

Effects of Social Structure on the Behaviour and Performance of Alternative Reproductive Phenotypes in Male Rock Shrimp, *Rhynchocinetes typus*

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Abstract

Males that adopt alternative mating tactics within a conditional strategy often undergo costly morphological changes when switching to the next phenotype during ontogeny. Whether costs of changing to a subsequent reproductive phenotype are outweighed by a higher mating probability may depend on the frequencies of different phenotypes in a group of competitors. Benefits and costs associated with different phenotype frequencies depend on interactions within and between alternative phenotypes, but the underlying behavioural mechanisms have rarely been studied. Herein, we used the rock shrimp *Rhynchocinetes typus* as a model: ontogenetic male stages of this species differ in morphological and behavioural traits that indicate alternative reproductive phenotypes. The small, subordinate, male stage (typus) develops via several intermediate stages (intermedius) to the dominant male stage (robustus): in competitive interactions the typus males usually employ the sneaking tactic, while the robustus males invariably employ the monopolizing fighter tactic. In laboratory experiments, we manipulated phenotype frequencies to examine whether there are frequency-dependent effects on searching behaviour, aggressiveness and mating probability. With increasing frequency of robustus males, the rate of aggressive interactions among them increased. Furthermore, robustus males increased walking velocity when more than one robustus male was present. In contrast, typus males did not adjust their searching or aggressive behaviour. The increase of aggressive interactions among robustus males provided more opportunities for typus males to seize a temporarily unguarded female. While typus males exploit fights among robustus males that produce mating opportunities for them, robustus males benefit from typus males, which reveal the presence of receptive females. We suggest that each phenotype benefits from the presence of the other phenotype and suffers costly interference among individuals of the same phenotype. Whether frequency-dependent effects on the mating probability of subordinates also affect their ontogenetic switchpoint should be examined in future studies.

Introduction

Mating success of alternative reproductive phenotypes largely depends on the frequencies at which different phenotypes occur in a population. Traditionally, it has been suggested that each phenotype does better than the other when it is rare (Maynard Smith 1974; Singh & Sisodia 2000), leading to the concept of negative frequency-dependent selection to explain the coexistence of genetically determined alternative phenotypes in a population (Maynard Smith 1982; Gross 1996). Within this theoretical framework, alternative phenotypes are thought to exist at an evolutionarily stable frequency with equal average fitness of either phenotype (Maynard Smith 1982; Gross 1991, 1996) or to show cyclic oscillations, when more than two alternative phenotypes coexist (Sinervo & Lively 1996; Zamudio & Sinervo 2000). Evidence for frequency-dependent selection on genetically determined alternative phenotypes has been found for example in lizards (Sinervo & Lively 1996; Zamudio & Sinervo 2000; Bleay et al. 2007), ruffs (Lank et al. 1995; Widemo 1998), bluegill sunfish (Gross 1991), Atlantic salmon (Thomaz et al. 1997), damselflies (Svensson et al. 2005) and fruitflies (Fitzpatrick et al. 2007). However, when phenotypes are not genetically determined, as is the case in ontogenetically determined phenotypes, neither equal average fitness of alternative phenotypes nor frequency-dependent selection is required to maintain alternative phenotypes in a population (e.g. Shuster & Wade 2003). Instead, a conditional strategy is expected that has evolved under status-dependent selection, where the fitness of alternative reproductive phenotypes, relative to each other, depends on the competitive ability of individuals (Gross 1996). Males in poor condition (or low status) are thought to be unable to bear the costs associated with the more successful reproductive phenotype and are therefore forced to adopt a behavioural tactic that yields a lower average fitness (e.g. Dawkins 1980; Hunt & Simmons 2001). To maximize overall fitness, frequency-dependent selection has been suggested to affect a status-dependent switch between alternative reproductive phenotypes (Repka & Gross 1995; Gross 1996; Gross & Repka 1998). Whether frequency dependence does occur or not depends on the relationship of costs to benefits in interactions within and between alternative phenotypes, but empirical studies about frequency-dependent effects within non-genetically determined, conditional strategies are rare (e.g. Eadie & Fryxell 1992; Pfennig 1992; Simmons et al. 2004).

Using different frequencies of ontogenetic male stages that employ alternative behavioural tactics, our study examines changes in behaviours and mating probabilities depending on the respective social environment.

Alternative reproductive phenotypes usually differ in their ability to monopolize resources or mates, with the less successful phenotype parasitizing members of the more successful phenotype (e.g. Taborsky et al. 1987; Arak 1988). Typically, monopolizing tactics are used by dominant individuals, while parasitic tactics are usually employed by subordinate individuals that avoid direct confrontations due to their lower competitive ability. As dominants are thought to suffer from parasitic interactions with subordinates, and subordinates suffer from competition with other subordinates, it is usually assumed that with increasing frequency of subordinates in a population the fitness functions of both dominants and subordinates decline (e.g. Barnard & Sibly 1981; Eadie & Fryxell 1992). However, the frequency of dominant and subordinate phenotypes may also affect only one of either phenotypes (Parker 1984; Sherratt 2001), and Simmons et al. (2004) showed that the mating success of both dominant and subordinate males may also decline with increasing frequency of the dominant phenotype. Hence, fitness consequences of variable phenotype frequencies are presumably quite diverse, depending on the underlying mechanisms of mating behaviour and their susceptibility towards changes in the social structure. For example, in a fighter–sneaker system it may be common that the mating success of subordinate sneakers considerably depends on aggressive interactions among dominant fighters that leave a female temporarily unguarded. This mechanism has been identified as ‘distraction sneaking’ in the hawk–dove–sneaker model of Dubois et al. (2004), which predicts that sneakers have high success when they are rare and aggression between hawks is common, and low success when they are frequent and aggression between hawks is rare. Hence, dominants do not necessarily suffer from a high frequency of subordinates, favouring the relatively costly fighting tactic of the dominants. Herein, we test how dominant and subordinate male phenotypes react to and are affected by changes in alternative phenotype frequencies.

Similar as social status, the probabilities of encountering alternative phenotypes can also influence the success of either phenotype. For example, sneaker males might reduce searching at high frequencies of fighter males, and instead succeed with

a more stationary sneaking behaviour. On the other hand, a very low frequency of dominant fighter males could mean that increasing locomotor activity is beneficial for subordinates, as it would increase the encounter rate with females not (yet) monopolized by dominant males. Hence, local social structure may affect both searching behaviour and the spatial distribution of alternative reproductive phenotypes, which can have important fitness consequences for either phenotype (Gross 1991). Based on these considerations we expect that dominant and subordinate males show frequency-dependent changes in searching behaviour, aggressiveness and mating probability. Using a marine shrimp as a model species, we predicted increasing aggressiveness of dominant robustus males with increasing frequency of dominants, and that simultaneously the mating probability of subordinate typus males would increase. Furthermore, typus males were expected to reduce and robustus males to increase their locomotor activity at increasing frequency of robustus males.

Methods

The Model Organism

The rock shrimp *Rhynchocinetes typus* Milne Edwards 1837 is very common on shallow subtidal hard-bottoms (0–40 m) along the coast of Chile (Vasquez & Castilla 1982). Three different reproductive phenotypes are distinguished among male rock shrimp: they reach sexual maturity in the female-like typus stage, and during growth they pass through various intermediums moult stages until they reach the terminal robustus stage, which is characterized by strongly developed third maxillipeds and first chelae, which are used to guard females and as weapons in intra-sexual combats. The mating system is described as 'neighbourhood of dominance' (Correa & Thiel 2003a) with a strong dominance hierarchy among males of the order typus < intermediums < robustus (Correa et al. 2003). Robustus males occur in proportions of 2–5% in natural populations (Correa & Thiel 2003b). The size classes of the different males stages are highly overlapping (Correa & Thiel 2003b), indicating a conditional strategy of switching to the next ontogenetic stage. Robustus males have high resource holding power (RHP, a measure of fighting ability *sensu* Parker 1974). They take over females from subordinates and defend them against other males by holding them between their pereopods in the so-called cage state (Correa et al. 2000,

2003). While guarding the female, they delay spermatophore transfer and perform behaviours thought to stimulate ovulation in the female. This behavioural tactic has been termed 'guard' and was identified as the primary mating tactic because all males perform it in a competition-free situation (Correa et al. 2003). Subordinate males also hold the female in the cage state, but cannot defend a female against intermediums and robustus males. Therefore, typus males avoid direct competition with the dominants, and rapidly seize the female and transfer spermatophores immediately without stimulating the female (Correa et al. 2003). This behavioural tactic has been termed 'sneak' and was called the secondary (alternative) mating tactic. Under natural conditions, robustus males always employ the guarding tactic, whereas typus males normally use the alternative sneaking tactic. Moreover, subordinates may take advantage of brief mating opportunities when females are temporarily left unguarded during fights between robustus males (Correa et al. 2003), which corresponds to 'distraction sneaking' as described by Dubois et al. (2004).

Collection and Maintenance of Rock Shrimp

Rock shrimp were collected during the months Aug.–Oct. 2004 in Bahía La Herradura in Coquimbo, Chile (29°59'S, 71°22'W). Collections were made in the shallow subtidal zone (3–6 m) using a diver-operated 'airlift sampler' (Correa & Thiel 2003b) and baited traps. Immediately after capture, shrimp were transferred to flowing seawater tanks in the laboratory, where the sex of all individuals was identified. Maintenance took place under natural light conditions and temperature ranges of 10–13°C.

Individuals of different sex were maintained in separate tanks with *ad libitum* food supply (ascidian colonies of *Pyura chilensis* with their epibionts). To ensure sexual maturity, only males >13 mm cephalothorax length and reproductive (i.e. ovigerous) females were selected for this study (Correa & Thiel 2003b; I. Hinojosa, pers. comm.). Three male stages (typus, intermediums and robustus) were distinguished on the basis of morphological characteristics provided by Correa et al. (2000) (Table 1). Each morning, recently moulted females were collected from the holding tanks and isolated in individual plastic containers (20 × 20 × 15 cm) with flowing seawater. These females were then used in the experiments 36–48 h after moulting, when they become fully receptive (for further details see Correa et al. 2003; Hinojosa & Thiel 2003).

	Typus	Intermedius	Robustus
Characters (after Correa et al. 2000)			
Hairs on first chelipeds	No	Yes	Yes
Relationship, last segment third maxilliped/ carapace length	<<1	>1 and <2.1	>2.1
Number of spines at tip of third maxilliped	7	7	1
Number of teeth at tip of propodus of first cheliped	4	4	1
Measurements			
Cephalothorax length (mm; $x \pm SD$)	13.6 \pm 0.7	16.7 \pm 1.2	19.3 \pm 1.8
Antenna length (mm; $x \pm SD$)	74.5 \pm 9.4	87.0 \pm 10.3	96.0 \pm 17.2

Table 1: Morphological characters and measures of three ontogenetic male stages of *Rhynchocinetes typus*

Table 2: Experimental set-up

	Treatment 1	Treatment 2	Treatment 3
No. males (Typ., Int., Rob.)	19, 4, 1	14, 8, 2	9, 12, 3
Density (δ , σ)	24, 2	24, 2	24, 2
Replicates with focal typus male	7	7	7
Replicates with focal robustus male	7	7	7
Total no. replicates	14	14	14
No. males in all replicates (T, I, R)	266, 56, 14	196, 112, 28	126, 168, 42

The number of the treatment refers to the number of robustus males. The treatments are referred to as 'phenotype frequency'.

Experimental Design

The aim of this experiment was to examine the searching and monopolization behaviour of robustus and typus males within assemblages of different frequencies of ontogenetic male stages. Experiments were conducted with assemblages of 24 males in three different male proportions (hereafter called 'phenotype frequencies' – see Table 2). These male assemblages competed for two receptive females, thus the operational sex ratio (OSR) was 12:1 in all treatments. This is at the lower range of the naturally occurring OSR, which has been estimated to vary between 15 and 81 males per receptive female (Correa & Thiel 2003b).

Within each replicate, the behaviour of one randomly selected individual (hereafter called 'focal animal') was examined in a large observational arena. The focal animal was either in the terminal moult stage (robustus) or in early intermoult stage (typus). For each treatment, we conducted seven replicates with focal typus males and seven replicates with focal robustus males between Aug. and Oct. 2004 (Table 2).

All experiments were conducted at night between dusk and midnight, when rock shrimp are most

active (Miranda & Kong 1970; Arana & Henríquez 1983). In a large tank (135 \times 62 cm), we produced an observational arena (93 \times 62 cm) using a hermetic glass divider. This observational arena was subdivided into 15 \times 10 equal squares (6.2 \times 6.2 cm) with a xylene-free marker pen. The experimental tank contained no rocks or other structures to avoid competition for refuges. Refuges are mainly used during the day but are of minor importance during mating (Thiel & Correa 2004). Water depth was 15 cm. A tent of black mesh was set up around the experimental tank to exclude possible light disturbances from the outside.

All observations were recorded on video-tape with an infrared-sensitive video camera. To achieve better illumination, a lamp built of 18 IR-diodes (940 nm) was installed. An observation period lasted 30 min, with a preceding acclimation phase of 20 min. The acclimation phase was recorded as well to avoid disturbance through camera adjustment. Focal animals and females were marked shortly before the acclimation phase using a small piece of reflective tape, attached on the abdomen with cyanoacrylate glue. Shrimps stayed calm throughout the marking procedure (<30 s) as they were held by hand just above the water surface at the inner edge of the tank in a way that they had contact with seawater at least with one antenna and some pereopods. Marked shrimp were released into the tank and observed for a few minutes, which confirmed in all cases that they behaved normal and showed no apparent signs of unusual behaviour due to the small piece of tape on their abdomen. Also the unmarked shrimp did not seem to be affected by these marks on the focal animals and on receptive females.

The male assemblages were kept together in trays (60 \times 40 \times 25 cm) with aerated and flowing seawater for 2 d to allow the development and stabilization of a hierarchy structure (see also Dennenmoser & Thiel 2007). All shrimps were deprived of food for 24 h

prior to the experiments to exclude the influence of a variable hunger level on searching behaviour.

Females were tested for receptivity before starting the experiments by allowing them to interact with a robustus male (see also Van Son & Thiel 2006). If the male started to form the typical cage state within 20 min, shrimp were separated immediately and the female was used in the following experiment, which was initiated within 15–90 min after this test. Both receptive females were acclimated together under a plastic bell, which was placed in the middle of the observational arena. After 20-min acclimation time, the experiment started with the removal of the plastic bell. To ensure that the OSR was identical in all replicates, we only considered replicates in which both females mated during the 30 min of the experiment. If one (or both) female(s) did not mate during that time, the replicate was repeated. Similarly, if one of the males moulted during the experiment or the remainder of the night, the replicate was repeated as individuals may change their behaviour during the pre-moult and moulting phase, and the presence of moulting individuals may affect the behaviour of conspecifics (Adams & Moore 2003). All focal animals were used only once in the experiments, whereas non-focal individuals were used up to three times in these competition experiments with a recovery period of at least 48 h between replicates. After each replicate, the experimental tank was cleaned with fresh water and a sponge, and rinsed again with salt water. The different replicates of each treatment were conducted in a randomly assigned order.

Behavioural Observations

We quantified different behaviours using a computer program for behaviour analysis (OBSERVER 2.0), Noldus Information Technology, Wageningen, The Netherlands. Behaviours were classified as mutually exclusive activities. Animals could be walking or resting without visible locomotion, they could be contacting a female or mating, attacking another male or fighting. Walking was defined as visible locomotion, whereas resting was defined as no visible locomotion for longer than 2 s. Contact was defined as physical touching of individuals with any part of the body or thoracic appendages such as maxillipeds, chelipeds or antenna. Mating was defined as holding a female in the so-called cage state for at least 1 s. In this position, the male holds the female in a cage formed by the pereopods, the third maxillipeds and the abdomen (Correa et al. 2000, 2003).

As measures for locomotor activity we used walking velocity, walking activity and area covered by focal animals. Walking velocity was measured as square changes per minute walking without contact with the female, based on the 150 squares marked on the bottom of the tank (square dimension was 6.2×6.2 cm). A square change was defined as both eyes crossing a line or changing a square diagonally. Walking activity was defined as the percentage of time spent walking compared to the total time without contact to a female. The time without contact to the female includes both the time before first contact with a female and the time between female losses and the next female contact. The area covered was obtained by counting the number of different squares visited during the experiment. Furthermore, we measured pre-contact and pre-seizure times as the time until a focal male established first contact with a female and as the time a focal male needed to seize the female after first contact with her respectively.

While behavioural data obtained from focal animals were used to calculate measures of individual searching behaviour, data of all males present in a replicate were used for the analyses of aggressiveness and mating probability. Aggressiveness was quantified as attack-frequency of all males from a replicate for seven of 14 randomly selected replicates in each treatment. Attack was defined as acceleration directed towards a conspecific within antenna range. The attacking individual usually turned its head in the direction of the conspecific after direct body contact, followed by a longer agonistic interaction or pursuit (see also Dennenmoser & Thiel 2007). Fights between robustus males over a female were characterized by up-and down movements of chelae and third maxillipeds, and by grabbing each other's chelae with strong pulling and pushing (Correa et al. 2003). Mating probability in different social environments was measured for each male stage (typus, intermedium and robustus) as the proportion of males from that stage that seized a female at least once. For example, an average mating probability of 50% for intermedium males in treatment 1 means that in the 14 replicates of this treatment on average two of the four intermedium males present in this treatment seized a female. Furthermore, for each male that held one of the receptive females during the experiment, we recorded the male stage, holding time and the causes of female loss.

Data Analysis

All data were tested for normality and homogeneity of variances using the Kolmogorov–Smirnov and

Levene's test performed by SPSS 12.0 (SPSS 12.0, Chicago, Illinois, USA). We used two-way ANOVAS and *post hoc* Tukey tests to analyse measures of the searching behaviour of focal animals (locomotor activities and pre-contact time). Percentage data (walking activity) were arcsine square-root transformed before they were used in ANOVAS. Data of pre-contact time were square-root ($x + 0.5$) transformed as they failed the normality test. To compare attack-frequencies across treatments for each male stage, we used one-way ANOVAS and *post hoc* Tukey tests. As attack-data of robustus males failed the normality test, they were $\log(x + 1)$ transformed. We conducted a three-dimensional contingency table to test the overall hypothesis that the proportion of mating males is independent of male stage and phenotype frequency. Subsequently, we performed 2×3 contingency tables with *post hoc* chi-squared goodness-of-fit tests for each male stage to assess if the frequencies of mated/unmated males changed with increasing frequency of robustus males. To examine whether there were significant differences between treatments in the total number of male mates per female and in the time that females remained without mate, non-parametric Kruskal–Wallis tests were conducted, because data were not normally distributed. Furthermore, we conducted chi-squared goodness-of-fit tests for each treatment to test whether frequencies of first mating partners of females correspond to the frequencies of male stages present in each treatment. All tests were carried out with a significance level of $\alpha = 0.05$.

One robustus male of the first treatment moved during the first 10 min at unusually high velocities in a circle along the aquarium's edge without showing any reaction towards females or mating pairs encountered. After 10 min, this robustus male seized a female and guarded her until the end of the experiment. This robustus male was clearly ready to mate but not searching for mates during the first 10 min, and thus was not considered for statistical analysis of walking velocity. Furthermore, the first two replicates we conducted (one replicate in treatments 2 and 3 respectively) could not be considered for the analysis of the proportion of mating typus males and the number of mates per female, because initial problems with the illumination made it impossible to quantify whether some typus individuals mated multiply or not. However, this should not present a problem because the remaining 40 replicates still left 13 to 14 replicates per treatment for the statistical analyses (Table 2).

Results

Locomotor Activity of Focal Males

Locomotor activity was affected by phenotype frequency with robustus males walking faster when there was more than one robustus male in the group (Fig. 1a, Table 3). Walking velocities were also significantly influenced by male stage (Table 3), with typus males being faster than robustus males in the treatment with one robustus male (Fig. 1a). No significant interaction between male stage and phenotype frequency on walking velocity was detected (Table 3). Multiple comparison tests revealed that in typus males the walking velocities were independent of phenotype frequency, whereas in robustus males walking velocities were significantly lower in the treatment with one robustus than in the treatment with two robustus (Fig. 1a). Robustus males occasionally showed rapid movements after a fight with another robustus male, but this had no effect on the measures of average walking velocity.

Walking activity was neither influenced by male stage nor by phenotype frequency (Fig. 1b, Table 3), and neither was there a significant interaction (Table 3). The area covered within the 30 min of the experiment ranged from 12 to 134 of the 150 squares and was significantly influenced by male stage, but not by phenotype frequency (Fig. 1c, Table 3). Typus males covered a significantly larger area than robustus males in treatments with one and with three robustus males present (Fig. 1c). No interaction between male stage and phenotype frequency was detected (Table 3).

Mating Behaviour of Focal Males

Access to females was generally lower in typus than in robustus males (Fig. 3). In all, 17 (out of 21) focal typus males and all 21 focal robustus males established contact with a receptive female (Fig. 2a). Females frequently avoided to be seized by typus males but rarely by robustus males by rapidly moving away from the approaching male. Only one of the focal typus males seized a female, whereas 17 of all 21 focal robustus males started to mate within the experimental time (Fig. 2b).

No significant effect of male stage or phenotype frequency on pre-contact time could be found, and neither was there a significant interaction (Fig. 2, Table 3). The time from first contact to seizure (pre-seizure time) was generally short in robustus males (1.7 ± 3.6 min, $x \pm SD$), while the only focal typus

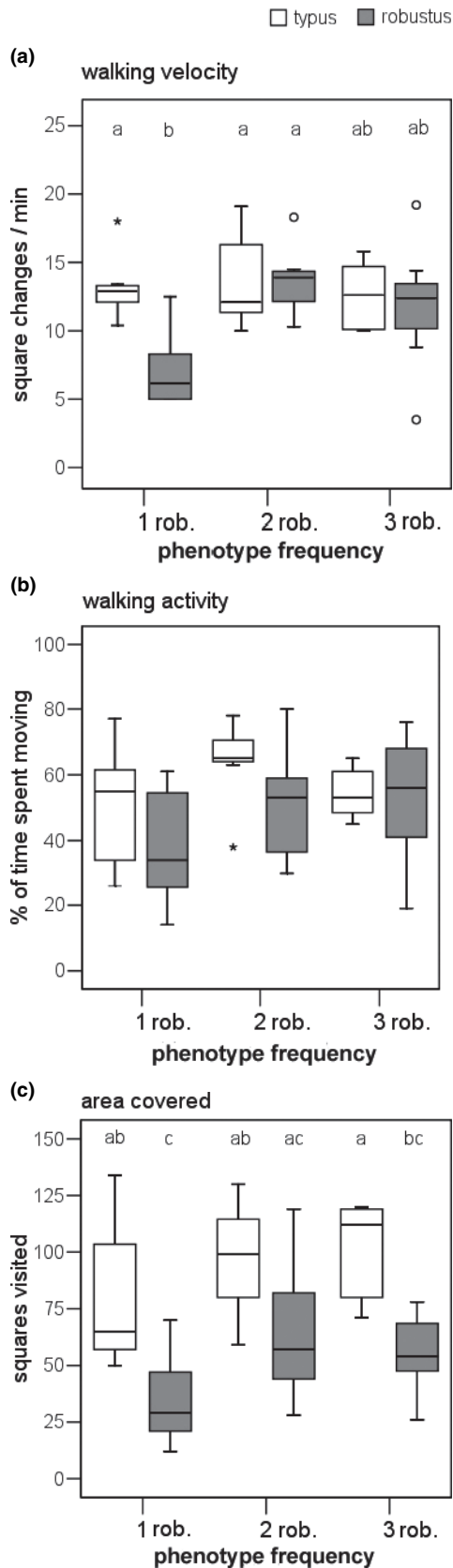


Table 3: Results of two-way ANOVAs for locomotor activities and pre-contact times (* $p < 0.05$)

	df	F	p
Walking velocity			
Male stage	1	5.139	0.03*
Phenotype frequency	2	3.987	0.028*
Interaction	2	3.183	0.054
Walking activity			
Male stage	1	3.062	0.089
Phenotype frequency	2	2.419	0.103
Interaction	2	0.49	0.617
Area covered			
Male stage	1	25.414	<0.001*
Phenotype frequency	2	3.071	0.059
Interaction	2	0.324	0.725
Pre-contact time			
Male stage	1	0.346	0.56
Phenotype frequency	2	0.702	0.503
Interaction	2	0.094	0.92

male that initiated mating seized the female 25.2 min after the first contact (Fig. 2b).

Mating behaviour of typus and robustus males corresponded to the sneaking and guarding tactics described by Correa et al. (2003). Furthermore, we observed that typus males that approached a stationary robustus male commonly were chased away by directed sideways moves of the large chelae of the robustus male towards the typus male. In such cases, the typus male often retreated rapidly but commonly remained within antenna range to the robustus male (up to a minute) (see also Dennenmoser & Thiel 2007).

Aggressive Behaviour of All Males

Attack-frequencies were dependent on both male stage and phenotype frequency. Typus males showed a constantly low rate of aggressive interactions that did not differ between treatments (Table 4). Robustus males increased their attack frequencies at higher proportions of dominants, while the tendency for a declining aggressiveness in intermediums males was not significant (Table 4). In all, 20 fights between robustus males (seven in the two-robustus treatment and 13 in the three-robustus treatment) over a female led to the liberation of the female out

Fig. 1: Locomotor activity of focal male rock shrimp; (a) walking velocity (b) walking activity (c) area covered. Boxplots show the median, interquartile range, outliers (○) and extreme cases (★). Different letters indicate treatments with significant differences (two-way ANOVA, followed by *post hoc* Tukey, $p < 0.05$).

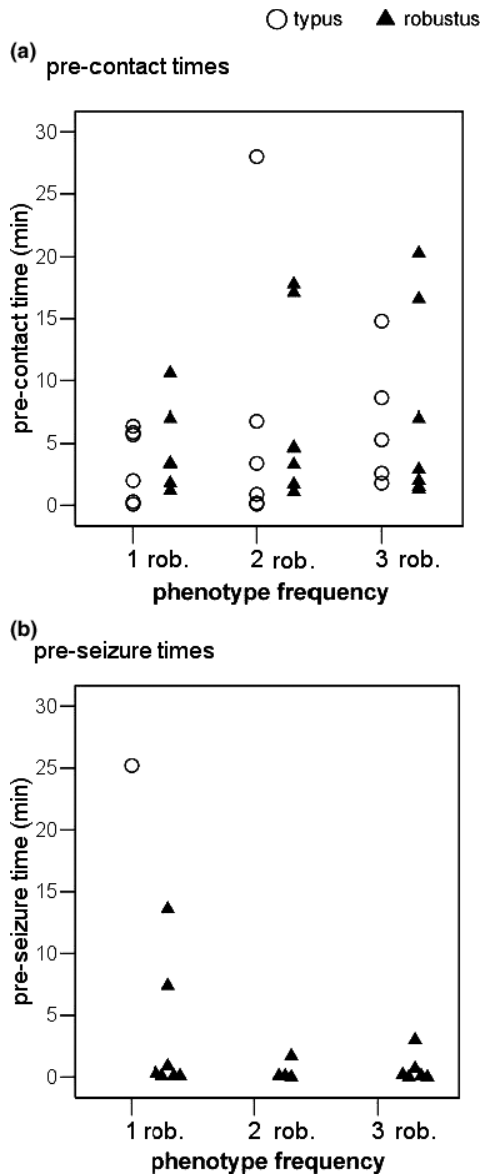


Fig. 2: Pre-mating times of focal male rock shrimp; (a) pre-contact times (b) pre-seizure times. Pre-contact time is the time from the start of the experiment until first contact with a female whereas pre-seizure time is the time from first contact with a female until first seizure.

Table 4: Attacks per male within 30 min ($x \pm SD$)

Male stage	Treatment 1	Treatment 2	Treatment 3	df	F	p
Typus	0.2 ± 0.04	0.2 ± 0.1	0.3 ± 0.2	2	1.528	0.244
Intermedius	1.1 ± 0.5	0.9 ± 0.2	0.6 ± 0.2	2	3.495	0.052
Robustus	0.4 ± 0.5	1.3 ± 0.9	2.8 ± 1.3	2	13.27	<0.001*

The number of the treatment refers to the number of robustus males present.

Results of statistical comparisons (one-way ANOVA) across treatments are given (* $p < 0.05$).

of the cage state, which gave a mating opportunity for three nearby subordinates (two typus and one intermedius male) in the three-robustus treatment. In the remaining 17 cases, the female was seized again by a robustus male after the fight, usually by the male that initiated the fight (in 15 of 17 cases).

Mating Probability of All Males

The 588 typus males present in all 42 replicates seized a female on 103 opportunities, and lost the female in 95 cases (93%) shortly after seizure (36 ± 66 s, $x \pm SD$), either due to female escape out of the cage state, or due to take-over by intermedius and robustus males. The 84 robustus males present in all replicates seized a female on 97 opportunities, and lost the female in 37 cases (38%), mainly due to fights with other robustus males (20 cases). Female escape out of a robustus male cage state happened very rarely, and usually the escaping female was immediately recaptured by the robustus male (in six of seven cases). In typus males, the proportion of mating males was significantly influenced by phenotype frequency, being lower in the two-robustus treatment ($6.6 \pm 3.3\%$), and higher in the one-robustus ($12.8 \pm 4.3\%$) and three-robustus treatments ($18.0 \pm 6.8\%$) (Fig. 3, Table 5). In robustus males, the proportion of mating males was not

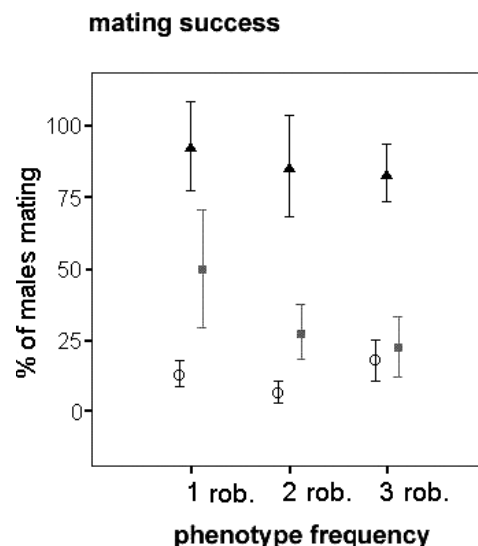


Fig. 3: Percentage of mating typus, intermedius and robustus males ($x \pm 95\%$ CI). Open circles (○) represent typus males, grey squares (■) represent intermedius males and filled triangles (▲) represent robustus males (for statistical comparisons see Table 5). Two replicates (out of a total of 42 replicates) had to be excluded from the analysis of typus males due to malfunction of the illumination, making it impossible to distinguish if some typus males mated multiply or not.

Table 5: Results of three-dimensional and subsequent 2 × 3 Contingency tables with *post hoc* chi-squared goodness-of-fit tests for differences between treatments in the proportion of mating males shown in Fig. 3 (**p* < 0.05)

Male stage	Treatments tested	χ^2	df	<i>p</i>
<i>3-Dimensional, mutual independence</i>				
		366.038	12	<0.001*
<i>3-Dimensional, partial independence</i>				
T, I, R	1, 2, 3	235.026	8	<0.001*
<i>2-Dimensional</i>				
Typus	1,2,3	9.196	2	0.01*
	1,2 (<i>post hoc</i>)	3.845	1	0.05*
	1,3 (<i>post hoc</i>)	1.369	1	0.242
	2,3 (<i>post hoc</i>)	8.232	1	0.004*
Intermedius	1,2,3	13.878	2	0.001*
	1,2 (<i>post hoc</i>)	6.828	1	0.009*
	1,3 (<i>post hoc</i>)	12.181	1	<0.001*
	2,3 (<i>post hoc</i>)	0.373	1	0.542
Robustus	1,2,3	0.935	2	0.627

p-values are Yates corrected if *df* = 1; numbers 1, 2 and 3 refer to the number of robustus males in the treatments. Two replicates (out of a total of 42 replicates) had to be excluded from the analysis of typus males due to malfunction of the illumination, making it impossible to distinguish if some typus males mated multiply or not; this affected one replicate with two and one with three robustus males; all 14 replicates from each treatment were considered for calculation of mating success of intermedius and robustus males.

significantly affected by phenotype frequency (Fig. 3, Table 5). In intermedius males, the proportion of mating males showed a significant decline from treatment 1 ($50.0 \pm 18.5\%$) to treatment 2 ($27.7 \pm 9\%$) and treatment 3 ($22.6 \pm 9.9\%$) respectively (Fig. 3, Table 5).

Females experienced variable numbers of different mating partners. In one-robustus and two-robustus treatments, we observed on average 2.7 ± 1.5 and 2.5 ± 1.3 different mating partners per female, respectively, whereas in the three-robustus treatment each female mated with 3.8 ± 2.1 different males ($x \pm SD$) (Kruskal–Wallis, $H = 6.203$, *df* = 2,

Table 6: First mating partner of the 28 females within each treatment (two females in 14 replicates per treatment). The expected frequencies are given in parentheses

	Typus	Intermedius	Robustus	χ^2	df	<i>p</i>
Treatment 1	16 (22.2)	7 (4.7)	5 (1.2)	15.477	2	<0.001*
Treatment 2	10 (16.3)	10 (9.3)	8 (2.3)	16.265	2	<0.001*
Treatment 3	15 (10.5)	11 (14)	2 (3.5)	3.214	2	>0.1

In parentheses the expected frequencies are given, assuming a first mating partner distribution proportional to the frequencies of male stages in the treatments.

Results of chi-squared goodness-of-fit tests for differences between observed and expected frequencies are given for each treatment (**p* < 0.05).

$n = 80$, $p = 0.045$). The first mating partner was most frequently a typus male (see Table 6). In treatments 1 and 2, the frequencies of different male stages as first mating partner differed significantly from the frequencies of male stages present (Table 6). A comparison of typus against pooled intermedius and robustus frequencies revealed that typus males were underrepresented as first mating partner in treatment 1 (chi-squared goodness-of-fit; $\chi^2 = 8.235$, *df* = 1, $p < 0.005$) and treatment 2 ($\chi^2 = 5.894$, *df* = 1, $p < 0.025$). In contrast, typus males were the first mating partner as often as expected from their frequency of occurrence in treatment 3 (Table 6). The time that a female spent being unmated was highly variable and decreased with increasing frequency of robustus males (treatments with one, two and three robustus males respectively: 13.4 ± 10.6 , 6.8 ± 7.4 , 3.5 ± 5.1 min) (Kruskal–Wallis, $H = 15.144$, *df* = 2, $n = 84$, $p = 0.001$).

Typus males could not control the movement of the female when holding her in the cage state. In three cases, the typus-female pair went to a stationary robustus male, which then disrupted the mating by displacing the typus male with his chelipeds. In the three-robustus treatment, it was observed on one occasion that a mating robustus male exchanged the female held in the cage state with the other female. It was also observed several times that robustus males showed no reaction towards a female until a subordinate male started to mate with that female.

Discussion

The results show that searching behaviour, aggressiveness and mating probability of alternative reproductive phenotypes in male rock shrimp are differently affected by variable phenotype frequencies. Typus males maintained relatively high walking velocities and low rates of aggressive interactions, whereas the dominant robustus males changed their behaviour, increasing both velocity as well as aggressive interactions with an increase in the number of dominant competitors. While the increased aggressiveness among robustus males seemed to provide more opportunities to sneak matings for typus males, robustus males were independent from phenotype frequency in their mating probability. This underlines that alternative phenotypes are differentially affected by a variable social environment. We suggest and discuss in the following that these differences might be linked to high interactions costs within, and low interaction costs between phenotypes.

The Influence of Social Structure on Locomotor Activity

Locomotor activities of *typus* males did not decrease with increasing frequency of *robustus* males, presumably because the high densities at which rock shrimp usually live disfavour long stays of passively waiting for sneaking opportunities near stationary *robustus* males, regardless of the frequency of male reproductive phenotypes. Costs of intra-tactical competition rapidly increase with the number of other approaching subordinates, and *typus* males may seek their mating opportunities by moving and actively searching for females under all tested phenotype frequencies, thereby avoiding a build-up of intra-tactical competition. *Robustus* males increased walking velocity in treatments with other *robustus* males around, most likely to find a receptive female before another competitor with equal or higher RHP may monopolize that female (see also Dennenmoser & Thiel 2007). A similar relationship between search intensity and competitor pressure has been found in common toads and field crickets. At high densities, when competitor pressure is supposed to be high, males call less to attract females and instead search more, whereas at low densities, when competitor pressure is low, males call more but search less (Höglund & Robertson 1988; Cade & Cade 1992). Consistently, Jirotkul (1999) reports decreasing courtship displays and increasing mate searching with increasing density in guppies. Dominants and subordinates often differ in susceptibility to interference (Ens & Goss-Custard 1984; Stillman et al. 1996), and usually dominants should experience an increasing competitor pressure with increasing frequency of dominants.

In the absence of other dominant males, moving fast may provide few benefits for a dominant male probably because it easily can supplant a subordinate male from any encountered female. Instead of searching actively for females, dominant rock shrimp may benefit more from attracting mates by chemical cues (Díaz & Thiel 2004), similar to common toads and field crickets, which would call to attract mates rather than searching for them at low population densities (Höglund & Robertson 1988; Cade & Cade 1992). Another benefit of low walking speed may also be a decrease in the risk of overlooking the receptivity of an encountered female, similar to what has been suggested for a wading bird, which moves more slowly when searching for cryptic prey (Goss-Custard 1977). Compared to subordinates, *robustus* males are preferred by females (Díaz & Thiel 2003) and furthermore they have longer antenna (Dennenmoser &

Thiel 2007), which is often positively correlated with female location efficiency in arthropods (e.g. isopods, Bertin & Cézilly 2005). Hence, *robustus* males have presumably a higher female location efficiency, which allows them to minimize locomotor activity in absence of other *robustus* males.

The Influence of Social Structure on Male Aggressiveness and Mating Probability

The level of aggressiveness in rock shrimp depends on both male stage and social environment. Subordinate *typus* males usually do not fight for females (Correa et al. 2003) and thus, their attack frequencies were independent of phenotype frequency. In contrast, the dominant *robustus* males aggressively fight for females (Correa et al. 2003). Hence, attack-frequencies among *robustus* males increased with the frequency of *robustus* males, creating more opportunities to sneak or to encounter a liberated female by chance for *typus* males. This mechanism is similar to 'distraction sneaking' as identified by Dubois et al. (2004), who predicted that sneakers have higher success when they are rare and aggression between fighters is common. Our results suggest that this prediction is only valid as long as there are not more females than can be monopolized by the *robustus* males: *typus* males also had an increased chance to mate in the first treatment, because one of the two females was not monopolized by the single *robustus* male. However, in this treatment *typus* males showed a much lower mating probability than *intermedius* males due to a disadvantage in RHP, while *typus* males were equally successful as *intermedius* males under a high *robustus* male frequency because *typus* males are better at sneaking (see also Dennenmoser & Thiel 2007). This may suggest that the more aggressive *intermedius* male stages are favoured when there are more females than can be monopolized by the dominant *robustus* males alone, while at high frequency of *robustus* males the less aggressive sneaking tactic of the *typus* male stage is favoured over the costly fighting tactic of *intermedius* males. Consistently, Isvaran (2005) argued that when more females are available, relatively costly reproductive tactics may be favoured by high mating benefits.

An alternative explanation for the variable mating probabilities of *typus* males could also be found in female rather than male behaviour. Female rock shrimp seem to reduce their reluctance to mate with increasing frequency of *robustus* males, as indicated by the decreasing time that females spent being

unmated, and by the increased acceptance of typus males as first mating partner in treatment 3. This is also in accordance with Thiel & Hinojosa (2003) who reported that females are seized significantly faster by typus males in presence than in absence of a robustus male. Hence, we cannot clearly distinguish whether typus males benefit from a reduced female resistance or from the increased frequency of sneaking opportunities. However, as under natural conditions up to four robustus males compete for each receptive female (Correa & Thiel 2003b), it is very likely that typus males frequently benefit from fights among robustus males that leave a female temporarily unguarded. The possible role of variable female behaviour on male mating success in different social contexts has seldom been studied (e.g. Krupa & Sih 1993; Sih & Watters 2005) and needs further research.

In contrast to the declining mating probability of intermedius males, robustus males always had a very high probability to mate, independent of phenotype frequency. This could mean that dominants are less susceptible to variability of social structure than subordinates, as had also been suggested for birds (great tits, Lange & Leimar 2004). However, the fertilization success of robustus males might have declined with increasing robustus frequency, due to increasing competition among robustus males and losses of matings to sneakers.

Robustus males seem not only to benefit when other powerful competitors are scarce but also as a result of typus males revealing the location of receptive females (Díaz & Thiel 2004; Thiel & Correa 2004). Robustus males have been shown to use visual cues produced by typus males scrambling for receptive females to find mates both in the laboratory (Díaz & Thiel 2004) and in the field (Thiel & Correa 2004). This mechanism of typus males revealing mates for robustus males is also supported by our observation that females mating with typus males provide a stronger cue for robustus males than unmated females, and by the fact that females first approach typus males but ultimately choose robustus males as mating partners (Díaz & Thiel 2003). Hence, both dominant robustus and subordinate typus males seem to benefit from each other's presence: subordinates sneak from the dominants, while dominants use subordinates as female finders. As both phenotypes exploit each other's behaviour, such interactions might best be termed mutualistic producer-scrounger cases (*sensu* Parker 1984; originally developed for parentally determined phenotypes). Herein, we use the term mutualistic producing-scrounging only to describe the

interactions between alternative phenotypes, without implying a frequency-dependent effect on phenotype fitness. A similar case has been found in Harris' sparrows, where dominants use subordinates as food-finders, which benefit from being tolerated in a high-quality patch that is defended against other dominants (Rohwer & Ewald 1981). Similarly, in ruffs and lance-tailed manakins dominant and subordinate males seem to benefit from each other's presence in attracting mates (Widemo 1998; DuVal 2007).

Outlook

Our results show that dominant phenotypes do not necessarily suffer from increasing frequency of parasitic subordinate phenotypes, as is commonly assumed (e.g. Barnard & Sibly 1981; Eadie & Fryxell 1992). Instead, dominant phenotypes might be independent or even benefit from an increasing frequency of subordinate phenotypes (see also Parker 1984). As a consequence, the relative fitness gain of switching to the dominant fighter phenotype is higher at high frequencies of subordinate sneaker phenotypes, which usually suffer from increasing intra-tactical interference. This might favour frequency-dependent selection on the switchpoint between alternative phenotypes, as benefits of switching to the fighter phenotype are more likely to outweigh the costs. Such a cost-benefit scenario may be especially important in ontogenetic phenotypes, where relatively few individuals survive to the dominant stage, causing high subordinate and low dominant frequencies. Here, dominants may have to outweigh the costs incurred by numerous subordinate sneakers. Dominants should counterbalance these costs either by (1) reducing aggressiveness among dominants (Dubois et al. 2004), (2) cooperating with subordinates (e.g. Taborsky 2001), (3) adjusting their mating tactic from female monopolization to female searching (e.g. Simmons et al. 2004), or by (4) mutualistic producing-scrounging, as shown herein for a marine shrimp.

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