

Martin Thiel · Ivan A. Hinojosa

Mating behavior of female rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea)—indication for convenience polyandry and cryptic female choice

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Abstract While studies on a wide diversity of organisms have demonstrated the importance of female behavior during matings, in crustacean studies, a strong bias towards male mating behavior prevails. Reproductively mature rock shrimp (*Rhynchocinetes typus*) exist as several ontogenetic stages that differ in their morphological and physiological capacities. In natural populations, the majority of males are in early ontogenetic stages (termed *typus*), many are in intermediate stages (*intermedius*), and few are in the terminal molt stage (*robustus*). Dominant *robustus* males, which have already demonstrated their biological fitness by surviving to this stage, have previously been shown to have a higher potential than subordinate *typus* males to defend receptive females against other males, and fertilize the entire clutch of a female. While females should thus show a preference for *robustus* males, they nevertheless frequently receive sperm from *typus* males. These observations suggested that females might have mechanisms to discriminate against sperm from subordinate males. In laboratory experiments, we observed that females avoided being seized by *typus* males for longer time periods in the absence of *robustus* males than in their presence. Following seizure, females that were initially held by *typus* males, required more time to initiate spawning than those held by *robustus* males. Many *typus* males transferred spermatophores to females before these started to spawn while *robustus* males waited until females began to spawn before they transferred spermatophores. Females manipulated spermatophores received from *typus* males for long time periods (minutes), but not those they received from *robustus* males. By accepting sperm from subordinate *typus* males, females may avoid further harassment (convenience polyandry), but they subse-

quently may discriminate against these subordinate males by delaying spawning and removing their sperm. These observations suggest that female behavior influences the outcome of matings, favoring fertilization of eggs by sperm from dominant males. Convenience polyandry and cryptic female choice may be common in other crustaceans as well.

Keywords Shrimp · Multiple mating · Female choice · Sperm removal · Male harassment

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Introduction

Females of many organisms receive sperm from multiple males, causing intense sperm competition (e.g. Birkhead and Møller 1992, 1998; Simmons 2001). Studies including a wide diversity of species have demonstrated that female behavior can have a strong influence on the outcome of sperm competition (Eberhard 1996). In general, it is thought that females discriminate against sperm from males of inferior quality (Simmons 2001). Thus, female choice of sperm is primarily expected to occur in species in which males of different quality participate in matings. Females may exert choice on male sperm by a variety of mechanisms, e.g. by remating with other males, by discarding sperm from one (or more) males, or by suppressing or delaying ovulation (Eberhard 1996). Since these female behaviors are often difficult to observe, they are said to result in cryptic female choice. Here we use the term cryptic female choice to refer to female behavior that is directed toward sperm and that biases the outcome of competition for fertilizations.

Females of many species engage both in overt and in cryptic mate choice (Eberhard 1996). In some species, though, the capability of females to engage in overt mate

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M. Thiel (✉) · I. A. Hinojosa
Facultad Ciencias del Mar,
Universidad Católica del Norte,
Larrondo 1281, Campus Guayacan, Coquimbo, Chile
e-mail: thiel@ucn.cl
Fax: +56-51-209812

choice is limited due to environmental conditions or the imposing behavior of males. Females may limit their resistance to male mating attempts if resistance increases the risk of predation or injury (Reynolds and Gross 1990; Rowe and Arnqvist 2002). Females of many of these species may obtain sperm from multiple males that differ in their quality (e.g. Arnqvist and Danielsson 1999; Cordero and Andrés 2002). In this case, females may use cryptic choice to select the sperm of high-quality males.

Cryptic female choice should be common in polyandrous species in which sexually mature males vary greatly in quality and the costs of precopulatory mate choice are high (Brown et al. 1997; Reyer et al. 1999; Pizzari and Birkhead 2000). These conditions occur in many crustacean species. Males may reach sexual maturity early during ontogeny when their secondary sexual characters are not yet fully developed. Consequently, these small males have a low potential to acquire important resources or defend females. Although not yet fully mature morphologically, small males often can subdue reproductive females and mate with them (Van der Meer 1994; Clark 1997; Jivoff and Hines 1998a; Jormalainen 1998). Females may resist such mating attempts but resistance may be costly (Arnqvist and Nilsson 2000; Jormalainen et al. 2001), and females may stop resisting after variable time periods. Forceful mating may be particularly common in crustacean species where males attach sperm externally to the female (e.g. Ra'anan and Sagi 1985). In many crustacean species, females receive sperm from multiple males that may differ substantially in their quality (Sainte-Marie et al. 1999; Clark and Caudill 2001), conditions favoring cryptic female choice. Nevertheless, female behavior has received relatively little attention with respect to its role in the outcome of sperm competition. In a first description of the mating behavior of *Rhynchocinetes typus*, we also paid most attention to the conspicuous mating behavior of males (Correa et al. 2000). Males of this and other crustacean species seize females and hold them with their pereopods for variable time periods, during which sperm transfer takes place. In *R. typus*, the males transfer several spermatophores to the ventral side of the female's abdomen, and fertilization occurs externally at the moment when the eggs are transferred from the female's gonopore to the pleopods, where females then incubate the developing embryos for several weeks. Females may mate sequentially with multiple males during one reproductive cycle, as has also been observed for several other crustaceans (e.g. Christy 1987; Diesel 1990, 1991; Koga et al. 1993; Sainte-Marie et al. 1999).

In the rock shrimp, *R. typus*, males first reach sexual maturity in the female-like typus stage. As they age and grow, males pass through several intermedium instars before reaching the terminal molt stage, termed robustus, which is characterized by highly developed 3rd maxillipeds and 1st chelipeds (Correa et al. 2000). All male stages can mate successfully in a non-competitive environment (Correa et al. 2000), but because they do not need to invest energy in further growth, robustus males

have a higher potential than typus males to engage in multiple matings and to fertilize the entire clutch of a receptive female (Hinojosa and Thiel 2003). Furthermore, in a competitive environment, robustus males can take over and defend receptive females against other male stages. Nevertheless, typus and intermedium males sometimes transfer spermatophores to females before robustus males encounter them or during struggles between dominant males (Correa et al. 2003). These observations suggest that females might prefer and benefit from mating with a robustus male since these have already proven their biological fitness by reaching the terminal molt stage. Therefore, we predicted that females should: (a) show a preference for dominant robustus males, and (b) exert cryptic female choice against sperm received from subordinate typus males.

Methods

Collection and maintenance of rock shrimp

Shrimp were collected during austral spring (October/November 2000) by scuba-diving in Bahía La Herradura, Coquimbo, Chile (29°59'S, 71°22'W). Shrimp were collected with a diver-operated airlift suction sampler (Wahle and Steneck 1991) in their natural habitat, shallow subtidal hard-bottoms. Immediately after capture, shrimp were transferred to the flowing-seawater laboratory where they were sexed and measured. Individuals of different sex were maintained in separate holding tanks in order to avoid uncontrolled matings. During the holding period, shrimp were fed with dead fish, crushed bivalves and the soft parts of ascidians. Females were maintained in groups of ~40 individuals, and each afternoon the tanks were checked for shed exuviae and for the corresponding molted females. These females were then held in separate small containers to be used the following day in the experiments. All shrimp were returned to their natural environment immediately after the experiments.

Experimental design

We only used the first and the last ontogenetic male stages since these differ most strongly in their morphological and physiological characters. If females distinguish between males, then it is most likely that they distinguish between these two male stages. All typus males were female-like in morphological appearance while the robustus males featured the strongly developed 3rd maxilliped and 1st cheliped, typical for this stage (for detailed criteria, see Correa et al. 2000). The experiments were conducted in glass aquaria (26 cm×30 cm surface area, 25 cm deep) that allowed free view for the observer. Previous experiments had demonstrated that shrimp apparently behaved normally in this experimental environment (Correa et al. 2000, 2003). All experiments were done during the day, because in the natural environment, rock shrimp are frequently found mating during the day (C. Correa and M. Thiel, unpublished data). We conducted direct observations because spawning contractions and other movements by females, which are held by the males in the characteristic cage state (see Correa et al. 2000), are difficult to quantify using video-recordings. Additional matings were staged in order to video-tape and describe these behaviors in detail. All experiments and video recordings (camera: JVC videomovie GR-AX606) were conducted during natural daylight in the laboratory, without use of artificial light sources.

Two types of experimental set-ups, with two sexually mature males plus a receptive female each, were used in this study. In one set-up, both males were in the typus stage (typus and typus), while in the other set-up one male was a subordinate typus and the other a

dominant robustus (typus and robustus) (Fig. 1). The rationale for this set-up was that, in a competitive situation, subordinate typus males differ in their mating behavior from that of dominant robustus males (Correa et al. 2003). Typus males typically transfer spermatophores as soon as they get hold of the female, while robustus males first employ behaviors thought to stimulate the female (Correa et al. 2000) before transferring spermatophores.

In each replicate experiment, the receptive female was introduced together with the males, but held under a plastic bell for 15 min before being released. Following release of the female, the behavior of the shrimp was observed initially for 30 min. If, during this time period, mating was initiated, we watched the shrimp for 30 min more. We recorded the moment at which a male first seized the female, when males transferred spermatophores and when the female started spawning. Fertilization occurs on the ventral side of the female's abdomen after spermatophores have been transferred. Preliminary observations had revealed that females occasionally manipulate their abdominal region. This behavior was described in detail and its duration was quantified.

Evaluation of the data and statistical analysis

We evaluated whether time until first seizure of the female differed between the two set-ups using the Mann-Whitney test. For this test, we did not consider for the second set-up whether the female was seized by a typus or by a robustus male.

Herein, our intention was to present the female with subordinate males only and with the possibility to chose between a subordinate and a dominant male. Since the mating sequence of multiple males is of great importance (see, e.g., Birkhead and Møller 1992, 1998; Pizzari and Birkhead 2000), we examined whether the ontogenetic stage of the male that first seized the female affected her behavior. In the first set-up (typus and typus), females were seized only by typus males, whereas in the second set-up (typus and robustus) the first male partner could have been either a typus or a robustus male. Thus, there were three first-male treatments, the first being typus in presence of another typus, termed "typus(typus)", the second being typus in presence of a robustus, termed "typus(robustus)", and the last one being robustus in presence of a typus, termed "robustus(typus)". In the second set-up, which results in two different first-male treatments, "typus(robustus)" and "robustus(typus)", one could suspect that replicates in these two treatments were not completely independent. However, all females used in this study

(10.6–15.4 mm carapace length, CL) were of similar size ranges and were randomly assigned to the different set-ups. Furthermore, a post-hoc analysis revealed that, in the second set-up, there were no significant size differences between females that were first seized by a typus male and those first seized by a robustus male (t -test: $t=1.194$; $df=17$; $p=0.249$). We therefore consider it justified (and necessary—see arguments above) to distinguish two first-male treatments in the second set-up.

We evaluated whether the first-male treatments had a significant effect on the duration of the following time intervals: (1) first seizure—start of spawning, (2) start of spawning—transfer of first spermatophore, and (3) duration of abdominal manipulation by the female. Since the data did not meet the requirements for parametric statistics, we utilized non-parametric tests (Kruskal-Wallis, followed by Dunn's Test). For all statistical comparisons conducted herein, the significance level was $\alpha=0.05$.

Results

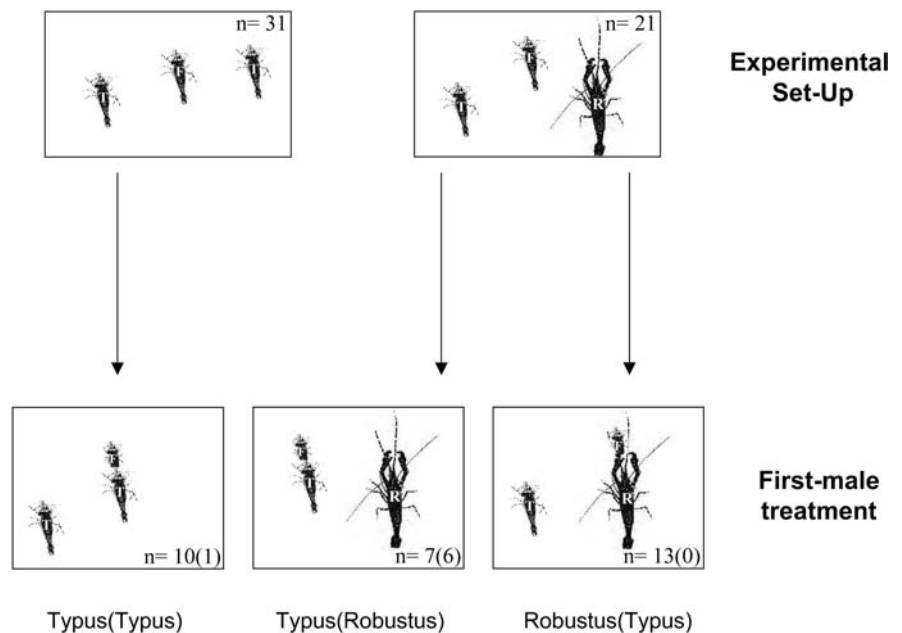
Male mating sequences

In the set-up with two typus males, females spawned following sperm transfer from a typus male in only 10 out of a total of 31 replicates. In nine of these ten cases, only one typus male mated (Fig. 1). When a robustus male was present, in all but one replicate, at least one male mated (Fig. 1). In six replicates, a typus male mated first, but later (within 1–15 min) was displaced by a robustus male. In only one case did the typus male mate without any intervention by the robustus male, while in the majority of replicates, the robustus mated and the typus male took no action (Fig. 1).

Timing of female behavior

The experimental set-up had a significant effect on the time that passed from the start of the experiment until first

Fig. 1 Scheme of the two experimental set-ups and the first-male treatments based on the ontogenetic stage of the males that was first to seize the female (n =number of replicates with the respective sequence; value in *parentheses* represents number of replicates in which female take-over by the other male occurred; female behavior was evaluated in relation to the first male mating with her)



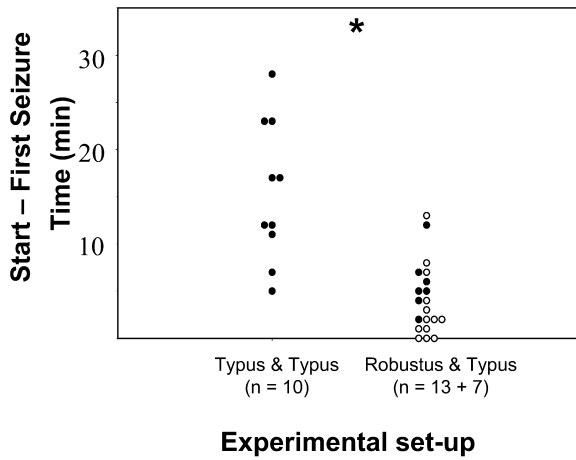


Fig. 2 Time interval from the beginning of the experiment until a female was first seized by a male; in the second set-up, *filled dots* represent typus males and *open dots* represent robustus males (n =number of replicates; * indicates significant differences between set-ups, $\alpha=0.05$)

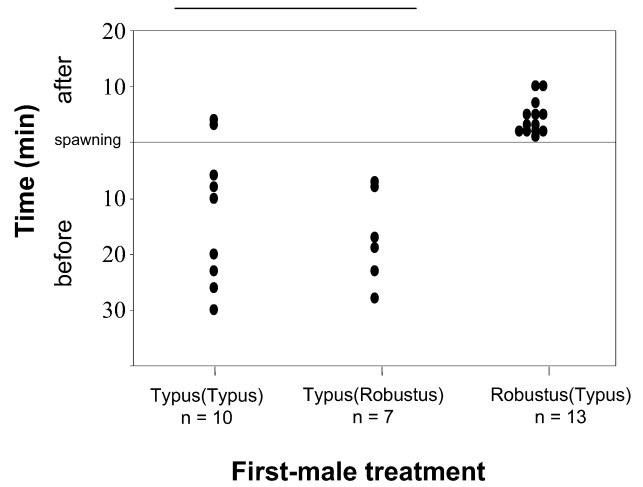


Fig. 4 Time interval between first spermatophore placement and first spawning contractions of the female; treatments connected by *lines* did not differ significantly (Kruskal-Wallis, followed by Dunn's test, $\alpha=0.05$); (n =number of replicates)

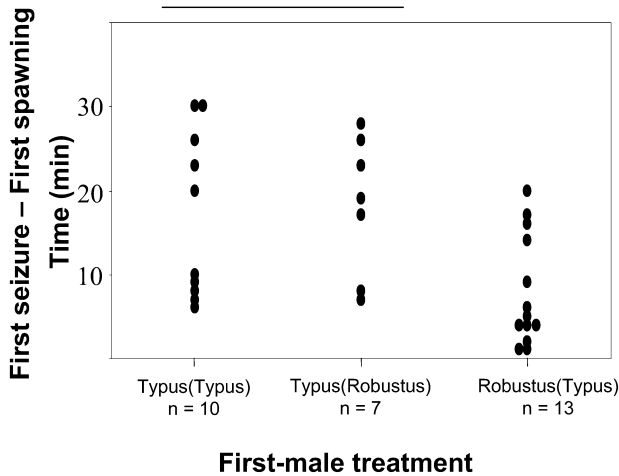


Fig. 3 Time interval between first seizure and first spawning contractions of female rock shrimp; treatments connected by *lines* did not differ significantly (Kruskal-Wallis, followed by Dunn's test, $\alpha=0.05$); (n =number of replicates; note that a female may have been taken over by the other male before the start of spawning)

seizure of the female (Mann-Whitney; $U_{20,10}=16$, $p<0.001$). In the set-up where robustus males were present, females were seized significantly faster than in their absence (Fig. 2). With only typus present, females evaded seizure for a much longer time.

The first-male treatment had a significant effect on the time from first seizure to spawning (Fig. 3) (Kruskal-Wallis, $H_2=9.536$, $p=0.008$). Females that were seized by robustus males started to spawn significantly faster than females seized by typus males (Fig. 3).

Synchronization between male and female behavior

In the robustus(typus) treatments, a close synchronization between male and female behavior was observed. Robustus males apparently waited until the female began spawning to place their first spermatophore on the female's abdomen (Fig. 4). Most typus males, in contrast, transferred spermatophores before the female started to spawn. There were significant differences between first-male treatments (Kruskal-Wallis, $H_2=16.983$, $p<0.001$). The interval between first spermatophore placement and first spawning contractions of the female was significantly longer in females seized by typus than in those first seized by robustus males (Fig. 4).

Female behavior after receipt of spermatophores

Many females that received spermatophores started to manipulate these with their 2nd pereopods (Fig. 5; see also S1–S3). Females opened their pleopods widely, stretching the filamentous spermatophores that were entangled between the pleopods and the abdominal sternites. They continuously directed their 2nd pereopods towards the pleopods and the abdomen, combing and grasping parts of the spermatophores with the chelate 2nd pereopods. During this process, females also frequently directed their pereopods towards their mouth region. While females manipulated spermatophores, parts of these were seen to disappear in the water column (see S3). During manipulation, females also occasionally beat their pleopods vigorously for a few seconds, thereby further expelling spermatophore material. All females that manipulated spermatophores in their abdominal region engaged in this behavior for at least several minutes (Fig. 6). This behavior was observed in most females that had received spermatophores from typus males, and the

Fig. 5A, B Drawing of female rock shrimp *Rhynchocinetes typus* manipulating spermatophore material attached to her abdominal region; the widely opened pleopods with the stretched spermatophore material and the manipulating pereopods can be seen. **A** Both 2nd pereopods directed towards abdominal region; **B** left 2nd pereopod directed towards mouth region; drawn after video-observations; male drawn without shading for clarity

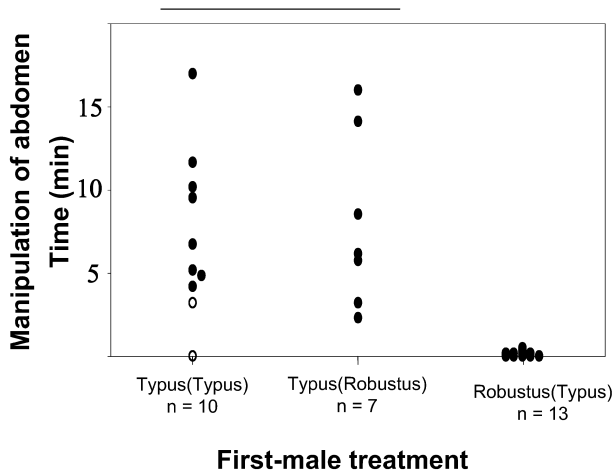
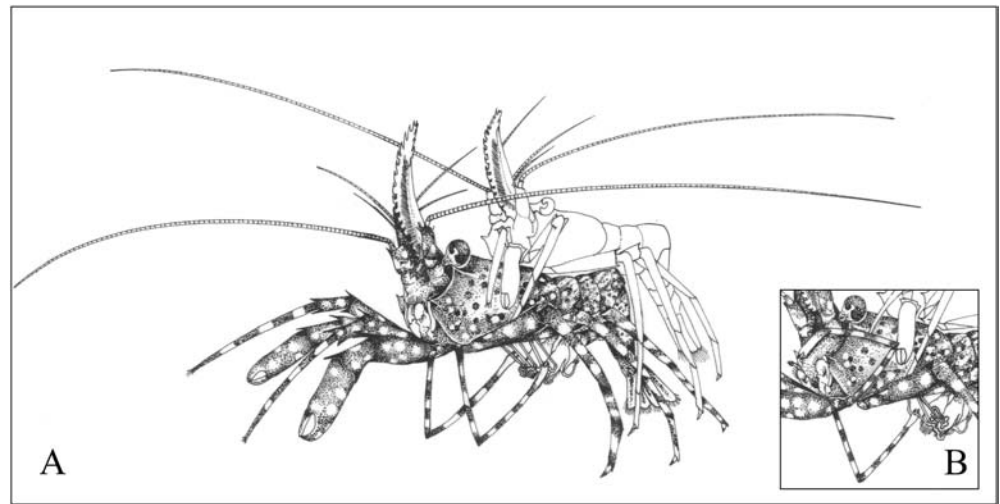


Fig. 6 Total time female engaged in manipulation of her abdominal region; treatments connected by lines did not differ significantly (Kruskal-Wallis, followed by Dunn's test, $\alpha=0.05$); (n =number of replicates; the two unfilled dots represent two typus males that transferred the first spermatophore after the female had started spawning, see also Fig. 4)

duration of the manipulation of the abdominal region was substantially longer in females first seized by typus males than by robustus males (Kruskal-Wallis, $H_2=17.804$, $p<0.001$). Two out of six females that had first received spermatophores from a typus male but subsequently were taken over by a robustus male, also manipulated their abdominal region briefly after the robustus male had started to transfer spermatophores. Both females had first manipulated spermatophores from the typus males, and they stopped manipulating shortly after the robustus males had transferred the first spermatophore. Two females that received the first spermatophore from a typus male after they had started to spawn did not (or only for short time periods) manipulate these spermatophores (Fig. 6). Females that first (and only) mated with robustus males occasionally touched their abdominal region briefly (2–30 s) before receiving spermatophores, but never

showed the extensive manipulation behavior directed towards spermatophores from typus males (Fig. 6).

Discussion

We found that receptive female rock shrimp *R. typus* behave differently toward subordinate typus males and dominant robustus males. Females appeared to evade seizure by subordinate males when dominant males were not present, and if seized by a subordinate, they delayed the beginning of spawning. Furthermore, females that received spermatophores from subordinate males actively manipulated these, thereby causing loss of at least some spermatophore material. All these behaviors are strongly suggestive of cryptic female choice. Here we argue that cryptic female choice in rock shrimp may have evolved in response to the limited ability of females to avoid mating attempts from subordinate males.

Male characters and female preferences in rock shrimp

Female preferences for certain males are expected when males differ in their phenotypic or genetic quality or in the resources they provide to their mates or young. Preferences may be based on male morphological, physiological, or behavioral traits (Eberhard 1996). During ontogeny, male rock shrimp pass through distinct morphological and physiological stages, resulting in high intra-sexual variance in these traits in reproductively active males. In contrast to early ontogenetic stages (typus), the terminal ontogenetic male stages (robustus) can defend a female against other males and guarantee successful fertilization of a female's clutch (Correa et al. 2003; Hinojosa and Thiel 2003). As we have shown here, subordinate and dominant males also differ in their mating behavior. Subordinate typus males transfer spermatophores to females as soon as they seize them, whether the females are ready to spawn or not. In

contrast, dominant robustus males wait until the females begin to spawn before they transfer their first spermatophores. Previous studies had suggested that this difference in male behavior could be due in part to the inexperience of the subordinate males (Correa et al. 2000). These studies showed that in a non-competitive environment, typus males guard females for shorter time periods and also engage in less stimulatory movements than do robustus males. Similarly, in a competitive environment, subordinate typus males transferred spermatophores within a minute of seizing a female, which was never observed in robustus males (Correa et al. 2003). As consequence of the morphological, physiological and behavioral differences, females should prefer dominant robustus males. Furthermore, robustus males, by surviving to this terminal molt stage, have already proven their biological fitness, thereby guaranteeing a fitness assurance to females using their sperm to fertilize their eggs.

In the present study, we found that female rock shrimp evaded seizure by typus males in the absence of dominant robustus males. Robustus males were fastest in seizing females, but in the presence of robustus males the successful typus males also quickly seized the female. Either females have a lower resistance to male advances when dominant males are present or typus males adjust their behavior in the presence of robustus males. In general, these results suggest that female rock shrimp have preferences for dominant males and exert active mate choice for these (see also Díaz and Thiel 2003). These observations coincide with those by Ra'anán and Sagi (1985) on female prawns, *Macrobrachium rosenbergii*, which attempted to evade subordinate males but readily mated with dominant males. Similarly, Snedden (1990) reported that female crayfish, *Orconectes rusticus*, showed a higher tendency to evade mating attempts from small-clawed males than from large-clawed males. Preference for certain males has also been shown for some fiddler crabs (Backwell and Passmore 1996). Female blue crabs (*Callinectes sapidus*) may exert subtle preferences by exhibiting resistance to males during pre-mating interactions, which effectively lead to matings with large males (Jivoff and Hines 1998b). In the isopod *Lirceus fontinalis*, females may perceive the condition of males, and prefer males in good condition (Sparkes et al. 2000). In general, it is assumed that females have a preference for dominant males, but in some species choosing a dominant male may be very costly (Qvarnström and Forsgren 1998). In these latter cases, females may (have to) mate with subordinate males.

Multiple mating in female rock shrimp

Given the great differences between ontogenetic male stages, it could be expected that female rock shrimp show preference for dominant males and only mate with these. Nevertheless, females frequently mate with multiple males including subordinate typus males (Correa et al.

2003). When approached by subordinate males, females do not strongly resist their mating attempts and are often captured within seconds of first contact (Correa et al. 2003; see also S1). In our experiments, where only two males were present, females evaded subordinate males, at least for some time. In nature, where the operational sex ratio (OSR) is strongly male-biased ($\gg 10$ males per receptive female; Correa and Thiel 2003), resistance may help little to evade male mating attempts since escaping females will continuously encounter other males. Furthermore, resistance to male mating attempts may be energetically costly or risky (Cowan 1991; Jormalainen et al. 2001). Receptive rock-shrimp females (and many other crustaceans) have just undergone the reproductive molt, and metabolic requirements for post-molt (and pre-mating) processes may be too high to permit an additional large investment in evasion. Sainte-Marie et al. (1999) also described how female snow crabs, *Chionoecetes opilio*, shortly after their reproductive molt showed little resistance to male mating attempts, since recently molted females are susceptible to injury (see also Donaldson and Adams 1989; Sainte-Marie and Hazel 1992; Rondeau and Sainte-Marie 2001). Female injury or even death as a result of male harassment has also been reported from other species (*M. rosenbergii*, Ra'anán and Sagi 1985; *Paralithodes camtschatica*, Paul and Paul 1990).

Rock shrimp occur at relatively high densities in their natural environment and, in particular, subordinate males predominate in the male population (Correa and Thiel 2003). Under these conditions, females may be exposed to a high degree of harassment from males (e.g. Cordero and Andrés 2002). Instead of constantly attempting to evade subordinate males via energetically costly escape movements, it may be preferable for females to accept seizure by approaching males. If in this situation females mate with multiple males, the term "convenience polyandry" applies (sensu Thornhill and Alcock 1983). This behavior is commonly observed in insects where receptive females experience frequent harassment from males (Rowe 1992; Blanckenhorn et al. 2000; Cordero and Andrés 2002), and it has also been suggested to occur in decapod crabs (Jensen et al. 1996; Sainte-Marie et al. 1999). In *R. typus*, receptive females are also exposed to harassment from males, in particular from the numerically super-abundant typus males. Evasion of continuous mating attempts by these subordinate males may be costly in nature and, consequently, females may simply accept some of the most persistent males. If subordinate males are then displaced by more advanced male stages, then female rock shrimp will typically receive sperm from multiple males (Correa et al. 2003).

Cryptic female choice in rock shrimp

While convenience polyandry has been identified in arthropods from both aquatic and terrestrial systems, little attention has been directed towards the fact that females that engage in this behavior can use sperm from different

males when fertilizing their eggs. Given female preferences for certain males, it could be expected that females engaging in convenience polyandry choose sperm from preferred males to fertilize their eggs. Observations of cryptic female choice in species that are exposed to frequent male harassment (Arnqvist and Danielsson 1999; McLain and Pratt 1999) indeed suggest that females may accept matings from low-quality males but subsequently discriminate against their sperm. We found that female rock shrimp behave in ways that may disfavor sperm from subordinate males. Females apparently simply delay the start of spawning when seized by subordinate *typus* males. However, we do not know whether this delay results from a failure of *typus* males to stimulate females to spawn (see above) or from active suppression of spawning by the female. Delay of spawning may effectively reduce fertilization success of sperm: spermatophores of rock shrimp start to disintegrate and spermatozoa unfold shortly after coming into contact with seawater (Dupré and Schaaf 1996). Following unfolding, spermatozoa may be dispersed by water movements, thereby becoming unavailable for fertilization. Female rock shrimp not only delay spawning, but also take a more proactive role in discriminating against sperm from subordinate males. Spermatophore manipulation resulted in loss of large parts of the spermatophore, and the fact that females only directed this behavior towards spermatophores from subordinate males further suggests cryptic female choice. However, it is not clear whether females discriminate against subordinate males or against spermatophores of all male stages that are transferred before females begin to spawn; most *typus* males placed spermatophore before spawning had started and no *robustus* males did. The fact that females did not (or for only a relatively short time) manipulate spermatophores from the two *typus* males that synchronized spermatophore transfer with the start of spawning, suggests that females discriminate against spermatophores placed during inappropriate moments. Regardless of the discrimination criteria females use (against subordinate males or against untimely spermatophores), the behavior is directed primarily against spermatophores from subordinate males, and thus can be interpreted as cryptic female choice. Accepting spermatophores from subordinate males may allow females to avoid male harassments; subsequent removal of these spermatophores may represent minor costs compared to evasion of or resistance to undesired males.

The potential for cryptic female choice in crustaceans

In many crustacean species, females mate with multiple males (e.g. Christy and Salmon 1984; Koga et al. 1993; Bauer 1996; González-Gurriarán et al. 1998; MacDiarmid and Butler 1999; Franke 2000; Hartnoll 2000; Clark and Caudill 2001; Zimmer 2001), and these males may vary substantially in important characters such as size, age, resource holding power, or physiological capacity. Some

of the best-documented cases are crabs from the genus *Chionoecetes*, where females mate multiply with males of different ages and sizes (Paul and Paul 1992, 1996; Urbani et al. 1998). In snow crabs, *C. opilio*, where up to 12 different ejaculates have been identified in the female spermathecae, females take a proactive role in mobilizing stored sperm when fertilization approaches (Sainte-Marie et al. 2000). In *C. opilio*, last males have precedence in fertilizing most eggs (Sévigny and Sainte-Marie 1996; Urbani et al. 1998), but it is not clear whether females actively manipulate sperm reservoirs from different males; multiple mating may simply be a female mechanism to top up their sperm stores to ensure future fertilizations (see also discussions in Paul and Paul 1992; Sainte-Marie and Lovrich 1994; Sainte-Marie et al. 1997). Several other observations from crustacean species in which females are known to mate multiply are highly suggestive of cryptic female choice. For example, Bauer (1992) observed that female penaeid shrimp copulated but did not receive sperm, and he discussed whether females might be capable of actively preventing insemination. In the caridean shrimp, *Heptacarpus sitchensis*, Bauer (1976) reported that females occasionally rejected a spermatophore during “cleaning activities”. Delay of spawning or active removal of spermatophores, as observed in *R. typus*, has also been reported from females of other crustacean species that mate multiply (Sainte-Marie and Lovrich 1994; MacDiarmid and Butler 1999), but present knowledge is too limited to interpret these observations as cryptic female choice. Future studies should focus on species in which females frequently engage in multiple matings.

Outlook

The behavioral observations presented herein indicate that female rock shrimp engage in convenience polyandry and, subsequently, in cryptic female choice. Convenience polyandry is relatively common in species where males harass receptive females (Rowe 1992; Cordero and Andrés 2002), and females of these species receive sperm from multiple (including undesired) males. While multiple matings and male variability are essential conditions for cryptic female choice to evolve (Eberhard 1996), they may not necessarily be sufficient. Other intrinsic (e.g. OSR) or extrinsic factors (e.g. predation pressure, availability of food resources, environmental complexity) may also influence the evolution of cryptic female choice in crustaceans. Based on our results and the theoretical considerations presented above, we propose that: (a) convenience polyandry is common in crustaceans, and (b) cryptic female choice is common among species with convenience polyandry. While convenience polyandry is not an essential precursor for cryptic female choice, it may nevertheless favor its evolution (Reyer et al. 1999; Pizzari and Birkhead 2000).

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