

Original Article

# Male fiddler crabs defend multiple burrows to attract additional females

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Males of many species defend resources to attract females. Surprisingly, defense of multiple female breeding sites (e.g., nests or burrows) appears to be rare, primarily reported in fish and birds. In fiddler crabs, burrows are a vital resource for reproduction and survival. Both sexes defend individual territories centered on a single burrow. We examined burrow acquisition and defense in *Uca capricornis* to test whether males defend multiple burrows as a novel strategy to acquire additional mates. When crabs were experimentally forced to acquire a new burrow, females often settled into an empty burrow near resident males. We documented more empty burrows around males than expected by chance and, in addition, larger males had a greater proportion of empty burrows in their immediate vicinity. We experimentally introduced crabs into empty burrows next to focal males: newly introduced males were soon evicted, whereas females were courted and stayed. These results suggest that male *U. capricornis* defend empty burrows as a strategy to obtain more mates. Intriguingly, however, *U. capricornis* tend to occur in socially monogamous pairs. This raises the possibility of sexual conflict within social pairs over the presence of additional females and that female–female competition might constrain male mating success. *Key words:* mating systems, polygamy, resource-holding potential, resource monopolization, sexual conflict, sexual selection. [*Behav Ecol* 22:261–267 (2011)]

The presence, proximity, and identity of nearest neighbors can have important consequences for both individual fitness (Krause 1994; Hirsch 2007) and population level processes (Mougeot et al. 2003). For example, neighbors can directly affect a focal individual's susceptibility to predation (Jakobsson et al. 1995; Barbosa et al. 2009) and parasites (Kleindorfer and Dudaniec 2009), mating success (Ziege et al. 2009), and feeding rates (Blanchard et al. 2008). Many species are territorial, meaning that individuals often control direct access to natural resources by excluding potential competitors from an area and, more broadly, can even influence who settles nearby.

Males often defend territories to exclude rivals (i.e., potential reproductive competitors) and to attract females (i.e., control access to resources used by females). In some species, males exclude females from prime habitat or reduce their access to critical resources. For example, both male and female hermit crabs (*Diogenes nitidimanus*) require a resource that is in short supply (shells) and intra- and intersexual fights over shells create conditions that reduce female growth rates (Asakura 1995). Similarly, in American redstarts (*Setophaga ruticilla*), socially dominant males force females to overwinter in poorer quality habitat (Marra 2000). One consequence of this type of male territorial behavior is to lower female survival and reproductive success. This can have important effects at the population level, such as lowering population density and generating a more male-biased adult sex

ratio (review: Rankin and Kokko 2007). On the other hand, there are occasions when territorial males preferentially allow females to settle nearby. For example, males sometimes defend female neighbors against male intruders, which reduces the likelihood that a female will lose her territory/resource (Milner, Jennions, and Backwell 2010). This suggests that males might preferentially allow females to become neighbors, especially if neighboring females are potential mates (Slatyer R, unpublished data). Similarly, in several fiddler crab species, large males prefer to have smaller males as neighbors (Bookmythe et al. 2010). Large males will actively assist smaller, but not larger, male neighbors when challenged by an intruder (Detto et al. 2010). Tolerance of lower quality neighbors by territorial males has also been shown to occur in at least 2 bird species: ruffs (*Philomachus pugnax*) (Lank et al. 1995) and lazuli buntings (*Passerina amoena*) (Greene et al. 2000).

A male's ability to defend resources that are required by breeding females can critically influence his capacity to mate with multiple females (i.e., to be polygamous; Shuster and Wade 2003). The ability of a male to defend natural resources is a function of the extent to which they are economically defensible. This is partly dependent on the spatial distribution of resources (Brown 1964; Emlen and Oring 1977). In general, clumped resources are more easily defended, enabling more competitive individuals greater control over access to resources (Kim and Grant 2007), which increases the potential for some males to be polygamous (e.g., Lindström and Seppä 1996). Female breeding sites (such as nests or burrows) are often a key resource defended by males. The ability to acquire and defend multiple breeding sites can potentially enhance male reproductive success by allowing several females to settle nearby. Surprisingly, however, defense of

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multiple breeding sites appears to be a taxonomically restricted behavior, primarily reported in fish and birds (e.g., Slagsvold and Lifjeld 1986; Slagsvold 1988; Dunn and Hannon 1991; Johnson and Kermot 1991; Petit 1991; Sato 1994; Rendall and Robertson 1994; Evans and Burn 1996).

In addition to resource distribution, the ability of a male to defend a limited resource economically depends, by definition, on his resource-holding potential (RHP). RHP is often positively related to body size or the expression of secondary sexual characters (Praw and Grant 1999; Temeles and Kress 2010). These traits therefore act as indicators of male RHP and are used during fighting assessment to either reduce the likelihood of initiating an encounter with a superior competitor (mutual assessment: Parker 1974; Jennions and Backwell 1996) or as a self-evaluative mechanism to determine one's own fighting ability/RHP (self-evaluation: Arnott and Elwood 2009). Females can also use a male's phenotype as a signal of his RHP and/or as a cue to the quality of the resources he is defending (reviewed in Kelly 2008). This leads to the general prediction that RHP, or a phenotypic cue thereof, is positively correlated with resource value and male reproductive success (Kelly 2008).

Here, we investigate sex differences in burrow acquisition and defense in the fiddler crab *Uca capricornis*. We were specifically interested in *U. capricornis* because it appeared to be a rare example of a species, other than a bird or fish, in which males might defend multiple breeding sites to increase their mating success. The species is native to northern Australia and lives in mixed sex populations on intertidal mudflats. Each crab occupies and defends a home burrow and a small area around the burrow. As with other species of fiddler crab, burrows are an essential resource acting as a refuge from predators, a source of water during the low tide period when crabs are active on the mudflat surface, and a site for breeding. Male *U. capricornis* court and mate with a female on the surface just outside her burrow. The female continues to defend her own burrow after mating, remains surface active and could potentially mate with several males before ovipositing. There is recent evidence that *U. capricornis* is possibly unique among fiddler crabs in that it forms socially monogamous pairs: a male and female can have overlapping territories and will attack same-sex crabs that approach their social partner (Detto and Backwell 2009). Casual observations of females temporarily without a burrow suggest that females sometimes occupy empty burrows adjacent to a male (cf. Murai et al. 1987; de Riveira et al. 2003). This raises the possibility that males could defend empty burrows to acquire additional mates and, in so doing, be polygamous. This would be a novel mating strategy for a fiddler crab, as studies of other species have consistently shown that males only defend their own burrow (Milner, Booksmythe, et al. 2010; Milner, Jennions, and Backwell 2010).

We used a series of simple experiments to investigate whether male *U. capricornis* defend more than one burrow and, if so, whether this is a strategy to obtain more mates. First, we determined whether females and males differ in the way they acquire a burrow. Second, we tested whether males were more likely to reside near empty burrows than expected by chance. Third, we tested whether males actively defend empty burrows against intruders. Finally, we examined how empty burrows arise and monitored their fate over time.

## MATERIALS AND METHODS

All experiments were carried out on *U. capricornis* in East Point Reserve, Darwin, Australia, from December to January 2003 and November 2009.

### Do females and males differ in how and where they acquire a new burrow?

To determine whether males and females differ in how they acquire a new burrow, resident male and female crabs were captured and then individually released at separate randomly chosen points on the mudflats far from their own burrow ( $N = 39$  of each sex). Each crab was monitored until it settled in a new burrow. We recorded: the time spent traveling, the total distance traveled (linear distance from release to settlement points), the number of interactions with other crabs, and how many fights or "digs" occurred (digs follow a fight and are an aggressive attempt to evict a crab from its burrow). The distance and sex of the nearest neighbor were noted. We then captured the focal crab and, as a measure of body size, recorded its carapace width using dial calipers ( $\pm 0.1$  mm).

### Are there empty burrows near resident males?

To determine whether males are more likely to have empty burrows around them than expected by chance, we counted the number of empty burrows around randomly chosen males and compared this with "control" locations. Seven nonoverlapping line transects were haphazardly placed throughout the mudflats. We attempted to cover the full range of habitat occupied by *U. capricornis*. Each transect was 16 meters in length and divided into 1-m segments. At each meter mark, we identified a focal male as the nearest male encountered on an imaginary line running perpendicular to the main transect from the mark. We counted the number of empty burrows in a circular area (radius 17 cm) centered on the control point or the focal male's home burrow. This corresponds to the average size area a male uses around his home burrow (Detto T, unpublished data). The matched control point was 34 cm from the meter mark on the opposite side of the transect line to the focal male. This distance ensured that there was no overlap between the 2 areas being sampled, even if the focal male's burrow was directly on the transect line. If a physical object obstructed a burrow count around the control point (e.g., a small puddle or tree trunk), a multiple of 34 cm (e.g., 68, 92 cm) was used until the first available unobstructed area was located. Crabs are fairly evenly dispersed throughout the lower part of the mudflat and the density of surface active crabs at our study site is approximately 7 crabs/m<sup>2</sup> (Detto and Backwell 2009), so the distance between focal crabs and the transect lines were unlikely to be influenced by fluctuations in the density of crabs. The number of empty and occupied burrows within each circular sampling area was counted. Finally, we captured the focal male and measured his carapace width and claw size.

### Do males defend empty burrows?

Even if empty burrows occur more frequently around males than in the control locations, it is conceivable that males might not necessarily defend empty burrows against occupancy. We therefore conducted an experiment to test whether males defend empty burrows and whether this depended on the sex of the intruder. Focal males with an empty burrow within 17 cm of their own burrow were haphazardly selected from sites across the mudflats. Male and female crabs to be introduced into burrows were then captured from sites well away from the focal male to ensure that they had not previously interacted with him. A single crab was then introduced into an empty burrow next to a focal male. The 2 crabs were then observed for 30 min after the introduced crab emerged from the burrow. We noted whether the introduced crab was evicted and/or courted.

After a crab was evicted, or when the trial had ended, both crabs were measured for carapace length and claw size (if male). The distance between the focal male's burrow and the empty burrow was also noted. Given that larger crabs tend to win fights (Fayed et al. 2008), we ensured that the introduced crab was slightly smaller than the focal male so that the focal male was more likely to initiate a fight. Each focal male was tested once (i.e., with either a male or a female intruder). Trials were not included in the analysis if the introduced crab failed to emerge after 15 min. Typically this occurred when a crab sealed itself into its new burrow and was therefore unlikely to emerge until after the next high tide or when the introduced crab rejected the empty burrow and wandered away from the burrow after reemergence. In total, we successfully introduced 27 males and 26 females to empty burrows and recorded the focal male's response.

### How are empty burrows created?

To determine how empty burrows were created, we observed males haphazardly chosen from sites across the mudflat ( $N = 80$ ). An area with a radius of 17 cm was drawn around the crab's burrow and all initially empty and occupied burrows were marked with numbered flags. The focal male's territory was then monitored for 1 h during the low tide period to determine how many empty burrows became occupied, how many new empty burrows were formed, and by what means (e.g., eviction, abandonment, and digging out of a new burrow).

### What is the fate of empty burrows over time?

We determined the length of time empty burrows remained open before being destroyed by the tides and if the rate of destruction depended on whether or not the burrow was subsequently occupied by a crab. We monitored 30 empty burrows just before the high tide by marking them with a small flag. Burrows were initially checked for a resident by pressing around the outside of the burrow that, in the soft mud, forces any crab inside toward the entrance where it becomes visible. Only unoccupied burrows were marked. We recorded burrow presence/absence, how the burrow was destroyed, and whether any crab utilized the empty burrow by checking twice daily for 5 days (immediately before and just after each diurnal high tide).

### Statistical analysis

All data were checked for normality and heterogeneity of variances. Parametric tests were used unless their assumptions could not be satisfied. In those instances, nonparametric equivalents were used. All data were analyzed using PASW Statistics v.18. All tests are 2-tailed unless otherwise stated, with  $\alpha = 0.05$ .

## RESULTS

### Do females and males differ in how and where they acquire a new burrow?

Males tended to interact with more crabs, fought significantly more often, were significantly more likely to try to dig out a resident, and traveled significantly farther than females to acquire a new burrow (Table 1). Released males were, on average, larger than females (reflecting the general size dimorphism in the adult population), but there was no correlation between size and any of the burrow acquisition

**Table 1**  
Male and female acquisition behavior following experimental displacement

	<i>N</i> (Pairs)	Males	Females	<i>t</i>	<i>P</i>
Size (mm)	38	15.1 (2.03)	13.6 (1.54)	4.258	<0.0001
Time (min)	39	62.3 (39.2)	57.7 (42.9)	0.551	0.585
Distance	36	173 (231)	130 (222)	2.562	0.015
No. of interactions	39	6.25 (4.33)	4.48 (3.48)	1.992	0.053
No. of nearest neighbors	36	4.84 (1.54)	5.05 (1.60)	0.697	0.490
Nearest neighbor distance	36	14.3 (7.07)	14.7 (6.14)	0.277	0.784
Fights	39	3.60 (2.98)	2.10 (2.52)	2.495	0.017
Digs	39	4.45 (3.26)	2.83 (2.71)	2.626	0.012

Summary statistics are mean ( $\pm$ standard deviation) (experiment 1).

behaviors for either sex (all  $P > 0.05$ , Table 2), with the exception of number of digs by males.

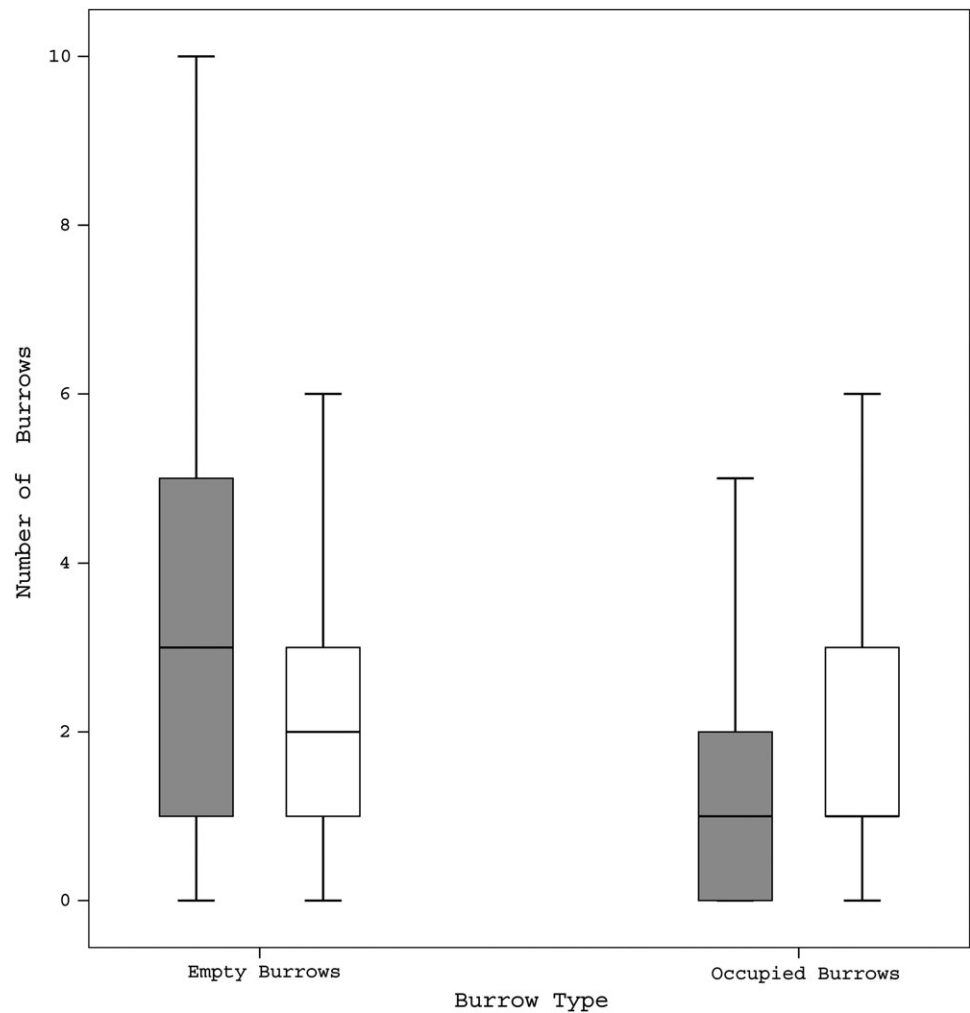
To acquire a new burrow, males were more likely to fight a resident burrow owner than locate an empty burrow (8 empty vs. 32 fight) compared with females (30 empty vs. 7 fights) (Fisher's Exact test,  $P < 0.0001$ ). In cases where the focal crab fought for a burrow, males were more likely to fight another male for a burrow (17 males vs. 9 females), whereas females were more likely to fight with another female (6 females vs. 1 male) (Fisher's Exact test,  $P = 0.03$ ). Males and females differed in the likelihood that they settled in a burrow next to a crab of the same sex. The proportion of females settling next to males was significantly greater than that for males. Specifically, focal females more often settled next to males (25 males vs. 9 females), whereas focal males settled next to each sex almost equally often (15 males vs. 19 female; Fisher's Exact test,  $P = 0.026$ ).

### Are there empty burrows near resident males?

There were a significantly greater number of empty burrows around a male's burrow than a matched control point ( $Z = 5.24$ ,  $N = 109$ ,  $P < 0.0001$ ). In contrast, the number of occupied burrows around control points was significantly greater than around focal males ( $Z = 2.62$ ,  $P = 0.009$ ) (Figure 1). In total, there were significantly more burrows around focal males than matched control points ( $Z = 2.646$ ,  $P = 0.008$ ) (all Wilcoxon tests,  $N = 109$ ). Finally, there was a significant positive correlation between male claw size and the proportion of empty burrows ( $r = 0.222$ ,  $P = 0.027$ ,  $N = 99$  as 10 males evaded capture) (Figure 2).

**Table 2**  
Pearson's correlation (*r* and *P* value) between carapace size and burrow acquisition behaviors

	<i>N</i>	Male	<i>N</i>	Female
Time (min)	39	0.221 (0.177)	40	0.013 (0.936)
Distance (cm)	28	0.100 (0.613)	38	0.287 (0.08)
No. of interactions	30	0.035 (0.856)	38	0.145 (0.383)
No. of nearest neighbors	38	-0.019 (0.912)	39	-0.085 (0.606)
Nearest neighbor distance	37	0.247 (0.141)	39	-0.051 (0.758)
Fights	39	0.287 (0.076)	40	0.270 (0.091)
Digs	39	0.323 (0.045)	40	0.165 (0.308)



**Figure 1**  
Box plot of the number of empty and occupied burrows around focal males ( $N = 109$ ; gray) and control points ( $N = 109$ ; white). Boxes represent the interquartile range around the median and error bars represent the range.

### Do males defend empty burrows?

When females were introduced into an empty burrow, they were significantly more likely to be courted than not to be courted ( $\chi^2_1 = 15.39$ ,  $P < 0.0001$ , 23 courted vs. 3 not courted) and significantly less likely to be evicted by the focal male than allowed to remain ( $\chi^2_1 = 15.39$ ,  $P < 0.0001$ , 23 remained vs. 3 evicted). When males were introduced, they were more likely to be evicted than allowed to remain ( $\chi^2_1 = 16.33$ , degrees of freedom = 1,  $P < 0.0001$ , 24 evicted vs. 3 remaining). None of the introduced males were courted (0 of 27). There was no size difference between females that were evicted and those that remained ( $t_{24} = 0.91$ ,  $N = 26$ ,  $P = 0.92$ ). The size difference between the introduced and focal males also had no influence on whether or not the intruder was evicted ( $t_{23} = 0.344$ ,  $N = 24$ ,  $P = 0.694$ ). There was no difference in body size between courted and noncourtied females ( $t_{24} = 0.308$ ,  $n = 25$ ,  $P = 0.910$ ), indicating that smaller females were equally likely to induce male courtship.

### How are empty burrows created?

During the 1-h observation period, the number of empty burrows within 17 cm of the focal male's burrow increased significantly from  $2.59 \pm 0.25$  to  $2.87 \pm 0.26$  burrows (mean  $\pm$  standard error) ( $t_{75} = 0.276$ ,  $P = 0.006$ ). Of the 80 males that we observed, there was no change in the number of empty

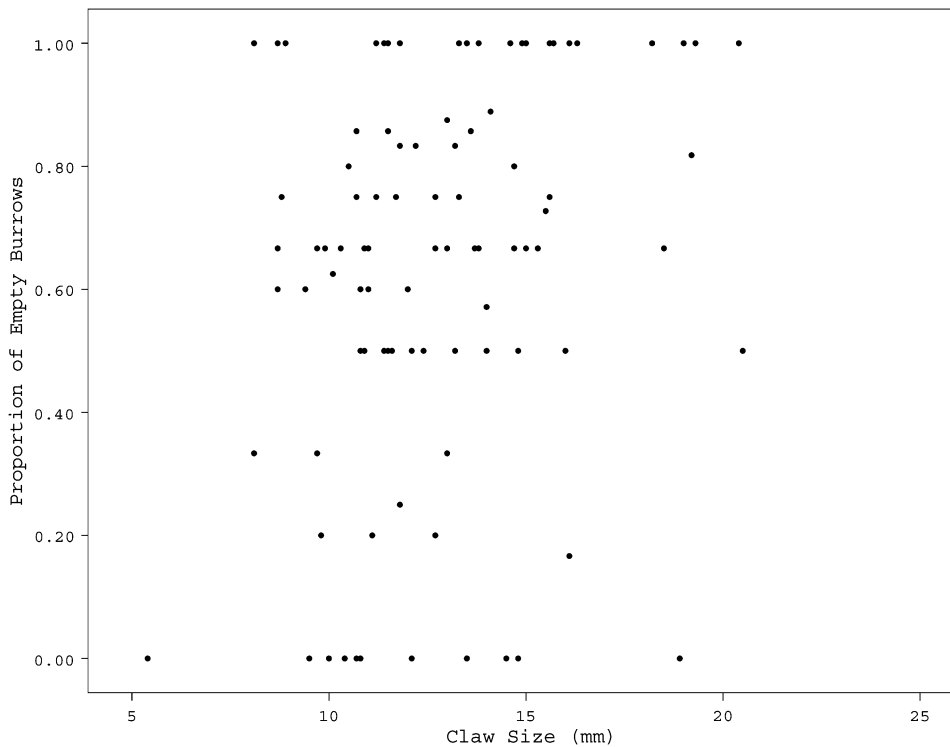
burrows surrounding 36 males. Of the other 44 males, 11 experienced a net loss in the number of empty burrows because a crab occupied one, whereas 33 experienced a net gain. Of the 33 newly empty burrows, 13 arose because the focal male evicted a crab and 13 were created when a crab abandoned its burrow and 3 were created because a crab dug a new burrow that it then did not occupy. We were unable to account for the origins of 4 burrows.

### What is the fate of empty burrows over time?

Occupancy by a crab had a marginally nonsignificant effect in delaying the destruction of an initially empty burrow (Wilcoxon–Gehan test,  $\chi^2_1 = 3.55$ ,  $P = 0.06$ ). Of the 30 burrows that were observed, 9 were destroyed after the first tidal cycle and 17 were destroyed by the fifth day.

### DISCUSSION

Male *U. capricornis* have a significantly greater number of empty burrows surrounding their own burrow than expected based on comparisons with adjacent control sites. This indicates that males either actively settle in areas with empty burrows, expel residents, and/or dig new burrows on their own. We suggest that these empty burrows allow additional females to settle near a male. In support of this claim, we found that territorial males treated males and females very differently



**Figure 2**  
Correlation between male claw size and the proportion of empty burrows within 17 cm of the male's burrow ( $r_s = 0.255$ ,  $P = 0.011$ ,  $N = 99$ ).

when they were introduced into an adjacent empty burrow. Focal males usually tried to evict introduced males, although introduced females were actively courted and allowed to stay. Furthermore, release experiments showed that burrowless females settle in empty burrows adjacent to a neighboring male. In contrast, burrowless males rarely attempt to occupy an empty burrow as they would have to fight for it and such burrows are likely of lower quality because of a lack of maintenance. Instead burrowless males acquire a burrow by evicting a resident male from its burrow.

Burrows are an essential resource for fiddler crabs as they provide a refuge from predators and water for gill replenishment (Zeil and Layne 2002). Burrow quality also influences female mate choice and subsequent reproductive success (Christy 1983; Backwell and Passmore 1996; Reaney and Backwell 2007). Previous studies of fiddler crabs have, however, always indicated that males defend a single home burrow. We suggest that male *U. capricornis* are potentially unique among fiddler crabs in that some males defend several reproductive sites to attract females, a tactic that has, as far as we are aware, previously been reported in only fish and birds (e.g., Slagsvold and Lifjeld 1986; Slagsvold 1988; Dunn and Hannon 1991; Johnson and Kermot 1991; Petit 1991; Sato 1994; Rendall and Robertson 1994; Evans and Burn 1996).

There are several ways that males might acquire empty burrows. During focal observations, 33 of 80 males acquired an additional empty burrow, and there was a small but significant increase in the number of empty burrows around focal males over the low tide period. Of these 33 males, 39% gained a burrow by evicting another crab, indicating that males actively compete for extra burrows. For another 39% of males, empty burrows were acquired when a nearby crab abandoned its burrow. Abandonment could be a preemptive behavior to avoid fighting with a larger male. Burrows might also be abandoned because they are of low quality and were only used as a temporary refuge during tidal inundation. We only observed 3 cases where new burrows were excavated, and this was always by a female. If this is generally the case, and females are the

workforce creating burrows, it suggests an additional advantage of allowing females to settle nearby: it would then enhance local resources (burrows). In the long term, it also remains unclear how empty burrows are maintained as there is a high probability that an unoccupied burrow will be destroyed by the incoming tide. This suggests that burrows around males, which are empty during the low tide period, are temporarily occupied by other crabs (i.e., those that have been evicted or abandoned their burrows) shortly before tidal inundation and then vacated in the next low tide period. This would explain the observed increase in the number of empty burrows over the monitored portion of the low tide period.

In general, larger male crabs have a greater ability to monopolize contested resources (i.e., greater RHP) (e.g., Jennions and Backwell 1996; Jaroensutasinee and Tantichodok 2003). Our finding that males obtain empty burrows by evicting neighbors is consistent with the fact that male size is positively correlated with the number of nearby burrows that are empty and negatively correlated with the number of occupied burrows. In most species, male RHP is positively correlated with resource value and male reproductive success (reviewed in Kelly 2008; Temeles and Kress 2010). Our findings suggest this is also the case in *U. capricornis* because defense of a greater number of empty burrows should increase the number of females that settle alongside a male and become available as mates.

Male reproductive success might also be elevated by defending more empty burrows because it increases the per capita likelihood that a visiting female will remain in a burrow. In fiddler crabs, females vary in how soon they mate prior to the optimal time for larval release (Crane 1975; Christy and Salmon 1984; Reaney and Backwell 2007). In some species, female mate choice is based on burrow size, and the preferred burrow size varies with the stage in the tidal cycle at which females seek out a mate (Backwell and Passmore 1996; Reaney and Backwell 2007; Milner, Detto, et al. 2010). This form of choice arguably arises because burrow dimensions influence the rate at which embryos develop. More generally, fiddler crabs seem

to prefer to occupy burrows with a diameter similar to their own carapace width. Males that defend several burrows will offer a greater size range of burrows to prospective mates and thereby increase the likelihood that any given visiting female will find a suitable burrow. Matings occur infrequently, so we were unable to test directly whether defending a greater number of empty burrows increases male mating success. This is, however, plausible given that our experiments showed that females prefer to settle in empty burrows alongside a male and that females occupying a previously empty burrow are actively courted.

Despite the potential for polygyny, it is unclear whether males actually end up defending more than one female for a prolonged period. If the operational sex ratio is male biased, then only a minority of males will be able to do so. Male, as well as female, behavior will also determine the extent to which polygyny can occur. In a previous study, male *U. capricornis* were observed to share part of their territory with a single female and defend her when she was approached by other males (Detto and Backwell 2009). In addition, females were observed to attack any female that entered the male's territory. Female aggression toward same-sex intruders has been reported in several other socially monogamous species (reviewed in Mathews 2002). Such behaviors suggest a form of short-term social monogamy but do not exclude the possibility that some males could maintain social bonds with 2 or more females. We have shown in the current study that male defense of empty burrows is likely to attract extra females onto his territory. It is therefore apparent that whether or not a male ends up defending more than one female in the longer term will depend on the extent to which female–female competition prevents settlement of another female. In *U. capricornis*, female aggression might be a mechanism to maintain exclusive access to the assistance that a male neighbor sometimes provides to a female when she is attacked by an intruding male (see Milner, Booksmythe, et al. 2010; Milner, Jennions, and Backwell 2010). This is a novel explanation for female–female competition that has not been reported in other taxa. An interesting question for future research is why a female would dig an extra burrow as this creates opportunities for competing females to settle near her social mate.

In sum, in *U. capricornis* males defend empty burrows that attract females and might allow them to mate polygamously and simultaneously defend several females. However, resident females might prevent males from mating with or defending other females on their territory (Detto and Backwell 2009), even though males provide no parental care and each female would have access to her own burrow. Future studies should investigate the extent to which the presence of more than one female reduces the effectiveness of the protection afforded to each female by a resident male.

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## REFERENCES

Arnott G, Elwood RW. 2009. Assessment of fighting ability in animal contests. *Anim Behav*. 77:991–1004.

- Asakura A. 1995. Sexual differences in life history and resource utilization by the hermit crab. *Ecology*. 76:2295–2313.
- Backwell PRY, Passmore NI. 1996. Time constraints and multiple choice criteria in the sampling behavior and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol*. 38:407–416.
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Ann Rev Ecol Evol Syst*. 40:1–20.
- Blanchard P, Sabatier R, Fritz H. 2008. Within-group spatial position and vigilance: a role also for competition? The case of impalas (*Aceros melampus*) with a controlled food supply. *Behav Ecol Sociobiol*. 62:1863–1868.
- Booksmythe I, Jennions MD, Backwell PRY. 2010. Investigating the 'dear enemy' phenomenon in the territory defense of the fiddler crab, *Uca mjoebergi*. *Anim Behav*. 79:419–423.
- Brown JL. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull*. 76:160–169.
- Christy JH. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behav Ecol Sociobiol*. 12:169–180.
- Christy JH, Salmon M. 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). *Biol Rev*. 59:483–509.
- Crane J. 1975. Fiddler crabs of the world, Ocypodidae: Genus *Uca*. Princeton (NJ): Princeton University Press.
- Detto T, Backwell PRY. 2009. Social monogamy in a fiddler crab, *Uca capricornis*. *J Crust Biol*. 29:283–289.
- Detto T, Jennions MD, Backwell PRY. 2010. When and why do territorial coalitions occur? Experimental evidence from a fiddler crab. *Am Nat*. 175:E119–E125.
- Dunn PO, Hannon SJ. 1991. Intraspecific competition and the maintenance of monogamy in tree swallows. *Behav Ecol*. 2:258–266.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*. 197:215–223.
- Evans MR, Burn JL. 1996. An experimental analysis of mate choice in the wren: a monomorphic, polygynous passerine. *Behav Ecol*. 7:101–108.
- Fayed SA, Jennions MD, Backwell PRY. 2008. What factors contribute to an ownership advantage? *Biol Lett*. 4:143–145.
- Greene E, Lyon BE, Muechler VR, Ratcliffe L, Oliver SJ, Boag PT. 2000. Disruptive selection for plumage coloration in a passerine bird. *Nature*. 407:1000–1003.
- Hirsch B. 2007. Costs and benefits of within-group spatial position: a feeding competition model. *Q Rev Biol*. 82:9–27.
- Jakobsson S, Brick O, Kullberg C. 1995. Escalated fighting behaviour incurs increased predation risk. *Anim Behav*. 49:235–239.
- Jaroensutasinee M, Tantichodok P. 2003. Effects of size and residency on fighting outcomes in the fiddler crab, *Uca vocans hesperiae* (Decapoda, Brachyura, Ocypodidae). *Crustaceana*. 75:1107–1117.
- Jennions MD, Backwell PRY. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol J Linn Soc*. 57:293–306.
- Johnson LS, Kermot LH. 1991. Effect of nest-site supplementation on the polygynous behavior in the House Wren (*Troglodytes aedon*). *Condor*. 93:784–787.
- Kelly CD. 2008. The inter-relationships between resource-holding potential, resource-value and reproductive success in territorial males: how much variation can we explain? *Behav Ecol Sociobiol*. 62:855–871.
- Kim JW, Grant JWA. 2007. Effects of patch shape and group size on the effectiveness of defence by juvenile convict cichlids. *Anim Behav*. 73:275–280.
- Kleindorfer S, Dudaniec R. 2009. Love thy neighbour? Social nesting pattern, host mass and nest size affect exoparasite intensity in Darwin's tree finches. *Behav Ecol Sociobiol*. 63:731–739.
- Krause J. 1994. Differential fitness returns in relation to spatial position in groups. *Biol Rev*. 69:187–206.
- Lank DB, Smith CM, Hanotte O, Burke T, Cooke F. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature*. 378:59–62.
- Lindström K, Seppä T. 1996. The environmental potential for polygyny and sexual selection in the sand goby, *Pomatoschistus minutus*. *Proc R Soc Lond B Biol Sci*. 263:1319–1323.
- Marra PP. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. *Behav Ecol*. 11:299–308.
- Mathews LM. 2002. Territorial cooperation and social monogamy: factors affecting intersexual behaviours in pair-living snapping shrimp. *Anim Behav*. 63:767–777.

- Milner RNC, Booksmythe I, Jennions MD, Backwell PRY. 2010. The battle of the sexes? Territory acquisition and defense in male and female fiddler crabs. *Anim Behav*. 79:735–738.
- Milner RNC, Detto T, Jennions MD, Backwell PRY. 2010. Experimental evidence for a seasonal shift in the strength of a female mating preference. *Behav Ecol*. 21:311–316.
- Milner RNC, Jennions MD, Backwell PRY. 2010. Safe sex: male–female coalitions and pre-copulatory mate-guarding in a fiddler crab. *Biol Lett*. 6:180–182.
- Mougeot F, Redpath SM, Lecke F, Hudson PJ. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. *Nature*. 421:737–739.
- Murai M, Goshima S, Henmi Y. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. *Anim Behav*. 35:334–342.
- Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. *J Theor Biol*. 47:223–243.
- Petit L. 1991. Experimentally induced polygyny in a monogamous bird species: prothonotary warblers and the polygyny threshold. *Behav Ecol Sociobiol*. 29:177–187.
- Praw JC, Grant JWA. 1999. Optimal territory size in the convict cichlid. *Behaviour*. 136:1347–1363.
- Rankin DJ, Kokko H. 2007. Do males matter? The role of males in population dynamics. *Oikos*. 116:335–348.
- Reaney LT, Backwell PRY. 2007. Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behav Ecol Sociobiol*. 61:1515–1521.
- Rendell WB, Robertson RJ. 1994. Defense of extra nest-sites by a cavity nesting bird, the tree swallow *Tachycineta bicolor*. *Ardea*. 82:273–285.
- de Rivera CE, Backwell PR, Christy JH, Verhencamp SL. 2003. Density affects female and male mate searching in the fiddler crabs, *Uca beebei*. *Behav Ecol Sociobiol*. 53:72–83.
- Sato T. 1994. Active accumulation of spawning substrate: a determinant of extreme polygyny in a shell-brooding cichlid fish. *Anim Behav*. 48:669–678.
- Shuster SM, Wade MJ. 2003. Mating systems and strategies. Princeton (NJ): Princeton University Press.
- Slagsvold T. 1988. Why are some birds polyterritorial? *Ibis*. 130:65–68.
- Slagsvold T, Lifjeld JT. 1986. Mate retention and male polyterritoriality in the pied flycatcher *Ficedula hypoleuca*. *Behav Ecol Sociobiol*. 19:25–30.
- Temeles EJ, Kress WJ. 2010. Mate choice and mate competition by a tropical hummingbird at a floral resource. *Proc R Soc Lond B Biol Sci*. 277:1607–1613.
- Zeil J, Layne J. 2002. Path integration in fiddler crabs and its relation to habitat and social life. In: Wiese K, editor. *Crustacean experimental systems in neurobiology*. New York: Springer-Verlag. p. 227–247.
- Ziege M, Mahlow K, Hennige-Schulz C, Kronmarck C, Tiedemann R, Streit B, Plath M. 2009. Audience effects in the Atlantic molly (*Poecilia mexicana*)-prudent male mate choice in response to perceived sperm competition risk? *Front Zool*. 6:17.