

MALE DOMINANCE HIERARCHY AND MATING TACTICS IN THE ROCK SHRIMP *RHYNCHOCINETES TYPUS* (DECAPODA: CARIDEA)

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A B S T R A C T

During ontogeny, male rock shrimp *Rhynchocinetes typus* develop from the typus morphotype through several intermedius stages to the robustus morphotype, the last molt stage, which features powerful third maxillipeds and chelae. In a competition-free environment, all male stages mate in a similar manner. They guard females for 23 min to 3 h and perform several behaviors before and after they transfer spermatophores. In the present study, we observed the mating behavior of three different ontogenetic stages of male rock shrimp in a competitive environment in which the three different male stages competed directly for access to receptive females. In the first set of experiments, two males of different ontogenetic stages were placed together with a receptive female. The results indicated the existence of a linear dominance hierarchy, being robustus > intermedius > typus. In the second experiment, we examined the behavior of subordinate males while two dominant-stage males competed for a receptive female. During agonistic displays of the two dominant-stage males, the female escaped from the embrace of her (dominant) mating partner. Some subordinate males used this opportunity to pair with the female and mate rapidly without courting, contrasting to their courting in a competition-free situation. In a competitive situation, subordinate males that gained access to a female deposited several spermatophores as soon as possible (within 1 min). At the beginning of both experiments, subordinates that interacted first with the receptive female rapidly transferred spermatophores. Thus, in a competitive environment, subordinate males may use an alternative mating tactic that is characterized by speed. The social environment may impose divergent selective pressures favoring the evolution of conditional alternative mating tactics.

Alternative reproductive behavior (*sensu* Austad, 1984) can be defined as any discontinuous variation in an aspect of reproductive behavior among one sex within a single population. Additionally, each behavior has associated with it differences in costs and/or benefits. Alternative reproductive behaviors occur in a wide variety of taxa and, when referring to particular aspects of the mating behavior, are commonly termed alternative mating tactics (AMTs—Waltz and Wolf, 1984; Taborsky, 1994; Cook *et al.*, 1997; Martin and Taborsky, 1997; but see Dominey, 1984). Each alternative may represent a fixed tactic during an individual's lifetime or may be employed by the same individual at different times.

The proximate causes of AMTs are commonly great imbalances in resource holding power (RHP is a measure of the absolute fighting ability of a given individual *sensu* Parker, 1974), caused, for example, by large morphological differences among competitors. Frequently, the ultimate cause in shaping and maintaining AMTs is thought to be strong

intrasexual competition for mating partners (e.g., Shuster, 1987; Clark, 1997; but see Emlen and Oring, 1977 for general discussion). A skewed operational sex ratio towards males (i.e., sexually active males being more abundant than receptive females) contributes to intrasexual competition (Emlen and Oring, 1977). Sexual selection then favors individuals better adapted for fighting (e.g., aggressive behavior combined with relatively well-developed fighting structures). Consequently, dominance systems may arise in which an individual's potential for access to scarce resources (e.g., receptive females) depends on its rank in a dominance hierarchy (e.g., McCann, 1981; Elnor and Beninger, 1995). Achieving a dominant status (relatively high RHP) may require costly resource investments such that individuals at a competitive disadvantage may improve their reproductive success by adopting an alternative tactic (avoiding direct competition) at relatively lower costs (Eberhard, 1982; Dominey, 1984; Taborsky, 1994, 1998; Emlen, 1997). Thus, the evolution of AMTs among

males can be expected in species with high intrasexual competition.

In a wide variety of crustacean taxa, intense male-male competition for mating opportunities exists (see e.g., Christy, 1987; Dick and Elwood, 1996). The proximate causes include the relatively short period during which females are receptive for mating, contrasted with the almost continuous readiness of males, asynchronous molting of females, high population densities, and polygamy (e.g., amphipod *Jassa marmorata*—Clark, 1997). Indeed, the allometric development of fighting structures—common in males of many crustacean species—is directly related to the importance of these structures in determining the outcome of direct encounters among males (e.g., Rubenstein, 1984; Conlan, 1989; Elner and Beninger, 1995; Barki *et al.*, 1997; Jivoff, 1997). However, very few cases of AMT have been reported for crustacean species (Ra'anan and Sagi, 1985; Laufer *et al.*, 1992; Clark, 1997; Sainte-Marie *et al.*, 1997; Shuster and Sassaman, 1997).

Commonly, males that employ AMTs are comparatively small and do not present large fighting structures (e.g., Ra'anan and Sagi, 1985; Shuster, 1987; Clark, 1997; Moczek and Emlen, 2000). These less-developed males can sneak efficiently past the more developed dominant males, as has been shown in the freshwater shrimp *Macrobrachium rosenbergii*, in which different male morphotypes are distinguished (Kuris *et al.*, 1987). Some of these males employ AMTs depending on their morph and social status. The large males with well-developed fighting structures are dominant and aggressive, and employ their fighting structures to get hold of and guard females during the mating process. Small but sexually mature males avoid direct competition and—instead of fighting—take advantage of their small size and agility to sneak toward the female and quickly transfer spermatophores (Ra'anan and Sagi, 1985).

Different male morphotypes have also been described for the marine rock shrimp *Rhynchocinetes typus* Milne Edwards, 1837 (Torres, 1983). Males first become mature during the female-like *typus* morphotype, after which they molt through various intermediate stages to the robustus morphotype, which is the final molt stage and is characterized by strongly developed third maxillipeds and first chelae (see also Fig. 1). *Rhynchocinetes typus* is very common on shallow (from 0 to approximately 40 m

depth) hard bottoms off the coast of Chile (Vásquez and Castilla, 1982). Oviparous females and juveniles were found in traps throughout the year (Vásquez and Castilla, 1982; Arana and Henríquez, 1983). The reproductive cycles of females are not synchronized (Correa, 2000). The sex ratio is about 1:1 throughout the year (Correa, 2000), but due to the short time period during which females are receptive after molting and the almost continuous sexual activity of males, the operational sex ratio should be strongly skewed towards males. Previous experiments revealed that in a competition-free environment, all ontogenetic male stages show similar mating behaviors, albeit accompanied by differences in mating investment (i.e., number of spermatophores placed during a single mating—Correa *et al.*, 2000). Males, after noticing a receptive female, seize and guard the female for a certain period (23 min–3 h), often until the female finishes spawning. During the mating process, males maintain females between their pereopods (in the cage state), employing various stimulatory and checking movements towards the female (for further details see Correa *et al.*, 2000).

The purpose of this study was to determine whether a dominance hierarchy exists between male stages. Based on the above, we hypothesized that males at a competitive disadvantage may adopt an AMT. In the present study, we describe the mating behavior of three ontogenetic male stages of *R. typus* in a competitive situation. We compare these observations with those from a recent study of male mating behavior in a competition-free situation (Correa *et al.*, 2000).

## MATERIALS AND METHODS

### Collection and Selection of Rock Shrimp for Experiments

Shrimp were collected using SCUBA diving from the shallow subtidal zone of Bahía La Herradura, Coquimbo, Chile (29°59'S, 71°22'W). Individual shrimp were caught with a hand-held net, placed in a collecting basket, and shortly thereafter transferred to flowing seawater tanks in the laboratory. Males and females were kept in separate tanks with *ad libitum* food supply (ascidian colonies with their epibionts, crushed mollusks, and dead fish) before they were used in the experiments. Water temperatures varied between 17.0° and 19.2°C.

Three ontogenetic male stages (*typus*, *intermedius*, *robustus*) were distinguished according to Correa *et al.* (2000). In order to ensure full sexual maturity of the first male morphotype (*typus*), we used only males greater than 15 mm carapace length, the largest males in this category. During ontogeny, males pass through several *intermedius* stages (~ 6

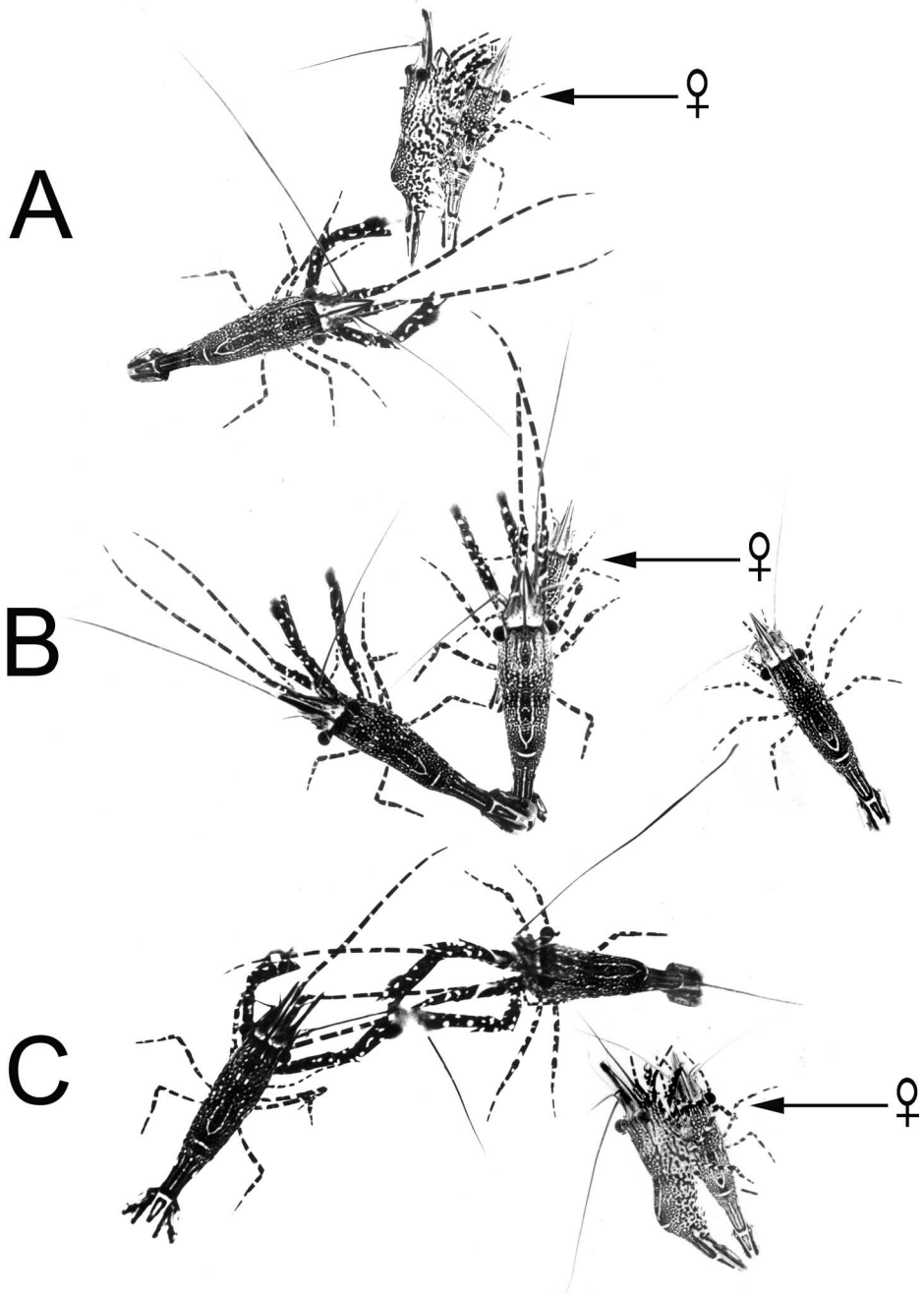


Fig. 1. Schematic representation of mating situations based on photographed and video-taped sequences among *Rhynchocinetes typus*. (A) First phase of experiments: subordinate male (typus) reacted first in capturing the female, robustus male at the left side; (B) Second phase of experiment 2: one robustus took possession of the female and is displaying towards the other robustus; subordinate typus at right side stays away from the two robustus; (C) Subordinate male is rapidly transferring spermatophores, taking advantage of a mating opportunity arising from aggressive interactions between robustus males. Video material available upon request.

instars, own unpublished estimation) before reaching the final molt stage, the robustus morphotype. For the experiments, we used late intermedius males, which require at most three additional molts before reaching the robustus stage. Males

were usually maintained without access to females for at least 5 d before being used in the mating experiments, but occasionally a male may have been used the day following its capture.

Recently molted and receptive females were collected each afternoon from the seawater tanks. When exuviae were found in the tanks, the recently molted females with still soft exoskeletons were identified and immediately separated into individual containers. These females were used for experiments to be conducted the following day (i.e., 12–36 h after molting), because preliminary observations indicated that females are not receptive immediately after molting but some hours thereafter.

All shrimp were returned to their natural environment after being used in the experiments.

#### Experiment 1: Male Dominance Hierarchy

To determine if there is a mating-related dominance hierarchy between the ontogenetic male stages, two males of different stages were placed with a receptive female in a 12-l glass aquarium. During an acclimatization period of 15 min, the males and the female were separated by a plastic partition, which was then removed, allowing contact between the shrimp. We used a continuous sampling method (*sensu* Lehner, 1996), observing this mating trio throughout the entire mating process, which sometimes lasted just over 3 h. During the observations, we collected both qualitative and quantitative data (see below). Five replicates of each of the three male-stage combinations were tested: robustus + typus, robustus + intermedius, intermedius + typus.

We designated a winner and a loser for each trial. Winners successfully mated and defended the female, with or without interacting aggressively with losers. Male stages that were found to win in the majority of replicates were characterized as dominants while loser males were characterized as subordinates. The total mating time and the number of spermatophore transfer events were recorded for dominants. Further, we recorded which male first initiated the mating process. Qualitative aspects of the agonistic behavior between males of different stages were contrasted with observations obtained from same-stage combatants (experiment 2, see below).

An *a posteriori* size analysis between shrimps of each experimental combination was performed (One-way ANOVA followed by Tukey test,  $\alpha = 0.05$ ). This comparison revealed that only in the intermedius + typus treatment were males different in size (typus:  $17.5 \pm 2.5$  mm; intermedius:  $22.8 \pm 2.7$  mm; mean carapace length  $\pm$  SD). It is expected that typus < intermedius < robustus in size, because this is the developmental order, but we attempted to use similar-sized males to examine mainly the effect of morphology rather than of size differences among the ontogenetic male stages. In this and in the following experiment, females were smaller than males, as would have been expected because in *R. typus*, there is a natural sexual size dimorphism in favor of males.

#### Experiment 2: Interactions Between Males and Observations of Male Mating Tactics

The purpose of this experiment was to provide those male stages that are at a competitive disadvantage (subordinates) with a mating opportunity while two dominant-stage males were fighting for access to the female. The initial phase of this experiment was identical to that of the first experiment: at the beginning, two males of different stages were competing for access to a receptive female. However, after one male became a winner (= dominant—see experiment 1), another male of the same ontogenetic stage was introduced into the aquarium. Thus, at this

moment, three males (two “dominant-stage” and one subordinate) + one receptive female were present in the aquarium. The rationale for the introduction of an additional dominant-stage male was to provoke aggressive interactions between these two males for access to the female. Preliminary observations had indicated that during these disputes, the female might temporarily be liberated, which could then provide a mating opportunity for the subordinate. Ten replicates of all possible combinations between dominant and subordinate male stages were tested: i.e., 2 robustus + 1 typus, 2 intermedius + 1 typus, and 2 robustus + 1 intermedius.

As in experiment 1, we used a continuous sampling method (*sensu* Lehner, 1996) in which we focussed particular attention on the behavior of subordinates. We recorded qualitative observations such as presence (or absence) of male behavioral events described in an earlier study (Correa *et al.*, 2000) and the manner in which these events were performed. In addition, we quantified the frequencies of potential mating opportunities for subordinates and their resulting behavior. We measured the time between the moment at which males seized females and at which the first spermatophore transfer event took place for both initial dominants and subordinates. Also, total mating time and number of spermatophore transfer events of subordinates were measured. We described qualitatively the agonistic behavior between males of the same developmental stage (the two “dominant-stage males”) and compared these observations with those from experiment 1 in which males of different developmental stages interacted.

An *a posteriori* size analysis between shrimps of each experimental combination was performed (One-way ANOVA followed by Tukey test,  $\alpha = 0.05$ ). Only in one treatment were males different in size: both intermedius were larger than the typus male (typus:  $16.3 \pm 1.2$  mm; first intermedius:  $20.8 \pm 1.1$  mm; second intermedius  $20.6 \pm 1.0$  mm).

#### Examination of the Initial Phase of the Mating Process

In the present experiments (with competitive environments), we were also interested in learning which male stage would initiate the mating process and in which manner. Because the first phase of both experiments 1 and 2 consisted of two different male stages competing for one receptive female, we analyzed these data together for every male-stage combination. Thus, we had 15 observations for each of the three male-stage combinations (5 replicates from the first experiment + 10 replicates from the second experiment) to examine how different male stages react upon encountering a receptive female in a competitive environment. We tested the null hypothesis that no differences exist between subordinates and dominants in taking the first mating initiative, employing a Binomial Test (i.e.,  $P_{\text{initiative}} = 0.5$  for both subordinates and dominants;  $\alpha = 0.05$ ).

#### Quantitative Analysis of Mating Effort Among Male Stages in Different Social Contexts

The present experiments provided us with data on total mating time and number of spermatophore transfer events for different ontogenetic male stages behaving as dominants (experiment 1) and as subordinates when mating opportunities arose (experiment 2). We compared these data with those obtained in a competition-free environment, which had been taken using the same experimental set-up and were conducted during the same season and by the same observers (Correa *et al.*, 2000), thereby permitting this comparison.

Table 1. Summary of data sources and sample size for two variables that were quantitatively evaluated: 1) total mating time and 2) number of spermatophore transfer events. Within each ontogenetic male stage, comparisons were made between males in competition-free vs. competitive environments.

Male stage	Social context		
	Competition-free	Competitive-environment	
		Subordinate	Dominant
Typus	Correa <i>et al.</i> , 2000, $n = 5$	experiment 2, $n = 10$	no data*
Intermedius	Correa <i>et al.</i> , 2000, $n = 5$	experiment 2, $n = 6$	experiment 1, $n = 5$
Robustus	Correa <i>et al.</i> , 2000, $n = 7$	no data*	experiment 1, $n = 10$

\* Typus males never were dominants and robustus males never were subordinates in our experiments.

Statistical comparisons were conducted on total mating time and the number of spermatophores transferred for each ontogenetic male stage in a competition-free and in a competitive situation. For each comparison a nonparametric two-sample test was performed (Mann-Whitney  $U$  test; Table 1 summarizes the sample size and data source for each comparison).

## RESULTS

### Male Dominance Hierarchy and Interactions Between Males

*A) Interaction Between Males of Different Ontogenetic Stages (Experiment 1).*—In all experimental mating trios (15 in total), females were mated by the more advanced ontogenetic male stage. In some cases, less advanced male stages also succeeded in performing spermatophore transfer events during a short interaction with the female. However, this only occurred at the beginning of the experiments, before the more advanced male had noticed the receptive female.

A linear dominance hierarchy (*sensu* Lehner, 1996) was identified between male stages, because in all treatments the more advanced ontogenetic stage finally won access to the female and then defended it against the other male until the end of the mating process. The dominant male stage is robustus, followed by the subdominant intermedius, with typus being the subordinate male stage. The status of each male in the dominance hierarchy was established by brief agonistic interactions between males. Dominants kept subordinates at a distance by repeated sideward sweeps of their first chelae either before or while guarding the female in the cage state. Direct agonistic interactions were usually unidirectional because small males assumed their subordinate role quickly and tried to avoid more developed males. Following establishment of the hierarchy, the mating process usually continued

without further interruption by the subordinate male.

*B) Interactions Between Males of Same Ontogenetic Stage (Experiment 2).*—Establishment of dominance status during interactions between males of the same stage often lasted several minutes and involved different interactions. Following addition of the second dominant-stage male in experiment 2, a stereotyped agonistic behavior was frequently observed, which consisted of a display phase followed or not by an aggressive phase (Fig. 1). At the beginning of the experiment, the dominant-stage males approached each other with the telson simultaneously displaying their first pair of chelae towards each other. Seen from above, this position gave the appearance of a “V” (Fig. 1B). Males maintained this position for variable time periods (from a few seconds up to several minutes), occasionally swaying back and forth over the substrate. In many cases, this display phase was sufficient to establish male status, and the encounter was terminated immediately thereafter, but this display phase was sometimes followed by an aggressive phase. During aggressive bouts, males abandoned the initial V position, faced their opponent directly, and with rapid movements attempted to grab the opponent’s chelae with their own (Fig. 1C). As soon as one male had grabbed his rival’s pair of first chelae, both males attempted to place the tips of their pointed maxillipeds towards the anterior region of their rival’s head. After a male had succeeded in placing his maxillipeds in that region, it pulled the opponent with its chelae, thereby effectively pushing its maxillipeds into the head region of the rival. This agonistic display terminated when one male changed its behavior from aggressive to submissive and tried to evade his rival. The winner rapidly recovered the female if she had been lost during this interaction. This stereotyped fighting be-

havior also was observed in one interaction between a large intermedium with a small robustus (winner). In one case (out of seven interactions that ended in aggressive bouts), we observed loss of a second chela as a consequence of the encounter.

While dominant males were competing and performing their agonistic displays, they often lost control over the female, thereby offering an ephemeral mating opportunity for subordinates (see sequence in Fig. 1).

#### Observations of Male Mating Tactics (Experiment 2)

Males that were at a competitive disadvantage as a consequence of their ontogenetic stage were able to modify their mating behavior according to the social environment. Herein subordinate males—i.e., all typus and intermedium with two robustus—had ephemeral mating opportunities (from a few seconds to some minutes). Results from the second phase of experiment 2 (i.e., when two dominant-stage and a subordinate male plus a female were present in the aquarium) demonstrated the importance of agonistic interactions between dominants for mating opportunities of subordinates. In 19 of 25 (76.0%) observations in which a dominant succeeded in mating, it lost hold of the female at least once as a result of agonistic interactions with another dominant-stage male. The number of mating opportunities for subordinate males during each replicate ranged from 1 to 9. In the majority of cases, subordinates used at least one of the mating opportunities that arose during conflicts between dominant-stages (13 of 19 cases; 68.4%). During these occasions, subordinate males took hold of the female, and some of them (6 of 13 cases; 46.2%) were able to perform one or more spermatophore transfer events before a dominant male recovered the female (Table 2).

The behavior of subordinates that used mating opportunities in a competitive environment was similar for typus and intermedium male stages but differed completely from the behavior of the same male stages in a competition-free environment (Fig. 2). During the brief mating encounters observed herein, subordinate males quickly seized the female and, without reaching a stable cage state, immediately performed repeated spermatophore transfer events (Fig. 3). They did not display any other behaviors before transferring spermatophores, and they avoided all direct encounters with

dominant males, which is why we termed their behavior a “sneak” mating tactic. Following successful spermatophore transfer events, the subordinate males continued mating in the usual manner as long as no dominant male attempted to recover the female. In contrast, dominants always delayed transfer of the first spermatophore for at least a few minutes (from 2 to 190 min, with exception of three robustus males in presence of a matched competitor; Fig. 3). Before transferring spermatophores, dominants guarded the female and performed other behavioral events such as they did in a competition-free situation (e.g., checking embrace, poking, pumping; see Correa *et al.* (2000) for detailed description of these behaviors; Fig. 2). This mating tactic was termed “guard.”

#### Examination of the Initial Phase of the Mating Process (Experiments 1 and 2)

The observation of the “sneak” mating behavior was not only restricted to subordinate males taking advantage of chances given by fighting males (as in experiment 2). At the beginning of both series of experiments, subordinate males occasionally seized and transferred spermatophores to the female before the dominant male took possession of the female. There was no significant tendency in whether dominant or subordinate males were the first to react to the presence of a receptive female, regardless of male-stage combination (Binomial Test,  $P > 0.50$  for every male-stage combination and for pooled data; Table 3). In 16 of 18 cases (88.9%) in which subordinate males first took hold of a female, they were able to perform spermatophore-transfer events using the sneak mating tactic before the dominant male intervened.

#### Quantitative Analysis of Mating Effort Among Male Stages in Different Social Contexts

When males are dominants in a competitive environment (i.e., intermedium competing with typus, and all robustus in experiment 1), they may seize or overtake a female once and then guard her throughout the entire mating process. Such matings of dominants lasted from 56 to 220 min, which did not differ from the duration of matings by the same male stages in a competition-free situation (see statistical analysis in Table 4; Fig. 4A). During this period, the mating couple maintained the cage state, and the male performed various stimulatory and/or sensitive events before and after

Table 2. Number of mating opportunities for subordinate males competing with two dominant-stage males and number of realized matings by subordinates; all data were taken from experiment 2; percentages of the first column are relative to the total number of replicates (10 for each mating trio) and the following are relative to each preceding column.

Male combination	No. of cases in which there was			
	At least one successful mating	A mating opportunity for subordinate male	A used chance (seizure by sub. male)	Spermatophore transfer events from sub. males
1 typus + 2 robustus	9 (90.0%)	7 (77.8%)	4 (57.1%)	4 (100%)
1 typus + 2 intermedius	7 (70.0%)	5 (71.4%)	3 (60.0%)	1 (33.3%)
1 intermedius + 2 robustus	9 (90.0%)	7 (77.8%)	6 (85.7%)	1 (16.7%)
Total	25 (83.3%)	19 (76.0%)	13 (68.4%)	6 (46.2%)

transferring spermatophores (Correa *et al.*, 2000). Dominants also performed as many spermatophore transfer events as they did in a competition-free situation (Table 4; Fig. 4B). In contrast, subordinate males, which are susceptible to attacks by dominants and relied on ephemeral mating opportunities, may engage in repeated seizures followed by short cage states (often < 1 min). Consequently, total mating times achieved by subordinates (i.e., all

typus and intermedius competing with robustus in experiment 2) in a competitive environment were significantly shorter than the mating times of the same male stages in a competition-free environment (Table 4; Fig. 4A). Because subordinate males were always interrupted in their mating attempts, the total number of spermatophore transfer events that they achieved was highly variable (from 1 to 18 events, see Fig. 4B), and they generally performed fewer

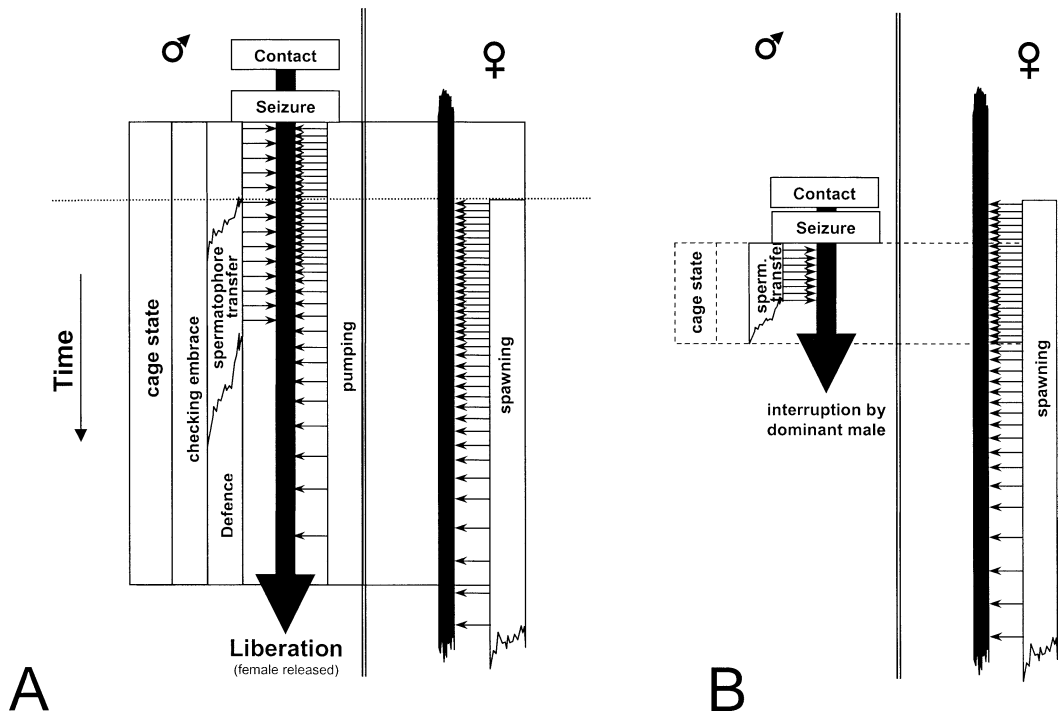


Fig. 2. Ethogram of behavioral states and events exhibited by male *Rhynchocinetes typus* during mating process in competition-free and in competitive environments. Horizontal arrows indicate specific behavioral events described in boxes (e.g., poking, spermatophore transfer, and pumping for males and spawning for females); dotted line shows the start of spermatophore transfer in males and initiation of spawning in females. (A) Behavior shown by all ontogenetic male stages in a competition-free environment (from Correa *et al.*, 2000) and by dominant males in a competitive environment. (B) Behavior shown by subordinate males in a competitive environment; mating pair does not necessarily form a stable cage state, and females may (as in example) or may not be spawning while subordinate males are transferring spermatophores.

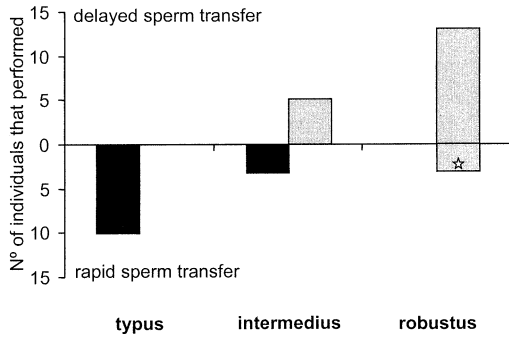


Fig. 3. Number of males performing either of two types of spermatophore transfer during experiment 2 (i.e., in a competitive environment). Rapid sperm transfer occurs within 1 min of pair formation, while delayed sperm transfer occurs at least 2 min after pair formation. Black columns represent individuals that are always subordinate, and gray columns represent dominant stages that had a matched competitor during the second phase of the experiment. Note that typus males were never dominants and robustus never subordinates. Intermedius males were dominant when combined with typus and subordinate with robustus. The star indicates a column including an individual that performed both delayed and rapid sperm transfer.

spermatophore transfer events than in a competition-free environment (Table 4).

#### DISCUSSION

Herein, we revealed the existence of a linear dominance hierarchy among ontogenetic male stages of *Rhynchocinetes typus* that are competing for mates (robustus > intermedius > typus). Dominant males easily gained access to receptive females when competing with subordinate males. The more developed males have a higher resource holding power (RHP *sensu* Parker, 1974) and thus hold an advantage both in taking over a female from a rival and in preventing female take-over by a rival (Iribarne *et al.*, 1995; Sainte-Marie *et al.*, 1997). Thus, older males will obtain most mating opportunities (e.g., Waltz and Wolf, 1984). Only when a dominant male had not yet perceived or could not direct his entire attention towards a receptive female did a subordinate male have a chance of gaining access to the female. During their mating attempts, subordinate males did not engage in mate-guarding or sophisticated courting (as they did in competition-free environments, Correa *et al.*, 2000), but rather immediately tried to transfer spermatophores onto the female's abdomen. Their behavior in a competitive environment was sufficiently different from that in a competition-free situa-

Table 3. First mating initiative by different ontogenetic male stages in mating experiments. Data were taken from experiment 1 and the first phase of experiment 2, in which two males of different ontogenetic stages competed to mate with the receptive female;  $n = 15$  replicates for each treatment; values in parentheses show percentage of replicates in which successful matings were observed; no significant differences were found between the numbers of dominant or subordinate males reacting first (Binomial Test,  $P \geq 0.50$  in each case).

Male combination	Successful mating occurred	No. of cases in which	
		Males taking the first mating initiative are	
		Subordinate	Dominant
typus + robustus	14 (93.3%)	8	6
typus + intermedius	12 (80.0%)	4	8
intermedius + robustus	14 (93.3%)	6	8
Total	40 (88.9%)	18	22

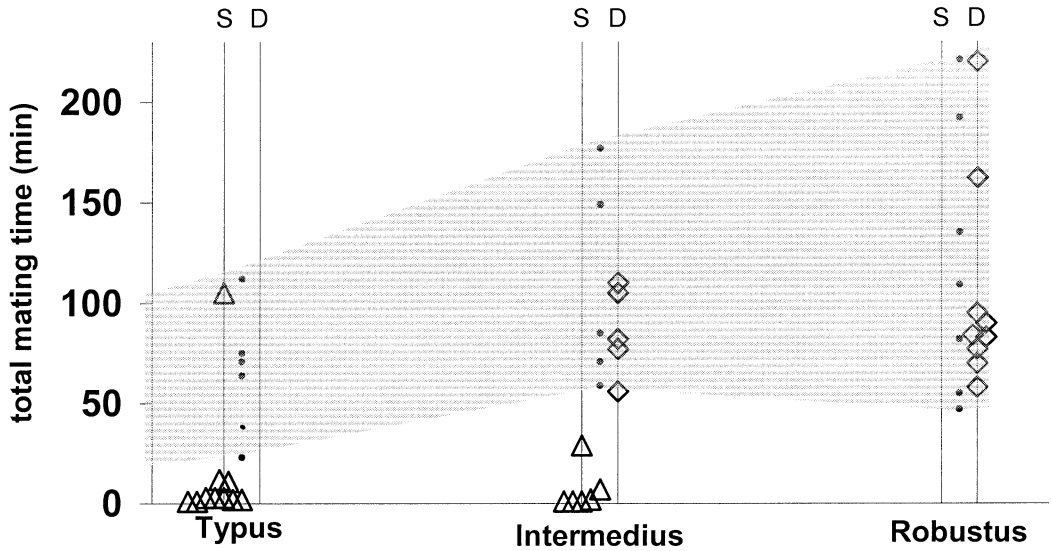
tion to be classified as an alternative mating tactic (AMT). Both morphology and social environment—by affecting the relative RHP of competitors—are important in determining which mating tactic each male employs.

#### Establishment of Dominance Rank Between Male Rock Shrimp

In all competitive encounters that we staged between male *R. typus* of different ontogenetic stages, the more developed male (with larger weapon structures than its opponent) quickly gained access to the receptive female as soon as it had noticed the female's presence. These observations are consistent with others made on species with different male morphs—larger or more developed males occupy higher social status (e.g., solitary bee *Centris pallida*—Alcock *et al.*, 1977; dung beetle *Onthophagus acuminatus*—Emlen, 1997; amphipod *Jassa falcata*—Borowsky, 1985; shrimp *Macrobrachium rosenbergii*—Ra'anan and Sagi, 1985; crab *Chionocetes opilio*—Elnor and Beninger, 1995).

In decapod crustaceans, relative body and/or weapon size (e.g., chelae) is important in determining relative RHP and, thus, the outcome of contests (Barki *et al.*, 1997; Sneddon *et al.*, 1997). When physical differences between rivals are too large, the chances that the less-developed individual could win are small (Hughes, 1996), and it is advantageous for it to withdraw. Accordingly, when different ontogenetic male stages of *R. typus* were competing for a female, the less-developed

## A Total mating time



## B N° spermatophore transfer events

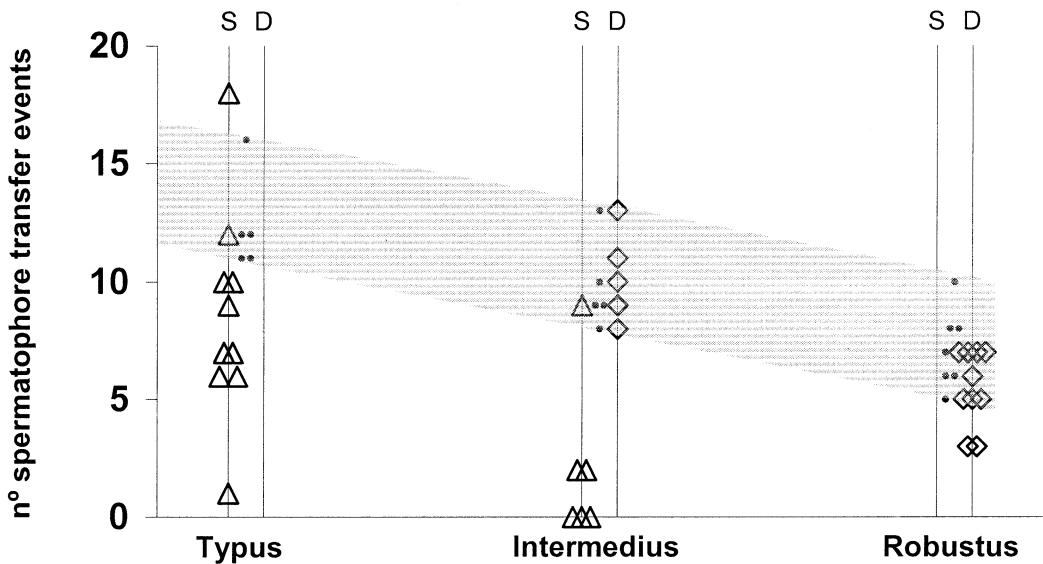


Fig. 4. (A) Total mating time and (B) number of spermatophore transfer events for the three ontogenetic male stages; only males that participated at least for a few seconds in a mating are shown; shaded area highlights range obtained for three male stages in a competition-free environment (●, data from Correa *et al.*, 2000); values representing subordinates are represented by  $\triangle$ , those representing dominants by  $\diamond$ .

male always withdrew immediately (experiment 1). In contrast, when contestants are matched in their fighting ability, as in interactions between *R. typus* males of the same ontogenetic stage (experiment 2), the smaller male may have

a considerable chance to win a contest, and, thus, an escalation could bring significant benefits (Parker, 1974; Hughes, 1996; see example in Sneddon *et al.*, 1997). In these cases *R. typus* exhibited a stereotyped (ritual-

Table 4. Summary of comparisons between males in a competition-free (CF) situation *versus* the same male stages in a competitive environment (COMP); two variables were compared: i) total mating time, and ii) number of spermatophore transfer events; for each group the sample size and mean  $\pm$  SD are presented; comparisons were done using the Mann-Whitney *U* test (*P* values with \* indicate significant differences with  $\alpha = 0.05$ ).

CF	COMP	Total mating time				No. sperm. transfer			
		CF	COMP	<i>U</i>	<i>P</i>	CF	COMP	<i>U</i>	<i>P</i>
R ( <i>n</i> = 7)♣	Dominant R ( <i>n</i> = 10 <sup>1</sup> )♥	120.1 $\pm$ 66.7	102.9 $\pm$ 49.6	32.0	0.770	7.1 $\pm$ 1.7	5.5 $\pm$ 1.6	17.5	0.088
I ( <i>n</i> = 5)♣	Dominant I ( <i>n</i> = 5)♥	108.2 $\pm$ 51.8	86.0 $\pm$ 22.0	10.0	0.602	9.8 $\pm$ 1.9	10.2 $\pm$ 1.9	10.5	0.676
I ( <i>n</i> = 5)♣	Subordinate I ( <i>n</i> = 6)♠	108.2 $\pm$ 51.8	6.8 $\pm$ 11.1	0.0	0.006*	9.8 $\pm$ 1.9	2.2 $\pm$ 3.5	2.0	0.018*
T ( <i>n</i> = 5)♣	Subordinate T ( <i>n</i> = 10 <sup>1</sup> )♠	69.0 $\pm$ 31.7	14.3 $\pm$ 32.1	4.0	0.010*	12.4 $\pm$ 2.1	8.6 $\pm$ 4.5	8.0	0.037*

♣ Data were taken from Correa *et al.* (2000).

♥ Data from experiment 1.

♠ Data from experiment 2.

<sup>1</sup> Note that these groups contain two types of competing males. Five data are for a robustus (dominants) competing with a typus and five are for a robustus competing with an intermedius; and seven cases of typus (subordinates) competed with robustus and three with intermedius.

ized) fighting behavior, which comprises primarily two phases: (A) display, consisting of the exhibition of male fighting structures, which is often but not necessarily followed by (B) a sequence of aggressive interactions (see Fig. 1). During the display phase, the two rivals have time to exhibit their own fighting potential and to evaluate their opponent's potential. Following assessment of the opponent's fighting potential, either the two males proceed to aggressive interactions, or one male retreats, avoiding direct encounters that may be too costly. In either case, these conventional fights (*sensu* Parker, 1974) resulted in the establishment of a dominance hierarchy between competitors. Similar to *R. typus*, in the freshwater shrimp *Macrobrachium rosenbergii*, agonistic displays between males of the same morph are ritualized and also involve different phases (a pre-escalated, escalated, and post-escalated fighting phase; Barki *et al.*, 1991). In contrast, when morphological differences between *M. rosenbergii* males are large, the smaller males usually evade direct interactions (Ra'anan and Sagi, 1985).

It should be noted that in experiment 2, males of different ontogenetic stages were in contact with each other before competing for receptive females, while males of the same ontogenetic stage were in contact only when attempting to gain access to receptive females. Thus, males of different ontogenetic stages could have evaluated their opponents before entering into direct competition, which was not possible for males of the same ontogenetic stage. The consistency of our results and the large morphological differences between males of different ontoge-

netic stages, however, led us to suggest that males of different morphological stages rarely enter into direct confrontation. This is supported by observations of many other species in which males with highly different RHPs rarely engage in aggressive interactions (Ra'anan and Sagi, 1985; Taborsky *et al.*, 1987; Shuster, 1989; Clark, 1997).

#### Primary and Alternative Mating Tactics in Rock Shrimp

Two mating tactics were identified in *R. typus* males. The tactic of attending and guarding the female throughout the mating process is employed by all male stages when in a dominance advantage (experiments 1 and 2) or in a competition-free situation (Correa *et al.*, 2000); this tactic was termed "guard." It can be considered the preferred tactic because all males perform it whenever the social environment allows (*i.e.*, the primary tactic *sensu* Taborsky *et al.*, 1987). In *R. typus*, it consists of a series of behavioral events before and after the actual spermatophore transfer events, and it may last for up to 3 h, during which dominants drive competitors away by aggressiveness (Correa *et al.*, 2000; present study). Given the dominance hierarchy among male stages, lower-ranked individuals have a very low chance of succeeding in performing this primary tactic. Instead, when dominants are present, subordinates are able to take advantage of ephemeral mating opportunities that arise during fights among dominant-stage males. They employ an alternative mating tactic, suggesting that they are able to assess the relative RHP of other males and adjust their respective behavior accordingly. This tactic was

termed "sneak" and is characterized by (1) rapidity, (2) simplicity (mounting the female and immediately transferring spermatophores), and (3) avoidance of direct competition with the dominants. This AMT, as observed in *R. typus*, is similar to those of other animals with variations in male morphologies (e.g., dung beetle *Onthophagus acuminatus*—Emlen, 1997; shrimp *Macrobrachium rosenbergii*—Ra'anan and Sagi, 1985; amphipod *Jassa marmorata*—Clark, 1997).

At the beginning of experiments 1 and 2, subordinate males had a chance to mate by reacting first to the presence of the receptive female. In a number of cases, they indeed initiated the mating process and successfully transferred spermatophores using the sneaking tactic. Thus, subordinate males utilized the sneaking tactic not only during direct competitive encounters between dominants, but also before the dominant males had even initiated the mating process. Because in some other species males at a competitive disadvantage also evade direct competition by means of rapidity (Ra'anan and Sagi, 1985; Shuster, 1989; Clark, 1997), one could have expected subordinates to react first to the presence of the receptive female. This was not confirmed in the present study, which is possibly due to the way in which male shrimp perceive the presence of receptive females; whereas in many other decapod crustaceans receptive females release sex pheromones into the water, triggering male searching behavior and provoking pair formation (Gleeson, 1991; Bouchard *et al.*, 1996), in most shrimp species, contact pheromones on the exoskeleton of recently molted females are of major importance in stimulating males (Bauer, 1979; Salmon, 1983). Male shrimp need to touch females in order to become aware of their receptivity. The fact that in our experiments equal numbers of subordinates and dominants initiated mating contact with a female may be the result primarily of their encounter rate with the female rather than of differences in mating tactics. It is likely that encounter rates with females in our laboratory experiments were similar for both subordinate and dominant males, while encounter rates in the field may be higher for subordinate stages due to their relatively high mobility and abundance (personal observations). In the field, visual stimuli (e.g., attraction to turmoil centered around receptive females) may addi-

tionally affect encounter rates between males and receptive females. Given that in nature shrimp occur at high densities and are continuously moving, thereby frequently touching other shrimp, receptive females will probably be easily detected. This most likely leads to disputes similar to those in our laboratory experiments.

Switching to an alternative tactic may be better than using the primary tactic when a male is not in a position to successfully fight with other males, for example, as a consequence of a weak RHP (Alcock *et al.*, 1977; Thornhill, 1981; examples in Ra'anan and Sagi, 1985; Taborsky, 1994; Clark, 1997). Following the establishment of an individual's status in the dominance hierarchy (see previous section), male shrimp either employ the sneak or guard mating tactics. However, when morphological differences between competing male stages are small, both competitors may be reluctant to abandon the primary tactic (guard). This may be, in our present experiments, reflected by the fact that intermedium males competing with robustus males (and to some extent *typus* competing with *intermedius*) were more reluctant to change from their primary tactic (guard) to the alternative (sneak; see last column in Table 2). In a situation in which the competitors' RHPs are highly unequal (e.g., *typus* vs. *robustus*), subordinate males may always switch to the alternative tactic (see last column in Table 2).

Thus, *R. typus* could be considered a species whose males exhibit a pure conditional mating strategy (*sensu* Dominey, 1984): Males employ one of two mating tactics depending on their relative RHP, i.e., depending on their own ontogenetic stage and on that of other competing males. In the field, it is likely that in addition to the quality of a direct competitor (e.g., ontogenetic state), the number of additional competitors—by affecting the operational sex ratio—may also influence the mating behavior of a male (Iribarne *et al.*, 1995; Jivoff and Hines, 1998; Jirotkul, 1999; Kvarnemo and Simmons, 1999).

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