Dishonest signalling in a fiddler crab

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Animal communication theory predicts that low-frequency cheating should be common in generally honest signalling systems. However, perhaps because cheats are designed to go undetected, there are few examples of dishonest signals in natural populations. Here we present what we believe is the first example of a dishonest signal which is used commonly by males to attract mates and fight sexual rivals. After losing their large claw, male fiddler crabs (*Uca annulipes*) grow a new one which has less mass, is a less effective weapon and costs less to use in signalling than an equivalent-length claw of the original form. Males with original claws do not differentially fight males with regenerated claws even though they are likely to win. Regenerated claws effectively bluff fighting ability and deter potential opponents before they fight. During mate searching, females do not discriminate against males with low-mass, regenerated claws, indicating that they are deceived as to the true costs males pay to produce sexual signals. Up to 44% of males in natural populations have regenerated claws, a level unanticipated by current signalling theory. The apparent rarity of cheating may be an artefact of the usual difficulty of detecting cheats and dishonesty may be quite common.

Keywords: cheating; dishonesty; signalling

1. INTRODUCTION

During courtship and aggressive interactions, the interests of the senders and receivers of signals often conflict (Johnstone 1997). Males should use the cheapest signals that are effectively transmitted and perceived. However, males that differ greatly in condition can produce cheap signals, making it difficult for receivers to assess a signaller's quality as a mate or his fighting ability reliably. Selection should therefore favour receivers who respond to expensive signals. Since receivers' responses determine whether signals evolve, most sexual and aggressive signals should be costly, honest indicators of male quality (Zahavi 1975; Berglund *et al.* 1996). Limits to the accurate assessment of signals make cheating possible, but only at low frequencies (Dawkins & Guilford 1991; Johnstone & Grafen 1993; Johnstone 1994), so that the cost of being deceived balances the benefit of reduced assessment.

Empirical studies demonstrating cheating of sexually selected signals are rare. Some authors have been able to create cheats experimentally (Rohwer & Rohwer 1978; Rohwer 1985; Fugle & Rothstein 1987; Veiga 1993), but there is only a single case of a natural bluff of fighting ability (Steger & Caldwell 1983) and no clear examples of naturally occurring dishonest mate choice signals. This is not surprising since there are logistic and conceptual problems in demonstrating cheating: cheats are designed to go unnoticed. Even if you identify an individual with a disproportionately large signal for its underlying quality, it is unclear how you can differentiate this from natural variation in the relationship between signal size and male quality. We have found a system in which this is possible. Following claw loss, most fiddler crab species regenerate a claw that is identical in form to the original (Crane 1975). In *Uca annulipes* and a few other fiddler crab species

(Yamaguchi 1973; Crane 1975), males instead regenerate claws that are lighter, more slender and less robust (leptochelous) than the original claws (brachychelous). For a given claw length, leptochelous claws have a smaller muscle mass than do brachychelous claws and they may thus be weaker and less effective weapons. Previous work has suggested that males use claw length in assessing an opponent's fighting ability (Jennions & Backwell 1996) and claw length is a predictor of mating success (Backwell & Passmore 1996). Here we investigate whether long but weak leptochelous claws are dishonest signals to both male and female conspecifics.

The fiddler crab *U. annulipes* lives in mixed-sex colonies on intertidal mudflats. Males use their single, greatly enlarged claw to fight other males and to attract females with a waving display. The major claw length, waving rate, velocity of the wave down stroke and leadership in groups of synchronously waving males all affect male sexual attractiveness (Backwell & Passmore 1996; Backwell *et al.* 1998, 1999). Receptive females visit several males before staying in a male's burrow for mating and oviposition (Backwell & Passmore 1996). The male then abandons his burrow, leaving it to his mate. Males also leave their burrows to feed elsewhere, leading to frequent male–male fights for burrow ownership.

2. METHODS

We studied a population of *U. annulipes* in the Saco de Inhaca, Inhaca Island, Mozambique, from July to December 1998. All work was carried out on a 100 m × 50 m intertidal mudflat. For statistical analysis, the data used in all multiple ANCOVAs were log transformed, outliers were removed and the α coefficient levels were adjusted using Bonferroni's correction. The results of all *G*-tests are presented with William's correction. When non-significant results were obtained, the power of the test was determined for a medium effect using the method outlined in Cohen (1988).

(a) *Brachychelous and leptochelous claw characteristics*

We collected and measured males of the two claw types. The males were collected by digging up seven $1\,m \times 1\,m$ plots and by catching surface-active individuals. Using dial calipers with a $0.1\,mm$ accuracy, we measured the carapace width and the following claw parameters: propodus length (hereafter referred to as claw length), dactyl length (movable finger) and manus length (palm). The measurements were highly repeatable (see Backwell & Passmore 1996). Claws were defined as leptochelous ($n = 614$) or brachychelous ($n = 1084$) based on the presence or absence of tubercles on the pollex and dactyl, respectively. ANCOVA was used to test for differences in the dactyl and manus lengths using claw length as the covariate.

We collected 20 males of each claw type, paired for claw length (difference in claw length $< 0.2\,mm$). We caused the males to autotomize their claws, which we then dried at $60\,°C$ for 24 h, and recorded their mass on a Mettler AE 163 balance with $0.001\,g$ accuracy. We used a paired t-test to compare the dry mass of equivalent length brachychelous and leptochelous claws.

(b) *Claw regeneration*

To determine whether leptochelous claws were a result of claw regeneration, we captured and marked (individually numbered plastic tags glued to the carapace) males with brachychelous claws. We caused them to autotomize their major claw and housed them for five months in cages on the mudflat within the boundaries of the natural population. The males were housed either in individual cages (30 cm high aluminium meshing buried in the sediment to a height of 15 cm, forming a round cage with a diameter of 30 cm; a solid ring around the open cage top prevented most males from escaping) or in a communal cage of 30 males (same design but a $1\,m \times 1\,m$ square). After five months we recaptured as many males as possible (escape prevented the recapture of some males) ($n = 14$ from the individual cages and $n = 12$ from the communal cage). Using the claw parameters above, we compared the claws that were regenerated by these caged males with the claws of leptochelous males in the population.

To determine whether the differences between leptochelous and brachychelous claws are permanent, we captured, measured, marked and housed leptochelous males (as above) for five months. We remeasured the claws after five months ($n = 42$ initial readings and $n = 29$ final readings) and compared the initial and final morphology using ANCOVA.

(c) *Male–male aggression*

We located 100 pairs of fighting males by searching the mudflat for naturally occurring fights which had reached the grappling stage. We then captured both males and identified their claw type. Using a goodness-of-fit G-test, we compared the proportions of same and different claw-type fights in the population to those expected if males initiate fights without regard to claw type.

We also collected 21 pairs of size-matched (claw length within $0.2\,mm$) males with the two claw types and allowed each of them 24 h to establish a burrow in an individual field cage (as described above). One size-matched brachychelous male was then released into each of the 42 cages. We observed each cage to determine whether the males engaged in a fight and identified the winner as the male that had possession of the burrow after the fight was complete. Using a G-test, we compared the proportion of fights won by the resident male when he was leptochelous to those won by brachychelous residents.

Finally, we captured and measured and then released 30 males of each claw type into the population of males. We followed these males and recorded the time elapsed and distance they travelled until they obtained a new burrow, the number of fights they had and whether they won their new burrow in a fight or occupied an empty one. We used t-tests to look for differences in time, distance and number of fights. We used a G-test to determine whether there was a difference in the proportion of leptochelous and brachychelous males which fought for new burrows or occupied empty burrows.

(d) *Female choice*

We tracked 61 mate-searching females (see Backwell & Passmore (1996) for details of the methods), catching each male visited by the female and, where possible, catching the male that was eventually chosen as a mate ($n = 39$). Using a G-test, we determined whether females visited leptochelous and brachychelous males in the proportion they were encountered in the population as a whole. We then determined whether females mated with leptochelous and brachychelous males in the same proportion that they visited them, again using a G-test.

(e) *Proportion of leptochelous males in three populations*

We collected 689 males that were active on the surface within the population of waving males during the periods of peak mating activity. We measured their carapace widths and claw lengths and noted whether they were leptochelous or brachychelous. We also selected two other spatially isolated populations of *U. annulipes* on Inhaca Island: one from the Station Mangrove and the other from the Airstrip Mangrove. We collected and measured males as above ($n = 431$ for the Station Mangrove and $n = 446$ for the Airstrip Mangrove) and calculated the proportion of leptochelous and brachychelous males in each of these populations.

3. RESULTS

(a) *Brachychelous and leptochelous claw characteristics*

Corrected for claw length, brachychelous claws had a longer manus than leptochelous claws (table 1 and figures 1 and 2). Although there was heterogeneity in the slopes of the regression lines of dactyl length for the brachychelous and leptochelous males, the lines intersected at a claw length of $489.39\,mm$. At all biologically meaningful claw lengths ($\leqslant 36\,mm$), leptochelous claws had longer dactyls than did brachychelous claws (table 1 and figures 1 and 2).

The leptochelous claws were significantly lighter than equivalent length brachychelous claws (paired t-test: leptochelous, $\bar{x} = 0.33\,g$ and s.d. $= 0.12$; brachychelous, $\bar{x} = 0.41\,g$ and s.d. $= 0.15$) ($n = 20$ pairs, $t = 4.99$ and $p < 0.001$).

(b) *Claw regeneration*

Corrected for claw length, the claws regenerated after autotomy did not differ from the population sample of leptochelous males in either manus or dactyl length (table 2) (power $= 70\%$). Regenerated claws differed from the population sample of brachychelous males for manus

Table 1. *Brachychelous* (*n* = *1082*) *and leptochelous* (*n* = *578*) *claw characteristics*

($\bar{x}$ (CI) = adjusted least-squares means (mm) and 95% confidence intervals.)

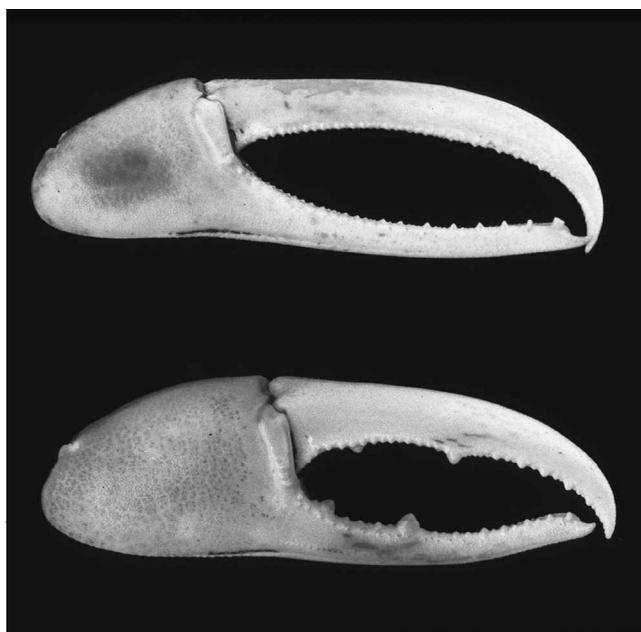|	brachychelous $\bar{x}$ (CI)	leptochelous $\bar{x}$ (CI)	interaction F (p)	effect F (p)
dactyl length	15.00 (14.00–16.00)	16.37 (15.37–17.38)	11.55 (0.001)	3026.81 (< 0.001)
manus length	10.64 (9.64–11.65)	9.66 (8.66–10.67)	1.89 (0.170)	2348.11 (< 0.001)

Figure 1. Leptochelous (top) and brachychelous (bottom) claws.

length (table 2). There was heterogeneity in the slopes of the regression lines of dactyl length for the regenerated and brachychelous claws. However, the intersection of the slopes was at 46.16 mm. At all biologically meaningful claw lengths ($\leqslant$36 mm), regenerated claws had longer dactyls than the claws of brachychelous males in the population (table 2). From this we conclude that leptochelous claws are the result of claw regeneration following claw autotomy. The same conclusion was reached by Yamaguchi (1973) for the brachychelous and leptochelous claws of a closely related fiddler crab *Uca lactea*.

The difference between the claw types appears to be permanent. Leptochelous males remeasured after five months showed no difference in manus length (initial readings $\bar{x}$(CI) = 10.74 mm (9.73–11.75) and *n* = 42 males and final readings $\bar{x}$(CI) = 10.72 mm (9.66–11.78) and *n* = 29 males) (interaction *F* = 0.85 and *p* = 0.36 and effect *F* < 0.00 and *p* = 0.99). There was also no difference in dactyl length between the initial and final readings (initial reading $\bar{x}$(CI) = 18.92 mm (17.91–19.93) and *n* = 42 males and final readings $\bar{x}$(CI) = 19.05 mm (18.03–20.07) and *n* = 25 males) (interaction *F* = 2.92 and *p* = 0.09 and effect *F* = 0.69 and *p* = 0.41).

(c) *Male–male aggression*

In naturally occurring fights, we found no difference between the observed proportions of the same and different claw-type fights and those expected if males initiate fights without regard to claw type (leptochelous–leptochelous, observed = 5 and expected = 3.9; brachychelous–brachychelous, observed = 69 and expected = 64; leptochelous– brachychelous, observed = 26 and expected = 32) (goodness-of-fit *G*-test *G* = 1.07, d.f. = 2, *p* = 0.58, *n* = 100 fights and power = 77%). Burrowless males did not preferentially challenge leptochelous residents.

Leptochelous males are competitively inferior. In forced fights, all of the brachychelous males (*n* = 21/21), but only 48% of the leptochelous males (*n* = 10/21) successfully defended their burrows during a fight with a brachychelous intruder (*G*-test: *G* = 18.33, d.f. = 1 and *p* < 0.001).

To determine whether leptochelous and brachychelous males differ in their ability to acquire new burrows, we released males individually on the mudflat. There was no significant difference between the two classes of males in the time they spent or the distance they moved before they acquired a new burrow, nor in the number of fights they initiated (*t*-tests: time *t* = 1.59 and *p* = 0.12, distance *t* = 0.56 and *p* = 0.58 and fights *t* = 1.52 and *p* = 0.14) (all d.f. = 29, all *n* = 30 and power all < 47%). However, there was a difference in how the males obtained new burrows. Most brachychelous males fought and won burrows (63%, *n* = 19/30) while most leptochelous males occupied empty burrows (70%, *n* = 21/30) (*G*-test: *G* = 6.66, d.f. = 1, *p* < 0.001 and *n* = 30).

(d) *Female choice*

The ratio of leptochelous to brachychelous males which attracted females to their burrows (0.20) did not differ from that expected based on the proportion of the two claw types in the surface-active population (0.21) (*G*-test: *G* = 0.17, d.f. = 1, *p* = 0.68, *n* = 175 and 689 and power = 99%). Furthermore, once a female visited a male, she was as likely to stay and mate with a leptochelous male (*n* = 14/40) as she was a brachychelous male (*n* = 25/135) (*G*-test: *G* = 2.05, d.f. = 1, *p* = 0.15 and power = 99%).

(e) *Proportion of leptochelous males in three populations*

The proportion of surface-active males with leptochelous claws varied between populations, ranging from 16 to 44% (Saco population 20.16% leptochely and *n* = 689 males; Airstrip population 15.92% leptochely and *n* = 446 males; Station population 44.08% leptochely and *n* = 431 males). In all three populations, there was a size-dependent increase in the frequency of leptochely, suggesting a greater cumulative probability of claw loss with male age (Saco population range = 7.5–45.2%, *r* = 0.85, *p* = 0.01 and *n* = 8 size classes; Airstrip population range = 11.1–26.2%, *r* = 0.86, *p* = 0.01 and *n* = 7 size
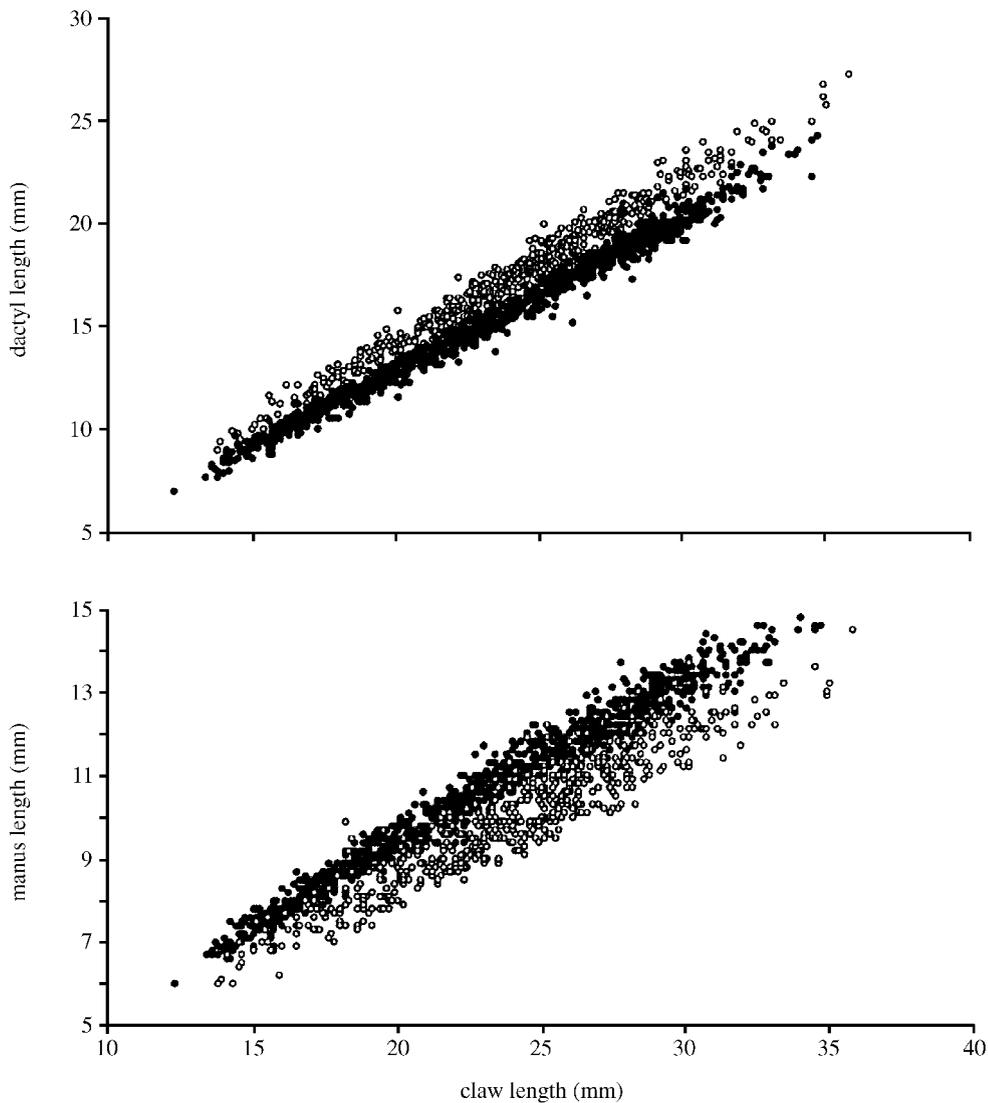
Figure 2. Dactyl and manus lengths of brachychelous ($n = 1082$) (filled circles) and leptochelous ($n = 578$) (open circles) claws.

Table 2. *Comparison between regenerated claws* ($n = 23$) *and brachychelous* ($n = 1081$)/*leptochelous* ($n = 596$) *claws in the population*

($\bar{x}$ (CI) = adjusted least-squares means (mm) and 95% confidence intervals.)

	leptochelous ($\bar{x}$ (CI))	regenerated ($\bar{x}$ (CI))	brachychelous ($\bar{x}$ (CI))	leptochelous/regenerated		brachychelous/regenerated	
				interaction F (p)	effect F (p)	interaction F (p)	effect F (p)
dactyl length	16.83 (15.83–17.83)	16.87 (15.85–17.88)	14.73 (13.73–15.73)	3.22 (0.07)	0.44 (0.51)	7.74 (0.005)	211.73 (< 0.001)
manus length	9.71 (8.69–10.73)	9.84 (8.84–10.85)	10.52 (9.52–11.52)	0.05 (0.83)	1.23 (0.27)	1.40 (0.24)	130.33 (< 0.001)

classes; Station population range = 17–67%, $r = 0.99$, $p < 0.01$ and $n = 6$ size classes).

4. DISCUSSION

In our study population of *U. annulipes*, 79% of males had heavy, robust major claws with a short dactyl, a large manus and pronounced tubercles in the gape (brachychelous). However, the rest (21%) had more delicate, lighter claws with a long dactyl, a much smaller manus and reduced tubercles (leptochelous). Leptochelous claws are grown following claw autotomy. The regenerated leptochelous claw form appears to be permanent since leptochelous claws remeasured after five months had not become more brachychelous in form. Further evidence for this comes from the size-dependent increase in the frequency of leptochely, which is presumably due to the greater cumulative probability of claw loss with male age.

For a given claw length, leptochelous claws must deliver a weaker gripping force than do brachychelous claws since the muscles in the manus close the pincers with a force at the tip which decreases with increasing dactyl length (Elner & Campbell 1981). They should thus be a less effective weapon in fights for burrows in which males forcefully grasp each other's claws. We tested whether leptochelous males are indeed less competent fighters by forcing size-matched males of the two claw types to fight a size-matched, brachychelous intruder. Leptochelous males are significantly less likely to win a fight with a similar-sized brachychelous male than are brachychelous males. Leptochelous males are thus competitively inferior.

Burrowless male *U. annulipes* tend to fight resident males with similar-sized but slightly smaller claws, probably because claw length predicts fighting success (Jennions & Backwell 1996). Presumably, males visually assess the fighting ability of potential opponents using claw length as a signal of strength. If males use claw type to assess an opponent's fighting ability, they should preferentially fight weaker, leptochelous males. We therefore compared the proportions of same and different claw-type fights in the population with those expected if males initiate fights without regard to claw type. We found no difference between the observed and expected proportions, indicating that burrowless males do not preferentially challenge leptochelous males. Long but weak leptochelous claws are therefore an effective visual bluff of fighting ability. Instead of regrowing a brachychelous claw after claw loss, males grow a less costly leptochelous claw that is indistinguishable from the original to males during pre-fight visual assessments of opponents.

Are the benefits to leptochelous males of bluffing fighting ability balanced by the costs during mate choice? To determine whether leptochelous males are less attractive as mates, we tracked mate-searching females. The ratio of leptochelous to brachychelous males that attracted females to their burrows did not differ from that expected based on the proportion of the two claw types in the population. Furthermore, once a female visited a male she was as likely to stay and mate with a leptochelous male as she was with a brachychelous male. Leptochelous males pay a lower cost of producing a signal which is just as attractive to females as that produced by males with more costly brachychelous claws. For example, since leptochelous claws have a lower mass than brachychelous claws, leptochelous males use less energy to wave at a given rate. Thus, even when in relatively poor condition compared with brachychelous males, leptochelous males can wave at the same rate. By choosing a leptochelous male, females are less reliably mating a male in good condition. This means that they are also less reliably mating with males providing a range of benefits which are generally positively associated with phenotypic condition and larger sexual traits (Møller & Alatalo 1999). If this positive association exists in *U. annulipes*, then leptochelous claws are dishonest signals of the fitness benefits females may enjoy when they mate with brachychelous males.

Leptochely can occur at very high frequencies within a population. As many as 44% of surface-active males can have leptochelous claws. Cheating is predicted by theory (Dawkins & Guilford 1991), but not at these high levels as the benefits are thought to decline rapidly as the frequency of cheats in the population increases (Dawkins & Guilford 1991; Johnstone & Grafen 1993; Johnstone 1994).

If negative frequency-dependent selection does not limit leptochely, what does and why do males first invest in the more costly brachychelous form of the major claw? We have shown that leptochelous males are more likely to lose their burrows. To determine whether they pay higher costs in finding a new one we released males of each claw type and followed them until they established a new residence. There were no significant differences between the two classes of males in the time they spent and distance they moved before they found a new burrow, nor in the number of fights they initiated. However, there was a difference in how males obtained new burrows. Most brachychelous males fought and won burrows while most leptochelous males occupied empty burrows. Final mate choice is based on burrow quality (Backwell & Passmore 1996). Since females do not discriminate against leptochelous males in mate choice, the empty burrows these males occupy are no lower in quality for mating and breeding (Backwell & Passmore 1996). Hence, neither the process nor the outcome of searching for new burrows seems to be more costly for leptochelous than brachychelous males. A higher frequency of burrow loss for leptochelous males is the only cost that seems to favour the brachychelous claw form. Small males are, on average, more often involved in fights since there are more males in the population that are slightly larger than them. The increased benefits of having a brachychelous claw when small may therefore select for the initial production of this robust claw form. As males grow, the relative frequency of fighting decreases and brachychely may be less advantageous. Moreover, larger males spend more time waving (Jennions & Backwell 1998). Thus, should claw loss occur, this may select for the development of a leptochelous claw that is less costly to wave.

Naturally occurring signal dishonesty is difficult to demonstrate, particularly when the variation in the trait occurs along a continuum. The discrete dimorphism between cheaters and honest signallers in this study allowed us to identify dishonest signallers easily. We were therefore able to show that leptochelous claws effectively bluff fighting ability as well as deceiving females as to the true costs males pay in order to produce courtship signals. The results of this study imply that cheating may be common but usually undetectable.

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