

SOCIAL MONOGAMY IN A FIDDLER CRAB, *UCA CAPRICORNIS*

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ABSTRACT

Fiddler crabs are generally considered polygamous as they tend to live in dense mixed sex colonies with numerous neighbours and individually defended territories. We show that the Australian fiddler crab, *Uca capricornis*, is socially monogamous based on behavioural experiments and observations of neighbouring males and females. The unusual relationship between neighbouring males and females in *U. capricornis* is selected for and maintained by intrasexual aggression and the ability to recognise and defend their partner.

KEY WORDS: fiddler crabs, pair bond, social monogamy

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INTRODUCTION

Mating strategies can involve anything from promiscuous liaisons to life-long monogamy, depending on ecological and social conditions. In the broadest sense, monogamy may be defined as a prolonged relationship between a single male and female. Exactly what constitutes a prolonged relationship determines the form of monogamy (Schein, 1975; Wittenberger and Tilson, 1980; Wickler and Seibt, 1981; Whiteman and Côté, 2004). Exclusive mating between a single male and female is considered genetic monogamy, whereas pairs that spend extensive periods of time together, with or without mating, are considered socially monogamous (Wickler and Seibt, 1983). These relationships may last for anything from an entire lifetime, to a succession of relationships lasting as little as a single reproductive cycle in serial monogamy. Identifying monogamy is further complicated by the existence of extra-pair copulations, the possibility that only a proportion of the population is monogamous, or that individuals may only spend part of their life in monogamous relationships (Wickler and Seibt, 1981).

Males generally maximise their reproductive success by mating with as many females as possible, which depends on the rate at which they encounter receptive females (Trivers, 1972). The time they spend with a particular female depends on the costs and benefits of searching for other females. Searching may be costly when population densities are low or male biased, or when females are receptive for a relatively short period of time and mate synchronously. Males may thus be pressured to guard females for some time before, during, and/or after mating (Orians, 1969; Emlen and Oring, 1977; Wickler and Seibt, 1981; Mathews, 2002a, b; Whiteman and Côté, 2004). If females can only mate once per clutch, then males may invest in pre-copulatory mate guarding. On the other hand, if females can mate with multiple males and there is last-male sperm precedence, then males should invest in post-copulatory mate guarding (Wickler and Seibt, 1981). Mate guarding will also make available females scarcer,

pressuring males to guard them for longer, which may lead to long-term heterosexual pairing (Grafen and Ridley, 1983).

Monogamous pairs may also form for territorial cooperation. Most monogamous pairs share a territory, and one or both sexes may benefit from shared maintenance and defence (Fricke, 1986; Wisendon, 1994; Mathews, 2002a; Morely and Balshine, 2002; Whiteman and Côté, 2004). In many animals, females may benefit from assistance in territory defence as they are often smaller than males and lack the necessary strength or weaponry to repel intruders.

Fiddler crabs (genus *Uca*) exhibit two general mating systems (Christy and Salmon, 1984; Salmon, 1987; Salmon and Zucker, 1988) that are not mutually exclusive; many species will utilise both, depending on environmental and social factors (Koga and Murai, 1997; Koga et al., 1998; deRivera and Vehrencamp, 2001; deRivera et al., 2003). Females may leave their burrows and wander through the colony, sampling different males, until choosing one and remaining in his burrow to mate and incubate her eggs. As females usually remain sequestered in the male's burrow after mating, such burrow-mating systems are more conducive to monogamy. On the other hand, surface-mating species, where males court burrow-owning females and mate with them outside her burrow (Salmon, 1987; Murai, 1992), are more likely to be polygamous. Females remain active on the surface after mating and can consequently mate with several males (Koga and Murai, 1997). However, in at least one surface-mating species, *Uca polita* Crane, 1975, males and females seem to form socially monogamous pairs, or 'resident breeding units' (von Hagen, 1993).

Uca capricornis Crane, 1975 are typical surface-mating fiddler crabs in many ways; they mate synchronously around spring tide, outside female-defended burrows and as females remain active on the surface after mating, they have the opportunity to mate with several males. In such situations, the last male to mate likely fertilises the majority of her eggs (Murai et al., 1987; Goshima et al., 1996).

However, preliminary observations suggest that *U. capricornis* meet certain conditions conducive to monogamy. Males could increase their reproductive success by mating with multiple females, but those who leave after mating may lose paternity to another male. Furthermore, the synchronised oviposition common to fiddler crabs means that if a male delays leaving until after oviposition, he is unlikely to find another receptive female. The low likelihood of successfully finding multiple receptive females may make it difficult for males to guard more than a single female. Furthermore, in *U. capricornis* males and females seem to live unusually close together and are more tolerant of each other than in other species and males are able to visually discriminate between their neighbours and unknown females (Detto et al., 2006).

The aim of this study was to determine whether there is in fact a special relationship between heterosexual pairs in *U. capricornis*. We also examined the mechanisms responsible for the formation and maintenance of these heterosexual pairs, with the aim of answering several questions crucial to understanding the adaptive significance of social monogamy: “why do individuals stay with their current partner?” and “why do individuals form a relationship with only a single partner?” (Wickler and Seibt, 1981; Morley and Balshine, 2002).

MATERIALS AND METHODS

This study was conducted on a large population of *Uca capricornis* in the vicinity of the mangrove boardwalk in the East Point Reserve, Darwin, Australia (12°24'35"S, 130°50'00"E). Fieldwork was conducted yearly from November to January in 2002-2006.

Natural Male-Female Interactions and Territoriality

The behaviour of *U. capricornis* is as yet undescribed. Consequently, we observed their behaviour for approximately 1100 h over 4 years to obtain a general picture of their social system and behaviour. Upon observing a mating we recorded, whenever possible, whether the individuals involved were male-female nearest neighbours living within 30 cm of each other, referred to here as $\text{Q}:\text{O}$ neighbours.

To obtain a more detailed description of the relationship between males and females, we recorded the natural interaction between $\text{Q}:\text{O}$ neighbours throughout the 14 day tidal cycle. We filmed the pairs from directly overhead with a Sony TRV110 camera for 30 min each. From the video, we documented any occasions where a male fought with an intruder who approached the female and observed the interactions between the male and female.

We also examined their territoriality. We digitised the video and tracked the crabs' positions every second (see Hemmi and Zeil, 2003) to determine how often each crab was nearer to his or her partner's burrow entrance than the partner was itself. We then documented territory size by converting the crab's position every second into a circle with a radius of 5 cm, as an estimate of the area covered by the crab as it moved. The result was a bitmap image of the overall area covered by the crab over half an hour, which we converted into an estimate of the actual area using the public domain Scion Image (Alpha 4.0.3.2) program (Scion Corporation). By aligning the male and female territories with their respective burrows we could also determine the area of overlap between them (see Fig. 1).

Sex Ratio and Distribution

To determine whether females may be a limited resource, we caught all of the individuals within 18 plots (4 m² each) and measured their carapace widths to calculate the sex ratio in relation to size.

We also recorded the location of the burrows within the plots, using XY coordinates, to determine whether the males and females were distributed

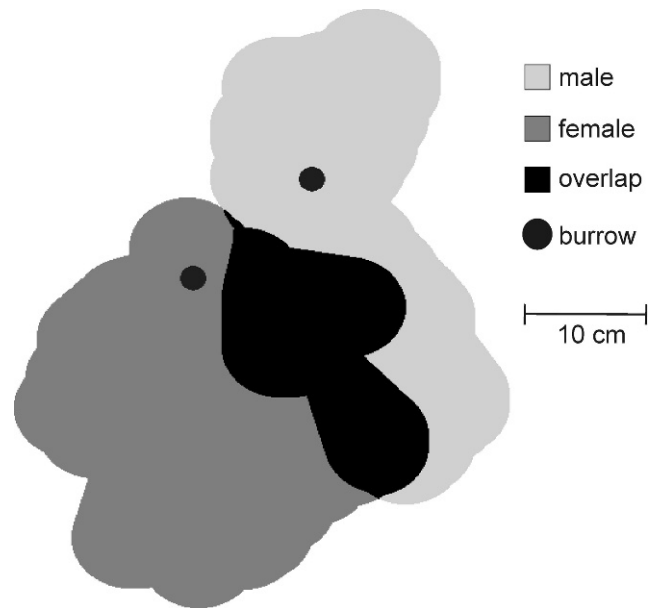


Fig. 1. Example of the territory covered by a male and female in a pair over 30 min.

independently of each other. We determined the distance to, and sex of, the nearest resident for every individual within each plot to compare the mean distance between $\text{Q}:\text{O}$ neighbours and between $\text{O}:\text{O}$ neighbours. We did not examine $\text{Q}:\text{Q}$ neighbours because the scarcity of females made such relationships rare. We also ran 500 iterations of a computer simulation in which the original crabs were randomly assigned to the existing burrow positions in each plot. We then compared the average simulated nearest neighbour distances between males and females to the observed mean distances between $\text{Q}:\text{O}$ neighbours in each of the 18 plots using a paired *t* test.

Tenure

Crabs may vacate their territories due to continued harassment by their neighbours (Zucker, 1977; Murai et al., 1987, 1996), because they are evicted, or for no apparent reason. To determine whether $\text{Q}:\text{O}$ neighbours were longer lasting than $\text{O}:\text{O}$ neighbours, we documented the number of crabs that were still present in their same burrows after 24 h. Each day, we randomly selected 20 focal males; 10 with male nearest neighbours and 10 with female nearest neighbours. To avoid catching and marking the crabs, which may affect their behaviour, we marked their burrows and identified each individual by drawing its unique carapace colour pattern. The following day, at the same time relative to low tide, we determined whether the crabs were in the same burrows. We marked a new set of 20 pairs each day over a full 14-day tidal cycle. These data suggested that crabs were less likely to change burrows during neap tide. We therefore repeated the protocol for six additional tidal cycles, taking a single reading of 20 pairs both at spring and neap tides. We were then able to compare the probability of females and males remaining in the same burrow, the probability of males with female or male neighbours remaining in the same burrow, and the probability of $\text{Q}:\text{O}$ neighbours and $\text{O}:\text{O}$ neighbours remaining together.

Neighbour-Stranger Experiment

To determine whether $\text{Q}:\text{O}$ neighbours have a special relationship compared to $\text{O}:\text{O}$ neighbours, we tethered different individuals near a focal male's burrow to see whether they were able to discriminate between their neighbour and a stranger of the same sex (see Detto et al., 2006). Tethering involved gluing a short length of cotton to the carapace and tying the free end to a nail stuck in the ground, allowing the crab to move but not leave the area. All tethering experiments were conducted in the 7 days between neap and spring tide when mating was most common, using only non-ovigerous females.

We selected 20 focal males with female nearest neighbours and 20 with male nearest neighbours. We tethered the neighbour 10 cm from the focal male's burrow, in the direction of the neighbour's burrow, and recorded the focal male's response. The trial ended when the focal male touched the tethered individual (approach), or after 5 min passed with no approach (ignore). We also presented the same focal males with unknown individuals of the same sex and size (± 1 mm) as the neighbour. The order of the two trials (neighbour or stranger) was random. During the stranger trial, we blocked the neighbour in its burrow by covering the entrance with a shell. The second trial was conducted 10 min after the first. Using Likelihood Ratio tests (preferable to χ^2 , see Zar, 1974), we determined whether the focal males of $\text{♀}:\text{♂}$ neighbours and $\text{♂}:\text{♂}$ neighbours were equally likely to approach their tethered neighbours. We also tested whether they were equally likely to approach strangers and neighbours.

Intruder Experiment

Males and females may be unable to associate with multiple partners because their partners aggressively repel same-sex intruders. To test this hypothesis, we located 15 $\text{♀}:\text{♂}$ neighbours and blocked the burrow of the male or the female (in random order). We tethered a size-matched same-sex or opposite-sex intruder (in a random order) halfway between the burrows. Once the focal individual emerged, we documented whether it responded aggressively by pushing or grappling with the intruder within 5 min. After each trial, we unblocked the burrow and allowed the pair to interact normally for 10 min before running the next trial. In this way, we observed the reactions of both pair members to same- and opposite-sex intruders. We then compared their responses using Likelihood Ratio tests.

Size-Assortative Pairing

Monogamous pairs are often sized matched (Schein, 1975; Morely and Balshine, 2002) and size-assortative pairing is predicted based on the costs of mate guarding (Jormalainen, 1998). Using the $\text{♀}:\text{♂}$ and $\text{♀}:\text{♀}$ neighbours collected during the different experiments ($\text{♂}:\text{♀}$: $n = 531$; $\text{♂}:\text{♂}$: $n = 215$), we examined whether the size of the nearest female or male neighbour was correlated with the size of the focal male.

RESULTS

Natural Male-Female Interactions and Territoriality

Of the 19 matings we observed, 8 were between $\text{♀}:\text{♂}$ neighbours. The remaining 11 matings involved wandering females that mated with a resident (1 observation), or wandering (2 observations) male, or unpaired resident females that mated with a wandering male who subsequently left (5 observations) or evicted (3 observations) the female. No females with a male neighbour within 30 cm were observed mating with a male other than their neighbour.

Mating generally occurred on the sediment surface at the female's burrow entrance, although we observed one instance in which the male entered his neighbour's burrow and sealed it behind them, presumably to mate. Males were never observed waving at females to attract them to their burrows for mating, but did wave at females when approaching them outside the females' burrows. Mating activity peaked around spring tide, although copulations were observed throughout the tidal cycle, and ovigerous females were commonly observed on the surface throughout the cycle.

The crabs' activity was concentrated around their burrows. The furthest a filmed male moved from his burrow was 22 cm, while the most a female moved was 15 cm. Male territories were larger than those of females (♂ : 992 cm² (SD 450), ♀ : 787 cm² (SD 300); paired t test: $t = -2.25$, $d.f. = 20$, $n = 21$, $P = 0.04$). On average, 38% (range: 14-84%, $n = 21$ pairs) of the females' activity range overlapped with their

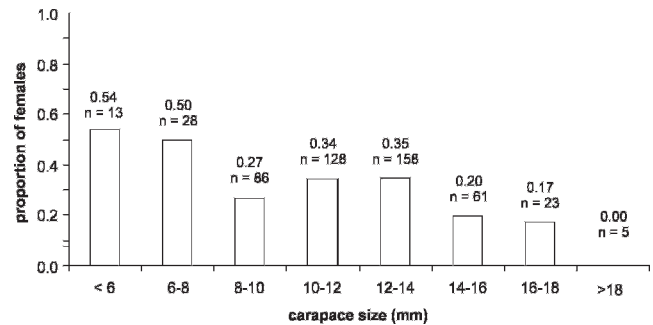


Fig. 2. The proportion of females at different size classes. The proportion of females and total sample size is shown above each bar.

neighbouring males'. The degree of overlap was not correlated with the distance between their burrows (Pearson's correlation: $r = -0.15$, $n = 21$, $P = 0.51$).

Males generally tolerated their female neighbour's presence. In 20 of the 21 pairs, females got closer to their partner's burrow than the male was himself. On average, females spent 21% of their time closer to the male's burrow entrance than the male himself (range = 0-65%, $n = 21$ pairs). Females also tolerated their neighbour, but were more likely to run back to their burrows if the male got too close. In 18 of the 21 pairs males got closer to the female's burrow than the female was herself, spending on average 14% of their time closer to the female's burrow entrance than the female (range = 0-55%, $n = 21$ pairs). The amount of time was also not related to inter-burrow distance (♀ Pearson's correlation: $r = -0.39$, $n = 21$, $P = 0.08$; ♂ Pearson's correlation: $r = -0.25$, $n = 21$, $P = 0.25$). When a wandering crab or another neighbour approached too closely, the crabs generally responded by running back to their burrow and chasing them away, except the few occasions when their view appeared to be obstructed by roots.

Although the vast majority of crabs lived in separate burrows, sometimes as close as 2 cm apart, males and females were occasionally observed sharing a burrow for an extended period. This arrangement appeared more stable than the temporary use of a resident's burrow by wandering crabs. How these associations are initiated, how common they are, and how long they last is unknown.

Sex Ratio and Distribution

There were an average of 7 crabs/m² active on the surface at any time ($n = 502$ crabs in 18, 4 m² plots). The sex ratio was strongly male biased, with only 30% females, and changed with size; females were significantly rarer in larger size classes (Spearman's correlation: $r_s = -0.905$, $P_{(2 \text{ tailed})} = 0.002$, $n = 8$ size classes; Fig. 2).

Males and females lived unusually close to each other. As predicted, the distance between naturally occurring $\text{♀}:\text{♂}$ neighbours (mean = 19 cm (SD 10.7), $n = 230$ crabs, 18 plots) was less than that between $\text{♂}:\text{♂}$ neighbours (mean = 20 cm (SD 11.2), $n = 255$ crabs, 18 plots; t test: $t = 1.94$, $n = 18$ plots, $d.f. = 17$, $P_{(1 \text{ tailed})} = 0.04$). The observed male-female inter-burrow distance was also less than predicted if males and females were randomly distributed

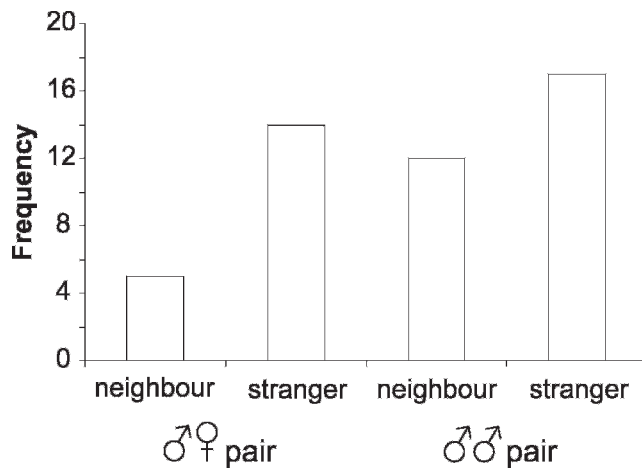


Fig. 3. Response of focal males in male-female and male-male pairs to their neighbour and to an unknown crab of the same sex and size. Bars indicate the number of trials in which the male approached the tethered individual ($n = 20$ trials per treatment).

within existing burrows (mean = 21 cm (SD 6.2), $n = 9000$; t test: $t = 2.05$, $d.f. = 17$, $P_{(1 \text{ tailed})} = 0.03$). Males and females were therefore not distributed independently of each other.

Tenure

Males and females were more likely to be found in the same burrow the next day around neap tides than during spring tides (Paired t test: $P_{(2 \text{ tailed})} = -6.088$, $d.f. = 6$, $n = 7$ activity cycles, $P = 0.001$). Females were more likely than males to be in the same burrow the next day (♀: 56% stayed, $n = 247$; ♂: 47% stayed, $n = 248$; $\chi^2 = 4.1$, $d.f. = 1$, $P = 0.04$). Males with female neighbours tended to be more stable than males with male neighbours (♂♀: 57% stayed, $n = 239$; ♂♂: 33% stayed, $n = 242$; $\chi^2 = 26.7$, $d.f. = 1$, $P < 0.001$). Overall, ♀:♂ neighbours were more likely to stay together, with both individuals found in their burrows on consecutive days, than were ♂:♂ neighbours (♂♀: 40% both stayed, $n = 231$; ♂♂: 23% stayed, $n = 236$; $\chi^2 = 14.8$, $d.f. = 1$, $P < 0.001$).

Neighbour-Stranger Experiment

Males treat female neighbours differently than male neighbours and intruders. Males were less likely to approach a female neighbour than an unknown female tethered in the same spot (neighbour: 5/20 trials, stranger: 14/20 trials; Fisher's exact test: $P_{(1 \text{ tailed})} = 0.005$). Males were equally likely to approach an unknown female (14/20 trials), a neighbouring male (12/20 trials) and an unknown male (17/20 trials) (Likelihood Ratio test: $\chi^2 = 3.27$, $d.f. = 2$, $P = 0.195$) (see Fig. 3).

Intruder Experiment

Males and females were equally likely to respond aggressively to intruders of the same sex (♂focal ♂intruder: 15/15 trials, ♀focal ♀intruder: 13/15 trials; Fisher's exact test: $P_{(1 \text{ tailed})} = 0.24$). Both males and females were less

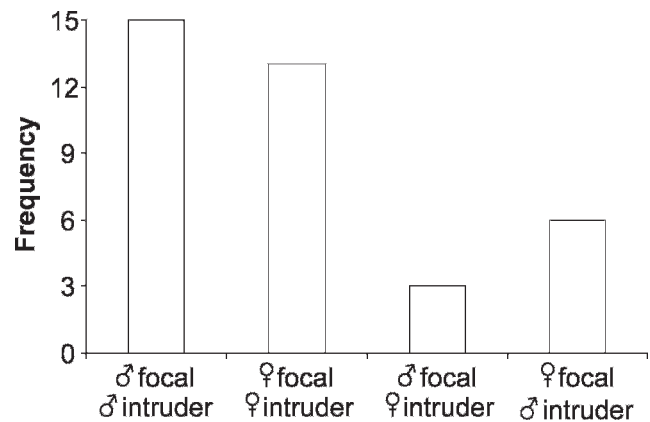


Fig. 4. Frequency of aggressive responses of focal males and females to same- and opposite-sex intruders ($n = 15$ trials per treatment).

likely to fight intruders of the opposite sex (♂focal ♀intruder: 3/15 trials, ♀focal ♂intruder: 6/15 trials; Fisher's exact test: $P_{(1 \text{ tailed})} = 0.21$) (see Fig. 4).

Size-Assortative Pairing

Female size was positively correlated with the size of her nearest male neighbour (Pearson's correlation: $r = 0.511$, $P < 0.001$, $n = 531$ pairs). Male size was also positively correlated with the size of his nearest male neighbour (Pearson's correlations $r = 0.296$, $P < 0.001$, $n = 215$), but more weakly than between ♂:♂ neighbours (comparison of correlation coefficients: $z = 3.185$, $P = 0.001$) (see Fig. 5).

DISCUSSION

The relationship between male-female nearest neighbours in *Uca capricornis* is unusual, both compared to the relationships between other conspecifics, and to heterosexual relationships in other fiddler crab species. Male-female pairs live closer together than ♂:♂ neighbours, and closer than predicted if they were randomly distributed. While the difference is quite small, the method used to calculate it is very conservative, based only on existing burrows when there are vast uninhabited areas of mudflat suitable for burrows. Despite their proximity, ♀:♂ neighbours are unusually tolerant of each other. Males discriminate between their female neighbour and unknown females, but treat males and strangers of either sex in the same way. This suggests that the tolerance exhibited by ♀:♂ neighbours is not simply related to the differential threats posed by males and females, but rather that the males learn to recognise their female neighbour, which is due to the female's unique carapace colour patterns (Detto et al., 2006).

Although a large proportion of the female's territory overlaps the male's larger territory, they do not share in territorial maintenance. Both sexes can construct and maintain their own burrows, and generally defend their own territories from intruding crabs of either sex. Females may benefit from assistance in territory defence, however, because they lack the enlarged claw with which to repel intruders. Males will defend their female neighbours from intruding males, which is uncommon in other surface-

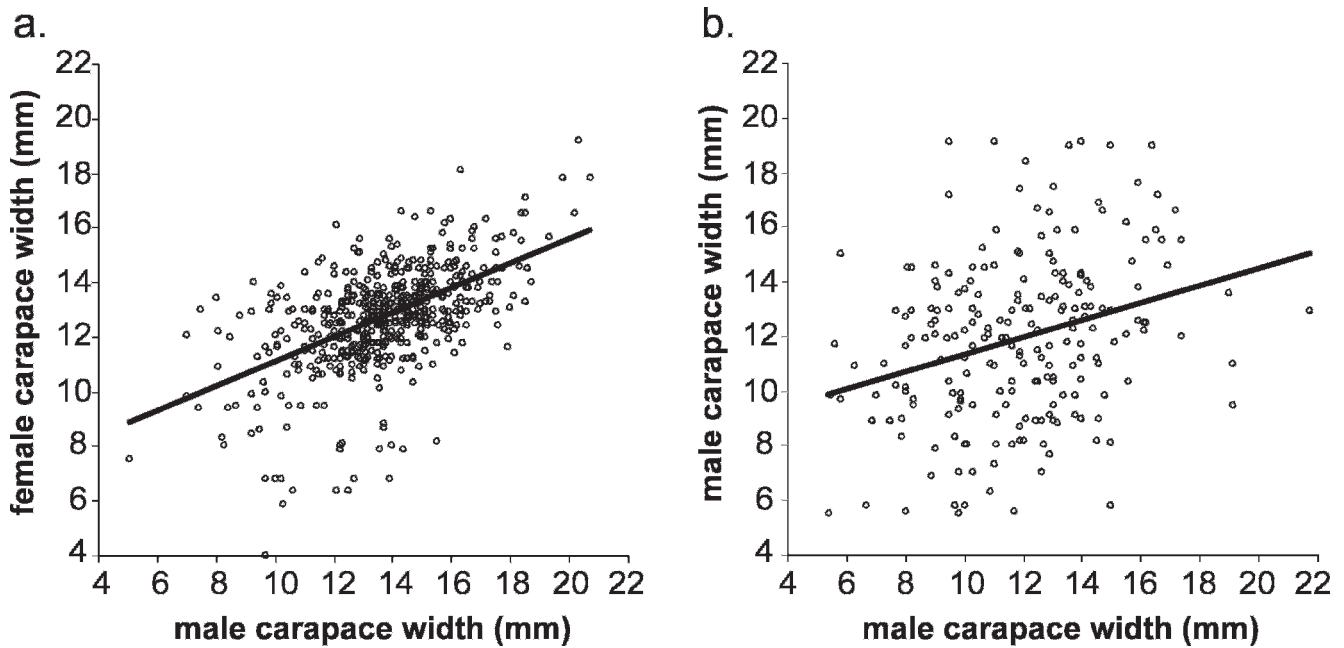


Fig. 5. Relationship between the size of individuals in male-female pairs (a) and male-male pairs (b).

mating fiddler crabs (Severinghaus and Lin, 1990). On the one filmed instance in which a burrowless wandering male approached a female, her partner ran over and chased him off. This behaviour was also witnessed in the field on numerous occasions. This may explain why females are more likely to stay in the same burrow. Males with a female neighbour are also more likely to remain in the same burrow than males with a male neighbour. When the crabs do change burrows, they are more likely to do so around spring tide, when mating activity peaks. This is probably due to males relocating in an attempt to find females (Severinghaus and Lin, 1990).

Male-female neighbours spent extensive and exclusive periods of time together, which fits the definition of social monogamy (Wickler and Seibt, 1983; Whiteman and Côté, 2004). However, we cannot make such definite claims about their mating system. The majority of the observed matings involved burrowless crabs. However unlike burrow-mating species, where mating is preceded by a conspicuous waving display, surface mating in *U. capricornis* is difficult to observe, and it is possible that our results were biased towards observations of burrowless crabs, which were more noticeable as they wandered through the colony. We cannot say how long ♀:♂ neighbours stay together, but it is highly unlikely to be for life. At some point the crabs no doubt leave their neighbours in search of new mates, at which point they may mate with a number of different individuals. However, ♀:♂ neighbours were never observed mating with other individuals, which suggests that once the crabs are in such a 'pair' they are truly monogamous.

Males could increase their reproductive success by searching for more females (Wickler and Seibt, 1981), but the energy expenditure, time away from foraging, predation risk, risks of encounters with other males, and the likelihood of increasing their reproductive success all influence the costs and benefits of searching for receptive females (Wittenberger

and Tilson, 1980; Grafen and Ridley, 1983; Mock and Fujioka, 1990; Wada et al., 1999; Mathews, 2002b; Morley and Balshine, 2002). These factors are in turn directly affected by the population density and sex ratio. Male biased or sparsely distributed populations increase the costs associated with searching and reduce the likelihood of finding a female. In snapping shrimps (Mathews, 2002b), amphipods (Dick and Elwood, 1996), and hermit crabs (Wada et al., 1999), male-biased sex ratios result in males remaining with one female for longer.

Uca capricornis are found at low densities compared to other fiddler crabs, with an average of only 7 crabs/m². Other surface-mating species reportedly live at densities of 19-60 crabs/m² to over 100 crabs/m² (Christy and Salmon, 1984). Females are particularly scarce in *U. capricornis*, comprising only 30% of this population. Even if males can find additional females after leaving their partner, they would most likely lose paternity to another male as females remain active on the surface after mating and can mate with several males, the last of whom fertilises most of her eggs (Murai et al., 1987; Goshima et al., 1996). As with most other fiddler crabs, *U. capricornis* oviposit around spring tide and release their larvae during the next spring tide, 12-14 days later (Salmon, 1987). Males can delay leaving their partner until after oviposition to ensure their paternity, but their reproductive synchrony means that any females they find are likely to have already oviposited (Emlen and Oring, 1977). The costs associated with searching for females and the low likelihood of successfully finding multiple receptive females in *U. capricornis* may select for males that guard females, but this does not explain why males guard only one female.

Males could theoretically increase their reproductive success by guarding a harem of several females. As males will readily court intruding females, it seems they would mate with multiple females if given the opportunity.

However, female *U. capricornis* do not depend on clumped resources that the males can defend, so males are forced to guard the females themselves. Females are sparsely and fairly evenly dispersed throughout the population, making it difficult for males to monopolise more than a single female at a time (Emlen and Oring, 1977). The male's ability to monopolise multiple females is further constrained by strong intrasexual aggression; female *U. capricornis* aggressively repel any wandering females that approach their territory. Similar behaviour has been credited with the promotion and maintenance of long-term monogamous pair bonds in *Trapezia* crabs (Huber, 1987), shrimps (Seibt and Wickler, 1979), burying beetles (Wittenberger and Tilson, 1980), numerous fish (Fricke, 1986; Hourigan, 1989; Hourigan et al., 1989; Reavis and Barlow, 1998; Carvalho et al., 2003; Harding et al., 2003), and house sparrows (Veiga, 1992).

Male *U. capricornis* apparently maximise their reproductive success by guarding individual females. The most effective method would be to sequester the female in a burrow after mating, as is common in burrow-mating fiddler crab species (Goshima et al., 1996; Yamaguchi, 1998; Murai et al., 2002). However, this would severely restrict the female's foraging time, and *U. capricornis* females continue to feed and defend their own territory during all stages of reproduction. In a number of other crustaceans, the male physically grasps his partner to guard her (Birkhead and Clarkson, 1980; Wada et al., 1999). While this isn't possible in fiddler crabs, the ability of *U. capricornis* to recognise their freely mobile partner (Detto et al., 2006) is equivalent to physical contact (Seibt and Wickler, 1979) as it allows them to track their partner and monitor their movements.

Males may benefit by guarding a single female, but why should females restrict themselves to a single male? The most likely explanation is that it is difficult for females to associate with other males because their partners repel any potential rivals. Consequently, even if females do not actually benefit from the relationship, it may be costly to resist (Wittenberger and Tilson, 1980). On the other hand, having a partner who will ward off other males has a number of possible advantages. Males can use their enlarged claw to easily evict a female from her burrow. Several unpaired females were evicted by males after mating with them, while females were less likely to be evicted if they had a male neighbour to defend her. Furthermore, *U. capricornis* males did not constantly court their female neighbour, and in fact ignored her when she was tethered near his burrow, whereas they approached and courted unknown females. By forming a relationship with a single male who recognises her and does not need to constantly assess her receptivity, she can forage without interruption. Finally, due to the strong competition for females, successful partners are likely to be strong competitors as weaker individuals will be replaced. This may explain why *U. capricornis* pair size-assortatively, as larger, competitively superior (Jennions and Backwell, 1996; Pratt et al., 2003) males are able to defend their access to larger, more fecund (Greenspan, 1980; Salmon, 1984; Salmon, 1987) females.

A number of crustaceans live in socially monogamous male-female pairs (Atema et al., 1979; Birkhead and

Clarkson, 1980; Anstensrud, 1992; Jormalainen, 1998; Mathews, 2002a; Rahman et al., 2003) which co-defend a single territory or enforce mate guarding by grasping their mate. Social monogamy seems unlikely in animals like fiddler crabs which defend individual territories and tend to live in dense colonies with numerous neighbours. *Uca vocans* Linnaeus, 1758, a typical surface-mating fiddler crab, live in strongly female biased populations of less than 20 crabs/m² (Christy and Salmon, 1984; Salmon, 1984). Males court several neighbouring females and make no effort to defend females they have just copulated with from rival males. *Uca thayeri* Rathbun, 1900 live at relatively low densities of 3-12 crabs/m² and males mate on the surface with several neighbouring females that they attempt to defend from intruders (Salmon, 1987). We suggest that there is an increasing trend for male fiddler crabs to guard their mates as population densities decrease. Monogamous relationships in *U. capricornis* appear to be due to the low population density, especially of females, combined with intrasexual aggression and the ability to recognise and defend their neighbour.

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