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Female rock shrimp *Rhynchocinetes typus* mate in rapid succession up a male dominance hierarchy

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Abstract The dynamics of male-male competition for mates and patterns of female choice depend critically on the social environment. We released newly molted sexually receptive females of the rock shrimp *Rhynchocinetes typus* in the field and recorded their interactions with males. In the dense aggregations in which these shrimp live, most females were encountered and seized by males within 2 min. Usually, females were first seized by subordinate males, and subsequently taken over by the dominant males. Many females (17 out of 23) had multiple mates during the 10-min observation period, and most of them received spermatophores from multiple males. Males used different mating tactics in accordance with their dominance status: subordinate males often used the sneaking tactic, seizing the female and immediately transferring spermatophores. In contrast, all dominant males used the primary mating tactic; they seized and stimulated the female before transferring spermatophores. Results from previous studies had indicated that females may reduce the fertilization chances of subordinate males by delaying spawning and removing spermatophores. We suggest that this capability in combination with the observed rapid mate succession may enable females to exploit male contest behaviors.

Keywords Shrimp · Polyandry · Contest induction · Female choice · Sexual selection · Mating systems

Introduction

The mating systems of many species are characterized by intense sexual selection and sperm competition (Andersson 1994; Birkhead and Møller 1998; Simmons 2001). Members of one sex (typically the males) compete for access to the other sex, offering the possibility to the members of the opposite sex (typically the females) to choose among competing mates (Andersson 1994; Eberhard 1996). In order to understand the mechanisms involved in mate competition and sexual selection, it is essential to know how many males compete for access to, mate with, and transfer sperm to females. While staged laboratory experiments provide useful information about the behaviors males use to compete for females, the outcome of sperm competition and the (sometimes cryptic) choices exerted by females (e.g. Van Gossum et al. 2001), they provide no information about the dynamics of mate competition, including the numbers of males involved in mating interactions, in the natural environment. Field studies have proven highly valuable in order to evaluate these dynamics (e.g. Backwell and Passmore 1996; deRivera et al. 2003; Forsgren et al. 2004).

A female approaching receptivity may become the object of several sequential contests while being guarded by a male. These contests may offer females the chance to sample different males and make an informed choice (e.g. Berglund et al. 1996; Gabor and Halliday 1997). The frequency, duration and outcome of these contests will not only determine which male is most likely to fertilize the eggs of a female, but also influence the degree of sexual selection (Andersson 1994; Birkhead and Møller 1998). Most studies on contest dynamics in crustaceans have been conducted with brachyuran species, in which the mating process often includes prolonged periods of pre-copulatory mate-guarding. In non-territorial caridean shrimp, mate-guarding is uncommon but contests may also develop around receptive females (Correa and Thiel 2003a). Our model species is the rock shrimp *Rhynchocinetes typus*, a marine caridean shrimp inhabiting the rocky subtidal of the southeast Pacific (Caillaux and Stotz

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2003). Physical and behavioral dimorphisms are pronounced in this species: while adult females have but one morph, adult males pass through several morphs as they grow and age. Similar characteristics have also been reported for some other marine and freshwater carideans (Bauer 2004). In *R. typus*, the first ontogenetic male stage (termed “typus”) is very similar to females in size and general morphology. At some point, males begin a progressive morphological and behavioral transition through several successive instars (altogether called “intermedius”) before reaching the final molt stage (“robustus”) (Correa et al. 2000). This transition is characterized by allometric growth of the third maxillipeds and first chelae, appendages with which males fight. In the laboratory, when males compete for mates, there is a linear dominance hierarchy among the male morphs according to age and size: typus < intermedius < robustus (Correa et al. 2003). Despite their disadvantage in direct competition, typus and intermedius males transfer spermatophores rapidly to a receptive female if they encounter her before she is guarded by a robustus or when brief mating opportunities arise during struggles between dominant males. Dominants always—and the other male stages in a competition-free environment—engage in sophisticated mating behaviors prior to and after the sperm transfer. In contrast to most other caridean shrimp (e.g. Bauer 1976; Bauer and Abdalla 2001), robustus males guard the female between their pereopods (in the so-called cage state) almost until the end of the spawning process (mating may last >3 h; Correa et al. 2000, 2003). This behavior was classified by Correa et al. (2003) as the primary mating tactic, which is in sharp contrast to the opportunistic mating behavior of subordinate males, identified as the alternative mating tactic.

The operational sex ratio (OSR) is highly male-biased in *R. typus* (Correa and Thiel 2003b). Subordinate males are most abundant in the field and thus they are most likely to first encounter a receptive female. For each receptive female present in the field, there are between two and four dominant males (robustus), suggesting that they may finally take over most of the daily available receptive females (Correa and Thiel 2003b). Whether female take-over by robustus males indeed occurs depends on a variety of factors, including their capacity to perceive and move towards receptive females. Equally important is the behavior of both the female and subordinate males. While in unstructured laboratory environments, robustus males quickly overtook females from subordinate males (Correa et al. 2003), it is not known how often or how fast this occurs in the highly complex and densely populated natural habitat of *R. typus*.

Robustus males have high resource holding and mating potentials and they can see a receptive female several shrimp body-lengths away (via tumultuous male activity around her—Díaz and Thiel 2004). We therefore predicted that robustus males will quickly move towards receptive females in the field, displace subordinate males and monopolize females.

Methods

Collection and maintenance of rock shrimp

We studied the mating behavior of rock shrimp in the field by: (a) releasing receptive females, and (b) searching for naturally occurring mating pairs. We observed the shrimp in their typical habitat on shallow subtidal hard bottoms composed of large boulders with crevices and caves (Caillaux and Stotz 2003). All observations were made in La Herradura Bay in Coquimbo, Chile (29°59'S, 71°22'W) at water depths of 3–9 m, where rock shrimp occur at high densities. The water in the seawater laboratory, where females were held before release, is pumped from near the release sites.

Females were collected with a diver-operated suction sampler, and maintained in the laboratory with ad libitum food (for details of sampling technique and area, see Correa and Thiel 2003b). Oviparous females were held in sexual isolation in groups of 25–30 females until molting, when they become sexually receptive (Correa et al. 2000). Receptive females were obtained in the laboratory following the method of Correa et al. (2003): every morning the holding tanks were checked for the presence of shed exoskeletons, whereupon the recently molted females were identified and placed together in a separate container. These females were released the following day in the field. Preliminary experiments had shown that female receptivity reaches its maximum 12–36 h after molting (Correa et al. 2000).

Experimental release of receptive females

Thirty-three receptive females were released and observed by a scuba diver in the field. For each dive, groups of receptive females (<7) were placed in a 10-l bucket and transferred from the laboratory to the field site in a small boat. Once at the diving site, the scuba diver took the females into a soft-mesh-cage and then searched the rocky subtidal for surfaces among large boulders (decimeters to meters in diameter) inhabited by high densities of rock shrimp. After locating a release site, the diver carefully settled near (20–30 cm) a group of shrimp and placed a transparent bell, 10 cm in diameter with a hole in the apex, onto the substratum. One receptive female was then carefully removed from the holding cage and put under the bell, where it was held for 3 min before it was released. During the 3-min acclimatization period, we recorded the presence/absence of robustus males within a radius of about 50 cm around the release site. After 3 min, we lifted the bell and the female joined the dense assemblage of conspecifics in the natural environment (start of experiment). We watched the female continuously for 10 min and recorded the sequence of males that attempted to mate with the female. For each male that seized the receptive female, we recorded ontogenetic stage (following Correa and Thiel 2003b), relative size compared to the previous male that held the female, duration of cage state with the female, number of spermatophore transfer events (STE), and the moment each STE occurred. The diver also noted the behavioral interactions of males with each other and with the female, specifically whether their mating behaviors corresponded to the tactics (primary or alternative mating tactics) seen previously in the laboratory. In addition to these male behaviors, we recorded whether female rock shrimp escaped from males attempting to seize her. Seven daytime dives were conducted during austral summer (from 30 January to 4 February 2000), and during each dive 3–6 females were released, completing a total of 33 replicate releases. A total of 29 females were followed over the entire 10-min observation period.

Scan sampling of natural mating pairs

Two surveys of naturally occurring mating pairs were conducted on the same day (22 December 2001) in the area where females were released. The first was conducted from 0840 to 1040 hours and the second from 1430 to 1630 hours. The surveys were made by swimming a transect across as many microhabitats inhabited by *R.*

typus as possible, continuously checking for the presence of mating pairs (i.e. couples in cage state). For every mating pair encountered, the ontogenetic stage of the male partner was recorded, after which the search was immediately continued.

Statistical analyses

During the experimental release of receptive females, whenever a female was seized by >1 male, we recorded whether the first or the last male partner was more developed (ontogenetically and/or in size). We used the chi-square goodness-of-fit test to test the null hypothesis that larger males were equally often first and last partners (Yates correction for continuity was utilized since $df=1$). Contingency tables were used to test whether the relative frequencies of ontogenetic male stages were similar between the first and last mating partners (2 types of mating partners×3 male stages; H_0 : first and last mating partners presented the same relative frequencies of ontogenetic male stages). Using a similar procedure, we compared the relative frequencies of ontogenetic male stages and their use of rapid and delayed STEs. During rapid STEs, the male seized the female and immediately (<1 min) transferred spermatophores (alternative mating tactic), while during delayed STEs, the male usually performs other behavioral events for >1 min before transferring the first of several spermatophores (primary mating tactic). When the type of STE could not be identified with certainty, for example, because males were interrupted, these males were not considered in the analysis (Contingency table; 2 types of STE×3 male stages; H_0 : males using rapid STE and males using delayed STE presented the same relative frequencies of ontogenetic male stages).

We tested whether male partners in natural pairings were randomly distributed between the three developmental ontogenetic stages. Herein we did not consider the net relative abundance of male morphs in the field (*typus* >>*intermedius* >>*robustus*, Correa and Thiel 2003b) as expected proportion, but rather the relative abundance of sexually active males under a conservative scenario. Therefore we performed a chi-square for goodness-of-fit test; H_0 : relative frequencies of ontogenetic male stages fit the operational sex ratio of 4 *typus*:7 *intermedius*:4 *robustus* per receptive female during the summer months, see estimates of OSR in Correa and Thiel (2003b). Frequency of occurrence data from the morning and the afternoon survey were pooled, since a Heterogeneity test revealed that proportions did not differ between morning and afternoon.

Results

Experimental release of receptive females

Our observations of receptive females in the field revealed a high level of male-male mate-competition.

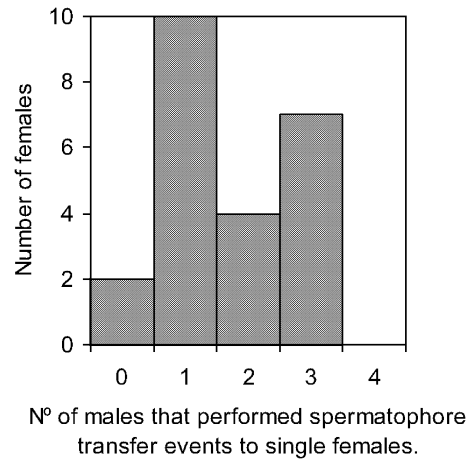


Fig. 2 Number of females *Rhynchocinetes typus* receiving spermatophores from different numbers of males in the natural environment; n=23 females that were seized by at least 1 male during the 10-min observation period

Twenty-nine of 33 released receptive females were observed throughout the entire 10-min observation period (Fig. 1). Twenty-three (79.3%) of these 29 females were seized by males who mated or attempted to mate with the female. Seventeen (73.9%) of the 23 females that were object of male approaches had multiple mating partners during the 10 min of observation (Fig. 1a–c). Many of the 23 females that were seized by males received spermatophores from 2–3 males (Fig. 2).

A high proportion of females that were released in the vicinity of *robustus* males were held by a *robustus* at the end of the 10-min observation period. Six of 8 females released in the presence of *robustus* males, but only 2 of 15 females released in absence of a *robustus*, were held by a *robustus* at the end of the observation period. Four out of the 23 females, with which males attempted to mate, exhibited escape responses. Two of these females subsequently escaped from different males. As a result of female escape responses, a total of nine males lost hold of the female following seizure. All these males were in the *typus* stage, which indicates that in addition to their social disadvantage, early male stages are less able to control females physically. Three of the four escaping females

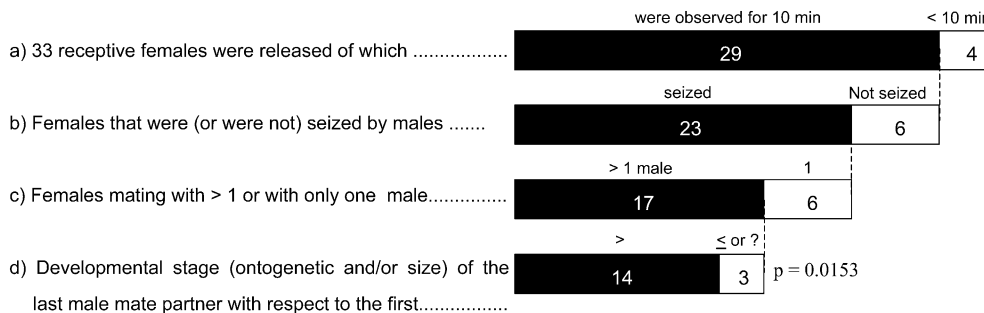


Fig. 1 Stepwise description of principal results from experimental release of receptive females *Rhynchocinetes typus* in the natural environment; probability value represents result of chi-square for

goodness-of-fit test (with Yates correction); H_0 : relative frequencies fit the ratio 1:1

Table 1 Number of males in the respective ontogenetic stage that were recorded as first and last male mating partner; only mating interactions with the 23 females that were seized by at least 1 male and that were observed during the entire 10-min observation period are considered

	Ontogenetic stage of male mating partners		
	Typus	Intermedius	Robustus
First male	16	6	1
Last male	8	7	8

had no robustus male in the vicinity at the start of the experiment.

When a male first encountered a female, he usually touched her with his antenna. In some cases, the first male to establish contact with the female rapidly attempted to seize her, while in other cases males did not react, even after repeated contacts. The majority of mated females were seized by a male within 2 min. For the 23 females that mated during the 10-min observation period, the average time from release until the first cage state with a male was 2.04 ± 0.42 min (mean \pm SE). In general, after the first males attempted to mate with the receptive female, other males from the immediate surroundings (<1 m) approached the mating pair. These males were attracted apparently by visual cues from the mating pair and by tumultuous activity produced by competing males.

There was a significant tendency for early ontogenetic male stages to initiate mating attempts, while late ontogenetic stages (particularly robustus) frequently guarded the female at the end of the 10-min observation period (Contingency table: 2×3 , $\chi^2 = 8.19$, $P = 0.0167$; Table 1). This sequence is exemplified by one female that was in mating contact with four different males during the 10-min observation period—the different males seized the female in the following chronological order: typus, typus, intermedius, robustus. In some cases, mate changes were initiated when a typus male lost hold of the female due to female escape reactions (see above). Occasionally a typus male also released the female in response to approaching fish, which was observed in three cases. However, in the majority of cases ($n = 27$), sequential changes in male mates resulted from male displacement by a larger or ontogenetically more advanced male. Consequently, when multiple matings occurred, the developmental stage of the last male partners (at the end of the 10-min observation period) tended to be significantly more advanced than the first-observed mates (Fig. 1d). These observations corroborate the existence of a strong dominance hierarchy: robustus > intermedius > typus.

Sixty males engaged in mating interactions with the 23 females during the 10-min observation period. This provided the opportunity to observe at least the beginning of the mating behavior for 36 typus, 15 intermedius and 9 robustus males. A higher proportion of subordinate than dominant males engaged in rapid spermatophore transfer events (Contingency table: 2×3 , $\chi^2 = 37.74$, $P < 0.0001$; statistical comparison only between the two safely identified types of STEs, i.e. rapid and delayed; Table 2). In

Table 2 Number of males in the respective ontogenetic stage that engaged in rapid or delayed spermatophore transfer events (STE); only mating interactions with the 23 females that were seized by at least 1 male and that were observed during the entire 10-min observation period are considered

	Ontogenetic stage of males engaging in STE		
	Typus	Intermedius	Robustus
Rapid STE	27	11	0
Delayed STE	0	2	8
Unknown	9	2	1

general, typus and intermedius males, after seizing the female, immediately performed several (one to eight) STEs, similar to the behavior of subordinates observed in the laboratory (i.e. alternative mating tactic). In contrast, all robustus and some intermedius seized the female without engaging in rapid STE, but instead performed other sensorial and/or stimulatory events—e.g. poking her ventral side as described in Correa et al. (2000)—in addition to aggressive displays against competitors (i.e. primary tactic). In the majority of these latter cases, we probably did not watch the shrimp long enough to see STEs, because males that use the primary mating tactic usually delay STE for several minutes until the female begins to spawn.

Scan sampling of natural mating pairs

A total of 22 mating pairs of rock shrimp were found during the 2 scan samplings in La Herradura Bay. In the majority of these pairs, the male partner was a robustus male. The relative frequencies of male mating partners (1 typus:1 intermedius:20 robustus) differed significantly from the expected ratio of 4:7:4 (scenario C of summer OSR of *R. typus*; Correa and Thiel 2003b; chi-square for goodness-of-fit test, $\chi^2 = 46$, $P < 0.001$).

Discussion

Our observations of receptive females in the field confirmed the existence of intense male mate competition in the rock shrimp *R. typus*. Even though females were observed for only 10 min, it was possible to witness several behaviors that provide a good image of the mating interactions of rock shrimp in their natural environment. The rapid succession of mates that females experience in the field offers them the opportunity to sample different males within a very short time period.

Male role in mate competition for receptive females

Most receptive females were first contacted by subordinate typus males, but additional males were rapidly attracted, apparently by visual cues generated by males mating with the female (Díaz and Thiel 2004). There

often was at least one dominant robustus male among the males attracted to a receptive female. The appearance of these dominant males dramatically decreased the chances of subordinates to guard the female (Correa et al. 2003). Since dominant males rapidly take over receptive females (8 out of 23 females were held by a robustus after <10 min), subordinates are prone to lose a female quickly. This may explain why many of the subordinate males immediately transferred spermatophores to the female's abdomen even though she had not yet begun to spawn.

The longer males guard the females before copulation, the higher is the risk that a more powerful competitor will displace them. Female take-over by larger males commonly occurs in crustaceans (Dick and Elwood 1989; Iribarne et al. 1996; Jivoff 1997; Sainte-Marie et al. 1997; Jormalainen 1998). In most polyandrous crustacean species, males struggle for females long before fertilization takes place. Consequently, small males have limited chances to gain fertilizations since sperm transferred during precopulatory mate guarding would usually be wasted (unless females store sperm and first males have precedence). The small males may simply take their chances, transfer spermatophores quickly and then attempt to control and guard the female until spawning and fertilization takes place. Dominant males in contrast, face a low risk of being displaced by competitors, and thus may delay spermatophore transfer in order to synchronize it with female spawning. Herein, this is exemplified by the fact that most robustus males used the primary mating tactic after seizing the female.

Female's role in mating competition

The majority of female rock shrimp observed in this study mated with and received sperm from several males. Some females mated with up to five different males in less than 10 min. Male displacement is common during mating interactions of rock shrimp (Correa et al. 2003; Thiel and Hinojosa 2003), but estimates obtained herein may be slightly higher than in a natural situation. Another study by Díaz and Thiel (2004) indicated that females may approach the vicinity of robustus males before they become receptive. We released females at randomly selected spots in their natural habitat, sometimes without a robustus male in the immediate vicinity. When robustus males are around, females may become quickly monopolized by these, resulting in relatively low numbers of sequential mates in a natural situation (but see next section).

Typically, females accept multiple matings in order to ensure fertilization (bet-hedging), for genetic benefits (trade up), or because costs of avoiding male advances are very high (convenience polyandry) (Jennions and Petrie 1997, 2000; Arnqvist and Nilsson 2000; Cordero and Andrés 2002; Fox and Rauter 2003). In rock shrimp, one male is usually sufficient to fertilize an entire clutch of a female (Correa et al. 2000), although there is evidence that robustus males have a higher fertilization potential

than typus males (Hinojosa and Thiel 2003). In general, though, it appears safe to assume that female rock shrimp do not require multiple matings, which suggests that they accept matings from subordinate males for other reasons. Herein, some females successfully evaded typus males, and none of these females was seized by a robustus during the 10-min observation period. Most females, though, tolerated seizure and sperm from subordinates despite the fact that they prefer dominant males (see, e.g., Díaz and Thiel 2003). Female crustaceans may incur injuries or even death caused by "ungentle" (sensu Donaldson and Adams 1989) male approaches (e.g. Ra'anan and Sagi 1985; Rondeau and Sainte-Marie 2001), and thus may accept matings from subordinate males in order to reduce the risk of injuries while awaiting the approach of dominant males. One major cost that females may incur as a result of this convenience polyandry could be that no preferred male appears on the scene in time. However, the results of our study show that robustus males are efficient in finding and monopolizing a receptive female within very short time periods. This suggests that the risk of not finding a preferred male is relatively low. Females often mate with subsequent males when these are of superior quality to first males (e.g. Gabor and Halliday 1997). Bateman et al. (2001) suggested that female crickets "bet-hedge" at the first copulation but, after assuring sufficient sperm supply, attempt to trade up and gain fertilizations from larger males. Pitcher et al. (2003) demonstrated that female guppies show no propensity to re-mate when subsequent males are of equal quality but trade up when second males present brighter ornamentation than first males. Similar changes of males along a dominance hierarchy as observed herein for *R. typus* may also be expected in other caridean shrimp, where some males present unique morphological characteristics (see examples in Bauer 2004).

Female exploitation of male-male competition

Several observations suggest that female rock shrimp may not only accept matings by subordinate males in order to reduce costs of male harassment, but also as a mechanism to induce indirect mate selection. If offered the choice between a subordinate typus and a dominant robustus male, most females first approached a typus male (Díaz and Thiel 2003), which often caused agitation in the nearby robustus males (personal observations). Several authors have suggested that reproductive females may provoke conflicts between males in order to mate with the winner of the contest, usually the larger male (Cox and LeBoeuf 1977; Christy 1987; Watson 1990; Berglund et al. 1996; Cunningham and Birkhead 1998; Semple 1998; Harari et al. 1999). In *R. typus*, dominants are attracted to mating pairs (see above), and due to their high resource holding power quickly displace subordinate males (Correa et al. 2003). Female rock shrimp may exploit this behavior, and induce contests in the vicinity of dominant males. This conclusion is also supported by the observa-

tion that typus males are able to seize females much faster in presence than in absence of a dominant male (Thiel and Hinojosa 2003). Perhaps in the presence of a robustus male, females readily accept any male. Typically, a robustus male immediately reacts towards and displaces subordinate males mating with a female. This sequence of events is highly predictable and consistent (sensu Shuker and Day 2001), allowing females to mate with a dominant male that has actively demonstrated its resource holding power. Several authors suggest that precopulatory choices by females are not costly in species that live at high densities (Reynolds 1996; Alatalo et al. 1998; Blanckenhorn et al. 2000; deRivera et al. 2003). As in lekking species (Reynolds and Gross 1990), the presence of many males may allow females to select males by inducing contests. Female rock shrimp may thus trade up among potential mates “by mating with a male who removed other males from contention by dominating in a contest” (Alexander et al. 1997)

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References

- Alatalo RV, Kotiaho J, Mappes J, Parri S (1998) Mate choice for offspring performance: major benefits or minor costs. *Proc R Soc Lond B* 265:2297—2301
- Alexander RD, Marshall DC, Cooley JR (1997) Evolutionary perspectives on insect mating. In: Choe JC, Crespi BJ (eds) *The evolution of mating systems in insects and arachnids*. Cambridge University Press, Cambridge, pp 4–31
- Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton, NJ
- Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. *Anim Behav* 60:145—164
- Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol* 38:407—416
- Bateman PW, Gilson LN, Ferguson JWH (2001) Male size and sequential mate preference in the cricket *Gryllus bimaculatus*. *Anim Behav* 61:631—637
- Bauer RT (1976) Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *J Nat Hist* 10:415—440
- Bauer RT (2004) Remarkable shrimps—adaptations and natural history of the carideans. University of Oklahoma Press, Norman, Okla
- Bauer RT, Abdalla JH (2001) Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology* 107:185—199
- Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc* 58:385—399
- Birkhead TR, Møller AP (1998) *Sperm competition and sexual selection*. Academic Press, London
- Blanckenhorn WU, Mühlhäuser C, Morf C, Reusch T, Reuter M (2000) Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. *Ethology* 106:577—593
- Caillaux LM, Stotz WB (2003) Distribution and abundance of *Rhynchocinetes typus* Milne Edwards (Crustacea Decapoda), in different benthic community structures in northern Chile. *J Mar Biol Assoc UK* 83:143—150
- Christy JH (1987) Competitive mating, mate choice and mating associations of brachyuran crabs. *Bull Mar Sci* 41:177—191
- Cordero A, Andrés JA (2002) Male coercion and convenience polyandry in a calopterygid damselfly. *J Insect Sci* 2:14
- Correa C, Thiel M (2003a) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Rev Chil Hist Nat* 76:187—203
- Correa C, Thiel M (2003b) Population structure and operational sex ratio in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J Crust Biol* 23:849—861
- Correa C, Baeza JA, Dupré E, Hinojosa IA, Thiel M (2000) Mating behavior and fertilization success of three ontogenetic stages of male rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J Crust Biol* 20:628—640
- Correa C, Baeza JA, Hinojosa IA, Thiel M (2003) Dominance hierarchy and mating tactics in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *J Crust Biol* 23:33—45
- Cox CR, LeBoeuf BJ (1977) Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317—335
- Cunningham EJA, Birkhead TR (1998) Sex roles and sexual selection. *Anim Behav* 56:1311—1321
- deRivera CE, Backwell PRY, Christy JH, Vehrencamp SL (2003) Density affects female and male mate searching in the fiddler crab, *Uca beebei*. *Behav Ecol Sociobiol* 53:72—83
- Díaz ER, Thiel M (2003) Female rock shrimp prefer dominant males. *J Mar Biol Assoc UK* 83:941—942
- Díaz ER, Thiel M (2004) Chemical and visual communication during mate searching in rock shrimp. *Bio Bull* 206:134—143
- Dick JTA, Elwood RW (1989) Assessments and decisions during mate choice in *Gammarus pulex* (Amphipoda). *Behaviour* 109:235—246
- Donaldson WE, Adams AE (1989) Ethogram of behavior with emphasis on mating for the Tanner crab *Chionoecetes bairdi* Rathbun. *J Crust Biol* 9:37—53
- Eberhard WG (1996) *Female control: sexual selection by cryptic female choice*. Princeton University Press, Princeton, NJ
- Forsgren E, Amundsen T, Borg AA, Bjelvenmark J (2004) Unusually dynamic sex roles in a fish. *Nature* 429:551—554
- Fox CW, Rauter CM (2003) Bet-hedging and the evolution of multiple mating. *Evol Ecol Res* 5:273—286
- Gabor CR, Halliday TR (1997) Sequential mate choice by multiply mating smooth newts: females become more choosy. *Behav Ecol* 8:162—166
- Harari AR, Handler AM, Landolt PJ (1999) Size-assortative mating, male choice and female choice in the curculionid beetle *Diaprepes abbreviatus*. *Anim Behav* 58:1191—1200
- Hinojosa I, Thiel M (2003) Somatic and gametic resources in male rock shrimp, *Rhynchocinetes typus*—effect of mating potential and ontogenetic male stage. *Anim Behav* 66:449—458
- Iribarne O, Fernandez M, Armstrong D (1996) Mate choice in the amphipod *Eogammarus oclairi* Bousfield: the role of current velocity, random assortment, habitat heterogeneity and male's behavior. *Mar Freshwater Behav Physiol* 27:223—237
- Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev* 72:283—327
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21—64
- Jivoff P (1997) Sexual competition among male blue crab, *Callinectes sapidus*. *Biol Bull* 193:368—380
- Jormalainen V (1998) Precopulatory mate guarding in crustaceans—male competitive strategy and intersexual conflict. *Q Rev Biol* 73:275—304
- Pitcher TE, Neff BD, Rodd FH, Rowe L (2003) Multiple mating and sequential mate choice in guppies: females trade up. *Proc R Soc Lond B* 270:1623—1629

- Ra'anan Z, Sagi A (1985) Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man). *Biol Bull* 169:592—601
- Reynolds JD (1996) Animal breeding systems. *Trends Ecol Evol* 11:68—72
- Reynolds JD, Gross MR (1990) Costs and benefits of female mate choice: is there a lek paradox? *Am Nat* 136:230—243
- Rondeau A, Sainte-Marie B (2001) Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. *Biol Bull* 201:204—217
- Sainte-Marie B, Sévigny JM, Gauthier Y (1997) Laboratory behavior of adolescent and adult males of the snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) mated noncompetitively and competitively with primiparous females. *Can J Fish Aquat Sci* 54:239—248
- Semple S (1998) The function of Barbary macaque copulation calls. *Proc R Soc Lond B* 265:287—291
- Shuker DM, Day TH (2001) The repeatability of a sexual conflict over mating. *Anim Behav* 61:755—762
- Simmons LW (2001) Sperm competition and its evolutionary consequences in the insects. Princeton University Press, Princeton, NJ
- Thiel M, Hinojosa I (2003) Mating behavior of female rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea)—indication for convenience polyandry and cryptic female choice. *Behav Ecol Sociobiol* 55:113—121
- Van Gossum H, Stoks R, De Bruyn L (2001) Frequency-dependent male mate harassment and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*. *Behav Ecol Sociobiol* 51:69—75
- Watson PJ (1990) Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). *Behav Ecol Sociobiol* 26:77—90