

ARTICLE

Takahiro Yamanoi · Kenji Yoshino · Koetsu Kon  
Seiji Goshima

## Delayed copulation as a means of female choice by the hermit crab *Pagurus filholi*

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**Abstract** Male hermit crabs perform precopulatory mate-guarding behavior during their reproductive season. As females generally cannot reject guarding attempts by males, male guarding prevents females from inspecting and choosing other male mates. However, as guarding males are often replaced by other males through competition for females during the guarding phase, females may be able to select males by delaying their copulation. To examine the possibility of female choice by hermit crabs, we investigated whether female *Pagurus filholi* that were being guarded in the field were ready to copulate and spawn. We found that about 30% of females guarded in the field were ready to spawn, indicating that guarded females delayed copulation with their current male. Our results suggest that by delaying copulation females may exploit male–male competition to “choose” dominant males. However, delaying copulation reduced the spawning potential of females. Hence, there is a trade-off between waiting for the opportunity to mate with a dominant male and decreased spawning success if females exploit male–male competition.

**Key words** Copulation delaying · Female choice · Hermit crabs · *Pagurus filholi* · Precopulatory mate guarding

T. Yamanoi  
Laboratory of Biodiversity Science, Graduate School of Agriculture and Life Sciences, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

K. Yoshino  
Center for Marine Environmental Studies, Ehime University, 2-5 Bunkyo-cho, Mastuyama 790-8577, Japan

K. Kon · S. Goshima  
Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate 041-8911, Japan

K. Yoshino (✉)  
Ariake Sea Research Project, Saga University, 1 Honjo-machi, Saga 840-8502, Japan  
Tel. +81-95-228-8846; Fax +81-95-228-8846  
e-mail: c1894@cc.saga-u.ac.jp

### Introduction

As females generally invest much energy in reproduction, they are selective when choosing their mates (Krebs and Davies 1993). Many studies on female choice have been conducted on females that can actively inspect and choose preferred males, for example, lekking animals (Mateos and Carranza 1999; Wilkelski et al. 2001), fishes (Houde 1988; Candolin 2000), anurans (Robertson 1986), crabs (Christy 1987), and insects (Steele 1986). However, because of male coercive behavior, females often may be unable to make their preferred choice.

One male coercive behavior likely to prevent females from choosing other males is contact mate guarding as seen in many aquatic crustaceans (reviewed by Jormalainen 1998). The decision to guard is made by the male, but the success of guarding depends on whether females can resist male guarding attempts (e.g., Strong 1973; Jormalainen and Merilaita 1993, 1995; Jivoff and Hines 1998; Sparkes et al. 2000, 2002). Hence, if females cannot resist male guarding attempts, male guarding behavior may restrict the ability of females to inspect and choose other males.

Most pagurid hermit crabs show precopulatory mate-guarding behavior in which males grasp the rim of the shell of a receptive female with their minor cheliped until copulation (e.g. Imafuku 1986; Elwood and Neil 1992; Goshima et al. 1996, 1998; Wada et al. 1996). Most guarding males are about 1.5–2.0 times larger in body size than females in *Pagurus filholi* (Yoshino et al. 2002), and there is no evidence that females can resist male guarding attempts (K. Yoshino, personal observation). Hence, once guarded, females are apparently restricted in their ability to choose males other than the current guarding male. After the precopulatory guarding phase, females and males ease partially out of their shells in a ventral to ventral position and copulate with their gonopores (located on the coxae of the fifth pereopods of males and the third pereopods of females) facing each other. After spermatophore transfer, males continue guarding until the female spawns in about 10 min. Females have no spermatecae and fully ovulate after

copulation (F. Tombe, unpublished data). Hence, females cannot exercise cryptic choice after copulation either by partly refraining from ovulation and absorbing clutches (e.g. Eberhard 1996; Reyer et al. 1999) or by removing spermatophores (e.g. Thiel and Hinojosa 2003). Are females of such species thus unable to choose males once they are guarded?

Females can avoid copulation with guarding males by withdrawing into their shells. In addition, as females release sex pheromones that attract males of various sizes (Imafuku 1986; Goshima et al. 1998; Yoshino et al. 2004), male–male competition occurs between guarding and rival non-guarding males. Guarding males are often replaced by larger, rival males (Yoshino et al. 2004). Females therefore could exploit this male–male competition and choose larger males than the current guarding male by delaying copulation.

The aims of this study are (1) to see if guarded female *P. filholi* delay copulation, and (2) to see if delaying copulation is costly. To achieve these aims, we used male “attempt tactics” specific to *P. filholi*. Attempt tactics are forcible copulation tactics where males that are similar in size to females try to copulate directly, instead of guarding. A male initiates this process by inserting his cheliped into female’s shell and forcibly pulling her out. Males much larger than females do not employ these behaviors because their chelipeds can be too large relative to the aperture of female shells to draw females out (Minouchi and Goshima 1998). Most females try to resist attempt tactics by fleeing or flicking their cheliped, but are often conquered and forcibly copulated by males within about 10 min (K. Yoshino and S. Goshima, unpublished data). Females will subsequently spawn if attempt tactics succeed. We can easily induce this forcible copulation in the laboratory by pairing a guarded female with a similarly sized male, which enables us to manipulate the timing of copulation. For the first aim, we need to know whether guarded females are ready to copulate and spawn. If not, females may be delaying copulation to ensure they are ready to spawn successfully rather than increasing the period during which males compete. In this study, we therefore investigated whether guarded females spawn after attempt tactics, and whether the number of hatchlings produced by females differed between females mated by attempt tactics and females mated by guarding tactics. For the second aim, we investigated the spawning potential and the number of hatchlings from females under several copulation-timing conditions using attempt tactics as an indicator of delaying costs.

## Materials and methods

### Study site and organism

All *P. filholi* were collected in 2002 on a rocky intertidal flat at Kattoshi, the southwest side of Hakodate Bay, southern Hokkaido, Japan (41°44′N, 140°36′E). Crabs were collected during low tide between April and July (Goshima et al. 1998), which is the main reproductive season of *P. filholi* at

this site. The body size of crabs was measured using an image analysis of a still video (NIH Image version 1.60) of the shield length (SL), which is the length of the calcified anterior portion of the cephalothorax. Minimum size of mature females is about 1.6 mm SL (Goshima et al. 1998). The mean size of guarding males at this site was about 4 mm SL compared to 2.5 mm for paired females (Yoshino et al. 2002). Female size was mainly distributed around 2.0–2.5 mm SL (Yoshino et al. 2001). The main size range of males that can perform attempt tactics was accordingly 2.0–2.5 mm SL. Average guarding period of *P. filholi* after collection from the field is about 2 days, following which the entire precopulatory guarding phase is estimated to last for 5 days at most in the field (Goshima et al. 1998). All crabs were released into their original habitats after each experiment.

### Experiment 1: spawning potential of guarded females

To determine whether guarded females delay copulation, we first investigated, using male attempt tactics, whether guarded females were ready to spawn. If guarded females were ready to spawn, the females would spawn after forcible copulation by attempt tactics. We collected guarding pairs from the field. As *P. filholi* is multivoltine, males often guard ovigerous females. We separated collected pairs and picked the female up with tweezers so the shell’s aperture was uppermost. When the female emerged from her shell we observed whether eggs were attached to her pleopods. In total, 40 guarding pairs, of which females were not ovigerous (assumed to be the first reproduction of the year), were used for the experiments.

The 40 pairs were randomly divided into two groups of 20 pairs. Females of one group were put individually into an experimental cylindrical plastic cage (5.1 cm diameter × 9 cm high) filled with fresh seawater. Small cages were used for the attempt-tactics group to increase the probability of the introduced male encountering the female during the experiment. A male of similar size (about 2.0–2.5 mm SL) was introduced to the female to induce copulation by attempt tactics. In general, males responded swiftly to the previously guarded female. However, as receptivity to female sex pheromones varies between males (i.e., some males do not copulate with receptive females), we repeated attempt-tactic trials up to three times if swift approach to females was not observed, to eliminate the possibility that the ripe female did not spawn due to being paired with a non-receptive male. We therefore assumed that females were not ripe enough to spawn if they did not spawn with the introduced males. Three hours later we examined whether females were brooding eggs as described above.

The other 20 females remained paired with their original males as a control group. In contrast to the attempt-tactics copulation group, we offered each pair a relatively large tank (19.5 × 12 × 7 cm high) to reduce unnecessary stress. Similarly, we checked the spawning of these females 3 h later. We analyzed by *G* test if the spawning frequency for females mated by males using attempt tactics was higher

than that of females mated by guarding males (control). If so, females either delay copulation or males are successful in forcing females to copulate and spawn prematurely.

#### Experiment 2: hatching success of females mated by males using the two tactics

To determine whether females mated by males using attempt tactics suffer a reduction in reproductive output, we compared the number of hatchlings from females spawned by guarding and attempt tactics in June 2003. If guarded females delay copulation, hatching success would not differ between females spawned by attempt tactics and guarding tactics. We collected guarding pairs from the field and put each pair into a small cylindrical cage (5.1 cm diameter  $\times$  9 cm high). Similar to experiment 1, we used only pairs whose females were non-ovigerous. These pairs were randomly divided into two groups. Females of one group ( $n = 24$ ) remained paired with their original male to represent natural spawning by guarding tactics (i.e., the females were allowed to decide their preferred copulation timing). Females of the other group ( $n = 32$ ) were offered a similar size male instead of the original male (i.e., females were forced to copulate with the male by attempt tactics).

After spawning, we reared females of both groups individually in their cages until hatching and counted the number of hatchlings produced by each female. Every day we counted the number of eggs that detached from each female's pleopods and the eggs that dropped out of her shell during rearing. Females release all eggs of a clutch after copulation (F. Tombe, unpublished data), so the difference in the number of detached eggs between the two groups indicates egg loss due to differences in mating tactics. For the attempt-tactics group, we used females that copulated on the day of collection to ensure that most females in this group experienced earlier copulation than they would have if guarded (2 of 32 cases were eliminated). Females in the guard group spawned on average after  $2.125 \pm 1.261$  days (mean  $\pm$  SD).

The SL of each female was measured by still video analysis (NIH image version 1.60). The number of hatchlings produced by females was analyzed by ANCOVA with female SL as a covariate, because female fecundity increases with size (Yoshino and Goshima 2001). First we tested for an interaction between our factor (copulation by attempt or guarding tactics) and the covariate (female SL). If no interaction was found, we treated the interaction as random error and pooled it in the error term. Including covariates in an ANCOVA is meaningless if the covariates' effects are not significant. However, we used covariates in statistical models if the effect was suspicious (i.e. if  $P < 0.1$ ). Data were not transformed.

#### Experiment 3: reproductive output and copulation timing

To see if delaying copulation is costly, we examined whether spawning ability and the number of hatchlings decreased as

the timing of copulation was delayed. We collected 60 guarding pairs and separated the sexes. Only non-ovigerous females were used for this experiment. The females were randomly divided into 4 groups of 15 individuals. Each group was assigned to copulate on the day of collection, or at 3, 7 or 10 days after collection. Each female was placed alone in an experimental cage (5.1 cm diameter  $\times$  9 cm high) filled with fresh seawater. Females were mated by males using attempt tactics as described for experiment 1.

For each group, we recorded the number of females that spawned, and analyzed by  $G$  test if the frequency of females that spawned decreased with copulation delaying. Females that copulated were housed at room temperature (20–25°C) under natural light. We counted the number of hatched zoea larvae produced by each female. Females under guarding may be unable to forage actively because of male grasping. Therefore, we did not feed the females during this experiment, but exchanged seawater every 3 days. The number of hatchlings was analyzed by ANCOVA in the same way as experiment 2. Data were not transformed.

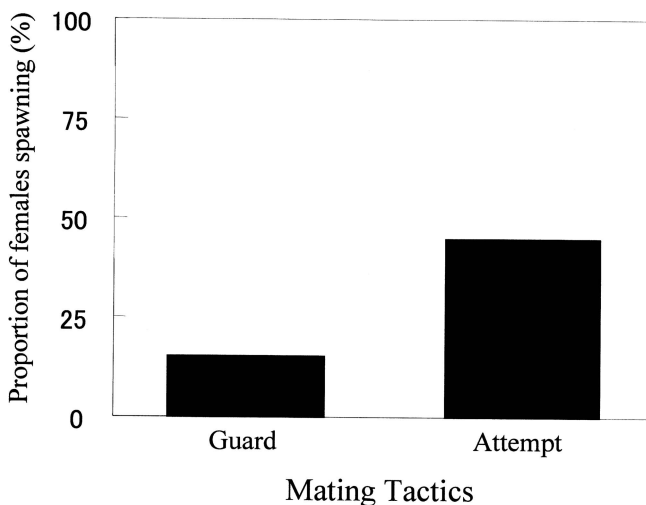
## Results

#### Experiment 1: spawning potential of guarded females

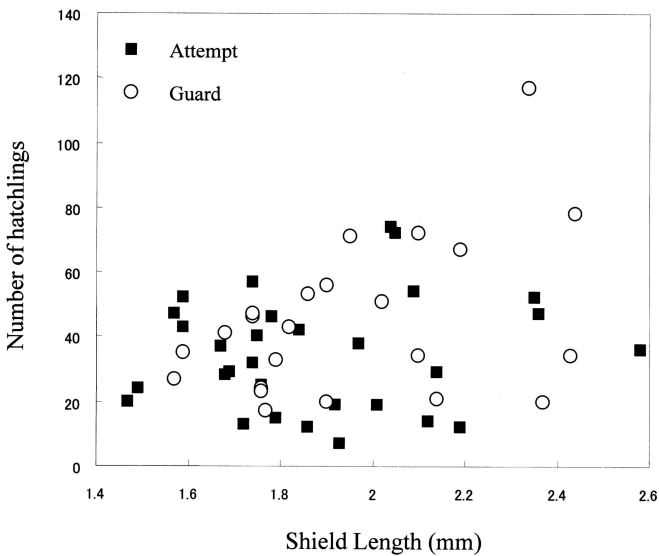
The proportion of females spawning within 3 h was significantly higher for females mated by males using attempt tactics than females mated by males using guarding tactics ( $G$  test,  $G = 4.44$ ,  $df = 1$ ,  $P = 0.035$ ; Fig. 1).

#### Experiment 2: hatching success of females mated by males using the two tactics

Two females from the guarding group and five females from the attempt group detached one egg, and one female in the



**Fig. 1.** Proportion of females spawning within 3 h mated by males using attempt (forcible copulation) and guarding tactics (control). Both sample sizes are 20

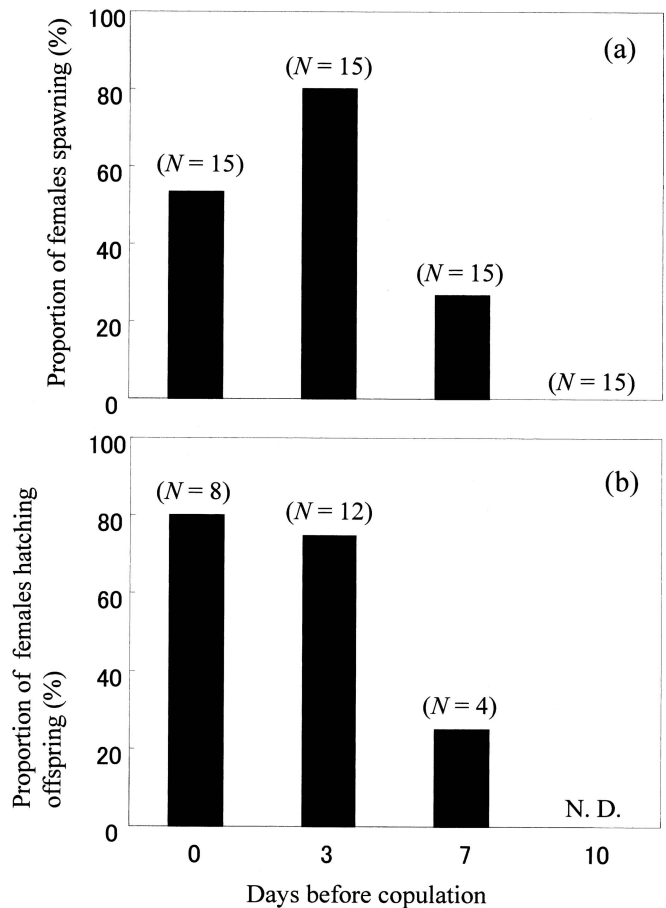


**Fig. 2.** Number of hatchlings from females mated using attempt and guarding tactics

attempt group detached four eggs. For the number of larvae produced by females, there was no interaction between mating tactics employed by males and female SL ( $F_{1,49} = 1.972$ ,  $P = 0.167$ ). There was no difference in the number of larvae produced by females between the guarding and attempt groups ( $F_{1,50} = 2.43$ ,  $P = 0.125$ ; Fig. 2) when controlling for female SL ( $F_{1,50} = 3.86$ ,  $P = 0.055$ ).

### Experiment 3: reproductive output and copulation timing

The proportion of females spawning varied depending on the timing of copulation (Fig. 3a:  $G$  tests,  $G = 27.17$ ,  $df = 3$ ,  $P < 0.001$ ). The number of females spawning decreased markedly between females that copulated at 3 days and 7 days after collection ( $G$  test,  $G = 8.80$ ,  $df = 1$ ,  $P = 0.003$ ,  $< 0.017$ ; type I error rate was adjusted by Bonferroni). Females did not spawn at 10 days after collection. In *P. filholi*, the ability to postpone spawning by females may last for about 3 days. However, females that spawned did not necessarily hatch their eggs (Fig. 3b). Though differences in the number of females hatching larvae following different delays before copulation was not statistically tested due to the small sample size, we compared the number of larvae hatched between females that copulated on the day of collection and females that copulated 3 days after collection. The interaction between female SL and days before copulation was not significant ( $F_{1,11} = 0.051$ ,  $P = 0.826$ ). The number of larvae hatched did not depend on the number of days before copulation (female SL,  $F_{1,12} = 4.62$ ,  $P = 0.053$ ; days before copulation,  $F_{1,12} = 0.123$ , 0.731). On average females that copulated on the day of collection hatched  $35.67 \pm 12.25$  ( $n = 6$ ) larvae compared to  $29.68 \pm 11.03$  ( $n = 9$ ) larvae hatched by females that copulated 3 days after collection. As eggs of females that copulated 7 days after collection did not hatch, except for one female that hatched four larvae, we could not compare the number of



**Fig. 3.** Proportion of females spawning when copulation was delayed for 0, 3, 7 and 10 days after collection from the field (a) and proportion of the females hatching offspring (b). *N.D.* indicates no data. The *number in parentheses* is the sample size. Note that proportion of females spawning are the percentages of the sample size of females hatching offspring out of 15 females

larvae hatched by this female statistically with that of the females of the other groups.

## Discussion

As reproductive success of male hermit crabs is proportional to the number of females they copulate with (Harvey 1990), it is adaptive for males to copulate swiftly and search for another female if females they guard are ready to copulate and spawn without deleterious effect on hatchlings. In this study, we found that several guarded females were mature enough to copulate and spawn (Fig. 1) without deleterious effect on the subsequent hatchlings (Fig. 2). Hence, the difference in the spawning proportion between females mated by attempt tactics and by guard tactics is not due to guarding males' copulation delaying but due to copulation delaying by females. At least 30% of females guarded in the field (Fig. 1; the difference of frequencies) had deliberately delayed their copulation with the guarding male.



Female *P. filholi* may exploit male–male competition to mate with the competition winner (i.e., the one with high resource holding potential) by delaying their copulation. Females of *P. filholi* near spawning release sex pheromones that attract males even after they are being guarded (Imafuku 1986). In the field, to what extent delaying copulation presents females with the opportunity to exploit male–male competition is unclear, however, a few cases of competition between non-guarding and guarding males have been observed in the field (K. Yoshino, personal observation). In the laboratory, aggressive competition between guarding males and non-guarding males is easily observed, and takeovers by non-guarding males often occur if they are larger than guarding males (Yoshino et al. 2004). In the isopod *Idotea baltica* (Jormalainen and Merilaita 1993, 1995) and *Lirceus fontinalis* (Sparkes et al. 2000, 2002), females aggressively struggle against male guarding attempts, which acts as female choice. Female blue crabs, *Callinectes sapidus* also have the potential to choose large males by resisting male guarding attempts (Jivoff and Hines 1998). In contrast to these species, female *P. filholi* cannot resist male guarding attempts, and therefore delaying copulation may be effective for choosing males of higher quality. Effectiveness of mate choice by controlling of reproductive timing has also been shown in other studies. In fallow deer, females have the potential to choose males by controlling their estrus (Komers et al. 1999). American lobsters have the potential to choose dominant males by controlling their molt timing (Cowan and Atema 1990).

The results of experiments 1 and 2 show females delay their copulation even after their eggs become fully ripe. However, we must note that about 50% of guarded females did not spawn after attempt tactics in the experiment 1. This suggests that female *P. filholi* attract males and induce male guarding behavior by sex pheromones before they are ready to spawn. Small males using attempt tactics do not succeed unless females are ready to spawn. Female sex pheromones may operate to attract large guarding males in advance so that females can avoid mating with small males employing attempt tactics. Most brachyuran females also attract males long before they mate (Christy 1987). Sex pheromones may also act as female choice in these species.

Delaying copulation may be effective for mate choice, but it can also be costly for reproductive output. The prolonged time to copulation decreased females' spawning potential (Fig. 3a). A similar example was also found in king crab (McMullen 1969). Delaying copulation for long periods after eggs have matured may deteriorate the subsequent embryonic development of eggs, which may cause partial or full absorption of clutches by females leading to decreased spawning potential. Another possibility is that females absorbed clutches as a result of starvation due to the present experimental design. If guarded females cannot actually forage in the field, delaying copulation will decrease spawning potential by prolonging starvation. Whatever causes the reduction in female spawning potential of *P. filholi*, excessive delay would be costly to female in terms of reduced output or missed opportunities for reproduction. When copulating, females must decide

between the cost of delaying and the benefit of mating with high quality males.

Our study showed that female *P. filholi* could delay copulation with guarding males by increasing the interval over which male–male competition can occur. Females may use this strategy to choose male mates actively while under male coercion. Female choice by exploitation of male–male competition is found in brachyuran crabs (reviewed by Christy 1987) and in rock shrimp (Thiel and Correa 2004). This mechanism of female choice may be important in many other crustaceans with precopulatory mate guarding, for example, in amphipods (Elwood and Dick 1990) and lithodid crabs (Goshima et al. 2000; Wada et al. 2000). There may be some other female strategies for choosing mates. We need to draw more attention to female mating behavior so as not to miss hidden female strategies for choosing mates.

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