

Surface Mating as an Alternative Mating Strategy in the Fiddler Crab *Uca lactea*

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ABSTRACT: The fiddler crab, *Uca lactea*, which lives on intertidal mudflats in Korea, exhibits both burrow mating and surface mating. We observed 17 cases of surface mating that occurred on Ganghwa Island, South Korea. Most surface-mating males did not build semidomes, structures that attract searching females for burrow mating. Based on the conclusion of a previous study that semidome building is condition-dependent, we suggest that food availability may influence the mating tactic of this species. In addition, there was a strong correlation between the carapace size of both sexes that surface-mated, which suggests that males use body size of females as a mating cue.

Key words: Alternative reproductive strategy, Burrow mating, Fiddler crab, Surface mating, *Uca*

INTRODUCTION

In many animal species, there is discontinuous variation in mating strategy and morphology among males (Andersson 1994, Choe and Crespi 1997, Shuster and Wade 2003). Evolutionary game theory has been used to understand the difference between mating strategies (Hamilton 1967, Maynard Smith 1982, Parker 1984). When the alternative strategies yield similar reproductive success, a mixed evolutionarily stable strategy (ESS) can exist in the following two ways.

First, each individual follows a particular strategy that is determined purely by genetic polymorphism and the population consists of the mixture of genotypes that makes for an overall evolutionarily stable state (Andersson 1994). Some strategies accompany distinct dimorphic or polymorphic characteristics as in the size of marine isopod *Paracerceis sculpta* (Shuster and Wade 1991). Other animals, such as the coho salmon *Onchorhynchus kisutch* (Gross 1984) or the cricket *Gryllus integer* (Cade 1979), show genetic variation in mating behavior.

Second, individuals are flexible in adopting mating strategies in response to what others do (Andersson 1994). Which tactic an individual chooses depends on diverse factors: relative frequencies of strategies, age, size, condition, strength, and other abilities of the individual and of the other members of population (Parker 1984) such as the mating strategies of the *Panorpa* scorpionflies (Thornhill 1984).

Fiddler crabs (genus: *Uca*) are semi-terrestrial animals that live

on intertidal mud or sand flats (Crane 1975). They can be divided into two groups according to their mating strategy. In the burrow-mating (BM) species, males defend their burrows and wave their enlarged claws to attract females. Receptive females enter multiple male burrows several times each before mating. In the surface-mating (SM) species, males search for females and mate at the entrance of female's burrow. In some species, however, males adopt both mating strategies.

Uca lactea lives on upper intertidal mudflats in Southeast and East Asia (Crane 1975). It employs both SM and BM strategies. Previously it has been reported that SM is the typical mating strategy of *U. lactea* (Murai et al. 1987). Contrary to this report, Kim and Choe (2003) observed in Korea that female *U. lactea* perform mate searching, which is prerequisite for BM, much more frequently. Here we report our observation on the occurrence and adaptive significance of SM in *U. lactea*.

METHODS

Study Area

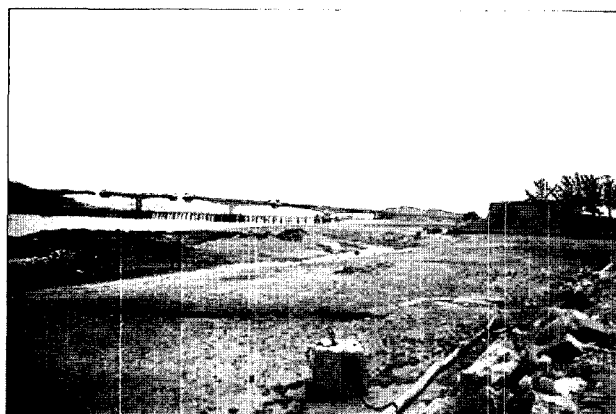
The study was carried out on intertidal mudflats in Choji-ri, Ganghwa Island, off the west coast of South Korea from June to August in 2000 and 2001. The study area was located on the southeast side of Ganghwa Island, approximately 200 m upstream from Ganghwa Bridge II (Fig. 1). All experiments and observations were carried out within a 20 × 20 m area of the mudflat. The maximum tidal range is approx. 1,000 cm. *U. lactea* lives on the upper

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(a)



(b)

Fig. 1. Scene of the study site at (a) high tide, and (b) low tide.

intertidal mudflat, 700 cm to 850 cm high in tidal range covering 400~500 m². This range is not inundated by the flood tides for 6~8 days per semilunar cycle. Crabs emerge from their burrows and remained active on the surface for about 7 h during the diurnal low tide each day. Crabs were not active on the surface before sunrise, after sunset, and in heavy rain.

Observation of Surface Mating

We observed SM only 3 times in 2000. From June to July 2001, we observed total 16 SM sequences. We recorded the duration of copulation using a stopwatch. When mating was terminated, we noted whether or not the female plugged the burrow entrance. Fifteen minutes after mating, we captured the male and female by plugging the burrows using a 1.2 m long bamboo stick. Then we measured the carapace width to the nearest 0.1 mm.

RESULTS

Burrow Mating

In the beginning of June, males began to build semidomes at

their burrows after the tides receded. Then males waved their enlarged claws constantly to attract females. A receptive female searching for a mate followed a courting male into his burrow. Then, she came out of the burrow and searched for another male. A female visited male burrows over 10 times, and rarely returned to previously sampled burrows. After sampling a number of different burrows/males, a female entered a male's burrow and did not come out for approximately 30 min. Then the male left the burrow and returned with mud to plug the burrow entrance. The synchronous waving behavior of courting males followed semilunar tidal rhythm. Though the males' activity peaked during the spring tides, their courtship peaked 3~5 days after the spring tides in Korea (Kim et al. 2004b).

Surface Mating

The male approached a neighboring female's burrow without waving his claw. During the approach, the female retreated into her burrow (Fig. 2a). At the burrow entrance, the male tapped the inside of the burrow using the second, third, and fourth ambulatory legs (Fig. 2b and c). If the female did not come out of the burrow, the male returned to his burrow. In most cases ($N=17$ out of 20), however, the female responded to the male by moving towards the burrow entrance. Using their second, third, and fourth ambulatory legs, the male gently pulled the female closer so that her abdomen touched his (Fig. 2d). Then, both the male and female abdomens' opened up and partially overlapped (Fig. 2e). After 6~11 min of coupling, the male and female separated and their abdomens closed up. After mating, the female did not plug her burrow but remained active on the ground. The males threatened their partner, presumably to prevent them from mating with other males.

Mating Duration and Pair Distance

Surface copulation lasted for 529 ± 104 s (mean \pm SD, range: 340~614s, $N=11$). Only one of SM males built a semidome and all



(a)



(b)



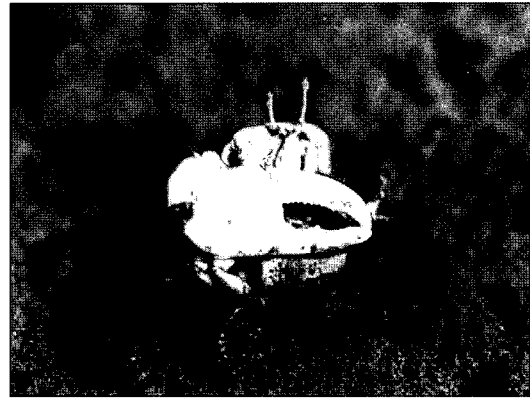
(c)



(d)



(e)



(f)

Fig. 2. Sequence of surface mating. (a) A male approaches to a neighboring female burrow. (b) The female is in her burrow and the male put his ambulatory legs into the burrow. (c) The male taps inside the burrow entrance vibrating the ambulatory legs. (d) The female comes out of the burrow. (e) The pair copulates on the surface of mudflat. (f) Surface mating scene of *U. lactea*.

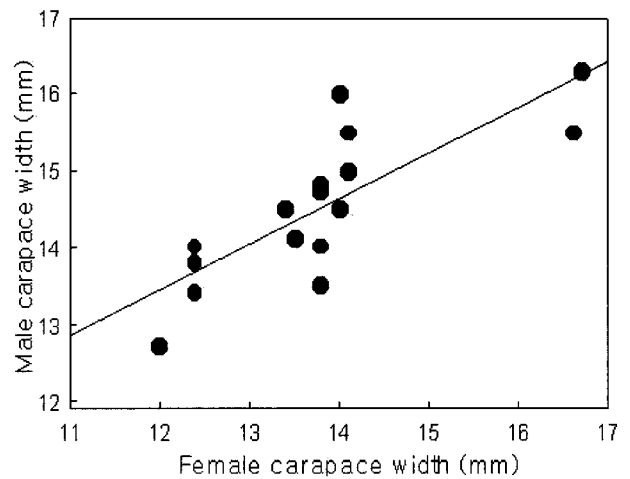


Fig. 3. The relationship of carapace widths between males and females that mated on the surface. Male carapace width (mm) = $6.334 + 0.593 \times \text{Female carapace width (mm)}$; $R^2 = 0.629$.

SM males did not wave their major claws before mating. The distance between the burrows of the two sexes who mated on the surface was 16.1 ± 7.1 cm (mean \pm SD, range: 6~30 cm, $N=16$). All the males approached the nearest female neighbor present on his chosen route.

Size-assortative Mating

The mean carapace width of males (14.52 ± 0.98 mm) was greater than that of females (13.80 ± 1.31 mm) (Wilcoxon signed

rank test, $Z = -2.66$ $N = 16$, $p < 0.01$). The carapace width of males showed strong correlation with that of females (Fig. 3, $r = 0.793$, $N = 16$, $p < 0.001$). Five out of the 17 males threatened females after mating and only one female plugged burrow entrance as a response to the threat. In only 2 out of 17 SM cases, females plugged their burrows for probable incubation after mating.

DISCUSSION

Uca lactea belongs to Indo-West Pacific clade among three suggested clades in *Uca* according to the phylogeny of mitochondrial 16s rRNA (Strumbaur et al. 1996). Based on other researchers' results, deRivera and Vehrencamp (2001) reported the major mating system of the Indo-West Pacific clade is surface mating. However, *U. lactea* displays both SM and BM strategies. In Korea, mate searching females were more frequently found than surface mating females. Mate searching by sampling male burrows can directly lead to BM. BM may be a dominant mating system of the population of *U. lactea* in Korea. This pattern contrasts with reports in Japanese population in which SM occurred more frequently than BM (Yamaguchi 1971, Murai et al. 1987). The relative ratio of mating strategies could be different even in the same species depending on the environment.

The mitochondrial phylogeny proposes two possible scenarios in the evolution of mating tactics of genus *Uca* (Strumbauer et al. 1996). First, the Indo-West Pacific clade may have lost the 'derived character' represented by BM. Second, BM may have evolved at least three times independently. Without consideration of environmental factors, it is hard to determine which scenario is more plausible for the evolution of the mating system.

What is the main ecological factor that determines mating systems of *Uca* species? To address this question, two possible factors have been strongly suggested. Koga et al. (1998) proposed that the mating system of *Uca* is influenced by predation pressure. Males, in high predation pressure, increased the relative frequency of surface mating because female searching is costlier when predation risk is high. The other factor is operational sex ratio suggested by deRivera and Vehrencamp (2001). According to this hypothesis, male searching should be associated with a strongly male-biased operational sex ratio. deRivera et al. (2003) supported the hypothesis by experimentally manipulating the density of individuals in *U. beebei*. Males searched more and females searched less when density increased.

Most males who mated on the surface did not build semidomes at their burrows. In our previous experiment, we found that semidome building is a condition-dependent behavior (Kim and Choe,

2003). Food availability may also influence mating strategies in *U. lactea*. When food is scarce and sufficient energy has not been secured, males cannot build structures and do much waving because semidome building and waving are energetically costly. SM males do not wave to attract females. This tactic consumes less energy than courting associated with BM. Therefore, males in poor condition may choose surface mating as an alternative tactic.

If the SM strategy is energetically cheaper, why don't all males choose this tactic? Even though the energetic cost of SM is smaller than that of BM, it provides less benefit in reproduction. We observed that a female mated for up to 3 times with different males in a day. Murai et al. (1987) demonstrated that ovaries of SM females in *U. lactea* were not fully developed. It suggests that SM females are not quite prepared to incubate immediately after mating. Considering there is high probability that females can obtain other males' sperm, SM is not an efficient strategy for males with respect to sperm competition (Koga et al. 2000). Although BM requires higher energetic cost, however, it could be more beneficial if the male mates in his burrow. He can ensure that his mate incubates his offspring by guarding her within the burrow.

Size-assortative mating is widely distributed in animals including fiddler crabs (e.g. Nakasone and Murai 1998). In our study, the body sizes of SM pairs showed significant correlation. Crespi (1989) proposed three possible causes for size-assortative mating: (1) Correlation in the body size between males and females in time and space; (2) Difficulties including physical constraints derived from size difference; (3) The success of larger males in male-male competition and preference for larger partners. In fiddler crabs, however, a clear mechanism remains to be uncovered. These results might suggest that males choose their partners fit for mating based on size. If a mating pair is mismatched in size, there could be mechanical difficulties with coupling of the sex organs and result in unsuccessful mating. Or, males might have an aesthetic preference for females of a similar size to himself.

To uncover the cause of size-assortative mating in fiddler crab species, diverse manipulation studies such as altering the size composition of neighboring crabs, are worthy of future study. Also, trade-off analysis in relation to various environmental factors should be applied to research adaptive significance of surface mating in fiddler crabs that take complex mating strategies.

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LITERATURE CITED

- Andersson M. 1994. Sexual selection. Princeton University Press, New York.
- Cade W. 1979. The evolution of alternative male reproductive strategies in field crickets. In: Sexual Selection and Reproductive Competition in Insects (Blum MS and Blum NA, eds). Academic Press, New York, pp 343-380.
- Choe JC, Crespi BJ. 1997. The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge.
- Crane J. 1975. Fiddler crabs of the world. Princeton University Press, Princeton.
- Crespi BJ. 1989. Causes of assortative mating in arthropods. Anim Behav 38: 980-1000.
- DeRivera CE, Vehrencamp SL. 2001. Male versus female mate searching in fiddler crabs: a comparative analysis. Behav Ecol 12: 182-191.
- DeRivera CE, Backwell PRY, Christy JH, Vehrencamp SL. 2003. Density affects female and male mate searching in the fiddler crab, *Uca beebei*. Behav Ecol Sociobiol 53: 72-83.
- Gross MR. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: Fish Reproduction: Strategies and Tactics (Postts GW and Wootton RJ, eds), Academic Press, London, pp 55-75.
- Hamilton WD. 1967. Extraordinary sex ratios. Science 156: 477-487.
- Kim TW, Choe JC. 2003. The effect of food availability on semilunar courtship rhythm in the fiddler crab *Uca lactea*. Behav Ecol Sociobiol 54: 210-217.
- Kim TW, Christy JH, Choe JC. 2004a. Semidome building as sexual signaling in the fiddler crab *Uca lactea* (De Haan) (Brachyura: Ocypodidae). J Crust Biol 24: 673-679.
- Kim TW, Kim KW, Srygley RB, Choe JC. 2004b. Semilunar courtship rhythm of the fiddler crab *Uca lactea* in a habitat with great tidal variation. J Ethol 22: 63-68.
- Koga T, Backwell PRY, Jennions MD, Christy JH. 1998. Elevated predation risk changes mating behavior and courtship in a fiddler crab. Proc Royal Soc London B. 265: 1385-1390.
- Koga T, Murai M, Goshima S, Poovachiranon S. 2000. Underground mating in the fiddler crab *Uca tetragonon*: the association between female life history traits and male mating tactics. J Exp Mar Biol Ecol 248: 35-52.
- Maynard Smith J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.
- Murai M, Goshima S, Henmi Y. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. Anim Behav 35: 1334-1342.
- Nakasono Y, Murai M. 1998. Mating behavior of *Uca lactea perplexa* (Decapoda: Ocypodidae). J Crust Biol 18: 70-77.
- Parker GA. 1984. Evolutionary stable strategies. In: Behavioural Ecology: An Evolutionary Approach, 2nd ed (Krebs JR, Davies NB eds). Blackwell, Oxford, pp 30-61.
- Shuster SM, Wade MJ. 2003. Mating systems and strategies. Princeton University Press, Princeton.
- Shuster SM, Wade MJ. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350: 608-610.
- Strumbauer C, Levington JS, Christy JH. 1996. Molecular phylogeny analysis of fiddler crabs: Test of the hypothesis of increasing behavioral complexity in evolution. Proc Natl Acad Sci USA 93: 10855-10857.
- Thornhill R. 1981. *Panorpa* (Mecoptera: Panorpidae) scorpionflies: Systems for understanding recourse defense polygyny and alternative male reproductive effort. Ann Rev Ecol Syst 12: 355-386.
- Yamaguchi T. 1971. The courtship behavior of a fiddler crab, *Uca lactea*. Kamamoto J Sci Biol 10: 13-37.
- Yamaguchi T. 2001. The mating system of the fiddler crab, *Uca lactea* (Decapoda, Brachyura, Ocypodidae). Crustaceana 74: 389-399.

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