

## Female rock shrimp prefer dominant males

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Evidence of female preference for dominant males during mating is reported for the rock shrimp *Rhynchocinetes typus*. Two sexually mature males of different ontogenetic stage were tethered at opposite sides of a large tank. Tethering restricted males from actively pursuing the receptive female but allowed females to choose between males. Surprisingly most (10 out of 11) females first approached the subordinate *typus* male, but after these initial contacts all females chose the dominant *robustus* male. Following antennal and corporal contacts of variable duration seven (out of 11) females initiated the mating process with the *robustus* male, while four females did not initiate mating during the 90 min observation period. The fact that all mating females selected the *robustus* shows strong female preferences for these males. It is suggested that female preference for large and dominant males is common among crustaceans with sexual size-dimorphism.

Sexual size-dimorphism is pronounced in many crustacean species in which males exhibit highly developed fighting structures (chela, pereopods). Males of these species may overtake females and hold them in a firm mating grip making it difficult to detect whether females have preferences. Despite these difficulties several studies indicate that females are capable of exerting preferences for certain males by exhibiting resistance to the advances of some males. For example, female tanner crabs resisted mating attempts from one-clawed males (Paul & Paul, 1996), and female crayfish resisted mating attempts from small males more efficiently than those from large males (Snedden, 1990). In isopods, females resist approaching males more intensively and successfully in less size-dimorphic populations (Jormalainen et al., 2000). While these reports indicate female preferences, in many species females offer little resistance to males because it may be costly and dangerous, sometimes even leading to the death of the female (see e.g. Ra'anan & Sagi, 1985). Instead of showing overt choices, females may exert their preferences for certain males in subtle, often cryptic, behaviours that are difficult to observe or quantify. It is for these reasons that female preferences are often little known in crustacean species with coercive male mating behaviour.

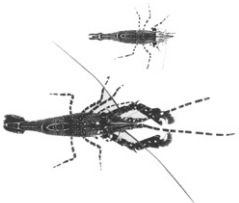
Receptive female rock shrimp, *Rhynchocinetes typus*, were studied to reveal whether they have preferences for certain males. Males of these shrimp undergo strong morphological changes during ontogeny: most males reach sexual maturity in the female-like *typus* stage, and during growth they pass through several intermedium moult stages before reaching the final stage, termed *robustus*. During male ontogeny, the 1st pereopods and the 3rd maxilliped experience strong allometric growth and are extremely developed in *robustus* males (see Correa et al., 2000). There exists a strong dominance hierarchy among males of the order *typus* < *intermedium* < *robustus* (Correa et al., 2003). All males are able to reproduce successfully, and usually males of all sizes immediately seize receptive females after making contact with them. Males differ in important behavioural and physiological characters: *robustus* males have a high resource holding potential and can defend females during the entire mating process (Correa et al., 2003), and furthermore they have substantially larger sperm supplies than subordinate males (Hinojosa & Thiel, 2003). For this reason, we hypothe-

sized that female rock shrimp may have preferences for *robustus* males. Since all males quickly seize receptive females when contacting them, females have little chance to exhibit their preferences overtly. We therefore conducted choice experiments in which we restricted male movements thereby enabling females to choose between males.

Rock shrimp were collected with a diver-operated suction sampler and maintained in the laboratory in tanks with flowing seawater and *ad libitum* food supply (for details see Correa et al., 2003; Hinojosa & Thiel, 2003). All experiments (N=11 replicates) were conducted in a large tank (140×60 cm surface area, 30 cm deep) that had flowing seawater during the acclimatization phase, but standing seawater during the 90-min long experiment. We tested whether females have a preference for the first (*typus*) or the final (*robustus*) ontogenetic male stage (males were distinguished using the criteria by Correa et al., 2000). One *typus* and one *robustus* each were randomly tethered at opposite sides of the experimental tank. A fine nylon thread was tied around each male at the suture between cephalothorax and abdomen and then fixed to the bottom of the experimental tank, leaving a leash of approximately 10 cm length. This allowed males to assume a natural position and to engage in courtship behaviours when the receptive female approached, but inhibited them from pursuing and seizing the female. Males were attached to the bottom of the tank 24 h before the actual choice experiment started. During the first 30 min after being tethered males frequently pulled on the nylon thread, but thereafter assumed a stationary position, apparently becoming accustomed to the nylon thread. After the 24 h acclimatization period, males behaved in a normal manner showing no signs of escape movements and the receptive female was introduced under a transparent bell. Following an acclimatization period of 30 min the female was released in the middle of the tank and we observed her behaviour for a maximum of 90 min.

Upon release, receptive females quickly approached one of the two males. Significantly more females first approached the *typus* than the *robustus* male (Table 1;  $\chi^2$  goodness-of-fit with Yates correction:  $\chi^2=7.45$ ,  $df=1$ ,  $P<0.05$ ). Only one female went directly to the *robustus* without visiting the *typus*. After contacting a male, females started to interact with them by mutual antennal contacts whereupon males became agitated

**Table 1.** Number of female rock shrimp *Rhynchocinetes typus* interacting with the subordinate typus male or with the dominant robustus male during different phases of the female choice experiment; following release, females were observed for 90 min; N=11 replicates.

	First visit	Last visit	Mating	
	Typus	10	0	0
	Robustus	1	11	7

and increased their movements. Males repeatedly attempted to pursue the female but could not because they were tethered. Female visits to the typus male extended over time periods ranging from 1 to 68.5 min ( $16.8 \pm 6.7$  min; mean  $\pm$  SE, N=10). Following these first visits to the typus, all females moved toward the robustus male. Upon first antennal contacts, robustus males reacted to females in a similar way as typus males, attempting to pursue the female actively (but being restricted by the tether). During these unsuccessful pursuits the robustus males raised their 3rd maxillipeds and 1st pereopods in an attempt to take the females into the cage state. Females often retreated when males made advances, but most females remained in the vicinity of the robustus. Some females revisited the typus, but then returned to the robustus. No female paid more than two visits to a typus, and at the end of the experiment all females were with a robustus (Table 1). Females that returned to the robustus quickly re-established antennal contact. With advancing time of their visits to robustus males, females apparently became more receptive towards the courting attempts from these. Females that had interacted with the robustus via mutual antennal contacts approached the head region of the robustus with their abdomen first. Often, females interrupted these advances, but seven females finally proceeded and were taken into the cage state by the robustus during the experiment (Table 1). Following initiation of the cage stage, the robustus males engaged in several other behaviours typical for this phase of the mating process (see Correa et al., 2000).

The fact that all females, which initiated matings, did so with the robustus clearly shows that female rock shrimp have a preference for these dominant males. It is not clear why most females first approached the typus. In the natural environment typus males are by far more abundant than robustus males, and consequently receptive females usually are first contacted by typus males, but then are taken over and monopolized by a robustus (Correa & Thiel, unpublished data), which are also preferred by females. This female preference for dominant

robustus males is not surprising since these can ensure undisturbed spawnings (Correa et al., 2003) and furthermore have a higher fertilization potential than subordinate typus males (Hinojosa & Thiel, 2003). Similar preferences of females for large and dominant males can also be expected in many other crustaceans with sexual size-dimorphism.

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