, males did not guard females treated with  $\text{MgSO}_4$  longer than untreated controls. We interpret this result as an indication that in dioecious species, males are more capable of forcing



**Fig. 2** Mean guarding time ( $\log_{10}$ -transformed) for four species characterized by two mating systems. Androdioecious species are reported in white; dioecious species are reported in gray. Error bars represent two times the standard error. Mate guarding time is expressed on a logarithmic scale

females into longer mate guarding because female resistance is not efficient, or that females are more willing to be guarded longer in order not to lose mating opportunities, so once the male approaches they will not resist strongly. Anesthetized females of the amphipod *P. fluviatilis* were not guarded longer than the non-treated control (Sutherland et al. 2007) and a similar result was reported for the isopod *Asellus aquaticus* and the amphipod *Gammarus zaddachi* (Jormalainen and Merilaita 1995). If female *L. badia* actually are willing to be guarded longer in order to attain a mating, then the level of the intersexual conflict over mate guarding duration should be lower in *L. badia* relative to *E. texana*.

It is also possible, though, that the  $MgSO_4$  treatment (effective for *E. texana*, in which treated hermaphrodites could not resist and were guarded significantly longer than controls; Benvenuto and Weeks 2011) might not have been sufficient to reduce female resistance for an adequate amount of time to be useful for this experiment. The treatment is temporary, and the chemical has an action that lasts sufficiently long for a species characterized by a very short receptive cycle (Table 1). In *L. badia*, the effect of the muscular relaxant might have been significantly reduced by the time the female was approaching receptivity and the male was interested in guarding. To avoid this problem, two studies on two crustacean species (the isopod, *Idotea baltica*, and the amphipod, *P. fluviatilis*) that guard longer than *L. badia* (average time=37 h in *I. baltica* and 4–5 days in *P. fluviatilis* vs. 7 h in *L. badia*), used daily application of treatment (alloferin in the first case and  $MgSO_4$  in the second) until the guarding started (Jormalainen and Merilaita 1995; Sutherland et al. 2007). In this way, the authors were sure to maintain the female in a constant relaxed state. Because we applied the treatment only once, it is possible that the effect of  $MgSO_4$  was too low to be effective by the time males started

guarding. However, a low female resistance in this species is compatible with the among-species comparisons (see below), so the potential reduction in the effectiveness of  $MgSO_4$  may not have had much of an effect on the current results.

#### Compromised mate guarding across species

In order to address the differences in mate guarding strategies between dioecious and androdioecious species, we compared the compromised mate guarding time of four species, characterized by the two mating systems. The four species expressed significantly different mate guarding times and, more importantly, differences in mate guarding duration were found between the two mating systems. As expected, mate guarding was significantly longer in dioecious than in androdioecious species.

We assessed the importance of male size as a covariate to account for the possibility that increased mate guarding duration was determined by higher energy available to larger animals. Empirical studies had supported the prediction that larger males can actually mate guard longer than small ones (Ridley and Thompson 1979; Ward 1983; Jormalainen et al. 1994a; Hatcher and Dunn 1997). We also added one additional covariate, the length of the female receptive cycle, to account for the possibility that males might make their guarding decisions at the beginning of the female's receptive cycle and thus guard their mates longer because they have a longer receptive phase. Size difference between the sexes was added as a covariate for mate guarding time to account for an increase in mate guarding duration when males were larger than their mates. Neither of these covariates significantly influenced the mate guarding duration.

The precopulatory mate guarding behavior noted in *L. badia* suggests that intersexual conflict is weaker in the

**Table 3** Schematic analysis of the strength of intersexual conflicts during mate guarding in dioecious vs. androdioecious species

MATING SYSTEM	♂ PERSISTENCE	♀ RESISTANCE	♂-♂ COMPETITION*	ENCOUNTER RATES*	♀ BENEFITS OF OUTCROSSING**
Androdioecious	<	>	<	>	<
Dioecious	>	<	>	<	>

Androdioecy	_____				
Dioecy		_____			

← Strength of intersexual conflict

Symbols > (higher than) and < (lower than) are measures of comparison between the two mating systems; \_\_\_ represents the strength of intersexual conflict (not to scale)

♂ male, ♀ female in dioecious system, hermaphrodite in androdioecious system

<sup>a</sup> Influenced by sex ratio

<sup>b</sup> Influenced by mating system

dioecious relative to the androdioecious clam shrimp species. Because females must outcross with males whereas hermaphrodites have the opportunity to self-fertilize, the former might be willing to accept a longer guarding phase. Moreover, dioecious males undergo higher male–male competition, and less frequent encounter rates, than do androdioecious males (due to the sex ratios typical of the two mating systems). This high male persistence, combined with possibly low female resistance, should result in a weaker intersexual conflict over the duration of mate guarding in dioecious than in androdioecious species (Table 3). This prediction appears to be correct: the two androdioecious species had significantly shorter compromised guarding times compared to the two dioecious species.

An alternative hypothesis is that in dioecious species there is a different resolution of the conflict with males controlling the duration of mate guarding since they are larger than females. If this is the case, the conflict, present in the past, was resolved to the advantage of males: an increase in male size could have been selected as a male strategy to prolong mate guarding duration (intersexual competition) as well as a response to direct or indirect male–male competition (intrasexual competition). Still, if we consider the difference between the median optimal guarding time for male (147.55 min) and female (18.94 min) *L. badia* vs. the median optimal guarding time for male (81.66 min) and hermaphrodite (1.53 min) *E. texana*, we notice that this difference is less than two times the length of the receptive cycle in *L. badia* while it is more than seven times the length of the receptive cycle in *E. texana*, suggesting a weaker conflict in the dioecious species.

The comparison of these two mating systems allowed us to test a prediction that indirectly follows from the graphical model of Jormalainen (1998): dioecious species should guard longer than androdioecious species (Table 3). This prediction was not made explicit in the model since the specific case of a comparison between mating systems has never been proposed nor investigated before. However, this difference in guarding duration flows directly from the graphical model outlined by Jormalainen (1998). Thus, the inter-mating system comparison performed here is a valuable extension of Jormalainen's model which validates the underlying theoretical assumptions and predictions of his model.

Numerous empirical studies have used Jormalainen's (1998) model as a theoretical framework for the study of mate guarding. Many studies have confirmed one of the basic assumptions of the model: the existence of differential costs between sexes, either as predation costs (Cothran 2004), energetic costs (Plaistow et al. 2003), feeding costs (Robinson and Doyle 1985; Benvenuto and Weeks 2011), or survival costs (Benesh et al. 2007). The role of intersexual power asymmetry, in the form of size difference between the

sexes, has also been investigated and verified to be important in influencing the guarding duration. Larger individuals are able to persist (males) or resist (females) more than smaller individuals, and thus they can better control the compromised mating time (Jormalainen and Merilaita 1993; Jormalainen et al. 1994a; Benvenuto and Weeks 2011). Finally, manipulative experiments have measured, in accordance with theory, longer optimal guarding times for males when female resistance was reduced (Jormalainen and Merilaita 1993; Jormalainen and Shuster 1999; Cothran 2008; Benvenuto and Weeks 2011) in species where female resistance plays an important role during the mate guarding conflict (but see Jormalainen and Merilaita 1995; Sutherland et al. 2007 for examples of species where this is not the case).

The mate guarding model proposed by Jormalainen (1998) makes specific predictions about mate guarding duration under various compromised intersexual scenarios. One level on which this model can be assessed is by creating a power asymmetry between the sexes (see above). An even more sophisticated approach consists of altering costs and benefits of the mate guarding pairs in order to shift the compromised time in a predictable direction. Species with different costs and/or benefits than the “standard” represent a great opportunity to test the model from this new perspective. We were able to measure a shift of the compromised mate guarding time in response to variation in costs and benefits between the sexes created by their respective mating systems. In this analysis, not only the costs but also the benefits (usually similar between males and females) vary between sexes and mating systems. Through this comparison, we were able to discern differences in mate guarding strategies and to explore the ideas of intersexual conflicts from a unique perspective, strengthening the validity of the antagonistic theory at the base of mate guarding behaviors.

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