A farewell to arms: males with regenerated claws fight harder over resources

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Physical strength and resource value are two key determinants of fighting success in most species. We investigated the role that resource value plays in determining fight outcome for a territory centred on a burrow in a fiddler crab, *Uca annulipes*. Males fought harder (escalated fights) for a territory during the mating period (when the burrow is also used for mating and breeding) than in the nonmating period (when it has value as a shelter). In both periods, having a burrow also allows access to the surrounding mudflat surface, where crabs forage. We confirmed earlier studies showing that males with regenerated claws are weaker competitors that are disproportionately evicted from their burrow during the non-mating period. Unexpectedly, however, males with a regenerated claw were not disproportionately evicted during the mating period. Fights at this time were also more escalated. We suggest this is because, when the disputed resource is also required for breeding, even weak males need to obtain and defend a burrow if they are to accrue any fitness. During the mating period, individuals with low resource-holding potential can improve their chances of mating if they escalate fights for burrows.

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Physical strength is the best predictor of fighting success in animal contests (Elias et al. 2010; Kasumovic et al. 2010). The role of resource value, however, is increasingly recognized as another important determinant of winning (Sigurjónsdóttir & Parker 1981; Barnard & Brown 1984; Haley 1994; Neat et al. 1998; Kotiaho et al. 1999; Gherardi 2006; Tricarico & Gherardi 2010; Doake & Elwood 2011). The propensity of an individual to initiate, escalate and win fights is determined by a resource's value to the contestant. Individuals are prepared to pay higher costs if the benefits of winning are greater (Enquist & Leimar 1987; Tricarico & Gherardi 2010). For example, access to gravid females generally provides a stronger incentive for males to compete than, say, a contest over food, because mating is more closely associated with fitness. If females require a resource for breeding (e.g. a territory), ownership of this resource is essential for males to reproduce successfully (reviewed in Kelly 2008). Weaker individuals cannot accrue fitness unless they overcome their inherent strength disadvantage (lower resource-holding potential; RHP) by escalating encounters and paying higher fight costs. There is mounting evidence that the consequences of winning or losing for different individuals influence fight escalation, duration and outcome (Harris 2010).

The relative value assigned by a contestant to a resource depends on its internal state and how this will affect its fitness (Tricarico & Gherardi 2010). The effect of changes in resource value has been investigated with respect to a male's state of sexual maturity (Dixon & Cade 1986), female presence (Kotiaho et al. 1999; Tachon et al. 1999), female abundance (Jennings et al. 2004), prior access to females (Brown et al. 2007), female mating status (Hoefler et al. 2009) and a male's previous mating experience (Judge et al. 2010). Here we report on a system in which we can examine fighting behaviour over a resource (a burrow and the surrounding territory) that differs in value between two periods owing to changes in the availability of mate-searching females.

In the fiddler crab *Uca annulipes*, a burrow and the surrounding area (i.e. territory) is a valuable resource used by both sexes as a refuge, foraging area and water supply. Each crab defends its own burrow. During the mating period, however, having a burrow has additional value for males. The surrounding territory is used as a site for court-ship of mate-searching females, which mate inside the male's burrow and then use it as an incubation site (Backwell & Passmore 1996). This increase in the relative value of a burrow should elevate a male's propensity to engage in more costly fighting tactics at this time. We therefore predicted that males will fight harder (longer and more escalated contests) during the mating period. Furthermore, in *U. annulipes* there are two classes of males: some have robust, original claws and others have lighter, weaker, regenerated claws (Backwell et al. 2000). We have previously shown that males with regenerated claws are more likely to lose fights (Backwell et al. 2000; for data on the closely related species, *U. mjoebergi*, see Reaney & Backwell 2007) and should therefore be at a disadvantage when competing to obtain a burrow to attract females.

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Study Species

As with many other fiddler crabs, male *U. annulipes* have a greatly enlarged major claw that is used in territorial contests and waved to attract mate-searching females. Females preferentially mate with large males that own high-quality burrows suitable for incubation (Backwell & Passmore 1996). Each individual owns and defends a territory that abuts those of his neighbours. Fiddler crabs feed on the sediment within their territory and use the burrow to escape predators and as a refuge from the heat and high tide (Smith & Miller 1973; Koga et al. 2001). A territory is also essential for burrow mating. In *U. annulipes*, there are two female mating tactics. Females sometimes mate on the mudflat surface, usually with their immediate male neighbours (Milner et al. 2010). This occurs throughout the semilunar tidal cycle. In addition, in each semilunar tidal cycle there is a 'mating period' in which many females leave their burrow in search of a male, mate with him underground and then remain in his burrow to incubate their eggs. Surface mating in the current study population was observed less often than burrow mating (S. Callander, personal observation). Studies of closely related species with comparable mating systems (e.g. Slatyer et al. 2012), and the observed occurrence of surface and burrow mating across the tidal cycle in *U. annulipes*, suggest that many females mate multiply. Females initially surface mate but then vacate their own burrow, sample males and burrow mate with another male within the same reproductive cycle. In the related species *U. mjoebergi*, females employ distinct mating tactics to confer different benefits. Females initially mate with male neighbours of any size and thereby gain protection in the form of burrow defence, but a female's mate choice decision when burrow mating is based on male phenotype and resource qualities (Slatyer et al. 2012). Crucially, the general reproductive physiology of fiddler crabs suggests that there is strong last-male sperm precedence (Diesel 1988). Indeed, recent paternity data using microsatellites in *U. mjoebergi* show that this is the case: although females mate multiply, the male with which a female eventually burrow mates gains almost all the paternity (Reaney et al. 2012). Thus, despite the presence of surface mating, it is still the case that a male's burrow is a vital resource to gain matings that lead to high paternity.

During burrow mating, the area around the burrow is used to court mate-searching females, and burrow quality is an important criterion during female mate choice (Backwell & Passmore 1996). After mating, a female remains in a male's burrow to incubate her eggs. Several aspects of the burrow (e.g. size, temperature and stability) influence her reproductive success (*Uca* genus; Christy 1983, 1987; deRivera 2005; Reaney & Backwell 2007). Consequently, a male is unable to attract a mate if he lacks a territory. Territory ownership is therefore even more valuable during the mating period.

When a male fiddler crab loses his large claw he regenerates a new claw. It has been shown in *U. annulipes* and a few other species of fiddler crab that the new claw has less muscle mass, a longer dactyl and fewer tubercles than the original one (Yamaguchi 1973; Crane 1975; Backwell et al. 2000; Lailvaux et al. 2009). These regenerated claws are inferior weapons, and males with regenerated claws are poorer fighters with lower RHP (Backwell et al. 2000; Reaney & Backwell 2007; Lailvaux et al. 2009).

In this study, we compared the territory acquisition behaviour and fighting success of males during the mating and nonmating periods.

METHODS

Mating and Nonmating Periods

We studied the fiddler crab *U. annulipes* in Chukwani, Zanzibar (6°13′21″S, 39°12′14″E) from August to October 2010. To define mating and nonmating periods operationally we delimited a 3 × 3 m plot within the population and each day noted the number of waving males at low tide. If there were ≥10 waving males, we classified the day as being during the mating period. As a result of the strong semilunar reproductive cycle, this measure clearly differentiated a mating and nonmating period (confirmed by an obvious difference in the presence or absence of mate-searching females). Females time their breeding to release their larvae at peak tidal heights to maximize offspring survival (Morgan & Christy 1995, 1997; Christy 2003).

Territory Acquisition

We experimentally created territory-seeking males by capturing territory owners and releasing them >2 m away from their own burrow. We then tracked them until they acquired a new territory. We released males with original claws that spanned the full population size range (13.8–32.0 mm). We temporarily marked males to avoid reusing them, and we moved to different areas of the mudflat between each release. We released 65 males during the mating period and another 65 during the nonmating period. We noted: (1) the method of burrow acquisition (evicted a male, evicted a female, occupied an empty burrow); (2) the distance travelled from release to burrow acquisition (the sum of the distance between all the burrows entered or fought over while searching); (3) the time taken to acquire a new burrow; (4) the number of fights; (5) the escalation level of each fight (low escalation = males pushed each other; high escalation = males grappled); (6) if the territory was acquired by evicting a male, his claw length and carapace width (mm) and whether he had an original or regenerated claw. We also recorded the claw length and carapace width of the released male.

We found that a significantly greater proportion of fights during the nonmating period involved a male with a regenerated claw being evicted (see Results). We then tested whether this was the result of: (1) males with regenerated claws being more available as opponents during the nonmating period; and/or (2) a greater propensity of released males to target these males when selecting an opponent during the nonmating period.

Claw Type of Surface-active Males

We determined the proportion of surface-active males with regenerated claws during the mating and nonmating periods by delimiting 50 × 50 cm plots and catching, measuring and recording the claw types of all males within each plot. We measured a total of 213 males in the mating period and 225 in the nonmating period. We excluded juveniles (carapace width ≤8 mm).

Targets of Territory-seeking Males

We captured, marked and released 100 original-clawed resident males during the nonmating period. We used different areas of the mudflat for each release to avoid reusing any crab. Released males sometimes fight with the nearest male to their release point. This might be an experimental artefact if males are simply trying to enter the closest available burrow. To ensure that there were no confounding effects of capture and release (e.g. scare response) on which crab a male chose to fight, we therefore documented the second fight of the released focal male, and noted whether his opponent had an original or a regenerated claw. This method has been successfully used in previous experiments on fiddler crabs (Milner et al. 2011; Milner 2012).

Statistical Analysis

All statistical tests were performed using SPSS 19.0 (SPSS Inc., Chicago, IL, U.S.A.) with $\alpha = 0.05$. Claw size and carapace width are highly correlated in *U. annulipes*. We used claw length in the analyses presented here, but using carapace width gave the same results. We compared burrow acquisition between the two periods with general linear models with claw size as a covariate and time period as a factor for continuous response variables, and with a log-likelihood ratio (LLR) test for mode of burrow acquisition.

RESULTS

Territory Acquisition

There was no difference in the mode of territory acquisition (LLR: $G_2 = 3.67$, $P = 0.16$) or in the time taken to acquire a territory between the mating and nonmating periods (mating: 762.52 ± 990.84 s; nonmating: 835.31 ± 935.89 s; $F = 0.24$, $P = 0.63$). However, males travelled significantly shorter distances (4.16 ± 5.62 m versus 6.95 ± 9.93 m; $F = 4.41$, $P = 0.04$) and engaged in significantly fewer fights during the mating period (4.15 ± 4.43 versus 5.85 ± 6.21 fights; $F = 3.88$, $P = 0.05$), but these fights significantly more often escalated to the grappling stage (33% versus 14%; Mann–Whitney U test: $Z = 3.65$, $P < 0.01$; (all tests: $N = 65. 65$).

The size of the residents that were attacked did not differ between the mating and nonmating periods ($F = 2.18$, $N = 45, 35$, $P = 0.144$,). Focal males were larger than the rivals that they evicted (24.1 ± 4.8 mm versus 20.6 ± 5.3 mm; paired t test: $t_{79} = 9.523$, $P < 0.001$). However, there were significantly more males with regenerated claws evicted during the nonmating period than during the mating period (43% versus 18%, respectively; Fisher's exact test: $N = 35, 45$, $P = 0.02$).

Claw Type of Surface-active Males

The proportion of surface-active males with regenerated claws did not differ between the mating (19.7%) and nonmating periods (19.1%; Fisher's exact test: $N = 213, 225$, $P = 0.90$). The increased proportion of males with a regenerated claw that were evicted during the nonmating period was therefore not due to their greater availability (Table 1).

Targets of Territory-seeking Males

We found no evidence that males with regenerated claws were specifically targeted by territory-seeking males during the nonmating period. Males with regenerated claws were attacked in approximately the same proportion that they occurred in the population (population: original claws = 182, regenerated claws = 43 (19.1%); males attacked by territory seeker: original claws = 85, regenerated claws = 15 (15%); Fisher's exact test: $P = 0.43$).

DISCUSSION

Territories are always valuable resources for male fiddler crabs, but during the mating period they are even more valuable because they become sites for courtship, mating and incubation. We found a difference in the fighting behaviour of males during the mating and nonmating periods. In the mating period a significantly greater proportion of fights escalated to the grappling stage, in which males interlock their large claws and twist. Fight escalation is a common indicator of the perceived value of a resource to the contestants (e.g. Elias et al. 2010). In *U. annulipes*, it seems that males are prepared to fight harder during the mating period, as the potential payoffs are greater.

We found no difference between the mating and nonmating periods in the likelihood that males with original claws acquired a territory by evicting a resident male or female, or by locating an empty burrow. In many fiddler crab species, male claw size appears to be used by males to assess fighting ability (e.g. Jennions & Backwell 1996), because larger clawed males tend to win fights (e.g. Morrell et al. 2005). Moreover, previous work using the same methods we deployed has shown that in *U. annulipes* (Milner 2012) and another closely related species, *U. mjoebergi* (Milner et al. 2011), males assess who to fight. There was, however, no difference in the size of the rival a male chose to fight between the two periods. Consistent with previous work in *U. annulipes* (Jennions & Backwell 1996), released, burrowless males tended to fight residents that were smaller than themselves. This suggests that released males did not alter their decisions about which males to challenge for a burrow between the mating and nonmating periods. There was also no difference in the time taken to secure a new territory between the mating and nonmating periods. However, in the mating period, males travelled a shorter distance and engaged in fewer, but more escalated fights before securing a new territory. It is possible that the shorter distance travelled is due to a change in the density of surface-active males between the mating and nonmating periods. This seems an incomplete explanation, however, because there is a correlation between the number of fights and distance travelled in both periods (mating period: $r = 0.650$, $P < 0.001$; nonmating period: $r = 0.688$, $P < 0.001$). This suggests that the shorter distance travelled in the mating period is primarily due to males winning a burrow after fewer fights. We suggest that one plausible explanation for these results is that released males fought harder and therefore won a territory sooner during the mating period as a result of a change in the value of the contested resource.

Regenerated claws are lighter and weaker, making males that possess them physically inferior fighters (Backwell et al. 2000; for data from *U. mjoebergi* see Reaney & Backwell 2007 and Lailvaux et al. 2009 for a direct measure of biomechanical strength). These males are therefore expected to lose a greater proportion of fights than males with an original claw. Previous work on *U. annulipes* found that males with a regenerated claw won approximately 50% fewer fights than equivalent-sized males with an original claw (Backwell et al. 2000). Additionally, territory-seeking males did not preferentially challenge residents with a regenerated claw, suggesting that they are unable to recognize regenerated claws (Backwell et al. 2000). We corroborated this finding in the current study, as males with a regenerated claw were not specifically targeted by territory-seeking males and were attacked in the proportion at which they occur in the population. We also found that during the mating and nonmating periods, males with regenerated claws were equally likely to be surface active: 19–20%

Table 1
Number (%) of males with original and regenerated claws that were evicted in relation to their population distribution during the mating and nonmating period

	Male population		Evicted males		Fisher's exact test (P)
	Original claw	Regenerated claw	Original claw	Regenerated claw	
Mating period	171	42 (19.7)	37	8 (17.8)	0.48
Nonmating period	182	43 (19.1)	20	15 (42.9)	0.01

of the surface-active males had a regenerated claw in both the mating and nonmating periods. These males are therefore equally available as opponents for territory-seeking males.

Given that males with a regenerated claw are equally available, equally likely to be targeted and less likely to win fights, we expected males with regenerated claws to be disproportionately represented among males evicted from their burrow. Indeed, this is what we found in the nonmating period. Although only 19% of the males in the population had regenerated claws, 43% of the males that were evicted (i.e. unable to defend their territory against an original-clawed intruder) had a regenerated claw. These results agree with previous work by Backwell et al. (2000) and a study of a closely related species (*U. mjoebergi*; Reaney & Backwell 2007).

Unexpectedly, however, males with a regenerated claw were not disproportionately evicted during the mating period, when 20% of males had regenerated claws, and 18% of the males evicted had a regenerated claw. Based on this finding, there appeared to be no disadvantage to having a weaker claw in the mating period. We suggest that this occurred because the physical disadvantage of having a less robust claw (i.e. all else being equal there is a decline in RHP) was compensated for by males with regenerated claws investing in more costly fighting tactics and escalating fights during the mating period. When a resource is required for reproduction, generally weak males (i.e. lower inherent RHP) must therefore fight harder, take more risks and pay greater costs in order to obtain the resource and accrue fitness. During the mating period, a territory is so valuable that weaker males are willing to escalate fights to defend a scarce resource even in the face of a divisive asymmetry in RHP.

Acknowledgments

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