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Factors influencing the onset and duration of receptivity of female purple rock crabs, *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837) (Brachyura: Grapsidae)

A.M. Brockerhoff*, C.L. McLay

School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

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Abstract

The effects of males, field, and laboratory conditions on the receptivity of females were tested in the New Zealand purple rock crab *Hemigrapsus sexdentatus*. Onset and duration of female receptivity is of interest because it influences the time available for mating and therefore the operational sex ratio (OSR), male–male competition, and the extent of sperm competition. Females were receptive once a year for a short time prior to oviposition. The breeding season was highly synchronised and lasted for about 3 weeks (from the end of March to mid-April; southern autumn), after which, almost all females carried eggs. We found few receptive females in the field (0% to 4.9%) during the breeding season despite a large number of crabs examined (935 in 1999 and 555 in 2000), suggesting that females are receptive for less than a day. The onset of the breeding season was the same for the wild crabs and those held in field cages, but the duration of receptivity increased to several days for caged females. The onset of the breeding season of females in the laboratory was earlier compared to females in the field and had, overall, a longer breeding season. Females isolated from males stayed receptive significantly longer (5.5 days) than females caged with males (3.3 days), suggesting that the duration of female receptivity is adjusted according to the presence or absence of males. Our results suggest that females have some control over their receptivity in relation to male presence, and this could influence the outcome of sexual selection.

Keywords: Female control; Female receptivity; Fertilisation window; Grapsidae; Hemigrapsus; Operational sex ratio

1. Introduction

Sexual selection, sperm competition, and female choice have been the subjects of many studies over the last two decades (see reviews of Anderson, 1994; Eberhard, 1996; Birkhead and Møller, 1998) especially in birds and insects. By comparison, little is

* Corresponding author. 1 Hare St., Christchurch 8004, New Zealand. Tel.: +64 3 343 1058; fax: +64 3 364 2024.

E-mail addresses: brockerhoff@paradise.net.nz (A.M. Brockerhoff), colin.mclay@canterbury.ac.nz (C.L. McLay).

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known on these subjects for marine invertebrates such as crustaceans. In particular, it is uncertain whether females have any control over the duration of their receptive period and the fertilization of their ova. More importantly, previously, there has been no way to determine female crustacean receptivity during the intermoult other than by inducing mating. Studies have been carried out on the general mating behaviour, mate choice, male–male competition, and sperm storage for marine crustaceans (Christy, 1987; Diesel, 1991; Subramoniam, 1993), but these revealed nothing about the factors influencing female receptivity. The time and duration of female receptivity determines the operational sex ratio (OSR, defined as the ratio of fertilisable females to sexually mature males at any given time; Emlen and Oring, 1977) and can influence the extent of male–male and sperm competition. For example it has been shown that the OSR influences female preference and male–male competition in guppies (Jirotkul, 1999). Under a male biased sex ratio, females of the hermit crabs *Pagurus filholi* and *P. lanuginosus* were guarded earlier and longer by males (Wada et al., 1999; Minouchi and Goshima, 2000).

Presently, there is little evidence that female crustaceans can control their receptivity. The onset and duration of crustacean female receptivity are known to depend upon internal factors such as the stage of moulting and development stage of the ovaries, and can be regulated by hormones (DeKleijn, 1998). In addition, external environmental factors such as the lunar cycle (Henmi and Murai, 1999; McCurdy et al., 2000), temperature (Berril and Arsenault, 1982; Flores and Negreiros-Fransozo, 1998), or a combination of both (Greenspan, 1982; Zimmerman and Felder, 1991; Caubet et al., 1998) can influence receptivity.

In many Crustacea, mating and moulting are linked, such that females are only receptive for a short time after moulting until the exoskeleton has hardened (i.e., postmoult mating Hartnoll, 1969, 2000). In these cases, the onset and duration of female receptivity (time available for mating) are determined by the moult cycle and are limited to several hours for *Cancer gracilis* (Orensanz et al., 1995), 5–12 h for the portunid crab *Callinectes sapidus* (Gleeson, 1991), and 6–50 h for the marine isopod *Paracerceis sculpta* (Shuster, 1989). However, receptivity may last for up to 21 days for the tanner crab *Chionoecetes bairdi* (Donaldson and Adams, 1989). In contrast, other Crustacea mate during the intermoult, when the exoskeleton is hard, commonly prior to oviposition (Hartnoll, 1969). The time and duration of female receptivity in these cases varies from a few days to several weeks and may include the days before and after oviposition. For example, females of grapsid crabs are receptive for 1–2 days (*Gaetice depressus*; Fukui, 1993) or 2–3 days (*Sesarma* sp. [*reticulatum*]; Zimmerman and Felder, 1991) and females of ocypodid crabs for an average of 11.4 days (*Macrophthalmus hirtipes*; Jennings et al., 2000) or up to 2 weeks (*Ilyoplax pusilla*; Henmi and Murai, 1999).

Some species are able to do both: mate while soft-shelled after moulting (primiparous) and subsequently when hard-shelled (multiparous), as found in the tanner crab *C. bairdi* (Donaldson and Adams, 1989) and the American lobster *Homarus americanus* (Waddy and Aiken, 1990). This is often a consequence of a terminal moult. Females in other species are assumed to be continuously receptive to mating after reaching a certain developmental stage. For example, females are receptive continuously in the marine isopod *Jaera hopeana* from the manca-II stage onwards (Franke, 1993) and after developing permanently mobile gonopore opercula in the case of the fiddler crab *Uca vocans* (Salmon, 1984), and in the grapsid crab *Pachygrapsus transversus* (Abele et al., 1986). For the fiddler crab, however, a peak of mating activities was observed during spring tides (Salmon, 1984). Overall, when both systems (postmoult and intermoult mating) are compared, it appears that intermoult mating allows more flexible timing of mating in relation to biotic and abiotic variables than the more physiologically determined behaviours associated with postmoult mating.

In this study, we examined the breeding behaviour of the intertidal crab *Hemigrapsus sexdentatus* (formerly known as *H. edwardsii* [Hilgendorf, 1882]). Our purpose was to determine factors that influence the onset and duration of the fertilisation window. Female receptivity was examined under field and laboratory conditions and in the presence or absence of males. A population in the field was monitored to obtain information on the spatial distribution and movement of the crabs, especially receptive females, before, during, and after the breeding season.