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# The effects of claw regeneration on territory ownership and mating success in the fiddler crab *Uca mjoebergi*

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Underlying male quality is often reflected in the condition of sexually selected traits. In fiddler crabs, male success in both intra- and interspecific interactions is highly dependent on the size of the major claw. However, males are often forced to autotomize their major claw. Claw regeneration significantly altered the structure of a males' major claw in *Uca mjoebergi*. We found, however, that claw regeneration did not affect signal quality. Both males and females were unable to visually distinguish a regenerated claw from an original claw. Although regenerated males were inferior fighters, males were able to compensate for this fighting disadvantage by avoiding fights with other males. Regenerated males were, however, less likely to acquire and defend high-quality territories and consequently suffered a decrease in mating success.



*Keywords*: claw regeneration; fiddler crab; mating success; signal quality; territory ownership; *Uca mjoebergi*

Sexually selected signals are notoriously costly to produce (Andersson 1994). In many species, only high-quality males can produce and maintain costly signals, allowing conspecifics to rely on these traits to honestly signal competitive ability or mate quality (Zahavi 1975). The relationship between signal costs and signaller quality, however, can be disrupted by several factors including disease (McGraw & Hill 2000), a change in resource availability (Kotiaho 2000) or a temporary loss of quality (e.g. a loss of competitive ability due to moulting or a loss of mate quality due to sperm depletion; Adams & Caldwell 1990; Kendall & Wolcott 1999). In some species, the relationship between signal costs and sender quality may be disrupted after the regeneration of a sexually selected trait.

Many invertebrates possess the ability to self-amputate (autotomize) major appendages. While autotomy can be hugely beneficial in terms of survival, the subsequent regeneration of a major appendage can be very energetically costly (e.g. Naya et al. 2007). Regrowing a lost appendage often requires a large shift in resource allocation that can affect somatic and reproductive growth (e.g. Niewiarowski et al. 1997). When an individual loses and regenerates a costly sexually selected trait, they may experience a reduction in overall condition that may be reflected in the quality of the regenerated trait. Appendages that have been regrown are also often structurally different from their nonregenerated originals (for review see Maginnis 2006). Consequently, regeneration can potentially affect male–male performance ability, competitiveness and mating success. In male wolf spiders, for example, regenerated legs are smaller than original legs and lack the conspicuous decorative tuft used in courtship and aggressive displays. As a result, leg regeneration negatively affects both male competitive ability and mating success (Uetz et al. 1996).

Male fiddler crabs (*Uca* spp.) produce one greatly enlarged major claw that can make up as much as 40% of their body mass (Crane 1975). They use their claw both as a weapon in agonistic encounters with other males and to attract mate-searching females. The length of the major claw is important in the assessment of fighting ability before physical contact (Jennions & Backwell 1996; Morrell et al. 2005) and as a predictor of male mating success (Backwell & Passmore 1996; Reaney & Backwell 2007). Males also attract females to their burrows by waving their major claw, often in synchrony with neighbouring males. Females have been shown to preferentially visit males with faster wave rates (Backwell et al. 1999, 2006).

Although the major claw is extremely important to males, they occasionally need to autotomize it during

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a predation attack, an escalated fight or a problematic moult. After autotomy, a male will regenerate a claw that is visibly distinguishable from his original major claw (Yamaguchi 1973) and often contains less muscle mass and a thinner exoskeleton. Regenerated claws are therefore lighter, more slender and less robust than original claws (Backwell et al. 2000). These morphological changes are permanent (Backwell et al. 2000) and decrease the physical strength of the major claw in *Uca mjoebergi* (S. P. Lailvaux, L. T. Reaney & P. R. Y. Backwell, unpublished data). As a result, claw regeneration significantly affects fighting success in both *Uca annulipes* (Backwell et al. 2000) and *U. mjoebergi* (S. P. Lailvaux, L. T. Reaney & P. R. Y. Backwell, unpublished data). Regenerating a new major claw is very costly (Allen & Levinton 2007) and males are presumably unable to regenerate an exact replica of their original claw. Males are therefore likely to be making the 'best of a bad job' by regenerating a weaker claw.

Does claw regeneration affect male fitness in other social contexts? Because a regenerated claw is structurally different from an original claw, the reliability of the signal, in terms of both the sender's fighting ability and his quality as a mate, may be compromised. Furthermore, if the production of a new major claw affects overall body condition (Hopkins 1982), males with regenerated claws may have less energy available for costly waving displays used to attract females (Matsumasa & Murai 2005). Both fighting and mating success are highly correlated with male size in *U. mjoebergi* (Morrell et al. 2005; Reaney & Backwell 2007), suggesting that the morphological changes that occur as a result of claw regeneration may be an important factor affecting male behaviour in many social contexts. In this study, we compared the behaviour of male *U. mjoebergi* with original and regenerated claws during (1) territory acquisition and defence and (2) courtship behaviour and determined if male mating effort and success was affected by claw regeneration.

# METHODS

## Study Population

We studied a population of the fiddler crab *U. mjoebergi* at East Point Reserve, Darwin, Australia between September and December 2004, 2005 and 2006. They occur in dense aggregations and both sexes occupy burrows that are essential for survival. Males will aggressively defend their burrows against wandering, burrowless males. During aggressive interactions, males first align their claws to assess relative size. Fights can then escalate into grapples, where males push and interlock claws (Morrell et al. 2005). There is a pronounced large-male fighting advantage in *U. mjoebergi* (Morrell et al. 2005).

Mate-searching females wander through the population of territory-holding males and visit the burrows of several before selecting a mate. The pair will mate in the males' burrow and the female will remain there for her entire incubation period. Males attract females to their burrows by waving their major claws, often clustering around a female and waving in synchrony. A females' initial decision to approach a male is based on claw size, with larger males having a mating advantage (Reaney & Backwell 2007), and courtship behaviour (Backwell et al. 1999). Final mate choice is, however, based on both male and territory quality (Backwell & Passmore 1996; Reaney & Backwell 2007). Burrow ownership is therefore also very important for male reproductive success.

## General Methods

All crabs were measured (carapace width and major claw length) to the nearest mm using dial callipers. It was often necessary to visually size-match pairs of males before running an experiment. This alleviates the need to capture and measure males before documenting their behaviour. Visual size-matching proved extremely accurate when checked by capturing and measuring the males after the experiment was completed (intraclass correlation: $r_1 = 0.68$, $P < 0.001$, $N = 27$ pairs). For brevity, we refer to males with regenerated claws as 'regenerated males' and males with original claws as 'original males'.

## Claw Structure, Prevalence and Neighbours

To determine whether regenerated and original claws were morphologically different, we measured regenerated ($N = 57$) and original ($N = 124$) claws for (1) claw length, (2) dactyl length (movable finger), (3) dactyl width, (4) manus width (palm), (5) manus height and (6) manus depth (mm). We then dried regenerated ($N = 48$) and original ($N = 108$) claws at 60°C for 24 h, which was sufficient to eliminate excess water but allow the claws to retain their original shape and structure. Each claw was then weighed using a Sartorius scale (0.1 mg).

We captured and measured all original and regenerated males within 25 randomly distributed $1 \times 1$ m plots to determine the prevalence of claw regeneration in the study population. To determine whether regenerated and original males differed in the identity and proximity of their neighbours, we located 35 pairs of visually sized-matched regenerated and original males. We recorded the distance to the three nearest burrows (cm), noting whether the burrows were empty or occupied and the sex of the occupants. We caught and measured the focal male and the occupants of the three nearest burrows.

## Territory Defence

Burrowless males wander through the population and selectively attack residents in an attempt to win their territories. To establish whether there was a difference in the attack rate of regenerated and original residents, we marked the burrows of regenerated ($N = 77$) and original ($N = 86$) males with numbered flags. For 30 min we noted how many times they were aggressively approached by wandering males.

We also measured burrow tenancy of 27 pairs of visually sized-matched regenerated and original males. We marked