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Alternative mating tactics and male mating success in two species of fiddler crab

Miranda L. Dyson[†] & Patricia R.Y. Backwell*

[†] Department of Environment, Earth & Ecosystems, The Open University, Milton Keynes, United Kingdom.

* Research School of Biology, The Australian National University, Canberra ACT 0200, Australia

Corresponding author: Miranda Dyson

Email: miranda.dyson@open.ac.uk

Telephone: +44 (0) 1908 653398

Running Title: mating tactics in fiddler crabs

Key words: male mating success; fiddler crab; alternative mating tactic

Abstract

1
2 The use of alternative male mating tactics can determine the strength of sexual selection on male
3 traits and have implications for sexual dimorphism. We examine size-based mating success in two
4 species of fiddler crabs where males use each of two alternative tactics to obtain matings. In *Uca*
5 *annulipes*, larger males were more successful when using the primary mating tactic (burrow mating)
6 but the full size range of males mated when using the secondary tactic (surface mating). In *Uca*
7 *urvillei*, both burrow and surface mating males were larger than the average sized male in the
8 population. Standardised directional selection gradients indicated that selection on male size was
9 stronger in *U. urvillei* than *U. annulipes*, reflecting the differences between species in male mating
10 success. Our results also showed that sexual size dimorphism was greater in the species with stronger
11 sexual selection on male size than in the species with weaker sexual selection. (150 words)
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Introduction

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3 Males and females of many animals use more than one tactic to obtain mates (Gross, 1996; Oliveira
4 et al., 2008; Taborsky, 1994), however alternative mating tactics are best known for males
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6 (Brockmann, 2001). The tactic adopted by individual males can be genetically determined and fixed
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8 over adult lifetime, or facultative, where individuals switch between tactics. The switch can be
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10 sequential, with one tactic used early in life and the other tactic later (e.g. blue headed wrasse, Gross,
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12 1982), or the tactics can be used simultaneously, with males switching between tactics within a
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14 breeding cycle or even a single breeding event (e.g. Guppies, Magurran & Seghers, 1994). In
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16 species, where switching between tactics is facultative and simultaneous, a male's decision to switch
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18 from one tactic to another can be determined by several factors including the availability of mates,
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20 the number of competitors present, population density, predation risk and female choosiness (Gross,
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22 1996; Henson & Warner, 1997; Ribeiro et al., 2010).
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32 The potential to use two different mating tactics can have profound evolutionary consequences. If
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34 male mating success depends on different, uncorrelated traits for each tactic, then a greater variety of
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36 males will mate and the strength of sexual selection will be low. If the same male traits determine
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38 mating success in both tactics, then there will be less variation in the trait for mated males. Mating
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40 success will be more highly skewed to those males with the traits that make them successful in both
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42 tactics, increasing the strength of sexual selection on those traits. In species where male size affects
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44 mating success and where growth is indeterminate, the strength of sexual selection is likely to affect
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46 sexual size dimorphism: strong sexual selection on male size would result in a greater degree of
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48 sexual size dimorphism compared to species with weaker sexual selection.
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57 Fiddler crabs comprise a group of nearly 100 species that occur in sub-tropical and warm temperate
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59 regions throughout the world. Sexual dimorphism is strong, with males having a greatly enlarged
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1 (sometimes brightly coloured) claw that females lack. In 15 species individual males use two tactics
2 in an attempt to secure matings with females (Ribeiro et al., 2010) and switch between tactics in a
3 facultative way during a single breeding cycle (Murai et al., 1987; Nakasone & Murai, 1998; Ribeiro
4 et al., 2010; deRivera & Vehrencamp, 2001; Christy & Schober, 1994; Christy & Salmon, 1984;
5 Yamaguchi, 2001). The primary tactic is active courtship which involves waving the enlarged claw
6 in attempt to attract the female into the male's own burrow (burrow mating). Waving is directed at
7 females that have left their own burrows to wander through the population of courting males
8 (Christy, 1987; Christy & Schober, 1994; Murai et al., 1987; Backwell & Passmore, 1996). After
9 approaching a male, the female follows him into his burrow then either remains to mate or leaves and
10 continues searching. If the female remains, the male enters the burrow and plugs it. Mating occurs
11 underground. The male guards the female for 1-4 days until she extrudes a clutch of eggs onto her
12 pleopods. The male then leaves, sealing the female in the burrow where she spends 12-20 days
13 incubating her eggs (e.g. Christy, 1987; Backwell & Passmore, 1996; Nakasone & Murai, 1998;
14 Yamaguchi, 2001; Reaney & Backwell, 2007). The secondary tactic males use to secure a mating is
15 to approach a feeding neighbouring female and attempt to mate with her on the surface, near her
16 burrow (surface mating). The male uses tactile signals, stroking the female with his legs and feeding
17 claw. Surface mating by males is unsolicited and mating attempts are sometimes unsuccessful, but if
18 the female is willing to mate she lowers her abdominal flap and allows copulation. After mating, the
19 male returns to his territory and both crabs resume feeding (Backwell & Passmore, 1996; deRivera &
20 Vehrencamp, 2001; Yamaguchi, 2001; Slatyer et al., 2012 and others). Surface mating is seldom
21 preceded by male courtship waving and it almost always occurs between crabs in neighbouring
22 territories (Murai et al., 1987; Nakasone & Murai, 1998; Yamaguchi, 2001).
23 Females always produce a clutch of eggs after burrow mating (Nakasone & Murai, 1998; Reaney et
24 al., 2012) but less frequently after surface mating (5% in *Uca mjoebergi*, Reaney et al., 2012; 11% in
25 *Uca perplexa*, Nakasone & Murai, 1998). Burrow mating is necessarily the last tactic used before
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1 fertilisation since males guard the female underground until she extrudes her eggs and can no longer
2 re-mate (Crane, 1975). Surface mating may result in fertilization but more often, females mate in a
3
4 male's burrow before ovulating.
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9 Studies on fiddler crabs have determined that male mating success in underground mating is
10 dependent on multiple factors including burrow characteristics (Backwell & Passmore, 1996, Reaney
11 & Backwell, 2007) wave rate (Reaney et al., 2008; Reaney, 2009) wave pattern (Backwell et al.,
12 1999; Milner et al., 2011; Kahn et al., 2014), UV (Detto & Backwell, 2009) and male size (Backwell
13 & Passmore, 1996; Nakasone & Murai, 1998; Reaney, 2009; Milner et al., 2011; Ribeiro et al., 2010;
14 Slatyer et al., 2012). Females of some species preferentially visit larger males but this preference can
15 vary with season (Reaney & Backwell, 2007; Milner et al., 2010) and also over a breeding cycle
16 (Backwell & Passmore, 1996). This variation is thought to reflect temporal changes in the costs of
17 and/or benefits of female mate choice.
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34 There are few studies that have examined whether, in fiddler crab species where males use both
35 tactics, size affects mating success in surface mating. Most studies have found that larger males
36 burrow mate more often than smaller males but that males of all sizes surface mate (Nakasone &
37 Murai 1998; Ribeiro et al., 2010; Slatyer et al., 2012). In some cases, however, there is no size
38 difference between surface mating and burrow mating males or between mated males and males in
39 the general population (Yamaguchi 2001). It has been suggested that surface and burrow mating
40 differ in their costs and benefits. Burrow mating is more likely to occur in small species living at
41 high densities in course-grained sediments (deRivera & Vehrencamp, 2001). Course-grain sediments
42 are thought to be beneficial since they transmit more oxygen than finer grained sediments. The
43 advantages of incubating in a male's deep burrow may only be feasible in oxygen-rich sediments
44 (deRivera & Vehrencamp, 2001). Density plays a role in the relative frequency of each tactic in *Uca*
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1 *uruguayensis* because the females' costs of searching for a mate are lower in high density
2 populations (Ribeiro et al., 2010) so they are less exposed to the risks associated with mate-searching
3 (e.g. predation, dehydration, overheating). At high densities, females may also benefit from leaving
4 their own territories to find a mate because they avoid the incessant attention from their male
5 neighbours in their high-density neighbourhood (Ribeiro et al., 2010).
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12 Clutch size may also influence the cost-benefit balance of the alternative mating tactics. In species
13 with small clutches, the eggs are fully protected by the abdominal flap and females are able to feed
14 on the surface during incubation without risking egg loss due to dehydration or abrasion (Henmi,
15 2003; Christy & Salmon, 1984). The quality of the incubation site would be less critical and
16 incubation may be equally successful in the male's or female's burrow (Henmi, 2003; Christy &
17 Schober, 1994; Christy & Salmon, 1984). In species with large broods, the eggs are much more
18 vulnerable since they protrude out of the abdominal flap. The quality of the incubation site should be
19 more important, and it may benefit females to search for males that have a burrow suitable for
20 incubation (see Christy & Salmon, 1984; Henmi, 2003).
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39 In this study we examine the mating systems of two South African species of fiddler crab, *U.*
40 *annulipes* and *U. urvillei*, both of which engage in surface and burrow mating. Our aim was to
41 determine the extent to which the use of alternative tactics by males affects their mating success. We
42 did this by determining the mean size of males that mated in their burrows and those that mated on
43 the surface. We then compared these with each other and with the mean size of males in the
44 population. If larger males are more successful when using either tactic, it should lead to a bias in
45 mating success towards large males and strong directional sexual selection on male size. However, if
46 large males are successful in one tactic but smaller males are more, or as successful in the other
47 tactic, there will be less skew in mating success with respect to male size, and directional sexual
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1 selection on size will be weaker. We also determined the population size distributions of females of
2 each species and compared sexual size dimorphism (the relative size of males to females) for each
3 species. The extent of sexual size dimorphism would be expected to differ depending of the strength
4 of sexual selection on male size.
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10 11 12 **1. Materials and Methods**

13 14 15 *2.1 Study Area.*

16 Data were collected from October 1992 to April 1993 at the Mangrove Conservation area of Durban
17 Harbour, South Africa (29°53'19"S; 31°00'45"E).
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22 23 24 *2.2 Population size distributions*

25 To determine the size distributions of male and female crabs, we demarcated areas of the exposed
26 mud flat using string. For *U. annulipes*, we demarcated four areas (300 x 20cm; 200 x 50cm; 200 x
27 50cm; 100 x 50cm) and collected a total of 147 males and 63 females. For *U. urvillei*, we demarcated
28 two areas (10 x 3m) and collected a total of 93 males and 69 females. We caught every sexually
29 mature crab within the plots and measured carapace width and claw length.
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38 39 40 *2.3 Size of burrow-mated males*

41 We located burrow matings by watching wandering females as they moved between courting males.
42 We caught males after they had sealed themselves underground with the females and measured their
43 carapace widths and claw lengths (when you remove the burrow plug, the male returns to the surface
44 to re-plug the burrow and can be easily caught). Immediately after measuring them, we placed them
45 back in the burrow and resealed it (unless we needed to use the *U. annulipes* burrow for another
46 study: see Backwell & Passmore 1996). We captured and measured 54 *U. annulipes* and 43 *U.*
47 *urvillei* burrow-mated males. The data collected on *U. annulipes* burrow matings (and the population
48 size distribution of *U. annulipes* males) were collected as part of another study (Backwell &
49 Passmore, 1996) but is reanalysed here.
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2.4 Size of surface-mated males

We collected and measured the males that we observed to surface mate. We approached the mating pair and watched the male as he decoupled and returned to his own burrow. We captured and measured him, and then returned him to his burrow ($n = 81$, *U. annulipes*; $n = 50$, *U. urvillei*).

Statistics: For both species we compared the mean sizes of the population, surface-mated and burrow-mated males using an ANOVA with LSD post-hoc tests. We ran the tests separately for carapace width, claw length and the size of the large claw relative to the carapace width (standardised residuals of claw length on carapace width). We calculated the linear standardised selection differentials (SSD) for claw length and carapace width for burrow-mated and surfaced mated males as well as for all mated males (burrow and surface mated) of each species. SSD was calculated as the mean trait value of the mated males – mean trait value of the population / standard deviation of the population (see Matsumura et al., 2012). We determined the size of males relative to females (sexual size dimorphism) for each species using a General Linear Model with carapace width as the dependent variable and sex and species as fixed factors. The residuals were normally distributed. The interaction term (sex*species) is a comparison of the sexual size dimorphism between the two species.

3. Results

3.1 Observations

In *U. annulipes*, burrow and surface mating are both common and easily observed. During burrow mating, females leave their territories and can sequentially visit up to 24 males (see, Backwell and Passmore, 1996) by approaching them and briefly entering their burrow. When a female selects a male, she enters his burrow followed by the male and if she does not re-emerge he returns to the surface and plugs the burrow entrance with sediment, sealing the pair underground. The female

1 remains underground to incubate a clutch of eggs after the male leaves. During surface mating, a
2 female that is feeding around her burrow entrance is approached by a neighbouring male (almost
3 always her closest neighbour). The female retreats to her burrow entrance, the male follows her and
4 touches her carapace and mouth area with his legs and feeding claw. If the female acquiesces by
5 lowering her abdomen, the pair mates on the surface very close the female's burrow entrance. After
6 mating, the male returns to his territory and both crabs resume feeding. Surface mating is not
7 preceded by male waving.
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19 Burrow and surface mating are also both common in *U. urvillei*. The population occurs within a
20 3.5m wide and ± 40 m long section of mudflat comprised of a sloping creek bank and the flatter
21 ground above it. Males have territories on the creek bank, in a strip of mud less than 1m wide and
22 parallel to the water, as well as on the flatter mudflat above the bank. Most females have territories
23 on the ± 2.5 m wide strip of flatter ground, very few live among the males on the creek bank. From six
24 months of observing this population, we found that, during the three-hour period before low tide
25 (falling tide) males and females stay in the vicinity of their territories. During the two hours after low
26 tide (rising tide), females (and a small number of males) leave their territories and walk down the
27 creek bank to the deep mud at the water's edge where they feed. In the last hour of the rising tide,
28 most females move back up the creek bank and onto the flatter area where they look for an empty
29 burrow. They occupy a burrow (on their own) until they leave again during the following falling tide.
30 Some females, leave the creek with the other females however, when they get to the area of male
31 burrows on the creek bank, walk along the length of the bank, among the waving males. These
32 females do not sequentially visit the burrows of multiple males, but walk straight to a single male
33 and enter his burrow. The male immediately seals the pair underground. All the burrow matings we
34 observed occurred in the last two hours of the rising tide. We also observed surface matings in both
35 the 'male zone' and in the higher 'female zone'. Males approached nearby resident females and
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1 touched their carapace and mouth areas. If the male was successful, mating took place on the
2 sediment surface very close to the female's burrow entrance.
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4 3.2 Male size and mating success 5

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7 In *U. annulipes*, the size (both carapace width and claw length) of the males that surface-mated were
8 no different to that of the males in the general population. However, burrow-mated males were larger
9 than both the surface-mated males and the general male population (Table 1 and 2; Figure 1). The
10 relative size of the large claw (standardised residuals of claw length on carapace width) did not differ
11 between the burrow-mated, surface-mated or population males (Table 2).
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21 In *Uca urvillei* there was no difference in the size (both carapace width and claw length) of males
22 that surface-mated or burrow-mated; but both categories of mated males were larger than the general
23 male population (Table 1 and 2; Figure 1). The relative size of the large claw (standardised residuals
24 of claw length on carapace width) did not differ between the burrow-mated, surface-mated or
25 population males (Table 2).
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41 The standardised selection differentials (Table 3) clearly show this pattern. There is strong
42 directional selection on male size (both carapace width and claw length) in burrow mating for both
43 species and in surface mating for *U. urvillei*. In surface mating for *U. annulipes*, there is weak
44 directional selection on male size. The selection differentials for all mated males (burrow- and
45 surface-mated) gives a more realistic measure of the total level of directional selection on males of
46 each species. From Table 3, it is evident that *U. urvillei* males are under strong directional selection
47 on both carapace width (SSD = 0.64) and claw length (SSD = 0.59) while *U. annulipes* is under
48 weaker directional selection for both measures of male size (SSD_{carapace} = 0.31; SSD_{claw} = 0.23).
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3.3 Sexual size dimorphism

In both species, males are larger than females with respect to carapace width and both male and female *U. urvillei* are a larger than male and female *U. annulipes* (GLM: sex F = 18.12, d.f. = 1; P < 0.001; species F = 336.24, d.f. = 1; P < 0.001). The interaction between sex and species was also significant (GLM: sex*species F = 10.37, d.f. = 1; P = 0.001) indicating that *U. urvillei* has a greater degree of sexual size dimorphism than *U. annulipes* (Fig. 2).

Figure 2 here

4. Discussion

Our results show that in both *U. annulipes* and *U. urvillei*, males that mated underground were significantly larger than the general population. This pattern has also been found in *U. uruguayensis* (Ribeiro et al., 2010), *U. mjoebergi* (Slatyer et al., 2012) and *U. perplexa* (Nakasone & Murai, 1998). In both species studied here, underground mating was initiated by females. In fiddler crabs, there is last male sperm precedence (Murai et al., 1987) so, by burrow mating with a male, the female ensures that he will father her offspring. In both *U. annulipes* and *U. urvillei*, burrow mating was preceded by vigorous courtship waving by males directed at females that wandered through the population. *U. annulipes*, females exhibited classic mate choice behaviour, visiting and rejecting several males before remaining to mate in the chosen male's burrow. This behaviour has been shown to result from females selecting males initially on the basis of male morphological traits (including size) and then on burrow quality (Backwell & Passmore, 1996). The selection of mates based on the quality of their burrows occurs in many other fiddler crab species (Christy, 1978; Christy, 1982; Christy, 1983; deRivera, 2005; Backwell & Passmore, 1996) and is thought to be due to the importance of the incubation site in successful larval development. In *U. urvillei*, although females burrow-mated with larger males, they did not visit and reject successive males after inspecting their

1 burrows (as in *U. annulipes*). They moved through the population of waving males, bypassing
2 several, and approaching the chosen male, entering his burrow and staying to mate. Since females
3 were never seen to reject the male after visiting his burrow, it can be assumed that females were not
4 selecting males on the basis of the characteristics of the burrow. Why would *U. annulipes* females
5 select mates based on their burrow quality but *U. urvillei* females not assess burrow quality? A
6 plausible answer is the difference in the clutch sizes of these two species. *U. annulipes* has large
7 clutches that protrude out of the abdominal flap and therefore require a burrow with a specific
8 microenvironment for successful incubation. *U. urvillei*, on the other hand, has small clutches that
9 are fully enclosed by the abdominal flap (Crane, 1975). It is likely therefore that incubation occurs
10 above ground while the females is actively foraging which negates the need for a burrow with a
11 specific microclimate for successful incubation

12 This study shows that for underground burrow mating, there is strong selection on male size in both
13 species. For *U. annulipes*, the selection differentials were 0.78 (carapace width) and 0.74 (claw
14 length); for *U. urvillei*, the selection differentials were 0.61 for both carapace width and claw length.

15 Surface mating in *U. annulipes* showed the same pattern found in many other fiddler crabs: surface-
16 mated male size did not differ from the size of males in the general population (Ribeiro et al., 2010;
17 Slatyer et al., 2012; Nakasone & Murai, 1998). In *U. mjoebergi*, a species that also has both mating
18 tactics, it was shown that burrow-mated males fertilised 98% of the clutch and the previously
19 surface-mated males fertilised only 2% of the eggs (Reaney et al., 2012). Surface mating is therefore
20 a low benefit tactic but since the male does not need to forfeit his burrow to the female, it is also a
21 low cost tactic. Why would females surface mate? It has been shown that surface-mating females
22 secured the help of their mated male neighbours in burrow defence (Slatyer et al., 2012). Females
23 appear to trade sex for protection and, since male neighbours are likely to be a random sample of the

1 male population, mating is indiscriminate with respect to size. In most fiddler crabs, including *U.*
2 *annulipes*, surface mating occurs between a female and one of her nearest male neighbours
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4 (Nakasone & Murai, 1998; Backwell & Passmore, 1996; Slatyer et al., 2012) and there is evidence
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6 that a female can be evicted by her neighbour after refusing to surface mate with him (*Uca lactea*,
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8 Murai et al., 1987). This would be a strong incentive for a female to surface mate neighbours,
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10 irrespective of their size, since even a small male is competitively superior to a clawless female
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12 (Booksmythe et al. 2010).
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19 In contrast, *U. urvillei* females surface-mated with the larger males in the population. This has not
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21 been found in studies of other fiddler crab species and it requires further investigation. Since surface
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23 mating occurred between a female and one of her nearest neighbours, there are two possible reasons
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25 for surface-mated males to be larger than the general population: (i) females live next to larger
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27 males; or (ii) females accept surface mating attempts from their larger (but not their smaller) male
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29 neighbours. In *Uca capricornis*, it has been shown that males defend empty burrows around their
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31 own territory and allow females to settle in those burrows (Mautz et al., 2011). Large males defend
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33 more empty burrows than small males and so larger males are more likely to be surrounded by
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35 females than are small males. It is possible that a system similar to this might explain how females
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37 could more often live next to larger males in *U. urvillei*. It seems less likely that females reject
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39 surface mating attempts from their smaller neighbours since this has not been found in any other
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41 fiddler crab species. Future work will examine this question.
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51 In *U. annulipes*, the alternate mating tactic (surface mating) did not favour larger males and the
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53 directional selection on male size was low (selection differentials of -0.11 and 0.00). The size range
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55 of males that mated (using both tactics) was therefore broad and this lowered the strength of sexual
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57 selection on male size: the selection differentials for all mated males (surface and burrow-mated)
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1 were 0.23 (CL) and 0.31 (CW). In *U. urvillei*, the opposite was true: in both surface and burrow
2 mating, large males were more successful. This results in a greater skew in male mating success and
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4 stronger directional selection on male size: the selection differentials for all mated males (surface and
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6 burrow-mated) were 0.59 (CL) and 0.64 (CW).
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11 Stronger sexual selection on male size should lead to greater sexual size dimorphism (John Christy,
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13 Pers. Comm.; see Soulsbury et al., 2014). Our results support this prediction in that in *U. urvillei*
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15 there is stronger sexual selection on male size and greater sexual size dimorphism than in *U.*
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17 *annulipes* where sexual selection on male size is weaker and sexual dimorphism less pronounced.
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25 However, the relationship between the strength of sexual selection on male size and sexual size
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27 dimorphism may not be straightforward in fiddler crabs. Due to last male sperm precedence (Murai
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29 et. al., 1987) fertilization success is likely to differ between surface and burrow mating. In *U.*
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31 *mjorbergi*, males that mate on the surface gain very low levels of paternity compared to males that
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33 mate in burrows (Reaney et al., 2012). For *U. urvillei*, the effect of this on the strength of selection
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35 would be small since selection differentials for both tactics are similar. For *U. annulipes*, however,
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37 the contribution of burrow matings to the total strength of directional selection on male size may be
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39 far greater than the contribution of surface matings; the strength of directional selection on male size
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41 would be stronger than that estimated from the combined differentials treating burrow and surface
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43 mating as equivalent. Future work should examine the relative contribution of surface and burrow
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45 mating to paternity in *U. annulipes*; and use the information to estimate a more accurate selection
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47 differential.
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58
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Table 1. Carapace width (CW) and claw length (CL) of males from the population; those that burrow-mated and those that surface mated.

Species	Male type	CW (cm) Mean (SD) N	CL (cm) Mean (SD) N
<i>U. annulipes</i>	Population	1.21 (0.23) 147	2.09 (0.65) 147
	Burrow-mated	1.39 (0.153) 54	2.57 (0.42) 54
	Surface-mated	1.21 (0.19) 81	2.02 (0.60) 81
<i>U. urvillei</i>	Population	1.96 (0.46) 93	2.73 (1.19) 93
	Burrow-mated	2.24 (0.33) 43	3.45 (0.95) 43
	Surface-mated	2.26 (0.37) 50	3.43 (1.07) 50

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Table 2. Results of ANOVAs and LSD (Least Significant Difference) post-hoc tests on size of population, surface-mated and burrow males. POP = population males; SM = surface-mated males; BM = burrow-mated males.

Species	Size measure	F (df)	P	LSD sub-sets		
				POP	SM	BM
<i>U. annulipes</i>	Carapace width	14.53 (2)	<0.001	*	*	< 0
	Claw length	16.24 (2)	<0.001	*	*	< 0
	Relative claw size	0.88 (2)	0.42	*	*	*
<i>U. urvillei</i>	Carapace width	11.98 (2)	<0.001	*	< 0	0
	Claw Length	9.60 (2)	<0.001	*	< 0	0
	Relative claw size	1.45 (2)	0.24	*	*	*

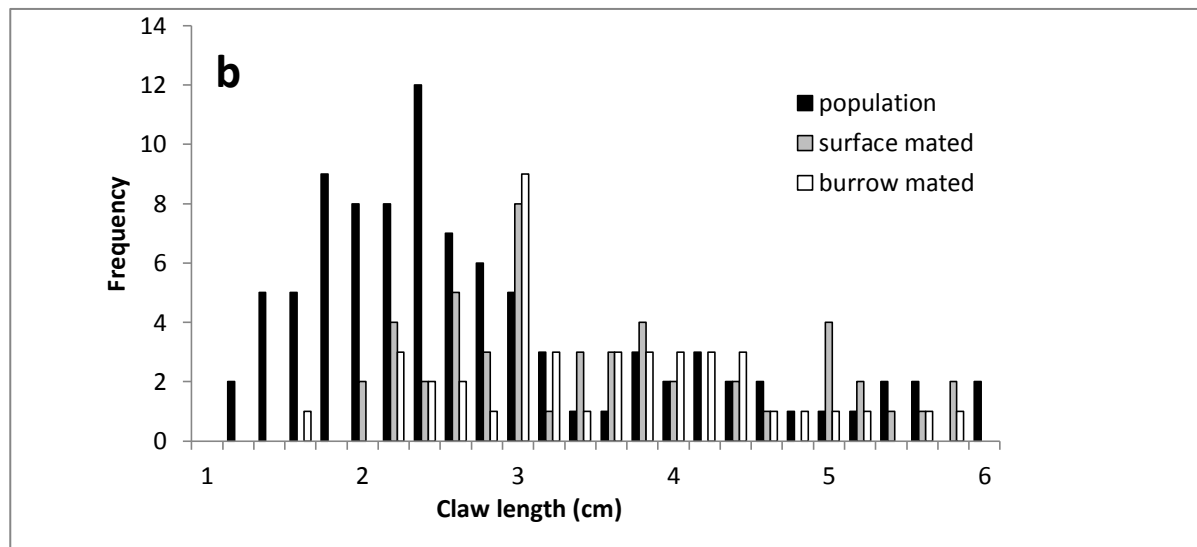
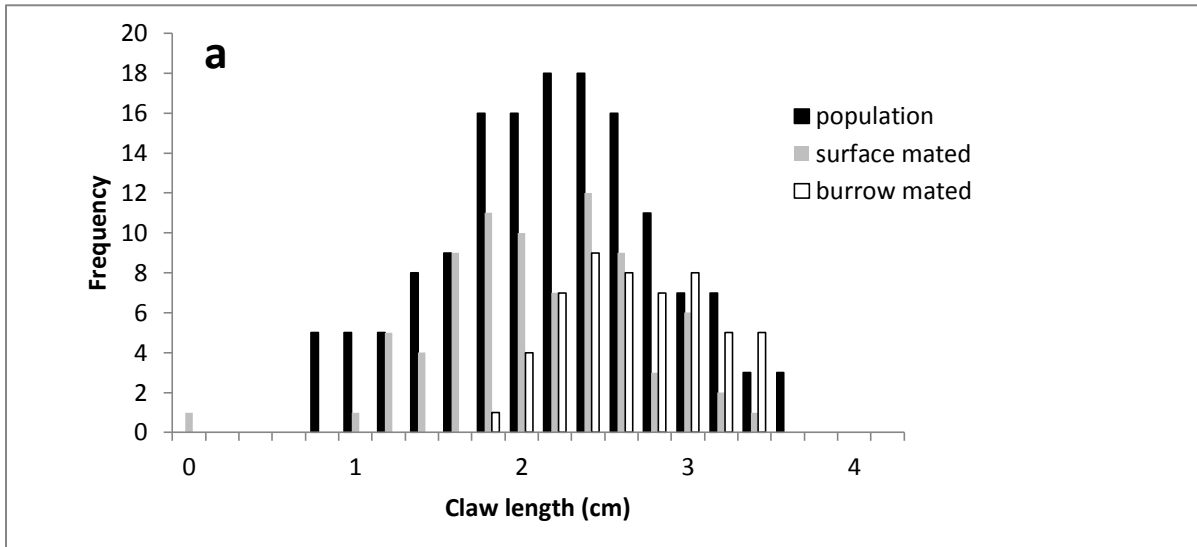
Table 3. Standardised selection differentials (SSD) for burrow-mated males (BM), surface-mated males (SM), and all mated males (BSM) in each species.

Species	Size measure	SSD		
		BM	SM	BSM
<i>U. annulipes</i>	Carapace width	0.78	0.00	0.31
	Claw length	0.74	-0.11	0.23
<i>U. urvillei</i>	Carapace width	0.61	0.65	0.64
	Claw Length	0.61	0.59	0.59

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Fig 1. The claw length of males in the population, males that surface-mated and males that burrow-mated for (a) *U. annulipes* and (b) *U. urvillei*.

Fig 2. The estimated marginal means of carapace width for male and female *U. urvillei* and *U. annulipes*.



Figure

