

How do weaponless male fiddler crabs avoid aggression?

Isobel Booksmythe · Richard N. C. Milner ·
Michael D. Jennions · Patricia R. Y. Backwell

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Abstract Mimicry of females enables weaker males in many species to avoid intrasexual aggression. In fiddler crabs (*Uca annulipes*), males use their major claw in aggressive interactions to acquire and defend a territory. Males that have autotomised their major claw will be disadvantaged in fighting, but might use their temporary resemblance to females to avoid costly aggressive encounters with other males. We investigated whether: (1) courting males mistake clawless male fiddler crabs for females; (2) clawless males are able to acquire, defend and retain territories as successfully as intact males; and (3) clawless males are more cautious than intact males. Clawless and intact males differed in burrow acquisition methods and fighting behaviour, but were equally successful at acquiring and retaining burrows. While courting males treated clawless males as female, we found no evidence that clawless males mimic the behaviour of females, or that they exploit the advantage of their mistaken identity. Clawless males further appear to avoid male aggression by altering their territorial strategies to minimise the potential for conflict.

Keywords Autotomy · Female mimicry · Fiddler crab · Territory acquisition · Territory defence

Introduction

In sexually dimorphic species, it can sometimes be advantageous for an individual to resemble a member of the opposite sex. Such mimicry can reduce intrasexual aggression, and in some cases improve mating success. For example, the plumage colouration of some male pied flycatchers (*Ficedula hypoleuca*) is very similar to that of females, enabling them to avoid aggressive encounters with other males and to obtain better quality breeding territories (Slagsvold and Saetre 1991). In the blennioid fish *Salaria pavo*, small males display the colour pattern and courtship behaviour of spawning females, allowing them to fertilise eggs laid by females in the nests of large males (Gonçalves et al. 1996).

Fiddler crabs (*Uca* spp.) provide a striking example of the morphological differences that can occur between males and females of the same species. Females are small, often drab, and have two small feeding claws, while males are larger, brightly coloured, and have one feeding claw and one greatly enlarged (“major”) claw (Crane 1975). The major claw is extremely important, as it is used both in a waving display for mate attraction and courtship, and as a weapon in aggressive interactions with other males. Claw length is a predictor of mating success (Backwell and Passmore 1996), and also acts as a signal of fighting ability (Jennions and Backwell 1996). Fighting plays an important role in the frequent territorial interactions experienced by male fiddler crabs. Each individual occupies a small territory containing a burrow, which is a vital resource for every crab, providing shelter from predation and tidal inundation (Crane 1975). The burrow must be defended against wandering individuals that have lost their own territories and will fight to evict residents. Additionally, residents fight their neighbours to expand their territory

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I. Booksmythe (✉) · R. N. C. Milner · M. D. Jennions ·
P. R. Y. Backwell
Research School of Biology (Botany and Zoology),
The Australian National University,
Canberra ACT 0200, Australia
e-mail: isobel.booksmythe@anu.edu.au

boundaries and increase their feeding area. Territorial fights are usually initiated by the intruding individual, and fighting is strongly size-assortative (Jennions and Backwell 1996). There is a close relationship between the size of residents and their burrows (Reaney and Backwell 2007). So, while it may be less costly for a large intruder to evict a smaller resident, there is then the added cost of enlarging the burrow.

Male fiddler crabs are able to autotomise their major claw, and do so to escape a predator (Backwell et al. 2000) or to emerge from a difficult moult (Maginnis 2006). While autotomy is preferable to death or serious injury, there are large costs associated with the loss of an appendage. Limb regeneration is a slow and energetically expensive process that diverts resources away from other functions such as reproductive activity and general growth (Juanes and Smith 1995). Furthermore, in several species of fiddler crab a regenerated claw is a lighter, less robust structure than an original claw (Crane 1975) and a less effective weapon (e.g., *U. annulipes*, Backwell et al. 2000). Although males with regenerated claws are able to deceive conspecifics in some mating and aggressive contexts, there is still a net cost to having a regenerated claw as territory defence is usually compromised (Backwell et al. 2000; Reaney et al. 2007).

One large cost of claw loss must occur immediately following autotomy. Until the next moult, a newly autotomised male has no claw at all, and the regenerating claw will not reach the size of the lost original for several moult cycles (Skinner 1985). In *U. annulipes*, for example, complete claw regeneration takes about 6 months (Backwell et al. 2000). Clawlessness presents a serious impediment to many aspects of life for a male fiddler crab. In many cases, a male that has lost his claw is also likely to have lost his territory (for example, through being removed by a predator or large rival). His first concern is, therefore, likely to be acquiring a new territory, which must be achieved without the use of weaponry. If successful, the autotomised male then has to retain ownership of the territory. Despite these difficulties, the fact that many males survive claw loss is demonstrated by the presence of males with regenerated claws. In *U. annulipes*, the proportion of individuals with regenerated claws was as high as 44% in one population (Backwell et al. 2000). This suggests that behaviours that ameliorate the costs of claw loss have arisen in fiddler crabs.

It is possible that clawless male fiddler crabs are mistaken for females, and as a result experience reduced aggression from other males. As the major claw is the main distinguishing feature, it is superficially difficult, for human observers at least, to tell clawless males from females except at close range. As the fiddler crab visual system does not involve high resolving power or visual acuity, relying instead on movement, colour, reflectance, and patterning

for species, sex, and individual recognition (Detto et al. 2006; Zeil and Hemmi 2006), it is likely that the major claw is an important cue for sex recognition in the crabs themselves. Female fiddler crabs can acquire and hold territories without the use of an enlarged claw. When searching for a burrow, female fiddler crabs use different tactics to males. While most males fight to evict residents of either sex, females are more likely to seek out unoccupied burrows (R.N.C. Milner et al., unpublished data). Females also obtain territories after mating as the male gives up his burrow for the incubation of eggs (Backwell and Passmore 1996). Despite having no apparent defence against them, burrow-owning females do not appear to suffer much harassment by burrow-seeking males (Jennions and Backwell 1996), who often bypass them to approach male residents. If clawless males use similar territorial strategies to females, or can deceive clawed males by mimicking female behaviour, they might also be successful in avoiding excessive harassment, and survive this vulnerable period.

Another potential cost of claw loss is increased susceptibility to predation. Limb autotomy increased susceptibility to predation in house crickets (*Acheta domestica*), due to a reduction in escape speed following limb loss (Bateman and Fleming 2006). Loss of a claw should not impede running in fiddler crabs. In fact, endurance capacity was greater for clawless than intact *Uca pugilator* males, and sprint speed was unaffected by claw presence or absence (Allen and Levinton 2007). However, other aspects of defence could be impaired in clawless individuals, as they have lost both a weapon and the opportunity to escape another predation attempt via autotomy. The behavioural decisions of individuals can be strongly influenced by their perceived risk of danger (Lima and Dill 1990). For example, in striped plateau lizards (*Sceloporus virgatus*) the distance from a predator at which individuals took flight was greater for individuals that had previously been captured than for control individuals. Of the previously captured individuals, those that autotomised their tail showed greater refuge use than intact individuals (Cooper 2007). A fiddler crab that has recently lost a claw to a predation attempt is likely to have a higher perceived risk of threat than one that has not. Consequently, a clawless male might be expected to exhibit greater caution than an intact male. A trade-off between predator avoidance and necessary activities such as foraging is found in most animals (Lima and Dill 1990). An increase in cautiousness could be costly if it results in reduced foraging time for a crab with the increased energetic requirements of claw regeneration. However, being more cautious might help clawless males avoid threats posed by conspecifics, as well as predators.

This study aims to examine whether clawless male *U. annulipes*:

1. Are recognised as male by resident males, or are courted like females
2. Are able to acquire and defend burrows as effectively as intact males
3. Can retain tenancy of a burrow for as long as intact males
4. Are more cautious than intact males after exposure to a threat

Together, these data will indicate whether clawless males are at a disadvantage in terms of male–male competition, and whether they are mistaken for females in a courtship context.

Methods

We investigated the effects of claw loss on male fiddler crabs, *U. annulipes*. This species occurs in dense mixed-sex populations on intertidal mudflats. Fieldwork was carried out on Inhaca Island, Mozambique (25°59'10"S, 32°56'35"E), during September and October 2008.

All the crabs used were caught as resident (burrow-owning) individuals and had original (non-regenerated) major claws. To remove the major claw, it was gently twisted forwards until the crab autotomised the limb. Claw removal was done immediately on capture to minimise additional stress on de-clawed males. The carapace width and major claw length of all crabs were measured using dial callipers to the nearest 0.1 mm. When size-matching was required, crabs were matched to within 1 mm using carapace width.

Can courting males recognise clawless males?

To determine whether courting male *U. annulipes* can distinguish between wandering females and clawless males, we released clawless male, intact male, and female crabs onto the mudflat and documented the waving response of resident courting males. Size-matched trios ($N=15$) of one female and two male crabs, were caught, measured, and marked with quick-drying white paint on the carapace. The major claw of one of the males was then removed. The crabs were individually released on the mudflat and tracked for 5 min as they moved through the population. The number of resident males within 20 cm of the focal crab and the number of these that waved at the focal crab were recorded. For a crab to be counted as waving, it had to directly face the focal crab and perform a full courtship wave. Data were analysed using linear mixed models in SPSS 17.0, with crab type (female/intact male/clawless

male), number of males passed and the interaction between these terms as fixed factors, and trio identity as a random factor.

Can clawless males acquire and defend burrows as effectively as intact males?

To determine how intact and clawless males acquire and defend burrows, we released males of both types onto the mudflat and tracked them as they searched for and established a territory. Eighty males were caught and their carapace width and claw length measured. The major claw of 40 males was removed. Each crab was individually marked and released back into the population. The release point was marked with a flag, and the crab was tracked until it acquired a burrow. The duration of the search, number of burrows the crab approached, whether it fought with male or female residents, method used to obtain the final burrow, and the straight-line distance between the release point and the final burrow were recorded. Once the focal crab had secured a burrow, it was observed for 1 h to record: whether it fought male and female neighbours and wandering individuals, whether it was aggressively approached by neighbours, and whether it sealed the burrow entrance, abandoned the burrow, or was evicted, within the first hour of occupation. We used Mann–Whitney U tests to compare continuous variables, and likelihood ratio tests to compare binomial response variables between clawless and intact males.

Can clawless males occupy a territory for as long a tenancy as intact males?

To determine whether clawless males retain burrows as successfully as intact males, we compared the length of tenancy for intact and clawless males experiencing similar pressures from neighbours. Size-matched pairs of males ($N=37$) were caught, measured, and marked, and one male in each pair was made to autotomise his claw. The marked males were placed in a pair of flagged empty burrows (the burrow entrance marked by a small, numbered flag) on the mudflat, whose male occupants we had previously evicted. The nearest neighbour to each flagged burrow was male, and the size of the nearest neighbour and distance to the nearest neighbour's burrow were judged by eye to be similar for each flagged burrow in a pair. After 30 min, the burrows were checked to see whether the new occupant had sealed the entrance. Flagged burrows were checked twice daily for the presence of the marked occupants until the male with the longer tenancy could be determined. We used a binomial test to analyse the effect of clawlessness on which male in a pair had the longer tenancy. Binomial response data were analysed using likelihood ratio tests ($df=1$).

Are clawless males more cautious than intact males following a threat?

To determine whether clawless males were more cautious than intact males after being exposed to a threat, we scared a pair of intact and clawless males ($N=20$ pairs) and recorded the time they took to re-emerge after retreating into their burrows. A resident clawless male was located by scanning the mudflat, and a nearby resident male with an original claw was identified. An observer sat approximately 1 m from both crabs and waited until all crabs in the area had resumed normal activity. When both focal crabs were on the surface, the observer stood suddenly to scare them into their burrows. The fiddler crab visual system is highly sensitive to movement and particularly to objects moving above the visual horizon (Zeil and Hemmi 2006). Thus, quickly standing elicits a threat response indistinguishable from that provoked by a predator (Jennions et al. 2003). The time from the scare to the re-emergence of each crab was recorded. When all crabs in the area had resumed normal feeding activity, the trial was repeated for the same focal pair. Both crabs were then caught and measured. Data were analysed using linear mixed models in S-Plus 7.0, with male type included as a fixed factor and male identity nested within pair identity as random factors. The significance of random factors was tested using a log-likelihood ratio test ($df=1$) of the model with and without the terms of interest. For fixed factor, we simply present the F-ratio for the parameter estimate.

Unless otherwise stated, all tests are two-tailed and alpha was set at 0.05. We used standard formulae to calculate the common effect size of Pearson's r for all tests (Cooper et al. 2009). If the intact male response was greater than the clawless male response, r was assigned a positive value.

Results

Can courting males recognise clawless males?

Released females and clawless males provoked the same level of courtship waving from resident males while released intact males provoked a much lower rate of waving. In the initial model, when all crab type categories were included, there was a significant interaction between crab type and the number of males passed ($F_{2, 27}=25.9$, $P<0.001$). The number of resident males waving at the focal crab increased strongly with the number of resident males passed for both females and clawless males, but barely increased for intact males (Fig. 1). When only females and clawless males were included in the model, the interaction between crab type and the number of males passed was not significant, and was removed from the model. In the final

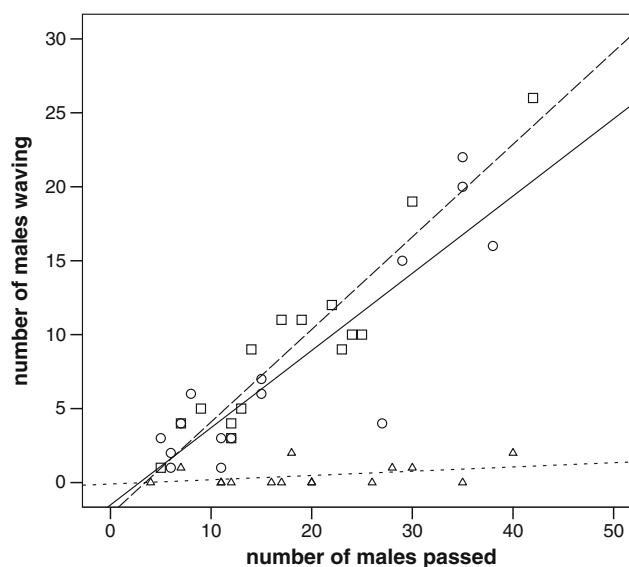


Fig. 1 Waving response of resident males to females (circles and solid line; $Y=0.522X-1.52$), clawless males (squares and dashed line; $Y=0.626X-2.165$) and intact males (triangles and dotted line; $Y=0.029X-0.1$)

model, there was no difference in the slope of the line for females and clawless males ($F_{1, 14}=2.85$, $P=0.11$), indicating that resident courting males responded in the same way to clawless males and females.

Can clawless males acquire and defend burrows as effectively as intact males?

Clawless males did not differ significantly from intact males in search duration, number of burrows approached, or the distance travelled during the search (Table 1). Compared to intact males, significantly fewer clawless males fought resident males, but significantly more fought resident females. Clawless and intact males also differed significantly in the method used to finally acquire a burrow, with clawless males significantly less likely than intact males to evict a resident, instead searching out empty burrows (Table 2). Although clawless and intact males differed in the behaviours they engaged in while searching, overall, these results do not indicate a difference in the ability of each type of male to acquire a burrow. After obtaining a burrow, fewer clawless males than intact males fought neighbouring males. Conversely, more clawless than intact males fought neighbouring females, although this difference was not significant ($P=0.07$). Clawless and intact males did not differ significantly in the likelihood they would: fight wandering male or female crabs; be aggressively approached by male or female neighbours; seal the burrow entrance; or abandon the burrow. However, significantly more clawless than intact males were evicted from their burrows within the first hour of occupation (Table 2).

Table 1 Burrow search parameter values for clawless and intact males

	Median (lower, upper quartiles)		Mann–Whitney U	Effect size (<i>r</i>)	<i>P</i> value
	Clawless males	Intact males			
Search duration (sec)	1,068 (382, 2381)	846.5 (329, 1629.8)	682	−0.13	0.26
Distance travelled (cm)	215 (87.4, 504.1)	228 (120, 390)	772.5	−0.01	0.94
Burrows approached	9.5 (4, 21.8)	8 (4, 19.5)	754	−0.05	0.66

Can clawless males occupy a territory for as long a tenancy as intact males?

$P=0.05$), even after controlling for the effect of pair identity ($LLR=5.55$, $P=0.02$).

In replaced pairs, intact males were no more likely to have a longer burrow tenancy than clawless males (clawless 54%; intact 46%; $P=0.85$). There was no difference in the likelihood that they seal their burrow entrance within the first 30 min of occupancy (clawless 13/24; intact 9/24; $G_1=1.35$, $P=0.25$). Crabs that sealed their burrow entrance were slightly more likely to be the longer tenant than crabs that did not seal, but this result was not significant (sealed 14/22; didn't seal 10/26; $G_1=3.05$, $P=0.08$).

Are clawless males more cautious than intact males following a threat?

Clawless and intact males did not differ in the time they took to re-emerge following retreat from a threat ($F_{1, 36}=0.84$, $P=0.36$). This result is not due to inaccuracy in measurement as there was significant repeatability in re-emergence time among individual males (log likelihood ratio=3.87, $df=1$,

Discussion

Burrow acquisition

While clawless male *U. annulipes* were not observed to actively mimic female behaviour, resident males courted wandering clawless males and wandering females equally. This was clearly different to their response to intact males, who were rarely courted. This suggests that clawless males are misidentified as females by male crabs. Whether males always perceive clawless males as female is unclear, although it is likely that at short range, cues besides the presence or absence of a major claw would indicate the sex of an individual. It is common in systems of mimicry for only one of multiple signals to be deceptive. For example, in Augrabies flat lizards (*Platysaurus broadleyi*), young males mimic females visually, but can still be identified as male by

Table 2 Incidence of aggressive, defensive, and other territorial behaviours in tracking and subsequent 1-h observations of clawless and intact males

	Observed/total		Likelihood ratio	Effect size (<i>r</i>)	<i>P</i> value
	Clawless males	Intact males			
Burrow-searching					
Fought males	14/40	38/40	15.58	0.670	<0.001
Fought females	29/40	19/40	5.28	−0.260	0.02
Acquired burrow by evicting resident	6/39	27/39	24.65	0.562	<0.001
1st hour of occupation					
Fought male neighbours	2/36	16/39	14.41	0.440	<0.001
Fought female neighbours	8/36	3/39	3.24	−0.209	0.07
Fought male intruders	13/36	18/39	0.78	0.101	0.38
Fought female intruders	3/36	1/39	1.28	−0.130	0.26
Aggressively approached by male neighbours	7/34	13/35	2.33	0.182	0.13
Aggressively approached by female neighbours	6/34	2/35	2.49	−0.187	0.12
Sealed burrow entrance	17/36	11/39	2.9	−0.196	0.09
Abandoned burrow	1/36	6/39	3.9	0.217	0.06
Evicted from burrow by intruder	11/36	4/39	4.95	−0.257	0.026

their scent (Whiting et al. 2009). While courting males were deceived, we found no evidence that clawless males exploited the advantage of their mistaken identity with behavioural mimicry of females.

Compared to intact males, burrow-searching clawless males fought significantly less often with resident males. Our observations suggest this was less a function of resident males' inability to recognise clawless males than of the tendency of clawless males to avoid approaching burrows owned by males (personal observation). Clawless males did not directly obtain burrows by deceiving male residents. On the single observed occasion when a resident male allowed a clawless male to enter his burrow, the resident followed the clawless male into the burrow as would happen in a successful mate-attraction event. At this point, the two crabs appeared to reach a stalemate in the burrow entrance where they both remained stationary for at least 2 h, when the tide covered the burrow and the observation had to be terminated.

Clawless males exhibited very different burrow acquisition methods to intact males, but they did not differ significantly in search duration, travel distance, or the number of burrows approached. This suggests that the strategy adopted by males that have lost their claw (that is, locating empty burrows rather than fighting to evict residents) is as successful as the normal male burrow-searching strategy. This raises a question: why do intact males fight and evict residents to obtain burrows, when they could instead search out abandoned burrows at no apparent extra cost? One reason might be that wandering intact males, unlike clawless males, present an obvious threat to residents, and are therefore less able to avoid fights initiated by defensive resident males. Such an unsolicited increase in fights could simply result in more opportunities to win burrows through fighting. However, this seems insufficient to explain the far greater likelihood that intact males evict a resident. Furthermore, intact males evicted both male and female residents in equal numbers, and resident females are unlikely to initiate fights with wandering males. Finally, previous studies and our observations suggest that territorial fights are mainly initiated by wandering males (e.g., Jennions and Backwell 1996).

Another explanation for the differences observed is that the burrow-searching strategy employed by clawless males could impose costs not measured in our study. For example, the quality of a male's burrow is an important criterion assessed by females searching for mates in *U. annulipes* (Backwell and Passmore 1996), and burrow structural qualities can be affected by factors such as substrate composition (Lim 2006). Abandoned burrows may be damaged or of poor structural quality, or situated in resource-depleted or otherwise lower quality habitat. Consequently, for an intact male, it might be worth the cost of fighting to acquire a high-quality, well-situated burrow.

Burrow ownership

In the first hour after obtaining a burrow, clawless and intact males did not differ in the number of aggressive approaches from neighbours of either sex, but clawless males had significantly fewer fights with male neighbours, suggesting there are some key behavioural differences between clawless and intact males. Clawless males might initiate fewer fights with male neighbours, and/or exhibit greater caution than intact males, retreating as soon as a neighbouring male displays aggression to avoid any escalation of the encounter. While our experimental results showed that clawless males were not more cautious than intact males after exposure to a threat, the threatening stimulus presented was like that of a potential predator rather than a conspecific competitor. Although studies of other fiddler species have found higher predation on both males (*Uca beebei*, Koga et al. 2001) and females (*U. pugilator*, Bildstein et al. 1989), sex biased predation has not been shown in *U. annulipes* (Walker 1972), suggesting the predator-avoidance benefits of hiding for longer would not differ for *U. annulipes* with or without a major claw.

Once resident, clawless and intact males did not differ in the number of fights they had with wandering males or females. However, clawless males were more frequently evicted by wandering crabs, indicating they were more likely to lose these fights when they occurred. Despite this vulnerability, clawless males do not appear to be specifically targeted by burrow-searching individuals. Differences in the burrow quality of clawless and intact males might contribute to the pattern observed. If clawless males tend to occupy poorer quality burrows, the benefit from evicting a clawless male is reduced as well as the cost. Depending on their own condition, intruders could therefore be choosing between two roughly equal strategies: reduced costs for reduced benefits or increased costs for greater gain.

Our tracking observations showed that newly resident clawless males had a greater likelihood of eviction within the first hour of burrow occupancy. The replacement experiment, however, showed that clawlessness did not predict shorter burrow tenancy. These apparently contradictory results could be explained by the greater (though not significant) likelihood for intact males to abandon a burrow. The method we used to assess burrow tenancy did not allow for a detailed examination of the reasons for departure from a burrow, and was only intended to provide a broad measure of the general ability of each male type to retain a burrow.

In summary, clawless male *U. annulipes* experience reduced aggression from males, which might be a result of their temporary resemblance to females. However, we found no evidence that clawless males mimic the behaviour of females, or that they exploit the advantage of their

mistaken identity. Even so, an incidental resemblance to females decreases aggression directed at burrow-searching clawless males, increasing the probability that they will survive to regenerate a claw. Clawless males further appear to avoid male aggression by altering their territorial strategies to minimise the potential for conflict.

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