

# Competition for food and mates by dominant and subordinate male rock shrimp, *Rhynchocinetes typus*

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## Summary

Differences in size and resource holding power of males should affect how each competes for food and females. Subordinate males often search for undefended resources, whereas dominant males aggressively take over resources and usually defend them against nearby competitors. Furthermore, during ontogeny males may gain reproductively, and early developmental stages may value food over females, while the opposite may be true for dominants. Based on these assumptions we hypothesized that subordinate and dominant males would differ in their behaviour during resource location and acquisition. Subordinate males should spend more time searching over larger areas compared to dominant males, and compete more aggressively for food than for females, while dominants should do the reverse. In a laboratory study using rock shrimp, *Rhynchocinetes typus*, we found that subordinate males (called *typus*) searched more actively and over a larger area than dominant males (*robustus*) in non-competitive contexts. In a competitive context with food, *typus* males also showed higher searching activity than *robustus* males, but in competition for females these differences disappeared: *typus* males decreased and *robustus* males increased searching. Subordinate *typus* males competed more aggressively for food than for females, whereas *robustus* males competed more aggressively for females than for food. The dominance of *robustus* males was evident only in competition for females but not for food. Our study is one of only a few about the ontogeny of locomotor performance in invertebrates and shows that male searching behaviour and the use of aggression are affected by competitive ability, female mate preferences and ontogenetic changes in subjective resource value.

**Keywords:** competition, foraging, mating, alternative tactics, searching, locomotor activity, RHP, subjective resource value.

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## **Introduction**

Acquisition of food and females plays an important role in the evolution of social systems and alternative competitive tactics. Recent studies have compared the monopolization of food and females in order to contribute to a general theory of resource competition and monopolization (Blanckenhorn et al., 1998; Kokko et al., 1999; Grant et al., 2000). Prerequisites for the monopolization of a resource are the economically defendable distribution and abundance of resources in time and space, the ability of an individual to exclude conspecifics from resources, and the motivation to monopolize the resource, i.e., how much an individual values the contested resource. Resources are considered to be economically defendable when they are clumped in space, dispersed in time or predictable in both (Brown, 1964; Emlen & Oring, 1977). It has been shown repeatedly that monopolization of both food and mates increases as the clumping of resources in space increases (Monaghan & Metcalfe, 1985; Theimer, 1987; Vahl et al., 2005), the temporal clumping of resources decreases (e.g., Grant & Kramer, 1992; Grant et al., 1995; Blanckenhorn et al., 1998), or when resource availability becomes predictable (Grand & Grant, 1994; Goldberg et al., 2001). While resource characteristics are generally thought to affect individuals of variable age or size in different ways, few studies on intraspecific plasticity in resource acquisition behaviour have been conducted (for exception see Vahl et al., 2005, and references therein).

When food or mates can be easily monopolized, the use of aggression and dominance hierarchies within groups are expected (Isbell, 1991; Lott, 1991). Individuals within dominance hierarchies usually compete via interference competition as they limit each other's access to resources, e.g. by resource stealing (kleptoparasitism, e.g., Brockmann & Barnard, 1979) or time wasting through encounters and fights (e.g., Ens & Goss-Custard, 1984). Dominance hierarchies may be settled by relative body size, size of weapons, aggressiveness or signals of fighting ability (Qvarnström & Forsgren, 1998). Most commonly, dominants and subordinates differ in resource holding power (RHP, a measure of fighting ability *sensu* Parker, 1974) due to differences in body and weapon size (e.g., Christenson & Goist, 1979). Such differences between dominants and subordinates may not only affect the ability of resource defence and monopolization, but also the way in which resources are acquired, i.e., by active searching or by resource stealing (klep-

toparasitism). When resources can easily be taken over by stronger competitors, subordinates may be forced to avoid dominants and to search over larger areas for undefended resources, which are mostly in habitat patches of poor quality (e.g., Ens & Goss-Custard, 1984; Parker & Sutherland, 1986).

In mating systems with male dominance hierarchies two alternative ways of kleptobiotic resource acquisition can be found: the dominant fight tactic and the subordinate sneak tactic (e.g., Howard, 1978; Taborsky et al., 1987). While dominants fight to take over females from conspecifics, subordinates – besides actively searching for a female – often wait near a mating dominant (instead of avoiding them) and take advantage of a mating opportunity when the female gets free, e.g., during the attack of another dominant male. Locomotor activity of subordinates may be determined by a trade-off between time spent actively searching for undefended females and passively waiting for sneaking opportunities beneath a guarding dominant male. If mating success depends mainly on female encounter rates, high locomotor activity and mobility should be favoured in subordinate males (Ghiselin, 1974). Locomotor activity of dominant males may depend on whether females actively search for males and prefer to mate with dominant males. If females search for dominant males, dominants have less need to search for females than subordinate males, allowing them to reduce search activity and predation risk. Consequently, it can be expected that subordinates (which search over large areas for undefended females) are less aggressive than dominants (which take over and defend females against nearby competitors) during competition for females.

Animals search and fight not only for females, but also for other resources such as food, shelter or territories. The outcome of contests for such resources will not only depend on asymmetries in resource holding power, but also on resource value asymmetries between contestants (Maynard-Smith & Parker, 1976), or on an interaction of both (e.g., Lindström & Pampoulie, 2005). Females and food might be of different subjective value to dominant and subordinate males due to a changing trade-off between somatic growth and gamete production during ontogenetic development. Small subordinates should invest mainly in growth to overcome their competitive disadvantage, whereas large dominants can invest all surplus energy in gamete production (Hinojosa & Thiel, 2003). Food of high quality should therefore be of special interest for subordinates, as it allows faster growth and spending more

time searching for females. Differences in searching activity between subordinates and dominants are thought to further enhance these resource value asymmetries: highly mobile subordinates will have higher energy demands than more sedentary dominants. It is, thus, expected that subordinate males value high-quality food more than dominants, and that they compete aggressively for food resources. Despite their ability to monopolize high-quality food, dominant males might have little need to do so, and instead invest more time in behaviours related to mating.

While the effects of resource dispersal in time and space and resource holding power on the monopolization of resources are well understood, studies considering effects of resource value on fighting behaviour usually focus on a pay-off asymmetry between contestants regarding the same resource (e.g., Enquist & Leimar, 1987, and references therein; Jennions & Backwell, 1996; Dearborn, 1998). Only a few studies have compared intraspecific competition for food and females in the same species (but see Blanckenhorn et al., 1998; Grant et al., 2000), and to our knowledge no study has yet examined the possible effect of a subjective resource-value asymmetry with respect to food and females on the behaviour of dominant and subordinate males. Herein, we compare behavioural differences between dominant and subordinate individuals across feeding and mating situations in order to understand the influence of asymmetries in RHP, subjective resource value and female choice on locomotor activity and aggressiveness.

## Materials and methods

### *The model species*

The rock shrimp *Rhynchocinetes typus* Milne Edwards 1837 is very common from 0 to approximately 40 m water depth on hard bottoms along the coast of Chile (Vásquez & Castilla, 1982), where it seems to prefer barren grounds with a high availability of refuges (Caillaux & Stotz, 2003). Males reach sexual maturity in the female-like *typus* stage, and during growth they pass through various intermedium moulting stages until they reach the terminal *robustus* stage, which is characterized by strongly developed third maxillipeds and first chelae. There exists a clear dominance hierarchy among males of the order *typus* < *intermedius* < *robustus* (Correa et al., 2003). Rock shrimp feature a mating system described as ‘neighborhoods of dominance’ (Correa

& Thiel, 2003a). Male-male competition is very strong as this shrimp lives at high densities (Caillaux & Stotz, 2003) and the operational sex ratio is highly male-biased (Correa & Thiel, 2003b). Females become receptive asynchronously (Correa & Thiel, 2003b), prefer to mate with dominant robustus males (Díaz & Thiel, 2003), and discriminate against subordinates by resisting their mating attempts and displacing their sperm (Thiel & Hinojosa, 2003). Robustus males have high resource holding power: they can take over females from subordinates and defend them during the entire mating process in the so called cage state between their pereopods (Correa et al., 2000, 2003). Subordinate males also hold the female in the cage state, but can neither defend a female against a robustus male nor control the movement of the female. Instead, subordinates sneak matings when females get free during fights between dominant males (Correa et al., 2003). While the mating success of robustus males primarily depends on their resource holding power, the mating success of subordinate males seems to depend on a successful trade-off between independent search and sneaking behaviour. Furthermore, robustus males invest more in gametic and less in somatic growth and therefore have larger sperm supplies than typus males (Hinojosa & Thiel, 2003). Robustus males have been reported to be inactive and slow in their movement compared to the more agile typus males (Díaz & Thiel, 2004). However, these observations were made during the day when the larger robustus males might be less active due to high predation risk by visual predators.

The objective of this study was to examine how dominant and subordinate males search for and monopolize food and females. We predicted that subordinate males would be less aggressive and that they would search more actively over a larger area than dominant males. Furthermore, we expected that subordinates would compete more aggressively and actively for food than for females, whereas dominants would do the reverse.

#### *Collection and maintenance of rock shrimp*

Rock shrimp were collected in Bahía La Herradura in Coquimbo, Chile (29°59'S, 71°22'W) during the months June to August (austral winter) and October to November (austral spring). Collections were made in the shallow subtidal zone (3-6 m) using a diver-operated 'airlift sampler' (Correa & Thiel, 2003b) and baited traps. All captured individuals were transferred to flowing seawater tanks in the laboratory. Maintenance took place under

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

	Typus	Intermedius	Robustus
Characters (after Correa et al. 2000)			
Hairs on 1 <sup>st</sup> chelipeds	no	yes	yes
Relationship, last segment 3 <sup>rd</sup> maxilliped/carapace length	<<1	>1 and <2.1	>2.1
Number of spines at tip of 3 <sup>rd</sup> maxilliped	7	7	1
Number of teeth at tip of propodus of 1 <sup>st</sup> cheliped	4	4	1
Measurements			
Cephalothorax length (mm; mean $\pm$ SD)	13.6 $\pm$ 0.8	15.7 $\pm$ 1.1	19.3 $\pm$ 2.0
Antenna length (mm; mean $\pm$ SD)	75.4 $\pm$ 8.8	79.9 $\pm$ 10.9	95.8 $\pm$ 12.3

natural light conditions, temperature ranges of 9-11°C (winter) and 12-15°C (spring).

The sex of all shrimp was identified immediately after capture. Individuals of different sex were maintained in separate tanks with ad libitum food supply (ascidian colonies of *Pyura chilensis* with their epibionts). In order to ensure sexual maturity, only males greater than 13 mm cephalothorax length and females with eggs were selected for the experiments (Correa & Thiel, 2003b; I. Hinojosa, personal communication). Three male stages (typus, intermedius, robustus) were distinguished based on the size and morphology of the 1<sup>st</sup> chelipeds and 3<sup>rd</sup> maxillipeds according to Correa et al. (2000) (Table 1). Recently moulted females were collected from the holding tanks each morning and separated into individual plastic containers (20  $\times$  20  $\times$  15 cm) with flowing seawater. These females were used in the experiments 36-48 hours after moulting, when they become fully receptive. During this post-moult period the exoskeleton will get sufficiently hard to prevent cannibalism, but the gonopores remain still soft enough to extrude the eggs (for further details see Correa et al., 2003; Hinojosa & Thiel, 2003).

#### *General experimental set-up*

We conducted two experiments to examine the searching and monopolization behaviour of both single males (non-competition experiment) and of males within assemblages (competition experiment) in a large observational arena. The randomly selected animals that we monitored in each replicate

(hereafter called 'focal animals') were either in the terminal moult stage (robustus) or in early intermoult stage (typus).

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 × 62 cm) we produced a smaller experimental area (93 × 62 cm) using a hermetic glass divider, in order to fit the experimental area to the proportion of a camera picture (3:2). This experimental area was divided into 15 × 10 equal squares (6.2 × 6.2 cm) with a xylene-free marker pen. Water depth in the tank was 15 cm. The experimental tank contained no rocks or other structures to avoid competition for refuges. Refuges are mainly used during the day and are no important component of mating behaviour (Thiel & Correa, 2004). A tent of black mesh was set up around the experimental tank to exclude possible light disturbances from the outside.

Video-taping with an infrared-sensitive video camera (Sony DCR-TRV 140 in super night-shot modus) was used for all observations. 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) because they had contact with seawater at least with one antenna and some pereopods.

All shrimps were deprived of food for 24 h prior to the experiments to exclude the influence of variable hunger levels on locomotor activities. If any individual moulted within an experiment or during the remainder of the night, the replicate was not considered. Four replicates were repeated due to this reason. Recently moulted individuals are easy to recognize through their soft exoskeleton and a change in colour from brown to a pale grey (Correa & Thiel, 2003b). After each replicate, the experimental tank was cleaned with freshwater and a sponge and again with salt water. The different replicates of each experiment were conducted in a randomly assigned order.

#### *Resources used in the experiments*

Resources used in the experiments were either receptive females or food. Females were tested for receptivity before starting the experiments by placing them together 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. Females were acclimated under a plastic bell (made from the upper part of a plastic bottle), which was placed in the middle of the observational arena. An experiment started with the removal of the plastic bell.

To obtain food items of equal quality, filets of fresh fish (*Trachurus murphyi*) were frozen for 24 h, defrosted and conserved in salt. Before used in the experiments, fish pieces were cut in small pieces ( $\approx 1.2 \times 0.8 \times 0.5$  cm) and put in a petri-dish (volume  $\approx 30$  ml) of sea water for 24 h. No fish older than one week was used in the experiments. In the competition experiment, fish pieces were sewed into small mesh bags ( $0.6 \times 0.6 \times 0.3$  cm) to prevent shrimp from dividing it into large pieces, what would have caused a change in competitor-to-resource ratio. Mesh size was 1 mm, allowing shrimps to pinch off very small fish pieces ( $<1$  mm), without completely consuming the food item within the experimental time.

In experiments with food as resource, an empty plastic bell was placed in the observational area for the duration of the acclimation time. The experiment started with the removal of the plastic bell and introducing the food at the same time. In experiments without resources the plastic bell was also placed in the observational area for the duration of the acclimation period and was removed to start the observational period.

#### *Non-competition experiment*

This experiment was conducted to determine stage- and resource-dependent differences in searching behaviour and resource handling in a non-competitive environment. Single males of both typus and robustus stages were surveyed within three different resource contexts: without resource, with one food item and with a receptive female. The number of replicates per male stage was 8 in treatments without resource and was reduced (for logistic reasons) to 7 in treatments with food and females. All treatments were run between June and August 2004.

If no mating occurred in experiments with females, the males were tested for capability to mate, which might be limited due to a trade-off between reproduction and growth (Thiel & Hinojosa, 2003). These assays were done by keeping male and female together in a small plastic container ( $20 \times 20 \times 15$

cm) with flowing seawater. In case the female carried an egg mass on the next day, it was isolated and observed for the following three days. A male was classified as 'capable to mate' when the female kept the egg mass for three days, which is a reliable indicator of successful fertilization (Correa et al., 2000).

#### *Competition experiment*

The aim of this experiment was to examine the searching and monopolization behaviour of dominant and subordinate rock shrimp in a competitive environment. The competition experiment was conducted with assemblages of 24 males. The male assemblages comprised 9 *typus*, 12 *intermedius* and 3 *robustus* males. This is close to the natural ratio of 8:10:3 (males above 13 mm CL) occurring in spring, when the proportion of *robustus* males in field populations reaches its maximum (Correa & Thiel, 2003b). Before being used in the experiment, the male assemblages were kept together in trays (60 × 40 × 25 cm) with aerated and flowing seawater for at least two days to allow the development and stabilization of a hierarchy structure (see also van Son & Thiel, 2006). A stabilization of hierarchy structure has been reported after one day in male freshwater prawn *Macrobrachium rosenbergii* (Barki et al., 1992).

Resources were either two females or two pieces of food, so that the ratio of competitor to resource was 12:1 in all set-ups. This is at the lower range of the naturally occurring operational sex ratio (OSR), which has been estimated to vary between 15 and 81 males per receptive female (Correa & Thiel, 2003b). For each treatment 7 replicates were conducted during austral spring (between October and November 2004). In these experiments it was important that both resources were available for males, because otherwise the competitor/resource ratio would not have been identical among the replicates. In one of the replicates with females, only one of the two females mated within the experimental time – this replicate was not considered and repeated for the analysis. All focal animals were used only once in the experiment, whereas non-focal individuals were used up to three times in this competition experiment with a recovery period of at least 48 h between the replicates.

*Behavioural observations*

We quantified different behaviours using a computer program for behaviour analysis (Observer 2.0). Behaviours were classified as mutually exclusive activities. Animals could be walking or resting without visible locomotion, being in contact with the tank's edge or not, they could be contacting a female or mating, contacting a food item or feeding, attacking another male or fighting. Walking was defined as visible locomotion, while resting was defined as no visible locomotion for longer than 2 s (Table 2). 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. In this position the male holds the female in a cage formed by the pereopods, the 3<sup>rd</sup> maxillipeds, and the abdomen (Correa et al., 2000, 2003). Feeding was defined as holding a food item with the chelipeds.

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 contacting the female, based on the 150 squares marked on the bottom of the tank (square dimension was  $6.2 \times 6.2$  cm). A square change was defined as both eyes crossing a line or changing to another square diagonally. Walking activity was defined as the percentage of time spent walking compared to the total time without contact with a female. The time without female contact includes both the time before

**Table 2.** Behavioural variables used in analyses.

Variables	Definition
Walk	Visible locomotion within 2 s
Rest	No visible locomotion for $\geq 2$ s
Square change	Both eyes crossing a line or changing a square diagonally
Attack	Directed acceleration towards conspecific
Mate	Holding a female in cage state
Feed	Contact a food item with chelipeds or 1 <sup>st</sup> pereopods
Walking velocity	Square changes per minute walking
Walking activity	Percentage of time spent walking
Area covered	Number of different squares visited
Pre-contact time	Time until first contact with a female or food
Pre-seizure time	Time between first contact and first seizure of a female
Pre-feeding time	Time between first contact with food and first feeding
Aggressiveness	Attack-frequency of all males present in a replicate

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 the proportion of time that focal animals spent with and without contact to the tank's edge.

For focal animals we also measured pre-contact and pre-seizure times. Pre-contact time was the time from the start of the experiment until a focal male established contact with a female for the first time. Pre-seizure time was the time a focal male needed to seize the female after first contact with her.

A very distinctive behaviour compared to all other shrimp was observed in three robustus males. Unlike other shrimps, they ran at high velocities in a circle along the tank edge (see outliers in Figures 2 & 4). These three robustus males were not considered for statistical analysis of walking velocity, as such behaviour of robustus males never has been observed in previous studies (e.g., Correa et al., 2000, 2003; Díaz & Thiel, 2003, 2004).

While behavioural data obtained from focal animals were used to calculate measures of locomotor activities, data of all males present in a replicate were used for the analyses of aggressiveness and sneaking success. In order to obtain a measure of male aggressiveness we quantified the attacks of all males present in a replicate in both food and female treatments – this was done for 6 randomly selected replicates out of all 14 replicates with food or females, respectively. Attack-distances were measured on the video monitor as eye-to-eye distance between the attacker and the victim with a precision of 4 mm.

An 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. Occasionally, a shrimp rapidly moved forward and even continued to advance in a straight line when another individual was in its path. In these cases body contact could occur, but both individuals usually turned their heads away from each other and thus, these movements were not considered as attacks. Attacks as recorded herein might lead to extensive agonistic interactions, which included a display phase that involved up- and down movements of chelae and 3<sup>rd</sup> maxillipeds, and on rare occasions turn into escalated fights, characterized by grabbing each other's chelae and strong pulling and pushing (Correa et al., 2003). Sneaking was

defined as acquiring a female that was liberated during a fight between two robustus males (Correa et al., 2003). Furthermore, for each male that held one of the receptive females during the experiment, we recorded the 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. We used two-way ANOVAs and post-hoc Tukey tests to analyse measures of the searching behaviour of focal animals (locomotor activities, pre-contact times). Percentage data (time spent without contact to tank edge, walking activity) were arcsine square-root transformed before they were used in ANOVAs.

To compare mating and feeding success of focal typus and robustus males, chi-square goodness-of-fit tests with Yates correction were performed. For a comparison of attack frequencies per male in food and female treatments we conducted a two-sample *t*-test for each male stage. A two-sample *t*-test was also used for comparing average attack-distances in food and female treatments for each male stage. To compare the sneaking success of typus and intermedius males, a chi-square goodness-of-fit test was conducted. All tests were carried out with a significance level of  $\alpha = 0.05$ .

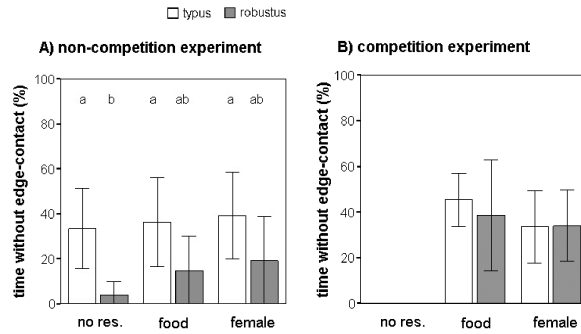
## **Results**

### *Non-competition experiment*

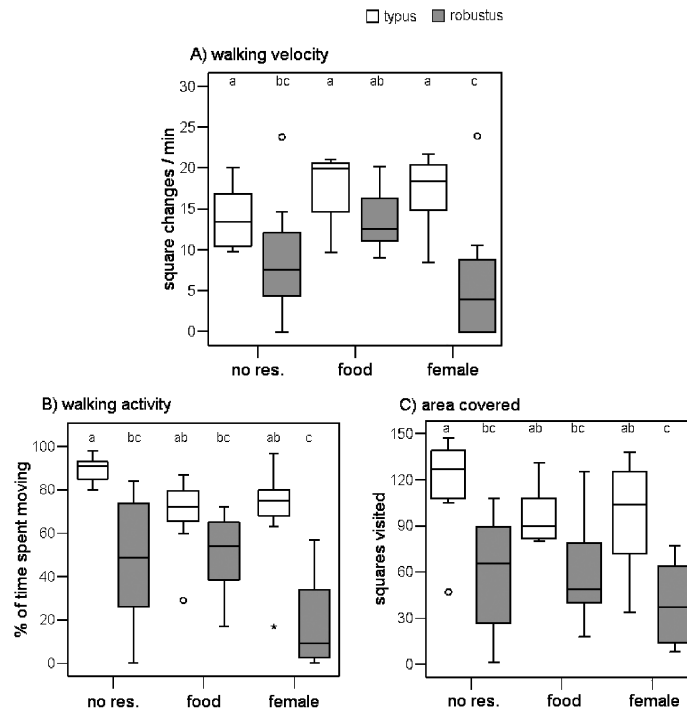
#### Locomotor activity of focal animals

In this experiment, typus males were highly active and moved across the whole observational area, whereas robustus males showed lower locomotor activities and remained more time with contact to the edge of the experimental tank (Figures 1 & 2). Differences between male stages in locomotor activity were most pronounced and always significant in treatments with females (Figure 2, Table 3).

Walking velocities were significantly influenced by both male stage and resource, and a significant interaction between male stage and resource on walking velocity was detected (Table 3). Multiple comparison tests revealed



**Figure 1.** Time spent without contact to the edge in A) non-competition experiments, and B) competition experiments. Different letters indicate treatments with significant differences (two-way ANOVA, followed by post-hoc Tukey,  $p < 0.05$ ).



**Figure 2.** Locomotor activity in non-competitive experiment: A) Walking velocity, B) Walking activity, and C) Area covered. Boxplots show the median, interquartile range, outliers (○) and extreme cases (★). Outliers are between 1.5 to 3 box lengths, extreme values more than 3 box lengths from either end of the box. Different letters indicate treatments with significant differences (two-way ANOVA, followed by post-hoc Tukey,  $p < 0.05$ ).

**Table 3.** Results of two-way ANOVA's for locomotor activities in non-competition and competition experiment (\* =  $p < 0.05$ ).

Variable	Non-competition			Competition		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
time without contact to tank edge						
male stage	1	27.688	0.000*	1	0.198	0.660
resource	2	2.325	0.112	1	1.606	0.217
stage*resource	2	0.922	0.406	1	0.261	0.614
walking velocity						
male stage	1	33.789	0.000*	1	1.855	0.186
resource	2	6.434	0.004*	1	0.28	0.602
stage*resource	2	4.276	0.022*	1	0.163	0.690
walking activity						
male stage	1	30.41	0.000*	1	16.163	0.001*
resource	2	4.73	0.015*	1	10.377	0.004*
stage*resource	2	2.415	0.103	1	3.603	0.070
area covered						
male stage	1	24.645	0.000*	1	11.482	0.002*
resource	2	1.41	0.257	1	4.584	0.043*
stage*resource	2	0.517	0.600	1	2.564	0.122

that walking velocity of typus males was independent of resource, while in robustus males walking velocities were significantly higher in treatments with food than in treatments with females and slightly (yet not significantly) higher than in treatments without resource (Figure 2A). Hence, typus males were found to move significantly faster than robustus males in treatments without resources and with females, but not in treatments with food.

Walking activity was significantly influenced by both male stage and resource (there were significant differences in walking activity between males without resource and males with female, post-hoc Tukey,  $df = 38$ ,  $p = 0.012$ ), but no interaction effect of male stage and resource on walking activity was detected (Table 3, Figure 2B). Typus males were more active than robustus males in treatments without resource and with females (Figure 2B).

During the 30 min of the experiment the males covered between 1 and 142 of the 150 squares of the experimental arena. The area covered was significantly influenced by male stage, but not by resource (Table 3, Figure 2C). No interaction effect of male stage and resource on area covered was

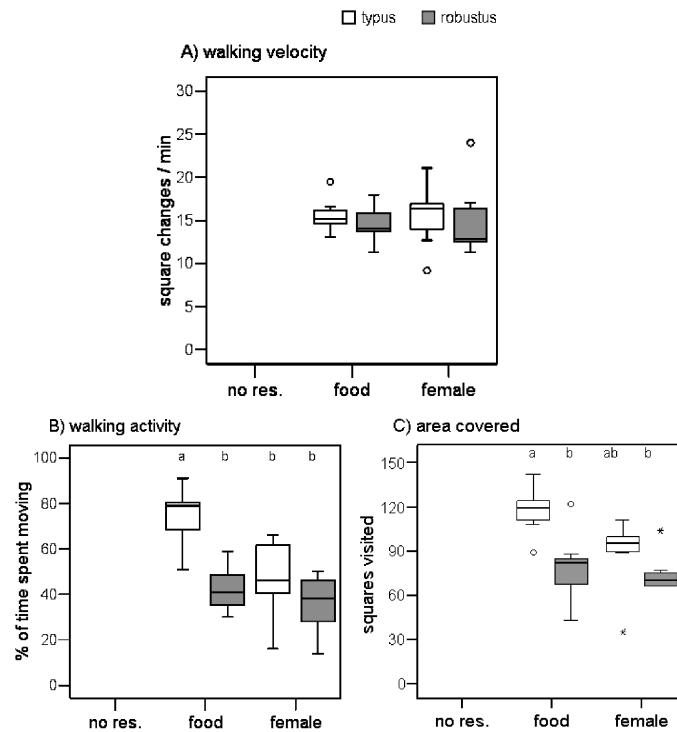


### Competition experiment

#### Locomotor activity of focal animals

Similar as in the first experiment, *typus* males were more active and covered a larger area than *robustus* males (Table 3). However, since both *typus* and *robustus* males moved across the whole observational area, there was no difference in the time spent without contact to the tank edge between the two male stages (Table 3, Figure 1). In contrast to the first experiment, neither male stage nor resource had a significant effect on walking velocity (Table 3, Figure 4A).

Walking activity was significantly influenced by male stage and by resources, but no interaction effect of male stage and resource on walking ac-



**Figure 4.** Locomotor activity in competitive experiment: A) Walking velocity, B) Walking activity, and C) Area covered. Boxplots show the median, interquartile range, outliers (○) and extreme cases (★). Outliers are between 1.5 to 3 box lengths, extreme values more than 3 box lengths from either end of the box. Different letters indicate treatments with significant differences (two-way ANOVA, followed by post-hoc Tukey,  $p < 0.05$ ).



within the experimental time. The pre-contact time with females was neither significantly different between male stages (two-way ANOVA,  $F = 1.436$ ,  $df = 1$ ,  $p = 0.243$ ) nor to pre-contact times with food ( $F = 0.111$ ,  $df = 1$ ,  $p = 0.742$ ) (Figure 5A). The pre-seizure time seemed to be higher in typus males ( $N = 2$ ) than in robustus males ( $N = 5$ ), which in most cases seized the female immediately, but the low number of typus matings did not allow a statistical comparison (Figure 5B).

Females showed escape behaviour towards typus males but not towards robustus males. Consequently only 2 of 7 focal typus males seized a female, whereas 5 of 7 focal robustus males started to mate within the experimental time (chi-square goodness-of-fit,  $\chi^2 = 1.143$ ,  $df = 1$ ,  $p = 0.285$ ) (Figure 5). One of the two robustus males that did not mate showed no reactions towards females encountered during the experiment, whereas the second robustus male was observed to mate shortly after the experimental time.

#### Competition for food and females in all males

Food-holding individuals rapidly moved backwards when being attacked, and thus an attacking shrimp often missed the food item. However, due to the high number of contenders some attacking conspecifics usually could reach the food item and pinch off a small piece from it with its chelipeds. A food item often was held by several shrimp (up to 8) at the same time. Chelipeds were used to hold the food and not to defend the food items. Males rapidly lost the food item to attacking conspecifics, if they did not hold it firmly with their chelipeds. Only 2 intermedius and 1 robustus male were observed to exclude all other conspecifics from the food through backwards moving.

The 126 typus males present in the 14 replicates seized a female on 34 opportunities, but they all lost the female shortly ( $13.4 \pm 15.6$  (SD) s; range: 1-80 s) after seizure, either due to female escape or to take-over by intermedius and robustus males. The 42 robustus males present in the 14 replicates seized a female on 66 opportunities, and lost the female in 42 cases (63.6%), mainly due to fights with other robustus males.

On two occasions it was observed that a mating robustus male exchanged the female held in the cage 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. Typus males could not control the movement of the female. In some cases the typus-female

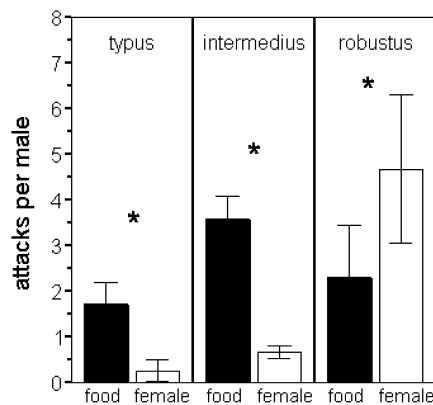
pair went to a stationary robustus male, which then disrupted the mating by displacing the typus male with his chelipeds.

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, which approached a stationary robustus male, commonly were chased away by directed sideways moves of the large chelipeds of the robustus male. In such cases the typus male often stayed within antenna range to the robustus male (up to a minute) rather than leaving immediately. This behaviour of typus males was observed with both paired and unpaired stationary robustus males.

#### Aggressive interactions among males

Considering all males present in the replicates, a total of 39 fights between robustus males over a female led to the liberation of the female, which gave a mating opportunity for 13 subordinates (10 typus and 3 intermedius males). In the remaining 26 cases the female was seized again by a robustus male after the fight. The higher sneaking success of typus compared to intermedius males, despite a lower number of typus males present, indicates that intermedius males are less efficient than typus males in exploiting sneak opportunities (chi-square goodness-of-fit,  $\chi^2 = 111.616$ ,  $df = 2$ ,  $p < 0.001$ ).

Typus males competed more aggressively for food than for females (Figure 6). The same pattern was observed in the generally more aggressive intermedius males, which seemed to be the most aggressive competitors for



**Figure 6.** Attacks per male (mean  $\pm$  SD) within 30 minutes competition for food and females of typus, intermedius and robustus males; ( $\star = p < 0.05$ ,  $t$ -test).

food. Robustus males competed more aggressively for females than for food, and were the most aggressive competitors for females (Figure 6). Mean attack distances of competing males were generally longer in competition for food than in competition for females: Typus males attacked over distances of  $7.9 \pm 2.5$  cm (mean  $\pm$  SD) in food treatments, and  $4.2 \pm 0.7$  cm in female treatments ( $t$ -test,  $df = 70.5$ ,  $p < 0.001$ ). Intermedius males attacked over distances of  $8.8 \pm 2.8$  cm in food, and  $5.2 \pm 0.9$  cm in female treatments ( $t$ -test,  $df = 217$ ,  $p < 0.001$ ). Robustus males attacked over distances of  $8.8 \pm 1.7$  cm in food, and  $7.0 \pm 1.5$  cm in female treatments ( $t$ -test,  $df = 70.4$ ,  $p < 0.001$ ).

## Discussion

Our results show that subordinate and dominant males differ in how they search for females and food. In general, subordinate males are much more active and cover a wider search area compared to dominant males. However, in a competitive situation these differences between subordinate and dominant males were only pronounced with food resources, but disappeared with females. Furthermore, subordinate males competed more aggressively for food than for females, whereas dominant males competed more aggressively for females than for food. This could suggest that differences in locomotor activities and aggressiveness are closely linked to RHP, subjective resource value and female preferences for the dominant males.

### *The influence of RHP and subjective resource value on locomotor activities*

Differences in locomotor activities between dominant and subordinate males may reflect different trade-offs or abilities in resource monopolization. For example, dominant male lizards typically exhibit greater levels of activity than subordinates (DeNardo & Sinervo, 1994), and it has been suggested that higher endurance and maximum running speeds of dominants are advantageous for territory defence (Robson & Miles, 2000; Perry et al., 2004). This is certainly not the case in rock shrimps, where locomotor activities are lower in dominant than in subordinate males, and reflect searching for resources rather than territory defence. Higher searching activities of subordinates are usually expected when subordinates suffer some socially mediated interference costs from the presence of dominants (e.g., Stahl et al., 2001;

Rands et al., 2006, and references therein). However, we found no evidence that subordinates avoided dominants or suffered high interference costs from the presence of dominant competitors. Hence, the overall higher locomotor activity of *typus* males seems to indicate differences in searching efficiency, in subjective resource value and in resource acquisition tactics.

In competition for females *typus* males decreased walking activity, whereas *robustus* males increased walking activity as well as walking velocity and consequently covered a larger area compared to a non-competitive situation. This can be explained by different mating tactics, which are determined by RHP. The subordinate *typus* males, which usually employ a sneaker tactic, stayed not only around paired, but also around unpaired stationary *robustus* males. Since females prefer the dominant *robustus* males (Díaz & Thiel, 2003) and locate these via waterborne chemicals (Díaz & Thiel, 2004), subordinate males may take advantage of the attractiveness of the dominant *robustus* males and wait near them for approaching females, similarly to what can be found in hotshot lek mating systems (e.g., Beehler & Foster, 1988). Thus, waiting for mating opportunities might have led to a decrease in subordinate walking activity compared to a non-competitive situation. In contrast, dominant *robustus* males that employ a guarding tactic might increase their locomotor activities in a competitive situation looking for opportunities to take over females from subordinates, or to find a female before another dominant male monopolizes her (Dennenmoser & Thiel, unpubl. data).

So why are the dominant *robustus* males not more active than *typus* males in competition for females? Dominants and subordinates may differ in a trade-off between mate searching and predator avoidance that is affected by searching efficiency and the number of mating opportunities (e.g., Kålås et al., 1995). Thus, if females are highly mobile and choosy, the preferred dominant phenotype benefits from increased searching efficiency and high numbers of mating opportunities, allowing to reduce the costs of predation risk while moving. Furthermore, mating subordinates provide visual cues that are detectable over large distances for dominant males (Díaz & Thiel, 2004). Hence, searching for take-over opportunities could simply be more effective and require less locomotor activity than searching independently (at least during daytime), similar to what has been found in foraging wading birds (Stillman et al., 2002).

In competition for food, differences in searching activity between subordinates and dominants may be enhanced by subjective resource value asymmetries: the highly mobile and still growing subordinates will have higher energy demands than the more sedentary and full-grown dominants, and therefore invest more into the location of the food source. This may explain why *typus* males employ higher locomotor activities than *robustus* males despite social costs of moving, being usually higher for subordinate than for dominant males (e.g., Martín & López, 2000). Similarly, Kreiter & Wise (1996) suggested that in a fishing spider adult females employ higher locomotor activities than juveniles due to increased energy requirements during yolk production.

Up to now, only few studies on the ontogeny of locomotory performance in invertebrates are available (but see Kreiter & Wise, 1996; Kirkton & Harrison, 2006). In grasshoppers, an ontogenetic change in locomotor performance has been related to stage-dependent requirements during predator escape, food-finding and migration (Kirkton & Harrison, 2006). In contrast, in male rock shrimp an ontogenetic change in locomotor behaviour seems to be related to changing RHP and mating tactic, subjective resource value, and female choice for the dominant males.

#### *The influence of RHP and subjective resource value on aggressiveness*

In competition for females, *typus* males were rarely aggressive because they avoided direct confrontations with the dominant males and instead employed the alternative sneaking tactic, which has also been observed in previous studies (Correa et al., 2003; Thiel & Hinojosa, 2003). In competition for food, no alternative to the use of aggression other than searching independently could be observed; hence subordinates seemed to be equally aggressive as dominant males despite much lower body and weaponry size. Chelipeds could not be used as weapons, because they were employed to hold the food. Therefore the risk of being injured during an attack is probably low for subordinates compared to the benefit of obtaining a piece of high-quality food. Generally, small males are expected to be as aggressive as their larger opponents when resources are scarce, of high value, and RHP is not a perfect determinant of fight outcome (Morrell et al., 2005), which fits our observations. If food items are not defendable through fighting, a linear dominance hierarchy based on RHP can not be established, supporting the view that

dominance hierarchies may not only depend on individual characteristics, but also on the contested resource (Qvarnström & Forsgren, 1998) and the social context (Chase et al., 2003; Dingemanse & Goede, 2004).

Thus, the use of aggression depends on both the defensibility of the resource and the fighting ability of the contestant, as predicted by resource defence theory (Brown, 1964; Emlen & Oring, 1977). However, as attack frequency may also be affected by resource value (Temeles, 1989; Dugatkin & Ohlsen, 1990), our results could suggest that *typus* males value food over females, whereas *robustus* males value females over food. Such an ontogenetic change in subjective resource value of food best explains the high attack frequencies of *intermedius* males in competition for food: they should gain more from investing into somatic growth and RHP than any other male stage, because they are less efficient in sneaking than *typus* males and yet still cannot defend a female against *robustus* males.

#### *Ontogenetic change in RHP and subjective resource value*

Increasing RHP and dominance status during ontogeny is usually accompanied by increasing body and weapon size (i.e., growth), which requires higher energy investment than maintenance of dominance status, once achieved. The food requirements and relative investment in somatic growth should therefore be greater for subordinate males than for dominant individuals, at the expense of investments in gamete production. Accordingly, a changing trade-off between somatic and gametic investment may reflect a switch between alternative mating tactics. For example, in bluegill sunfish sneaker males invest equally in somatic and gametic growth, whereas satellite males invest proportionally more in somatic growth, while the dominant parental males invest proportionally more in gametic growth (Neff et al., 2003). A similar pattern has also been found in rock shrimp (Hinojosa & Thiel, 2003). Since successful mate guarding reduces the risk of sperm competition, investing relative more into body size and RHP may be the better alternative than investing relatively more into sperm production in the face of high sperm competition, especially when numbers of mating opportunities are low (Alonzo & Warner, 2000; Neff et al., 2003).

Considering that subordinates usually experience a higher risk of sperm competition and lower numbers of mating opportunities than dominants, subordinates receive higher benefits from investing relatively more in somatic

than in gametic growth, whereas dominants obtain higher returns from investing relatively more in gamete production. Hence, there is a pay-off asymmetry (resource value asymmetry) sensu Maynard-Smith & Parker (1976) between subordinates and dominants with respect to food and females. Since the resource value affects the intensity of aggressive behaviour and resource defence (Temeles, 1989; Lindström & Pampoulie, 2005), ontogenetic stages differing in dominance status may differ in aggressiveness with respect to food and females, as has been shown herein for a marine shrimp. The present study supports the idea that fighting behaviour also depends on asymmetries in the subjective value that competitors place on a resource ('own resource value-dependent persistency' sensu Gherardi, 2006), which furthermore appears to affect searching behaviour and the degree to which different kinds of resources are monopolized.

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