

What are the consequences of being left-clawed in a predominantly right-clawed fiddler crab?

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Male fiddler crabs (genus *Uca*) have an enlarged major claw that is used during fights. In most species, 50% of males have a major claw on the left and 50% on the right. In *Uca vocans vomeris*, however, less than 1.4% of males are left-clawed. Fights between opponents with claws on the same or opposite side result in different physical alignment of claws, which affects fighting tactics. Left-clawed males mainly fight opposite-clawed opponents, so we predicted that they would be better fighters due to their relatively greater experience in fighting opposite-clawed opponents. We found, however, that (i) a left-clawed male retains a burrow for a significantly shorter period than a size-matched right-clawed male, (ii) when experimentally displaced from their burrow, there is no difference in the tactics used by left- and right-clawed males to obtain a new burrow; however, right-clawed males are significantly more likely to initiate fights with resident males, and (iii) right-clawed residents engage in significantly more fights than left-clawed residents. It appears that left-clawed males are actually less likely to fight, and when they do fight they are less likely to win, than right-clawed males. The low-level persistence of left-clawed males is therefore unlikely to involve a frequency-dependent advantage associated with fighting experience.

Keywords: frequency-dependent; laterality; sexual selection; male–male competition; mate choice; polymorphism

1. INTRODUCTION

A partial explanation of the ‘lek paradox’ is that negative frequency-dependent selection maintains additive genetic variation for sexually selected traits (Pryke & Griffith 2006; Zajitschek *et al.* 2006). Female guppies, for example, prefer males with rare colour patterns, which might explain why males are highly polymorphic for coloration (Farr 1977; Eakley & Houde 2004). Traits that increase male attractiveness are also often used as weapons (e.g. antlers and horns) and negative frequency-dependent selection during fights might similarly maintain variation. In many species, males with large weapons compete directly for females, while others pursue alternative mating tactics. This can lead to discrete male morphs with frequency-dependent reproductive success. For example, in the dung beetle, *Onthophagus taurus*, horned males fight for access to females while hornless males sneak matings. Paternity tests show that the *per capita* success of hornless males declines as their frequency increases (Hunt & Simmons 2002).

The costs and benefits of being a rare morph have been extensively investigated in humans, where individuals who define themselves as left-handed are in the minority in all populations (Raymond & Pontier 2004; Faurie *et al.* 2005). Left-handedness confers an advantage

in interactive sports like tennis or boxing (Raymond *et al.* 1996; Brooks *et al.* 2004), but not when opponents compete indirectly (e.g. athletics or swimming). This is presumably because the population-level bias creates an asymmetry in the experience contestants have with opposite-handed opponents. Left-handers are rare so they more often compete against opposite-handed opponents. It has even been suggested that population variation in the proportion of left-handers reflects differences in the intensity of selection on males to win fights (Faurie & Raymond 2005). Controversially, there is also some evidence that left-handedness is costly, such as greater susceptibility to diseases (e.g. Geschwind & Behan 1982) or accidents (e.g. Coren & Halpern 1991), although other large-scale studies have reported no such effects (Steenhuis *et al.* 2001; Abel & Kruger 2004). In principle, however, the eventual handedness ratio should depend on both negative frequency-dependent selection and any frequency-independent costs of left-handedness (Billiard *et al.* 2005).

Many animals preferentially use one appendage for specific tasks (Bisazza *et al.* 1996; Lonsdorf & Hopkins 2005) and behavioural laterality (unequal use of one side of the body) occurs in numerous contexts. For example, *Junco hyemalis* birds prefer to use their right eye to scan for predators (Franklin & Lima 2001), individual New Caledonian crows consistently hold tools on the same side of their beak (Rutledge & Hunt 2004) and different toad species consistently prefer to jump to the same side

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when escaping predators (Lippolis *et al.* 2002). In some cases, behavioural laterality is associated with strong morphological asymmetry (e.g. Hori 1993). Fiddler crabs (genus *Uca*) offer a textbook example because in all 92 species, males have a single enlarged claw on either the left or right. This major claw is used as a weapon and, in most species, is also waved at females during courtship. In 90 species, left- and right-clawed males are equally common and their fighting and mating behaviour is indistinguishable, implying either no selection or negative frequency-dependent selection on laterality (e.g. Jennions & Backwell 1996; Pratt *et al.* 2003). In two species, however, 91–99% of males are right-clawed (*Uca vocans* and *Uca tetragonon*). To date, no one has examined the consequences of morphological asymmetry in these species.

There is some evidence that handedness is heritable in humans (McManus 1991) but less information on behavioural laterality in other animals (but see Bisazza *et al.* 2000; Hopkins *et al.* 2006). In contrast, many morphological asymmetries are heritable (e.g. Hori 1993), although in the 90 species of *Uca* where left- and right-clawed males are equally common it has been suggested that claw asymmetry is not heritable. Experiments show that when a juvenile loses a claw it regenerates into a smaller feeding claw, while the other claw develops into the major claw. Loss is presumably random with respect to body side (Morgan 1923; Ahmed 1976; Yamaguchi & Henmi 2001). This proximate mechanism does not readily explain the bias in right-clawed species, although the existence of these species implies that there once was, and might still be, heritable variation in the likelihood of directional claw loss.

Fights between two male fiddler crabs whose major claws are on the same or opposite sides are very different. This could have important fitness effects. When males fight they first face each other, touch claws and push each other. Often one male will then retreat but, if the fight escalates, they interlock claws and grapple. During fights, only males of opposite clawedness can align their claws from base to apex. There might therefore be a difference in the ability to judge a rival's strength when claws are lined up in the same or the opposite direction (figure 1). When grappling, the claws of males of opposite clawedness interlock in front of their bodies, while those with the same clawedness must extend their claws away from the body before interlocking (figure 1). This clearly influences fighting style and could affect the outcome if males differ in their experience in engaging in each type of fight.

Here we test for possible morphological and behavioural differences between left- and right-clawed males in the fiddler crab *Uca vocans vomeris*. This species is reported to have 96–99% right-clawed males (McNeil 1920; Williams & Heng 1981; Jones & George 1982). Owing to their rarity, left-clawed males should be relatively more experienced at fighting opposite-clawed males. We therefore predict that they will have a clear advantage during fights. However, the fact that they are rare suggests that there are frequency-independent costs associated with being left-clawed. We therefore tested whether left-clawed males display behaviours associated with lower fitness (e.g. less time spent on surface feeding or less likely to attract females).

2. MATERIAL AND METHODS

(a) Study species

Our study species is often designated *Uca vocans dampieri*, a subspecies of the widespread *U. vocans*. Some authors elevate the six subspecies to species status, but the phylogenetic relationships and taxonomy of fiddler crabs are poorly resolved. Salmon (1984) conducted relevant behavioural work on *Uca vocans vomeris* in Townsville, Queensland. We can clearly demonstrate that the population in Darwin is identical to that of *U. v. vomeris* in Townsville for 500 bp of the 16S RNA mitochondrial gene (see Sturmbauer *et al.* 1996; J. S. Keogh & P. R. Y. Backwell unpublished data).

We studied *U. v. vomeris* in Darwin, Australia from October to December in 2004 and 2005. Crabs live in mixed-sex colonies on intertidal mudflats. Every crab owns a burrow that provides a refuge during high tide. At low tide, crabs emerge to feed on organic matter in the mud around their burrow. Aggressive interactions and courtship occur throughout the low-tide period. The enlarged major claw of males is used during fighting but, unlike other fiddler crabs, it is less clear whether males wave to attract females (Nakasone *et al.* 1983). Courting males stroke females with their legs or minor claw, but mating is seldom preceded by claw waving (Salmon 1984). Unusually for a fiddler crab, females do not seem to search for mates (Christy & Salmon 1984, 1991). Instead, males visit females and mate at the burrow entrance (Nakasone *et al.* 1983; Salmon 1984). Underground matings inside burrows have been documented, but it is unclear whether these were in male or female burrows (Nakasone *et al.* 1983). Females are continuously receptive and mate multiply, but only do so with a few of the many males that court them.

When a male courts a female at the burrow entrance of the female, it either approaches a nearby female and later returns to its burrow ('sallying'), or permanently leaves its burrow to seek out females ('aggressive wanderer'; see Salmon 1984). Aggressive wanderers can spend most of the low-tide period moving through the population, fighting resident males and searching for females. They settle only in a burrow towards the end of the low-tide period. These males have a higher encounter rate with females, which tends to increase their mating success (Salmon 1984), but they also make contact with more males than with non-wandering residents. Wanderers fight resident males for burrows and larger males more often win these encounters. The benefits are unclear though as wanderers invariably move on and allow the original resident to reclaim its burrow. A common mating tactic used by resident males is to back up to a wandering female and push it towards their burrow entrance ('herding'). The success of herding at our study site is low. We have not seen it lead to a mating in three seasons of observations. It might, however, be the way in which mating in burrows is initiated (Nakasone *et al.* 1983).

(b) Density, body size, laterality and claw morphology

We demarcated 64 plots (1 m²) haphazardly placed throughout the population. We then captured and measured the carapace width and claw length of all males within each plot and noted their clawedness ($n = 423$). Systematic collection of all males in each plot ensures unbiased information on the size distribution of males of each claw type. We also actively searched for left-clawed males and similar-sized right-clawed males to study claw morphology in greater depth. We then

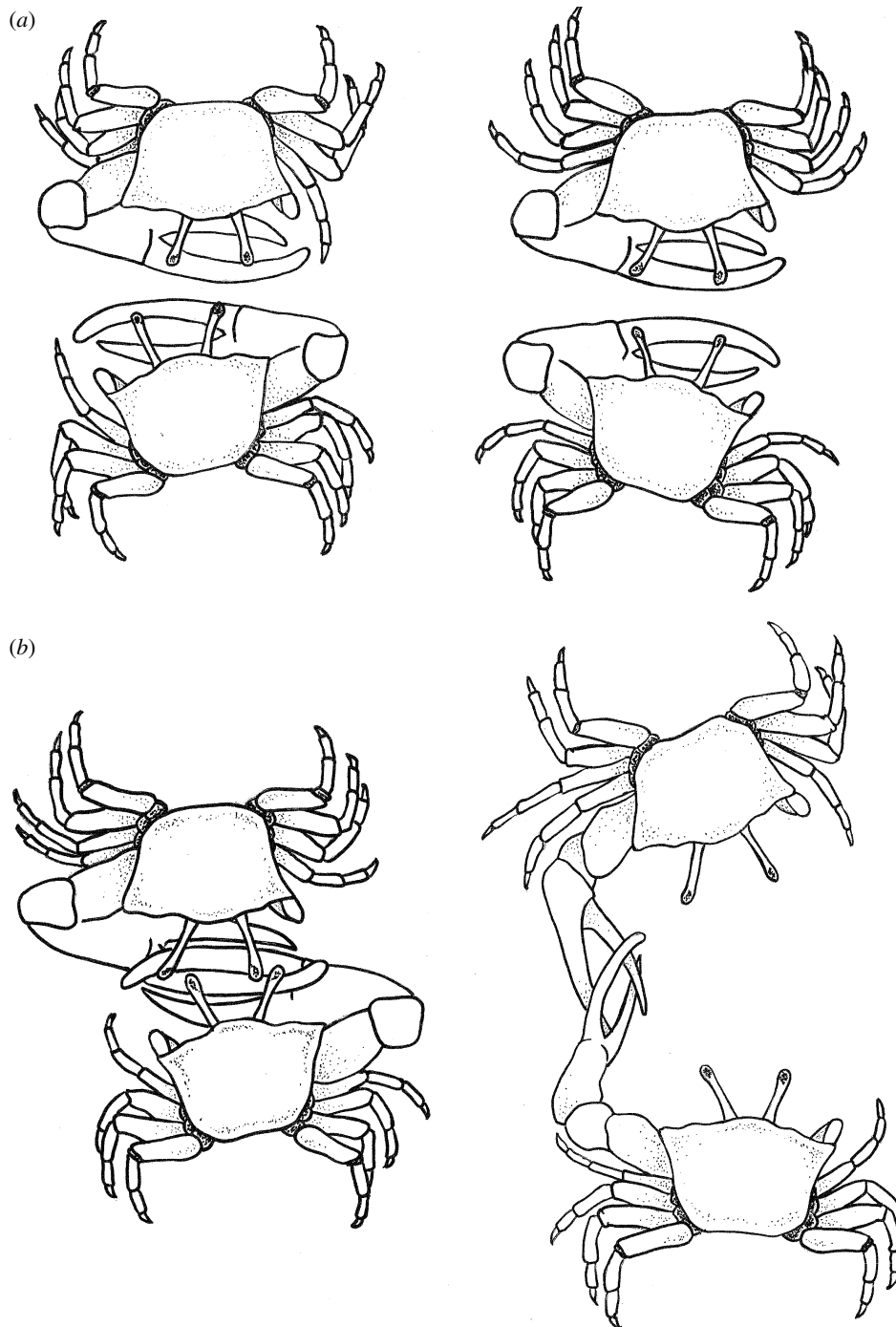


Figure 1. The difference in claw alignment during (a) the pushing phase and (b) the grappling phase of fights between two males of the same or opposite clawedness.

measured carapace width and seven claw parameters for 30 left-clawed and 30 right-clawed males (claw, dactyl and manus length; manus and dactyl height; pollex shelf length; manus width) and used MANOVAs to investigate potential differences. First, we treated carapace width as a covariate and the seven claw measures as dependent variables. Second, we treated claw length as a covariate and the other six claw measures as dependent variables. All measurements were log-transformed.

Left-clawed males were rare (approx. 1.4%, see §3). Sample sizes for all subsequent experiments therefore represent a major effort to obtain data (e.g. on average, to capture 30 left-clawed males, we had to assess 2150 crabs in an area of 326 m²). We were further constrained by the need to match males by size (which affects fighting behaviour) and

location (as density, crab size and sex ratios vary spatially). This greatly increased the area and number of crabs we had to survey to find suitable left-clawed males.

(c) *Burrow tenancy*

To test whether left-clawed males are better at defending their burrow, we located 26 pairs of size-matched males of opposite clawedness that held burrows less than 2 m from each other but were not immediate neighbours so they did not interact. Size was matched by eye (in a pilot study, $r_1 = 0.90$, $n = 20$ pairs). We marked both burrows with small flags. Males have distinct carapace patterns that we photographed for individual identification. We then documented which focal male was the first to leave its burrow by opportunistically checking male identity when the burrow occupant was surface active. We

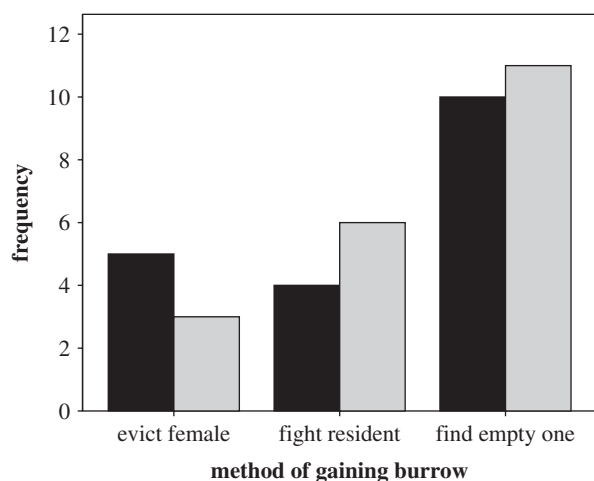


Figure 2. The number of released left- and right-clawed males that obtained a new burrow in each of three possible ways (both $n=19, 19$). ■, left-clawed; ▒, right-clawed.

used a binomial test to determine whether left- or right-clawed males were more likely to leave their burrow first. We assume that longer residency indicates increased fighting ability (but see §4).

(d) Success as wandering males: experimental release trials

To test whether left-clawed males are more likely to win fights when wandering, we captured, measured and released 19 size-matched pairs of left- and right-clawed males onto the mudflat. We then monitored them until they acquired a burrow. We alternated between releasing a left- and a right-clawed male, but both males from a given pair were released at the same site. We documented how each male obtained a new burrow (fought a male, evicted a female or occupied an empty burrow). We also noted how long it took to obtain a burrow and how many times each male (i) fought with resident males, (ii) had a non-contact interaction with another male, (iii) interacted with females and (iv) entered burrows. We used a log-likelihood ratio (LLR) test to determine whether left- and right-clawed males obtained burrows in the same way. We used Wilcoxon matched-pairs tests to compare the time until burrow acquisition and the number of interactions or burrows entered.

(e) Success as a resident

To test whether left-clawed males are better fighters, or have lower success at gaining mates, we located another 35 pairs of left- and right-clawed males using the same criteria described for the burrow tenancy study. We recorded male behaviour for 30 min with alternating instantaneous scans at 1 min intervals (15 scans per male). We used LLR tests to compare the proportion of males that (i) engaged in mating activities (courted/mated), (ii) fought and (iii) retreated into their burrow. We compared the proportion of scans during which a male engaged in each activity using Wilcoxon matched-pairs tests.

(f) Fight outcome

We did not document the fighting success of left-clawed males in experimentally staged fights because they avoided initiating fights in a pilot study. We therefore used the natural fights that

occurred during our 30 min observation. We documented 37 fights involving 13 left-clawed and 24 right-clawed residents who all fought right-clawed, wandering males.

Unless otherwise stated, summary statistics are presented as mean \pm s.d. and tests are two-tailed ($\alpha=0.05$). The approximate power to detect a medium strength effect was calculated for $\alpha_2=0.05$ using tables for equivalent parametric tests in Cohen (1988).

3. RESULTS

Within the sixty-four 1 m² plots, we located 423 males. The mean population density was 6.61 males m⁻² (range 1–18). The mean carapace width of males was 9.66 ± 3.11 mm, mean claw length was 10.20 ± 5.83 mm and the two measures were highly correlated ($r=0.98$, $p<0.001$, $n=423$). Only 6 out of 423 males were left-clawed (1.4%). They spanned the full population size range and were not confined to a particular size class. Using the 60 males (30 of each clawedness) for which we had all seven claw measurements, there were no detectable morphological differences between left and right claws, regardless of whether we controlled for carapace width or claw length (MANOVAs; carapace: $F_{7,51}=0.602$, $p=0.751$; claw: $F_{6,52}=0.332$, $p=0.917$). Using the combined dataset of 483 males, we could test with greater statistical power for any effect of clawedness on the relationship between the carapace width and the claw size. There was no difference in the slope ($F_{1,479}=1.84$, $p=0.176$) or elevation ($F_{1,480}=0.20$, $p=0.888$) of the relationship for left- and right-clawed males (both $n=36, 447$). Thus, left and right claws do not differ in absolute size relative to body size or in shape for a given claw length.

In 10 out of the 26 pairs of left- and right-clawed resident males that we located, we could not tell which male left its burrow first because both were replaced by a new male between the same successive observations. In 13 out of the 16 remaining pairs, the right-clawed male retained its burrow for a longer period of time (Binomial test, $p=0.021$).

There was no difference in the way in which left- and right-clawed wandering males obtained a new burrow ($G_2=1.78$, $p=0.41$; figure 2). There was also no significant difference in the time taken to acquire a burrow, the number of burrows entered or the number of non-contact interactions with other crabs (power $\approx 32\%$). However, right-clawed males initiated significantly more fights with resident males ($p=0.03$, table 1).

There was no difference in the proportion of left- and right-clawed resident males that attempted to mate (LLR=2.97, $p=0.09$; 5/35 versus 11/35) or that fought (LLR=1.48, $p=0.22$; 12/35 versus 17/35), nor in the rate at which left- and right-clawed males attempted to mate (power $\approx 54\%$) but, on average, right-clawed males engaged in a greater number of fights ($p=0.04$, table 2). Although the proportion of time spent inside the burrow did not differ for left- and right-clawed males (power $\approx 54\%$; table 2), fewer right-clawed males entered their burrow (LLR=3.97, $p=0.046$; 18/35 versus 26/35). The likelihood that a fight ending with the resident winning was unaffected by clawedness (LLR=0.22, $p=0.64$; 10/13 versus 20/24; power $\approx 31\%$).

Table 1. Behavioural differences (mean \pm s.d.) between released males prior to obtaining a new burrow ($n=19$, 19). (The p -values from Wilcoxon matched-pairs tests. Values are in bold if $p < 0.05$.)

	time taken to obtain a burrow (min)	non-contact interactions with males	interactions with females	burrows entered	fight with resident males
left-clawed male	3.37 \pm 2.86	1.63 \pm 1.71	0.53 \pm 0.61	2.32 \pm 2.33	0.42 \pm 0.77
right-clawed male	3.91 \pm 2.76	2.53 \pm 2.23	0.68 \pm 0.67	2.47 \pm 1.61	0.95 \pm 1.03
Z	0.72	1.34	0.88	0.80	2.16
p	0.47	0.18	0.38	0.43	0.03

4. DISCUSSION

Although most male *U. v. vomeris* possess a major claw on the right, approximately 1.4% of males were left-clawed. This value is similar to that reported in other populations (0% of 34 males, McNeil 1920; 4% of 644 males, Williams & Heng 1981; 2.7% of 2784 males, Barnwell 1982 and 1% of 417 males, Jones & George 1982). The existence of the predominantly right-clawed species *U. vocans* and *U. tetragonon* makes it plausible that, given a common underlying proximate mechanism, there are heritable genetic differences for the propensity to develop a major claw on one side of the body between them and other *Uca* species. By extension, it seems probable that there is, or at least was ancestrally, additive genetic variation for morphological asymmetry in claw growth.

Directional asymmetry in a sexually dimorphic trait used during fights raises two obvious questions. First, why do left-clawed males still occur? Second, are there any selective advantages or disadvantages of this rare phenotype? When there is some additive genetic variation for claw asymmetry, then left- and right-clawed males should have equal fitness at equilibrium frequencies. In *U. v. vomeris*, this would involve negative frequency-dependent selection that favours left-clawedness for some components of fitness, combined with frequency-independent costs so that the equilibrium frequency is not one to one.

Studies of contests in humans reveal an advantage of being left-handed because its rarity means that they have greater experience fighting opposite-handed opponents (Raymond *et al.* 1996). This experiential advantage is further magnified in any species where there is a 'winner effect' such that previous fight outcome affects the outcome of subsequent fights (Hsu *et al.* 2006; Rutte *et al.* 2006). In *U. v. vomeris*, we therefore predicted that left-clawed males would have a fighting advantage. When defending or fighting for a burrow, they should be more likely to engage in fights than retreat or pursue alternate tactics. They should also be more likely to win fights. To our surprise, however, three separate lines of evidence indicate that left-clawed males are *less* successful.

First, right-clawed males retained their burrow for a significantly longer period of time than left-clawed males, which implies that left-clawed males are worse fighters. Some males do, however, voluntarily leave their burrow to search for females, so these data provide only circumstantial evidence that right-clawed males are better at defending burrows. Second, when males were experimentally removed from their burrow and forced to wander, there was no difference in the tactics used by left- and right-clawed males to obtain a new burrow. However, right-clawed males were significantly more likely than left-clawed males to initiate fights with resident males.

Table 2. Behavioural differences (mean \pm s.d.) between residents ($n=35$, 35). (The p -values from Wilcoxon matched-pairs tests. Values are in bold if $p < 0.05$.)

	number of mating attempts	number of fights	time spent in burrow
left-clawed male	0.22 \pm 0.65	0.37 \pm 0.55	2.20 \pm 2.91
right-clawed male	0.40 \pm 0.69	0.69 \pm 0.83	1.82 \pm 2.88
Z	0.95	2.05	0.88
p	0.34	0.04	0.38

Third, although resident males do not initiate fights with wanderers, right-clawed residents engaged in significantly more fights than left-clawed residents. This occurred because a significantly greater proportion of left-clawed males retreated into their burrow during focal observations thereby avoiding fights. If a fight did occur, however, there was no significant difference in the proportion won by left- and right-clawed residents.

We were unable to collect data on mating success, but there was no significant difference in the proportion of left- and right-clawed resident males that attempted to mate ($p=0.09$). Even so, right-clawed males were more than twice as likely to attempt to mate (31.4% versus 14.3%), so this trend is worthy of further investigation. In addition, Salmon (1984) showed that males which were more likely to mate also made more forays away from their burrow and more often engaged in fights. In our study, right-clawed males initiated more fights when wandering, were less likely to retreat into their burrow when resident and fought more often when residents. This all implies that right-clawed males are more likely to mate.

Our data did not reveal a left-clawed fighting advantage in *U. v. vomeris*. In fact, although our data are limited due to the inherent rarity of left-clawed males, these males seem to be less likely to fight than right-clawed males. There are at least three possible explanations for this. First, there might be positive frequency-dependent selection on fighting success for right-clawed males. Although possible, we can think of no plausible reason why this should be the case. Second, the rarity of left-clawed males and their reduced fighting ability might be causally related. It is possible that left-clawedness is associated with a developmental pathway that affects general performance. If so, this might explain the rarity of left-clawed males. The main argument against this explanation is, however, that there is no difference in the relative size and shape of left and right claws. There was also no obvious trend for left-clawed males to be smaller than right-clawed males, suggesting that, given indeterminate growth, there is no difference in longevity between the morphs. Third, it might

be easier to assess an opponent's strength when it is of the same clawedness (Hyatt & Salmon 1978). As such, left-clawed males might be generally inclined to avoid fights as they are more likely to escalate an encounter with a larger opponent which they are unlikely to defeat.

The persistence of left-clawed males in *U. v. vomeris* is puzzling. The simplest explanation is to dismiss it as an aberration with no heritable basis. One could argue that it arises due to accidental early loss of the right claw in young crabs, forcing them to switch from the usual developmental pathway of right-claw production to producing a major left claw. We note, however, that published reports and our own informal observations of many populations of *U. v. vomeris* indicate that left-clawed males occur at about the same level (1–4%) in most populations. We would argue that this is too consistent a phenomenon and, from a long-term evolutionary perspective, too common a morph to be so readily dismissed with a non-adaptive explanation. A strong bias towards right-clawed males in *U. v. vomeris* has probably evolved from an ancestral species with an equal ratio of left- to right-clawed males, which makes us hesitant to assume that claw laterality is not heritable. As with any trait seemingly associated with below-average fitness that persists at similar but very low frequencies in many populations, an adaptive explanation is worthy of further investigation (for a similar case of an extremely rare, but heritable, male morph, see Pryke & Griffith (2007)).

This research conformed to the ethical guidelines of The Australian National University.

We thank R. Milner for reading a draft and J. Keogh for drawing figure 1. Funding was provided by an ARC Discovery grant (to P.R.Y.B.). This study was also supported by a Grant-in-Aid for Scientific Research (C) (no. 14540584) from the Japan Society for the Promotion of Science (JSPS).

REFERENCES

- Abel, E. L. & Kruger, M. L. 2004 Left-handed major-league baseball players and longevity re-examined. *Percept. Mot. Skills* **99**, 990–992. (doi:10.2466/PMS.99.7.990-992)
- Ahmed, M. 1976 Study of normal and aberrant sexual types of Venezuelan fiddler crabs *Uca cumulanta* and *Uca rapax*. *Bull. Mar. Sci.* **26**, 499–505.
- Barnwell, F. H. 1982 The prevalence of male right handedness in the Indo-west Pacific fiddler crabs, *Uca vocans* (Linnaeus) and *U. tetragonon* (Herbst) (Decapoda: Ocypodidae). *J. Crust. Biol.* **2**, 70–83. (doi:10.2307/1548114)
- Billiard, S., Faurie, C. & Raymond, M. 2005 Maintenance of handedness polymorphism in humans: a frequency-dependent selection model. *J. Theor. Biol.* **235**, 85–93. (doi:10.1016/j.jtbi.2004.12.021)
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L. J. & Vallortigara, G. 1996 Right-pawedness in toads. *Nature* **379**, 408. (doi:10.1038/379408a0)
- Bisazza, A., Facchin, L. & Vallortigara, G. 2000 Heritability of lateralization in fish: concordance of right–left asymmetry between parents and offspring. *Neuropsychologia* **38**, 907–912. (doi:10.1016/S0028-3932(00)00018-X)
- Brooks, R., Bussiere, L. F., Jennions, M. D. & Hunt, J. 2004 Sinister strategies succeed at the cricket World Cup. *Proc. R. Soc. B* **271**(Suppl.), S64–S66. (doi:10.1098/rsbl.2003.0100)
- Christy, J. H. & Salmon, M. 1984 Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biol. Rev. Camb. Phil. Soc.* **59**, 483–509.
- Christy, J. H. & Salmon, M. 1991 Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *Am. Zool.* **31**, 329–337.
- Cohen, J. 1988 *Statistical power analysis for the behavioral sciences*, 2nd edn. Mahwah, NJ: Lawrence Erlbaum Assoc, Inc.
- Coren, S. & Halpern, D. F. 1991 Left-handedness: a marker for decreased survival fitness. *Psychol. Bull.* **109**, 90–106. (doi:10.1037/0033-2909.109.1.90)
- Eakley, A. L. & Houde, A. E. 2004 Possible role of female discrimination against 'redundant' males in the evolution of colour pattern polymorphism in guppies. *Proc. R. Soc. B* **271**(Suppl.), S299–S301. (doi:10.1098/rsbl.2004.0165)
- Farr, J. A. 1977 Male rarity or novelty, female choice behavior, and sexual selection in guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae). *Evolution* **31**, 162–168. (doi:10.2307/2407554)
- Faurie, C. & Raymond, M. 2005 Handedness, homicide and negative frequency-dependent selection. *Proc. R. Soc. B* **272**, 25–28. (doi:10.1098/rspb.2004.2926)
- Faurie, C., Schiefenhover, W., Le Bomin, S., Billiard, S. & Raymond, M. 2005 Variation in the frequency of left-handedness in traditional societies. *Curr. Anthropol.* **46**, 142–147. (doi:10.1086/427101)
- Franklin, W. E. & Lima, S. L. 2001 Laterality in avian vigilance: do sparrows have a favourite eye? *Anim. Behav.* **62**, 879–885. (doi:10.1006/anbe.2001.1826)
- Geschwind, N. & Behan, P. 1982 Left-handedness: association with immune disease, migraine, and developmental learning disorder. *Proc. Natl Acad. Sci. USA* **79**, 5097–5100. (doi:10.1073/pnas.79.16.5097)
- Hopkins, W. D., Wesley, M. J., Russell, J. L. & Schapiro, S. J. 2006 Parental and perinatal factors influencing the development of handedness in captive chimpanzees. *Dev. Psychobiol.* **48**, 428–435. (doi:10.1002/dev.20165)
- Hori, M. 1993 Frequency-dependent natural-selection in the handedness of scale-eating cichlid fish. *Science* **260**, 216–219. (doi:10.1126/science.260.5105.216)
- Hsu, Y. Y., Earley, R. L. & Wolf, L. L. 2006 Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biol. Rev. Camb. Phil. Soc.* **81**, 33–74. (doi:10.1017/S146479310500686X)
- Hunt, J. & Simmons, L. W. 2002 Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle *Onthophagus taurus*. *J. Evol. Biol.* **15**, 784–795. (doi:10.1046/j.1420-9101.2002.00442.x)
- Hyatt, G. W. & Salmon, M. 1978 Combat in fiddler crabs *Uca pugilator* and *Uca pugnax*—quantitative analysis. *Behaviour* **65**, 182–211.
- Jennions, M. D. & Backwell, P. R. Y. 1996 Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* **57**, 293–306. (doi:10.1006/bjil.1996.0017)
- Jones, D. S. & George, R. W. 1982 Handedness in fiddler crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda, Ocypodidae). *Crustaceana* **43**, 100–102.
- Lippolis, G., Bisazza, A., Rogers, L. J. & Vallortigara, G. 2002 Lateralisation of predator avoidance responses in three species of toads. *Lateralality* **7**, 163–183.
- Lonsdorf, E. V. & Hopkins, W. D. 2005 Wild chimpanzees show population-level handedness for tool use. *Proc. Natl Acad. Sci. USA* **102**, 12 634–12 638. (doi:10.1073/pnas.0505806102)
- McManus, I. C. 1991 The inheritance of left-handedness. *CIBA Found. Symp.* **162**, 251–281.
- McNeil, F. A. 1920 Studies in Australian carcinology. No 1. *Rec. Aust. Mus.* **13**, 105–109.
- Morgan, T. H. 1923 The development of asymmetry in the fiddler crab. *Am. Nat.* **57**, 269–273. (doi:10.1086/279921)

- Nakasone, Y., Akamine, H. & Asato, K. 1983 Ecology of the fiddler crab *Uca vocans vocans* (Linnaeus) (Decapoda: Ocypodidae) II: relation between the mating system and the drove. *Galaxea* **2**, 119–133.
- Pratt, A. E., McLain, D. K. & Lathrop, G. R. 2003 The assessment game in sand fiddler crab contests for breeding burrows. *Anim. Behav.* **65**, 945–955. (doi:10.1006/anbe.2003.2152)
- Pryke, S. R. & Griffith, S. C. 2006 Red dominates black: agonistic signaling among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. B* **273**, 949–957. (doi:10.1098/rspb.2005.3362)
- Pryke, S. R. & Griffith, S. C. 2007 The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *J. Evol. Biol.* **23**, 1512–1521. (doi:10.1111/j.1420-9101.2007.01332.x)
- Raymond, M. & Pontier, D. 2004 Is there geographical variation in human handedness? *Laterality* **9**, 35–51.
- Raymond, M., Pontier, D., Dufour, A. B. & Møller, A. P. 1996 Frequency-dependent maintenance of left handedness in humans. *Proc. R. Soc. B* **263**, 1627–1633. (doi:10.1098/rspb.1996.0238)
- Rutledge, R. & Hunt, G. R. 2004 Lateralized tool use in wild New Caledonian crows. *Anim. Behav.* **67**, 327–332. (doi:10.1016/j.anbehav.2003.07.002)
- Rutte, C., Taborsky, M. & Brinkhof, M. W. G. 2006 What sets the odds of winning and losing? *Trends Ecol. Evol.* **21**, 16–21. (doi:10.1016/j.tree.2005.10.014)
- Salmon, M. 1984 The courtship, aggressive and mating system of a “primitive” fiddler crab (*Uca vocans*). *Trans. Zool. Soc. London* **37**, 1–50.
- Steenhuis, R. E., Ostbyte, T. & Walton, R. 2001 An examination of the hypothesis that left-handers die earlier: the Canadian study of health and aging. *Laterality* **6**, 69–75. (doi:10.1080/13576500042000025)
- Sturmbauer, C., Levinton, J. S. & Christy, J. 1996 Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. *Proc. Natl Acad. Sci. USA* **93**, 10 855–10 857. (doi:10.1073/pnas.93.20.10855)
- Williams, M. J. & Heng, P. K. 1981 Handedness in males of *Uca vocans* (Linnaeus, 1758) (Decapoda, Ocypodidae). *Crustaceana* **40**, 215–216.
- Yamaguchi, T. & Henmi, Y. 2001 Studies on the differentiation of handedness in the fiddler crab, *Uca arcuata*. *Crustaceana* **74**, 735–747. (doi:10.1163/156854001317015562)
- Zajitschek, S. R. K., Evans, J. P. & Brooks, R. 2006 Independent effects of familiarity and mating preferences for ornamental traits on mating decisions in guppies. *Behav. Ecol.* **17**, 911–916. (doi:10.1093/beheco/ar1026)