Mate competition in the velvet swimming crab *Necora puber*: effects of perceived resource value on male agonistic behaviour

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**Abstract** Male velvet swimming crabs [*Necora puber* (L.)] were observed to engage in long and vigorous agonistic interactions to gain possession of a sexually receptive female. The role of agonistic behaviour in male mate competition in this species was examined by investigating the effect of the perceived presence of sexually receptive females on interactions between males. Exposing male crabs to water conditioned by sexually receptive females resulted in prolonged interactions, with a greater incidence of potentially injurious behaviour than interactions between control crabs, exposed only to sea water. Male-conditioned water also resulted in more offensive behaviour, but these interactions were of shorter duration and not significantly different from sea water controls. Agonistic superiority was strongly correlated with contestant relative size when males were exposed to male-conditioned water or sea water, but not when exposed to female-conditioned water. Overall, the results conformed with the general predictions of game theoretic models in relation to the influence of resource value on agonistic behaviour. Crabs were more persistent and probably incurred greater fitness costs in the perceived presence of a sexually receptive female, when interactions may have been resolved on the basis of factors more closely related to actual fighting ability than the relative body sizes of contestants.

**Introduction**

In many species, agonistic behaviour mediates competition for mates or for resources necessary for mating, often, but not always, between males (Huntingford and Turner 1987; Harvey and Bradbury 1991). In these cases, reproductive success of males may be largely dependent on contest success, giving rise to intrasexual selection for morphological or behavioural characteristics associated with agonistic capability.

In several species of crab, reproductively successful males tend to be larger than unpaired males (Edwards 1966; Hazlett et al. 1977; Hazlett 1979; Berrill 1982; Wilber 1986; Asakura 1987; Christy 1987; Diesel 1988; Sekkelsten 1988; Smith 1992; Norman and Jones 1993) and the chelipeds, which are used in agonistic displays, are often sexually dimorphic (Dingle 1983). Lee and Seed (1992) noted that male shore crabs (*Carcinus maenas*) paired with females had larger chelae than average. Assortative mating of this kind may arise because agonistic behaviour mediates male mate competition and the ability of males to acquire and defend females is positively related to body and weapon size (Dingle 1983), but other explanations are possible, such as female mate choice (Christy 1987), size-related male ability to subdue potential mates (Arnqvist 1992) or male size-related costs of pre-copulatory pairing (Elwood and Dick 1990).

Field data indicate that competition among male crabs for sexually receptive females is likely: the operational sex ratio (Emlen and Oring 1977) of crab populations is often heavily male-biased (Wilber 1986; Choy 1988; Sekkelsten 1988; Smith 1990; Norman and Jones 1993), particularly when the relatively short period of female sexual receptivity is taken into account. In many species of crab, copulation takes place only when the female’s exoskeleton is soft after ecdysis (Hartnoll 1969). However, direct observation of mate competition in aquatic crabs under natural conditions is difficult, due to their cryptic and often nocturnal activity patterns, particularly during the vulnerable post-moult period. In several species there is pre- and post-cop-
The value of resources to an animal can be defined in terms of the increment to the individual's Darwinian fitness that is gained by acquiring them (Krebs and Kacelnik 1991). Being essential for reproduction, receptive females are clearly a valuable resource for males, particularly when future mating opportunities are limited (Enquist and Leimar 1990). The sequential assessment game is a game theoretic model of assessment and decision rules by animals during contest competition for resources, in which a contestant's decision to continue or retreat is based on the value and accuracy of its estimate of its own fighting ability (the ability to inflict and avoid injuries) relative to the opponent (Enquist and Leimar 1983). This model predicts that a contestant's persistence will be positively related to its perception of resource value and, providing its opponent continues, the degree of assessment of relative fighting ability (likely to equate with contest duration), the accuracy of the final estimate and the total cost incurred (reduction in fitness) are also predicted to increase with perceived resource value (Enquist and Leimar 1987). An extended version of the sequential assessment game that includes several behavioural options further predicts that prolonged interactions will involve more types of progressively more costly assessment behaviour, leading ultimately to direct assessment of relative fighting ability through injurious fighting (Leimar 1988; Enquist et al. 1990).

The present study investigates agonistic behaviour as a potential mechanism of intrasexual selection in the velvet swimming crab *Necora puber* (L.). Velvet swimming crabs are relatively common on hard substrata in Northeast Atlantic coastal waters (Ingle 1980). Individuals do not show site attachment (Norman 1989), and the reproductive biology of *N. puber* is typical of portunids (González Gurriarán 1985; Choy 1988). Pre-copulatory pairing can last up to 9 d and post-copulatory pairing up to 3 d. Copulation occurs after the female mouls, and females can spawn more than once after a single insemination. Sex pheromone release by sexually receptive females has been inferred in several species of portunid, and is thought to serve to attract males (Bachau 1986; Dunham 1988). Female *N. puber* have not been shown to produce a sex pheromone, but this seems likely since the reproductive behaviour of this species is similar to those portunids for which there is evidence for a sex pheromone.

The operational sex ratio in *Necora puber* populations is often male-biased (Choy 1988; Norman and Jones 1993), reproductively successful males tend to be larger than average, in one population at least (Norman and Jones 1993), and the chelipeds are sexually dimorphic (Smith 1990). Males fight readily when they encounter each other and, outside the breeding season, superiority in these interactions is largely dependent on the relative body sizes of opponents (Smith et al. 1994). In the present paper, the role of agonistic behaviour in mate competition is examined by describing interactions between males in pre-copulatory pairs and single males and by investigating quantitatively the effect on male agonistic behaviour of the perceived presence (odour) of a sexually receptive female. The results are interpreted in the light of predictions of the sequential assessment game.

### Materials and methods

**Interactions between single and paired males**

To determine whether male *Necora puber* fight for receptive females, three interactions between single males and males paired with females in the pre-copulatory guarding position (Hartnoll 1969) were observed. Single males and pre-copulatory pairs were collected by divers from rocky sites in shallow sublittoral areas of the Firth of Clyde, Scotland. They were placed in a glass observation tank and allowed to settle overnight, with the single male and the pair separated by a vertical partition. In each of the three cases, the paired male was smaller than the single male and the female was smaller than both males.

The observation tank (104 litres) had an arena of 64x42 cm, a layer of gravel = 2 cm deep, and was supplied with water pumped from the Firth of Clyde (12°C, 32‰S). Water inlets and outlets at each side of the tank helped minimize circulation of water across the partition. The tank was constantly illuminated with subdued green light, similar to the intensity and spectral composition of daylight in the *Necora puber* habitat in the Firth of Clyde in summer. After the settling period, the partition was removed by remote control and the crabs' subsequent behaviour was recorded with a video system.

**Interactions between single males**

Encounters between single males were staged during the period of peak breeding activity in July–September 1989. During encounters, males were exposed to one of three types of test water: water conditioned by females (see below), water conditioned by males, or sea water in which no crabs had been kept. Crabs to be observed and those used to condition test water were collected by divers from the Firth of Clyde in July and August. Females found paired with males in the pre-copulatory guarding position were assumed to be sexually receptive or imminently so (Hartnoll 1969) and were used to prepare female-conditioned water. Males to be observed were held in individual holding tanks in a flow-through sea water system prior to observation.

Encounters were staged between 09.00 and 20.00 hrs by placing one male in each side of the observation tank described above and allowing them to settle for 1 h while separated from each other by the partition. The sea water supply (12 to 14°C, 30 to 32‰S) was turned off during the settling and observation periods. Five minutes after the start of the settling period, test water was allowed to drain into the observation tank from a 4.5-litre glass container, via polythene tubing and a Y-connector which divided the water into each half of the tank. Delivery of test water took ≈ 15 min.

Female- and male-conditioned water was prepared by holding six crabs of the appropriate sex for 12 h in a 150-litre tank with partitions to prevent them injuring each other. The water in these tanks was aerated, but not renewed. These crabs were not fed during the course of the experiment, to avoid contamination of the water with food odour. If female crabs moulted during the course of the experiment, they were used only until one day after their moult, since the period of sexual receptivity ends as the new exoskeleton hardens (González Gurriarán 1985). Since females may release pheromone intermittently, the lability of a putative pheromone is unknown and males may not always respond visibly to pheromone (Dunham 1988), the proportion of tests where female pheromone was present in the