Animal Behaviour 79 (2010) 735–738

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The battle of the sexes? Territory acquisition and defence in male and female fiddler crabs

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ARTICLE INFO

Article history:
Received 24 September 2009
Initial acceptance 30 November 2009
Final acceptance 17 December 2009
Available online 20 January 2010
MS. number: 09-00631

Keywords:
fiddler crab
sexual dimorphism
territoriality
territory defence
Uca annulipes

In many territorial species males invest substantially in weapons, which they use in fights to acquire and maintain territories that ultimately give them access to females. Females often live within male territories or in female-only areas that are segregated from males. Under these circumstances, females do not have to compete directly with males for space, and in the context of territory acquisition and defence there is therefore no cost to being weaponless. In fiddler crabs, however, weaponless females hold territories among well-armed males. How do they do this? Observations and replacement experiments were carried out on *Uca annulipes* to determine how males and females acquire and defend territories. Weaponless females were as capable as well-armed males of both acquiring and defending a burrow. Females acquired burrows by seeking out empty ones, while males acquired them by evicting male and female burrow owners. After acquiring a burrow, males mainly fought with male neighbours and females with female neighbours. Both sexes were equally likely to be evicted from their burrow and the likelihood that they remained on their territory for 24 h or more was the same. Males and females thus used different strategies of burrow acquisition and defence, and the male strategy appeared to be more costly. We discuss possible explanations for these differences.

In many sexually dimorphic species, males have large imposing weapons while females are weaponless (Andersson 1994). Males fight to acquire and maintain territories that ultimately give them access to females, or they directly engage in contests for the females themselves (Emlen 2008). In such circumstances females often live within male territories (Lopez & Martin 2002) or in female-only areas that are segregated from areas occupied by reproductively active males (Ruckstuhl 2007). In these cases, females do not compete directly with males for space or resources, and in the context of territory defence and acquisition there is therefore no cost to females of being weaponless (see Marra 1999). In fiddler crabs, however, males and females live in the same area, and weaponless females must maintain territories adjacent to those of well-armed males. Females are able to obtain and defend territories even when space is limited and therefore extremely valuable (Crane 1975).

Fiddler crabs live in dense mixed-sex colonies. Both males and females defend territories containing a central burrow. Burrows are a vital resource as they provide shelter from tidal inundation, predation and desiccation (Smith & Miller 1973; Koga et al. 2001). They are also used during reproduction as a site of mating and incubation (Backwell & Passmore 1996). The territory surrounding the burrow consists of a small area of surface sediment that is used both as a source of food (organic matter deposited on the sediment each high tide) and as a platform for mating displays (Crane 1975). Territories are therefore essential for survival and reproduction in both sexes.

Fiddler crabs display pronounced sexual dimorphism. Females are small, usually dull coloured, with two small feeding claws. Males are large, often brightly coloured, with one feeding claw and one greatly enlarged claw (up to 50% of total body weight, making it the largest weapon relative to size in any animal; Crane 1975; Emlen 2008). The enlarged claw is used both for mate attraction and as a weapon during fights with other males (Allen & Levinton 2007).

Fights occur over territory ownership, either with burrowless, wandering intruders or with resident neighbours (Morrell et al. 2005). Males that lose their burrow, either through being evicted by another male or by forfeiting it to a female for incubation after mating with her, must quickly find a new burrow. To do so, they must fight and evict a resident male or female crab, find an unoccupied burrow or dig a new one (Jennions & Backwell 1996). Fights between males begin with opponents lining up and pushing their major claws against each other, and can escalate to a grapple where the claws are interlocked. Fights often last over a minute and can be extremely costly (Jennions & Backwell 1996). As females are weaponless and therefore disadvantaged in physical combat, the least costly method for a male to gain a new territory would

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doi:10.1016/j.anbehav.2009.12.030

presumably be to evict a resident female. How then do females obtain and defend territories within a population of heavily armed males? Our aim in this study was to investigate how well-armed males and weaponless females obtain and defend territories in the fiddler crab *Uca annulipes*.

METHODS

The study was carried out on Inhaca island, Mozambique (25°59′10″S, 32°56′35″E), during September and October 2008.

In *Uca annulipes*, mating occurs over 5–6 days each semilunar spring tide cycle, throughout the year (Backwell & Passmore 1996). Mating can occur underground in the male's burrow, or on the surface outside the female's burrow. Burrow mating is the most common type of mating. It occurs when a female leaves her burrow and wanders through the population in search of a mate. Once an appropriate male has been chosen, the female follows him back into his burrow. The male then seals himself and the female into the burrow by blocking the burrow entrance with a ball of mud and the pair mate (Backwell & Passmore 1996). After mating, the male vacates the burrow, leaving the female to incubate the clutch. Unlike burrow mating, surface mating mainly occurs between neighbours (Milner et al., in press) and can occur at any time during the tidal cycle (R. Slatyer & P.R.Y. Backwell, unpublished data). Following a surface mating, the female will return to her own burrow to incubate her clutch or go on to mate with a different male in another burrow (R. Slatyer & P.R.Y. Backwell, unpublished data).

Burrow Acquisition and Defence

To determine how female and male *U. annulipes* obtain territories, size-matched (within 1 mm for carapace width) male–female pairs were captured, measured and individually marked ($N = 40$ males, 40 females). One at a time, each crab was released and followed until a territory was gained. The sex of the crab released was alternated between trials. We recorded (1) distance travelled before acquiring a territory (straight-line measurement from release point to new burrow), (2) time spent searching for a territory, (3) number of burrows visited prior to acquiring a new territory, (4) whether the focal crab fought with burrow-owning males or females, and (5) method of territory acquisition (i.e. fought and evicted another crab or found an empty burrow). For male–male encounters, we classified interactions as fights if there was direct contact between the males' major chelae. For encounters involving females (female–female or male–female), interlocking of the ambulatory legs was classified as a fight. Behaviour classified as a fight was unambiguously associated with initiation of a contest between the two crabs.

Burrow Ownership and Defence

Following the acquisition of a territory, the focal crab was observed for 1 h to determine how female and male burrow owners defend new territories against both intruding and neighbouring crabs. We recorded (1) whether or not the crab was aggressively approached by a male or female neighbour (aggressive approaches included rapid movement towards the focal crab or antagonistic waves of the claw, if male, in the direction of the focal crab), (2) whether or not the focal crab fought with male or female neighbours or intruders (aggressive approaches that resulted in a fight were scored as a fight and not an aggressive approach), (3) whether or not the focal crab abandoned its burrow, sealed itself into the burrow by closing the entrance, or was evicted, and (4) whether the crab was still resident approximately 3 and 24 h after burrow acquisition (i.e. shortly before tidal inundation on the same and the following day).

Replacement Experiments

We performed replacement experiments to compare the responses of established burrow-owning (henceforth 'resident') males and females to new female and male neighbours while controlling for factors such as the distance to the nearest neighbour, and neighbour size and sex that could not be controlled for during the 1 h observations. Two similar-sized males that had similar-sized male neighbours (size matched by eye) at approximately the same distance away were removed from their burrows and replaced with a new male and female occupant ('replacement crabs') that were size matched to within 1 mm of each other using dial callipers. The pairs were then observed for 1 h and all interactions with neighbours (resident male and female neighbours) were documented: whether the neighbours aggressively approached the replacement crabs; whether the replacement crabs aggressively approached the neighbours; and whether the replacement crabs fought with their male or female neighbours.

Statistical Analysis

We tested for a difference between the sexes in the proportion of each assigned to one of two classes (e.g. did or did not fight a female neighbour) using log-likelihood ratio tests (LLR; $df = 1$). For continuous variables we tested for a difference between the sexes using Mann–Whitney *U* tests. All tests were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, U.S.A.); alpha was set at 0.05 and tests were two tailed. We used Bonferroni corrections to take into account multiple testing in each data set ($P_{\text{critical}} = 0.05/17 = 0.0029$ for the burrow acquisition experiment; $P_{\text{critical}} = 0.05/6 = 0.0083$ for the replacement experiment). It has, however, been suggested that presentation of effect sizes is a better approach than using Bonferroni correction when conducting multiple testing (see Nakagawa 2004). We therefore calculated the common effect size of Pearson *r* and the 95% confidence interval, CI, for all tests using standard formulae (Cooper et al. 2009). If the male response was greater than the female response, *r* was assigned a positive value.

RESULTS

Burrow Acquisition and Defence

Females did not differ significantly from males in the distance travelled, search duration or number of burrows they approached before obtaining a burrow (Table 1). Both sexes were equally likely to fight with burrow-owning females (19 of the 40 males tracked compared to 22 of 40 females tracked fought at least one female burrow owner). Males were, however, significantly more likely than females to fight with burrow-owning males (38 males versus nine females fought a burrow-owning male; Table 2).

Males and females differed significantly in their method of burrow acquisition: males were significantly more likely to evict a resident crab (evicted 13 females, 14 males, and one heterospecific crab), while 33 of 40 females found an empty burrow (Table 2). There was no relationship between male size and the method of burrow acquisition (ANOVA: $F_{2,36} = 0.211$, $r = 0.11$, $P = 0.811$). Females that evicted a resident crab either fought and evicted a female ($N = 4$) or stole a male's burrow by beating him back to it ($N = 3$). Such burrow 'sneaking' was only observed in females and involved no observable fighting (i.e. no fighting on the surface). Furthermore, there was no significant association between mating period (i.e. mating/spring tide and nonmating/neap tide) and whether males acquired a burrow by evicting a male or female ($\text{LLR} = 1.93$, $P = 0.165$) or by evicting a male or finding an empty burrow ($\text{LLR} = 0.622$, $P = 0.430$).

Table 1
Burrow search period for males and females

	Median (lower, upper quartiles)		Mann–Whitney *U*	Effect size (*r*)	*P*
	Males (*N*=40)	Females (*N*=40)			
Distance travelled (cm)	209 (114, 390)	210 (104, 690)	668.00	−0.103 (−0.32, 0.12)	0.355
Search time (s)	1006 (329, 1710.3)	951 (264.3, 1843)	780.50	0.021 (−0.20, 0.24)	0.851
Burrows visited	10 (3.3, 21.5)	9.5 (3.3, 16.8)	756.50	0.047 (−0.17, 0.26)	0.675

Following the acquisition of a burrow, males were significantly more likely than females to fight with their male neighbours and with intruding males (Table 2). Females were significantly more likely than males to fight with female neighbours (95% CI for effect size *r*: 0.27–0.62; although the difference is not significant if one controls for multiple testing using Bonferroni's correction). There was no significant difference between the sexes in the number of fights with intruding females, or the rate at which they were aggressively approached by male or female neighbours (Table 2). Furthermore, males and females were equally likely to abandon or seal their burrow, or to be evicted within the first hour, as well as being equally likely to retain their burrow 3 and 24 h after burrow acquisition.

Replacement Experiments

Replacement males were significantly more likely than replacement females to fight resident males, while replacement females were significantly more likely than replacement males to fight resident females (Table 3). There was, however, no significant difference between the sexes in the likelihood of a replacement crab being aggressively approached by resident males or females (Table 3). Replacement males were significantly more likely than replacement females to approach resident male neighbours aggressively (Table 3), but there was no significant difference in the likelihood they aggressively approached resident females (Table 3).

DISCUSSION

Burrow Acquisition

In *U. annulipes* well-armed males and weaponless females were equally successful at obtaining burrows; however, their methods of doing so differed significantly. While there was no significant difference in the distance travelled, time taken or number of burrows visited before obtaining a burrow, wandering males were significantly more likely than wandering females to fight with resident males and obtain burrows by evicting resident males and females. In contrast, most wandering females obtained an empty burrow and largely avoided aggressive encounters with males. The nine cases where females were aggressive towards males probably involved small males. Since both methods are equally successful, and obtaining an empty burrow is probably less costly than fighting for an occupied burrow, why do males not simply seek out empty burrows? Burrow quality is of particular importance to male *U. annulipes* as it is an important criterion assessed by females during mate choice (Backwell & Passmore 1996). Empty burrows are often of poor quality (i.e. are damaged, unstable owing to composition of the substrate or situated in low-quality habitat; Lim & Heng 2007). The costs incurred in obtaining a higher quality burrow by evicting another male would therefore probably be less than the benefits gained through an increased chance of mating (Backwell & Passmore 1996).

Given the difference in weaponry, and an approximately 1:1 adult sex ratio in this species (Litulo 2005), why do males not preferentially evict females? First, although not tested, female burrows are more likely to be of poorer quality than male burrows as females largely acquire empty burrows that have been abandoned. Because of the importance of burrow quality during mate selection (Backwell & Passmore 1996), males might avoid these burrows to some extent and seek out higher quality burrows owned by males. Second, male neighbours defend their female neighbours. Protecting female neighbours from wandering males increases a resident male's potential surface-mating opportunities (Milner et al., in press). As a result, regardless of the burrow owner's sex, a wandering male might still have to fight a resident male. Evidence of territorial coalitions has been found in the fiddler crab *Uca mjoebergi*, where males assisted familiar male neighbours

Table 2
Burrow search and defence periods for males and females

	Observed/total		Likelihood ratio	Effect size (*r*)	*P*
	Males	Females			
Search period					
Evicted resident to acquire burrow	28/40	7/40	23.68	0.545 (0.37, 0.68)	**<0.001***
Fought burrow-owning male(s)	38/40	9/40	49.91	0.790 (0.69, 0.86)	**<0.001***
Fought burrow-owning female(s)	19/40	22/40	0.45	−0.075 (−0.29, 0.15)	0.502
Resident period					
Fought male neighbour(s)	16/40	3/40	12.56	0.460 (0.27, 0.62)	**<0.001***
Fought female neighbour(s)	3/40	11/40	5.83	−0.269 (−0.46, −0.05)	**0.016**
Fought male intruder	16/40	3/40	12.56	0.460 (0.27, 0.62)	**<0.001***
Fought female intruder	1/40	2/40	0.35	−0.066 (−0.28, 0.16)	0.553
Aggressively approached by male neighbour	13/40	7/40	2.43	0.174 (−0.05, 0.38)	0.119
Aggressively approached by female neighbour	2/40	5/40	1.45	−0.135 (−0.34, 0.09)	0.228
Abandoned burrow	5/40	4/40	0.13	0.040 (−0.18, 0.26)	0.723
Sealed burrow entrance	9/40	15/40	2.16	0.164 (−0.06, 0.37)	0.142
Evicted from burrow	5/40	3/40	0.56	0.084 (−0.14, 0.30)	0.454
Present 3 h after burrow acquisition	13/24	16/24	0.79	0.128 (−0.16, 0.40)	0.375
Present 1 day after burrow acquisition	9/23	12/23	0.79	0.128 (−0.17, 0.40)	0.374

Significant results are shown in bold.
*$P < 0.05$ with Bonferroni correction.

Table 3
Burrow defence period for replacement males and females

	Observed/total		Likelihood ratio	Effect size (r)	P
	Males	Females			
Fought resident male	17/20	0/20	37.64	0.970 (0.94, 0.98)	**<0.001***
Fought resident female	0/20	8/20	13.11	−0.573 (−0.75, −0.32)	**<0.001***
Aggressively approached by resident male	17/20	16/20	0.17	0.066 (−0.25, 0.37)	0.677
Aggressively approached by resident female	0/20	0/20	0	0 (−0.31, 0.31)	1.00
Replacement crab aggressively approached resident male	8/20	0/20	13.11	0.573 (0.32, 0.75)	**<0.001***
Replacement crab aggressively approached resident female	2/20	2/20	0	0 (−031, 0.31)	1.00

Significant results are shown in bold.
*$P < 0.05$ with Bonferroni correction.

against intruders as it was often less costly than establishing new territory boundaries with a new, possibly stronger, male neighbour (Backwell & Jennions 2004). Similar defence coalitions occur in *U. annulipes* (Detto et al., in press).

Burrow Ownership and Defence

Well-armed males and weaponless females were equally successful at holding a territory over a 24 h period, and equally likely to be evicted from their burrow. These results are consistent with those recorded during the search period, which showed wandering males evicted equal numbers of males and females. Also consistent with the results obtained during the search period, resident males were more likely than females to fight with wandering males. We suggest that because of the asymmetry in fighting ability of males and females, females are less likely to retaliate to male intrusions or initiate defensive attacks towards passing males. Instead, females generally retreat into their burrow at the first sign of an approaching male. Furthermore, because females receive protection from their male neighbours as outlined above (Milner et al., in press), it might prove less costly in certain circumstances (i.e. when a female has numerous male neighbours) for wandering males to attempt to evict male rather than female burrow owners.

Male residents were more likely than female residents to fight a new male neighbour, while female residents were more likely to fight a new female neighbour (with the caveat that the trend for females was not significant if Bonferroni correction was applied; but see Nakagawa 2004). Fights between neighbours are caused by boundary disputes (including the establishment of new territory boundaries) and these fights appear to be sex assortative. We suggest that because of the asymmetry in fighting ability between the sexes, females are less likely to encroach onto a male's territory, and if they do they will simply retreat when threatened (i.e. no fight would be recorded and the interaction would be recorded as an aggressive approach). Furthermore, given that female neighbours appear to present males with potential mating benefits, agonistic behaviour towards neighbouring females could reduce male surface-mating success so that males might be more tolerant of female than male neighbour intrusions (Milner et al., in press).

In summary we have shown that although female *U. annulipes* are weaponless they are as capable as well-armed males of acquiring and holding burrows and territories. Females mainly acquired empty burrows, while males acquired burrows by fighting and evicting a resident. Males and females were equally likely to be evicted from their burrow, and equally likely to retain their territory for at least the first 24 h after burrow acquisition. The fact that females are weaponless and still competed successfully for the same general resource (although there might be a difference in the quality of the burrows they obtained) as well-armed males is an extremely interesting result that, to the best of our knowledge, has not been shown in any other species with such extreme sexual dimorphism in weaponry.

Acknowledgments

We thank Jessica Bolton and Tanya Detto for assistance and two anonymous referees for helpful comments. Research was funded by the Australian Research Council (to P.R.Y.B. and M.D.J.).

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