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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.

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

each male's burrow with a numbered flag and drew detailed images of each male (carapace patterning, handedness, leg coloration) for individual identification. Every hour, we noted whether both males still occupied their burrows and stopped recording once one male from the pair had been replaced by a new male resident.

## Territory Acquisition

To assess how males of the two claw types gained new territories, we caught and released sized-matched pairs of resident regenerated and original males ($N = 44$ pairs) into the population and followed them until they had gained a new burrow. Males were released at least 1 m from their original burrow. We recorded the time taken, distance travelled and whether the male fought a resident male for a burrow, evicted a female or found an empty burrow.

## Mating Effort

To determine whether regenerated and original males differed in their courtship effort, we videorecorded (Sony TRV16E digital camera) a cluster of naturally courting males that contained a regenerated male ($N = 20$ clusters). The regenerated male and his nearest courting original neighbour were then caught and measured. We determined the wave rate (waves/s) of the regenerated male and his nearest original clawed neighbour. To document the timing of each wave, the start of a wave was defined as the initial upward movement by the male's major claw from a horizontal motionless position, and the end of a wave was defined as the return of the major claw to a resting position. The start and end of each wave was determined using frame-by-frame analyses (0.04-s precision).

To further investigate possible differences in mating effort, we located visually size-matched pairs of regenerated and original males ($N = 18$ pairs) whose burrows where approximately 10 cm apart. We placed a tethered female 15 cm away, equidistance from the two males. To tether a female, we caught a wandering (burrowless) female and glued a thin piece of cotton string to the back of her carapace. This was then attached to a nail that was pushed into the mud. We videorecorded the time each male spent waving at the female, the total number of waves produced and the maximum distance each male travelled from his burrow while actively courting the tethered female (using a 5-cm grid drawn onto the sediment). Females were used in two trials (each with a different set of males) before being released and replaced with a new female.

## Mating Success

There are three stages to female choice in *U. mjoebergi*. (1) A female approaches a courting male by walking directly towards him and stopping just short of his burrow entrance. Many females stop at this point. (2) If the female is still interested, she will briefly enter the male's burrow for inspection before moving onto another male. (3) If,

however, the female remains interested in the male, she will stay in his burrow and the pair will mate underground (Reaney & Backwell 2007). We compared the success of original and regenerated males during all three stages.

To determine the success of original and regenerated males during the initial approach phase of the mating process, we marked the burrows of regenerated ($N = 77$) and original ($N = 86$) males with numbered flags during peak mating periods. We noted how often each marked male was approached by a mate-searching female over a 30-min period.

A 30-min observation period is sufficient to get a good sample size of female approaches but does not give sufficient data for burrow visits or matings. We therefore followed naturally sampling females ($N = 44$) through the population. Males that received a visit (female entered the males' burrow) or a mating (the female remains in the burrow) were marked by placing a numbered bead next to his burrow. To follow sampling females without disturbing them, we remained approximately 1.5 m away and dropped the numbered bead through a long, hollow pipe next to the visited or mated male's burrow. This method has been successful for following sampling females without affecting their sampling behaviour in a previous study (Reaney & Backwell 2007). We caught and measured the female and all visited and mated males.

## Statistical Analysis

All statistical analyses were performed in SPSS 14 (Chicago, IL, U.S.A.). We used paired analysis when analysing data for male pairs. All data were tested for normality before performing parametric analysis. Because male carapace width and major claw size were highly correlated (Pearson correlation: $r_S = 0.89$, $P < 0.001$, $N = 85$), we used only major claw size when analysing male size. Data are reported as mean $\pm$ SD.

## RESULTS

### Claw Structure, Prevalence and Neighbours

When controlling for claw length, regenerated claws had significantly longer and narrower dactyls and smaller manus and were significantly lighter than original claws (Table 1). Regenerated claws also often lacked teeth in the gape of the claw.

Males with regenerated claws made up 7.4% of the study population (20/269). The proportion of males with regenerated claws increased significantly with increasing carapace width (Mann–Whitney $U$ test: $Z = 2.83$, $P = 0.005$). At small carapace sizes (4–9 mm), 3.9% of males had regenerated claws while at large sizes (10–15 mm) this rose to 10.7%.

We found no significant differences in the distributions of sized-matched pairs of regenerated and original males within their neighbourhoods. They did not differ in the distance to the nearest neighbouring burrow (paired $t$ test: $t_{1,34} = -0.75$, $P = 0.46$; regenerated males: $12.8 \pm 5.8$ cm; original males: $11.9 \pm 5.7$ cm), the sex of the nearest

**Table 1.** Morphological measurements of regenerated and original claws

| Claw measurements | Regenerated claws | Original claws | F value | P value |
|---|---|---|---|---|
| Dactyl length (mm) | 13.48±2.23 (57) | 11.07±2.23 (124) | 308.3 | <0.001* |
| Dactyl width (mm) | 2.90±0.38 (57) | 3.01±0.44 (124) | 131.5 | <0.001* |
| Manus width (mm) | 7.96±1.08 (57) | 8.47±1.15 (124) | 383.7 | <0.001* |
| Manus height (mm) | 6.39±0.69 (57) | 6.32±0.79 (124) | 50.4 | <0.001* |
| Manus depth (mm) | 3.37±0.45 (57) | 3.38±0.50 (124) | 58.6 | <0.001* |
| Dry mass (mg) | 139.73±45.55 (48) | 136.11±53.53 (108) | 42.4 | <0.001* |

Data are presented as mean ± SD. Sample sizes are indicated in parentheses and * indicates a significant P value. F and P values were calculated when controlling for claw length.

neighbour (G test: $G = 0.27$, $df = 1$, $P = 0.61$; male/female neighbours: regenerated males: 23/12; original males: 25/10) or the distance to their nearest neighbouring male (paired $t$ test: $t_{1,34} = -1.68$, $P = 0.10$; regenerated males: $15.4 \pm 7.0$ cm; original males: $13.1 \pm 5.4$ cm). There was also no difference in the size of their nearest neighbouring male (paired $t$ test: $t_{1,34} = 0.52$, $P = 0.60$; regenerated males: $15.3 \pm 3.2$ mm; original males: $15.8 \pm 4.8$ mm).

## Territory Defence

Resident regenerated males were not preferentially challenged (aggressively approached) by other males (logistic regression: $\beta = -0.21$, $P = 0.55$; regenerated males: 28/77; original males: 27/86; controlling for body size: $\beta = 0.15$, $P = 0.41$). Regenerated males were, however, significantly more likely to vacate their burrows sooner than their size-matched neighbouring original male (20 regenerated males versus seven original males; binomial test: $P = 0.02$).

## Territory Acquisition

Size-matched original and regenerated males differed significantly in how they gained a new territory when released into the population. Whereas original males evicted mostly resident males (30/44), regenerated males avoided fights by evicting females or occupying empty burrows (26/44) (G test: $G = 6.69$, $df = 1$, $P = 0.01$; Fig. 1). However, regenerated and original males did not differ in the time they took (paired $t$ test: $t_{1,43} = -1.09$, $P = 0.28$; regenerated males: $7.4 \pm 6.4$ min; original males: $6.1 \pm 5.3$ min) or the distance they travelled (paired $t$ test: $t_{1,43} = 0.13$, $P = 0.90$; regenerated males: $135.0 \pm 103.1$ cm; original males: $138.1 \pm 137.9$ cm) until they had gained a new burrow.

## Mating Effort

We found no differences in the courtship behaviour of regenerated and original males. They waved to sampling females at the same rate ($F_{1,19} = 2.83$, $P = 0.11$; regenerated males: $0.39 \pm 0.08$ waves/s; original males: $0.39 \pm 0.12$ waves/s). Although regenerated males were significantly bigger than the nearest original male (paired $t$ test: $t_{1,19} = -5.29$, $P < 0.01$; regenerated males: $19.53 \pm 2.40$ mm; original males: $16.29 \pm 2.34$ mm), claw size did

not have a significant effect on wave rate ($F_{1,36} = 2.22$, $P = 0.15$). When presented with a tethered female, size-matched original and regenerated males spent equivalent amounts of time waving at the female (paired $t$ test: $t_{1,17} = -0.56$, $P = 0.58$; regenerated males: $71.2 \pm 34.4$ s; original males: $64.1 \pm 50.5$ s) and produced a similar number of waves (paired $t$ test: $t_{1,17} = -0.05$, $P = 0.96$; regenerated males: $22.4 \pm 16.4$; original males: $22.2 \pm 17.4$). Regenerated and original males also travelled similar distances towards the female (paired $t$ test: $t_{1,17} = -0.93$, $P = 0.37$; regenerated males: $9.28 \pm 5.0$ cm; original males: $7.78 \pm 5.3$ cm) during courtship.

## Mating Success

Regenerated males were approached by mate-searching females significantly more often than were original males (logistic regression: $\beta = -1.73$, $P = 0.01$), when controlling for male size ($\beta = -0.07$, $P = 0.23$, regenerated males: 11/77 (14.3%); original males: 3/86 (3.5%)).

Thirteen per cent (6/46) of the males that received a burrow visit from a female had regenerated claws. This was not significantly different from the proportion of
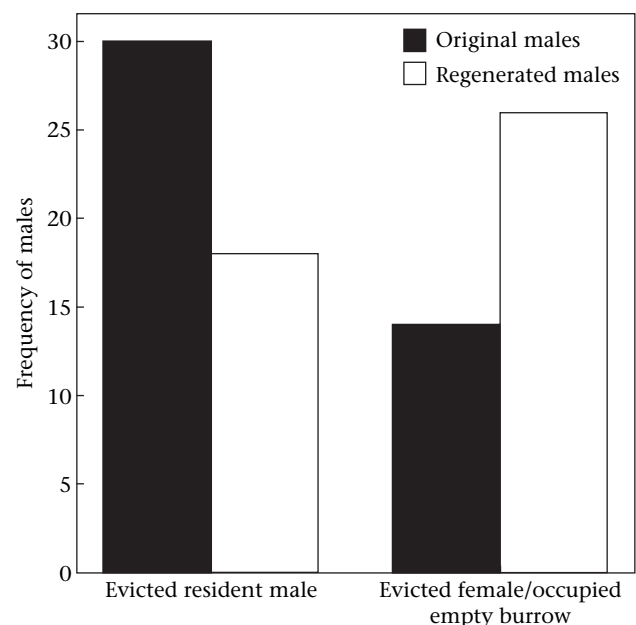


**Figure 1.** Territory acquisition by males with regenerated ($N = 44$) and original claws ($N = 44$).

regenerated males that naturally occur in the study population (7.4%; $G$ test: $G = 1.45$, $df = 1$, $P = 0.23$). There was no difference in the size of visited original and regenerated males ($F_{1,44} = 1.82$, $P = 0.18$; regenerated males: $17.83 \pm 3.89$ mm; original males: $15.81 \pm 3.37$ mm).

None of the 33 males that received a mating was a regenerated male. This was significantly lower than expected given the proportion of regenerated males that occurred in the study population (7.4%; $G$ test: $G = 4.80$, $df = 1$, $P = 0.03$).

## DISCUSSION

Regenerated major claws were structurally different from original claws in *U. mjoebergi*. For a given claw length, the dactyl was longer and more slender and the manus area was substantially reduced. Regenerated claws were also lighter than original claws, suggesting that they contain less muscle mass. A separate study has shown that the fighting success of males is compromised as a result of these morphological changes (S. P. Lailvaux, L. T. Reaney & P. R. Y. Backwell, unpublished data). Here we show that the inferior quality of regenerated claws also influenced behaviour during territory defence and acquisition and suggest that this translates into a decrease in male mating success.

Regenerated males maintained ownership of a territory for significantly less time than original males. Furthermore, when searching for a new territory, regenerated males tended to avoid fights with resident males, instead evicting females or searching for empty burrows. Although regenerated males did not suffer higher searching costs during burrow acquisition as a result of this behaviour, it may jeopardize the quality of the burrow they finally obtain. Burrow quality is extremely important to male reproductive success. While a female's initial decision to approach a male depends on claw size and courtship behaviour, final mate choice is strongly dependent on burrow quality. The structure (Backwell & Passmore 1996), size (deRivera 2005), stability (Christy 1983) and temperature (Reaney & Backwell 2007) of a burrow have all been shown to affect a female's final mate decision.

Although regenerated males did not experience a disadvantage during the early stages of mate attraction, where claw size and courtship behaviour are important for female choice (Backwell & Passmore 1996), they received significantly fewer matings than expected from their population frequency. The courtship behaviour of regenerated males was no different from that of original males and, as a result, a males' initial attractiveness was unaffected by claw regeneration. This suggests that females were discriminating against regenerated males during the final assessment of burrow quality. Regenerated males appear to be less successful at acquiring and maintaining good-quality territories. The frequent loss of territories and the avoidance of fights when searching for a new territory are therefore extremely costly in terms of the reproductive success of regenerated males.

Signal quality is often an honest indicator of male genetic quality (Andersson 1994). Male *U. mjoebergi* use claw size to predict an opponent's strength before deciding to engage in costly, aggressive interactions (Morrell et al. 2005). Females also use the relationship between claw size and male quality as a reliable means of selecting a mate (deRivera 2005; Reaney & Backwell 2007). Although male *U. mjoebergi* that have produced a new major claw are poor competitors and low-quality mates, this was not honestly reflected in the signal quality of a regenerated claw. Both males and females were unable to distinguish a regenerated claw from an original claw during the visual assessment process. Regenerated males did not position themselves among different neighbours compared to original males and were not specifically targeted by other males. This suggests that they were not immediately recognized as males with weak claws. Regenerated males were able to further conceal their inferior fighting ability by actively avoiding fights with other males when searching for a new territory. The low probability of encountering a male with a regenerated claw in this population may account for the observation that both males and females were unable to accurately assess the quality of a male based on claw type (but see Backwell et al. 2000). However, males paid a mating cost in terms of the quality of the burrow they were defending. Females were, therefore, still able to reliably select a high-quality male by rejecting low-quality burrows. Claw regeneration is, therefore, an important factor that affects male mating success in *U. mjoebergi*.

The results from this study differ from those found in *U. annulipes*, a closely related species (Rosenberg 2001). Although claw regeneration significantly affected fighting success in *U. annulipes*, males did not experience a mating disadvantage (Backwell et al. 2000). In contrast, claw regeneration affected both fighting behaviour and mating success in *U. mjoebergi* (this study; S. P. Lailvaux, L. T. Reaney & P. R. Y. Backwell, unpublished data). In *U. mjoebergi*, the low level of claw regeneration (7.4%) compared to *U. annulipes* (16–44%) may reflect the increased fitness costs experienced by males with a regenerated claw. One possibility is that the higher fitness costs have caused male *U. mjoebergi* to be more reluctant to autotomize their major claw in some contexts compared to *U. annulipes*. This aspect of claw regeneration in fiddler crabs certainly warrants further study.

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