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Functions of mudballing behaviour in the European fiddler crab *Uca tangeri*

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Abstract. European fiddler crabs place mudballs around their burrow openings. Both males and females placed mudballs, but there were major differences between the sexes in mudballing behaviour, suggesting that the female's mudballs were a by-product of digging out the burrow whereas the male's may have additional functions. When the male's mudballs were removed experimentally, the number and intensity of male–male agonistic interactions increased significantly. Experimentally visually isolated males spent longer making mudballs and less time waving. In a binary choice test, females were more likely to approach dummy males with mudballs, spent longer near these males and were more likely to enter their burrows than dummy males without mudballs. The same pattern was apparent for males with 30 rather than 20 mudballs. These results are consistent with a dual function for mudballs in *U. tangeri*: to reduce the number and intensity of aggressive interactions between neighbouring males and to attract females.

Uca tangeri is the only species of fiddler crab (genus *Uca* [Brachyura, Ocypodidae]) to be found in Europe, where it occurs on the southern coast of the Iberian peninsula (von Hagen 1962; Wolfrath 1993). Fiddler crabs are well known for their high degree of sexual dimorphism (Crane 1975). The genus *Uca* is also well known for the behaviour of building various structures from moist mud or sand at the entrance to their burrows. Structures built by males have been described for 14 of the 80 species of *Uca*. Low semi-domes (Christy 1988a) are built on one edge of the burrow entrance by *U. pugilator* (Christy 1982), *U. pugnax* (Greenspan 1984) and *U. minax* (Basan & Frey 1977), rims are built around the edge of the burrow by *U. panacea* (Salmon et al. 1978) and *U. galapagensis* (von Hagen 1968), tall wide hoods are built by *U. musica* (Zucker 1974), *U. leptodactyla* (Matthews 1930), *U. terpischores* (Zucker 1974) and *U. cumulanta* (Crane 1975) and tall narrow pillars are built beside burrows by *U. beebei* (Christy 1988a), *U. lactea* (Linsenmair 1967; Yamaguchi 1971), *U. latimanus* (Zucker 1981), *U. dorotheae* (von Hagen 1968) and *U. stenodactylus* (Müller 1986). The structures built by *U. tangeri* in a North African population were described as low massive semi-domes (i.e. hoods) on one edge of the burrow entrance (Müller 1983). However, preliminary observations of Portuguese populations found no trace of such structures; instead both sexes were seen to deposit mudballs resulting from the digging of the burrow (R. F. Oliveira, personal observation). Many species of fiddler crabs construct mudballs (P. Backwell, personal communication) although not all use material excavated from the burrow (Wada et al. 1994), but we are unaware of any detailed study of this behaviour in fiddler crabs.

Various suggestions have been made for the function of fiddler crab structures, but there have been few experimental studies. The semi-domes of some species may act as an object to provide anchorage to the male whilst engaged in forceful combat (Christy 1982) and hoods play a part in *U. latimanus* courtship (Zucker 1981). In *U. musica*, *U. terpsichores* and *U. beebei* the

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presence of hoods reduces the frequency of combats between territorial males and their construction is associated with high densities of male burrows (Zucker 1981). It has also been suggested that the pillars of *U. beebei* may function as guideposts to allow the resident male to find his burrow entrance quickly when escaping a predator and/or to attract females to the males' burrows (Christy 1988b). However, it is unlikely that the semi-domes and rims built by other *Uca* species function in this way because they are too low to appear above the crabs' horizon (Land & Layne 1995). Some other species from the same family build structures from excavated sand. Male ghost crabs, *Ocypode saratan*, place sand pyramids near the burrow and these structures apparently function in male spacing and female attraction (Linsenmair 1967) and *Ilyoplax* crabs produce various structures from mud excavated from their burrows (Wada 1984, 1994; Takayama & Wada 1992; Wada et al. 1994).

Our study looked for inter-sexual differences in mudball formation and deposition that might indicate the function of the mudballs of *U. tangeri*. We also studied the effects of experimental visual isolation on male mudballing behaviour, of mudball removal on male–male aggression and of females' responses to artificial burrows surrounded by varying numbers of mudballs.

METHODS

We conducted fieldwork during June and July 1996 in the Ria Formosa Natural Park, Algarve, Portugal, in the area of salt marshes and mudflats near Quinta da Marim and Cacela-Velha. Since the diameter of burrow opening in *U. tangeri* correlates closely with the carapace width of the resident crab (females, $r=0.95$, $N=40$, $P<0.001$; males, $r=0.93$, $N=40$, $P<0.001$; Lourenço 1995), we used this measure as an indication of crab size, thus avoiding disturbing the crabs. The orientation of burrows could be measured as a compass bearing as they began with a gentle downward slope; however, the orientation of burrows was not significantly different from a random distribution for either sex (F. Burford, unpublished data). We divided the area surrounding the burrow into 45° sectors, starting at 0° (i.e. pointing in the direction of the opening) and numbered them clockwise from 1 to 8. For most analyses we used four 90° sectors: front (sectors 1 and 8), rear (4 and 5), right (2 and 3) and left (6 and 7). We measured the distances from the nearest point of the burrow opening to the closest mudball, to the most distant one and to the centre of the main group of mudballs. The diameters of eight randomly selected mudballs were also measured and the number of mudballs in each sector noted. We noted the number of neighbours, within a 1.8-m radius, in each sector and measured the distance from the focal crab's burrow to each neighbour, and the diameter and orientation of each neighbour's burrow opening.

The interactions between crabs in an area of 4 m^2 were video-recorded for the 45 min either side of low tide as this is the time when most mudball placement occurs. On subsequent analysis of the video-recordings, we noted each occasion when the focal male placed a mudball and the sector in which it was placed. When the focal male was out of the burrow, we noted the activity of surrounding crabs (both neighbours and intruders, males and females) within 30 and 90 cm of the focal male's burrow. We categorized the activity of surrounding males as waving, mudball placing, fighting, approach or presence, and of females as approach or presence.

Experiment 1: Effects of Visual Isolation

To prevent males from seeing their neighbours, we enclosed focal male crabs with opaque barriers, 25 cm high, arranged in a square of 60 cm centred on the burrow opening. The enclosures were set up approximately 1.5 h before low tide and left undisturbed for 2 h to allow mudball construction to occur. After 2 h we observed the crabs for 20 min, noting each crab's behaviour at 2-min intervals. We scored six categories of crab behaviour: waving, placing mudballs, static beside the burrow opening, inside the burrow, feeding and agonistic interactions. There were four groups of focal males. The first group was completely isolated by the enclosure. The enclosures of the second group of males had the barrier at the back of the burrow removed, so these males were partially visually isolated. The third group was also isolated on only three sides, but in this group the frontal barrier was removed. A fourth (control) group was not enclosed but we marked the substratum with lines to show where an enclosure would have been placed (Fig. 1).

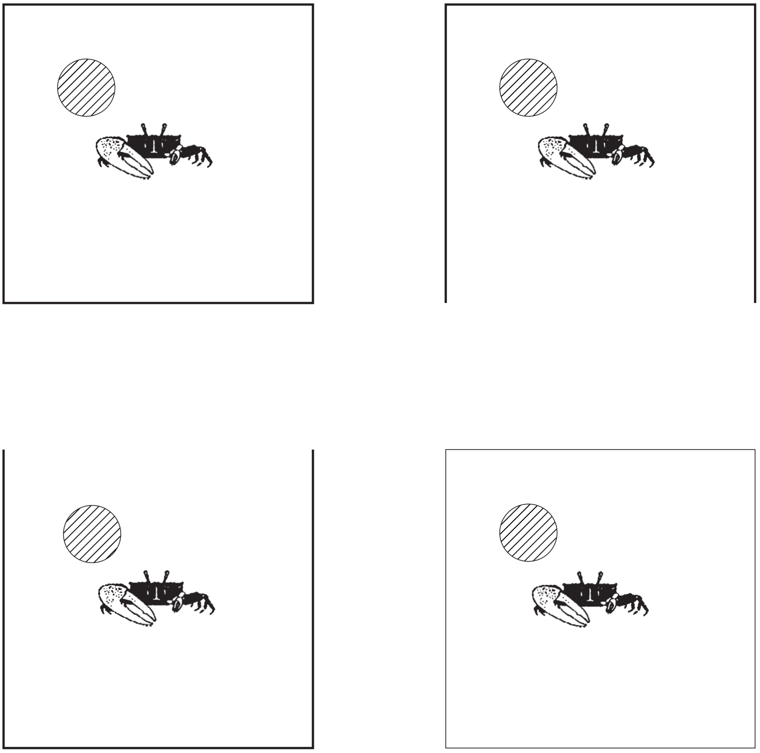

Figure 1. The four conditions of male visual isolation (completely enclosed; partially enclosed with front sector open; partially enclosed with back sector open) and the control group which was not enclosed. Thick lines indicate opaque barriers 25 cm high, thin lines indicate lines marked on the substratum in the absence of barriers.

Experiment 2: Effects of Mudball Removal

We noted the effects of removing and then replacing all of the mudballs around the focal crab's burrow in a 4 m^2 area. We recorded behaviour for 15 min before mudball removal, 15 min during mudball absence and 15 min after mudball replacement. We noted the number of male–male interactions and identified the opponent as either a resident male from within the marked 4 m^2 area or as an intruder (i.e. a male from outside the 4 m^2 area which had entered with the apparent purpose of fighting for a burrow). We scored the intensity of aggressive interaction on an increasing, five-point scale: (1) low intensity threat: major chela closed, held extended in front of the body; (2) high intensity threat: major chela opened, held in front of the body; (3) facing: opponents face, both threaten, one may jump towards the other snapping its claw; (4) pushing: opponents attempt to push each other backwards by locking claws; and (5) judo: opponents lock claws, one crab throws the other aside.

Experiment 3: Effects of Mudballs on Female Choice

We placed visually isolated females in the centre of a test arena of 1 × 1 m made from opaque barriers 25 cm high. In two opposite corners a zone of 40 × 40 cm was defined by a line drawn on the substratum. In each zone we dug a standardized burrow with a stick. The burrow opening diameter was 2.5 cm and the depth was 10 cm. Two resin-embedded dead males, matched for claw and carapace size, were placed in each arena, one by each burrow (Fig. 2). We noted the effects on females of two differences in the number of mudballs. The first difference compared the effect of the presence of 20 mudballs versus their absence. The second compared the effect of 20 mudballs versus 30 mudballs. We swapped the two males between zones on successive trials and changed mudballs between the two zones every two trials, so that each mudball category was presented to the females the same number of times at each location. The mudballs used had been

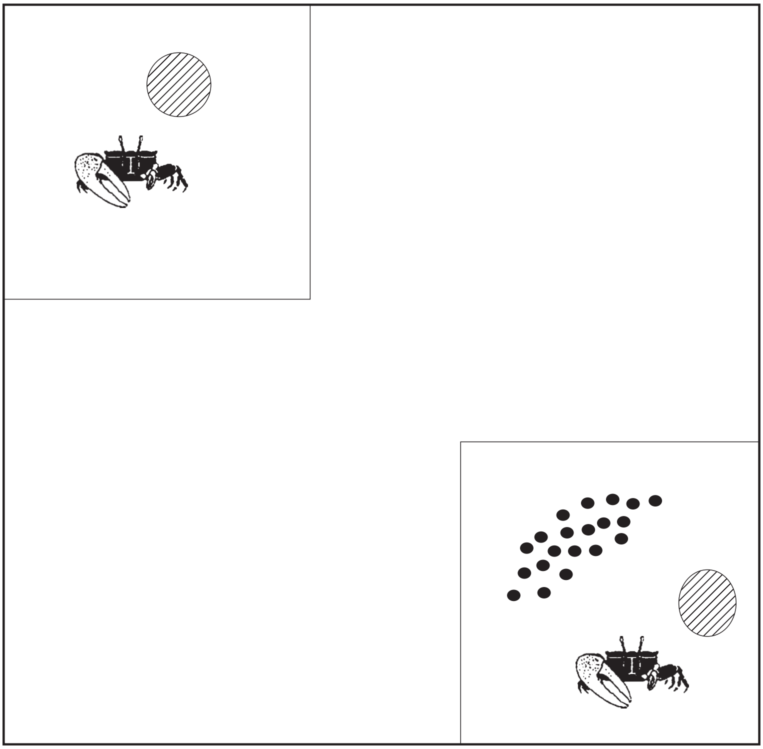

Figure 2. The arena used to test the effect of 20 versus 0 male mudballs on female behaviour. Thick lines indicate opaque barriers 25 cm high forming the boundaries of the arena, thin lines indicate lines marked on the substratum to delimit the zones around each dummy crab and its associated artificial burrow (⊘); ●: mudballs.

removed from males in the neighbourhood before the experiment and were matched for size between the two groups of mudballs. We collected the test females from the mudflats on the same low tide during which they were tested. The females varied between 13 and 30 mm in carapace width, and between 16 and 26 mm in carapace length. Each trial started with the introduction of one female to the centre of the arena, and lasted for 20 min unless the female stayed motionless in the centre (in which case the trial was abandoned) or the female entered one of the male's burrows and stayed there for 10 min without leaving (in which case the female was considered to have chosen the male and the test was ended). We recorded four behavioural variables in each trial: the zone first entered by a female (termed first approach); latency to female first entering a zone (termed latency to first approach); the time spent in each zone (termed time spent near); and the burrow that the female entered and remained in.

RESULTS

Mudballing Behaviour

Crabs made mudballs from material excavated from their burrows. A typical pattern of mudballing was that about 35 s after entering the burrow a crab would emerge carrying a mudball in the walking legs on one side (the side opposite the major chela for males) and deposit the mudball on the substratum surrounding the entrance. About 5% of mudballs were re-positioned, that is, the crab that had placed the mudball would return to it and move it slightly.

Although both sexes made mudballs, there were significant differences between them: males made more mudballs of larger diameter and placed them further from the burrow entrance than females (Table I, Fig. 3). Furthermore, there was a significant positive correlation between the total number of mudballs placed by males and the

Table I. Differences between the sexes in mudballing behaviour and of features of the burrow

Feature	Male	Female	*P*
Number of mudballs	47.7 ± 4.7 (26)	17.5 ± 3.5 (24)	<0.001
Mudball diameter	2.2 ± 0.1 (23)	1.7 ± 0.1 (24)	<0.001
Closest mudball	14.0 ± 2.1 (23)	6.8 ± 1.4 (24)	<0.01
Furthest mudball	43.4 ± 3.4 (23)	26.7 ± 2.7 (24)	<0.001
Centre of aggregation	28.1 ± 2.0 (23)	14.3 ± 1.7 (24)	<0.001
Burrow opening diameter	2.9 ± 0.1 (26)	2.6 ± 0.1 (24)	<0.01
Closest neighbour	46.7 ± 4.9 (26)	39.1 ± 4.3 (24)	<0.001
Number of neighbours	5.8 ± 0.8 (26)	4.1 ± 0.4 (24)	0.23

Mudball diameter (cm) is an average of eight randomly chosen mudballs per individual. Distances (cm) to mudballs and neighbours were measured to the nearest point of the burrowing opening (diameter in cm). Values are $\bar{X}$ ± SE (*N*). *P*-values are derived from Mann–Whitney *U*-tests.

average diameter of the mudballs ($r_s = 0.63$, $N = 23$, $P < 0.01$). Other differences between the sexes such as the diameter of the burrow opening (and hence carapace size, see Methods and Lourenço 1995) and the proximity and number of neighbours were small (Table I) and were unlikely to account for the sex differences in mudballing behaviour. For males, there were no significant correlations between crab size (taken from burrow entrance diameter) and the number of mudballs constructed ($r_s = 0.18$, $N = 26$, NS) or mudball diameter ($r_s = -0.13$, $N = 23$, NS). However, there was a significant correlation between female size (i.e. burrow entrance diameter) and the total number of mudballs constructed ($r_s = 0.45$, $N = 24$, $P < 0.05$). These observations are consistent with the idea that females produce mudballs as a consequence of burrow excavation whereas those of males probably have additional functions.

If mudballs function in burrow defence we would expect relationships between the number and placement of mudballs and features of neighbouring crabs. There was no significant correlation between the number of neighbours and the number of mudballs deposited by either sex (males: $r_s = -0.072$, $N = 23$, NS; females: $r_s = 0.34$, $N = 23$, NS). We did not find any significant relationships between large numbers, large size or proximity of neighbours and mudball placement in the four sectors around males (front, back, large claw side, small claw side) or females (front, back, right side, left side). However, males placed significantly more mudballs in front of the burrow opening ($F_{1,96} = 88.62$, $P < 0.001$; Scheffé post hoc test: $P < 0.001$) and the same tendency was apparent for females (Table II). The video-recordings showed that where males placed mudballs was affected by the behaviour of the surrounding males within a 90-cm radius of the burrow. The proportion of mudballs placed by the focal male in the front sector was significantly correlated with the proportion of waving activity by surrounding males in this sector ($r_s = 0.895$, $N = 7$, $P = 0.007$) as was the proportion of approaches by surrounding males in the large claw sector ($r_s = 0.788$, $N = 7$, $P = 0.035$). The proportion of fights between surrounding males in the large claw sector was significantly negatively correlated with the proportion of mudballs placed there by the focal male ($r_s = -0.859$, $N = 7$, $P = 0.013$).

Experiment 1: Effects of Visual Isolation

Visually isolated, fully enclosed, males spent a significantly greater proportion of the time placing mudballs than the controls ($\bar{X} \pm$ SE = 0.05 ± 0.024, $N = 10$; 0.0 ± 0.0, $N = 10$, respectively; Mann–Whitney *U*-test: $Z = -2.16$, $P < 0.05$). Fully enclosed males spent a significantly smaller proportion of the time waving than the controls ($\bar{X} \pm$ SE = 0.13 ± 0.049, $N = 10$; 0.47 ± 0.079, $N = 10$, respectively; Mann–Whitney *U*-test: $Z = -2.80$, $P < 0.01$) and a significantly greater proportion of the time feeding than the controls ($\bar{X} \pm$ SE = 0.14 ± 0.067, $N = 10$; 0.0 ± 0.0, $N = 10$, respectively; Mann–Whitney *U*-test: $Z = -2.16$, $P < 0.05$). Partially enclosed males did not show any significant differences from the controls regardless of whether the front or rear section was left open. These results show the importance of visual

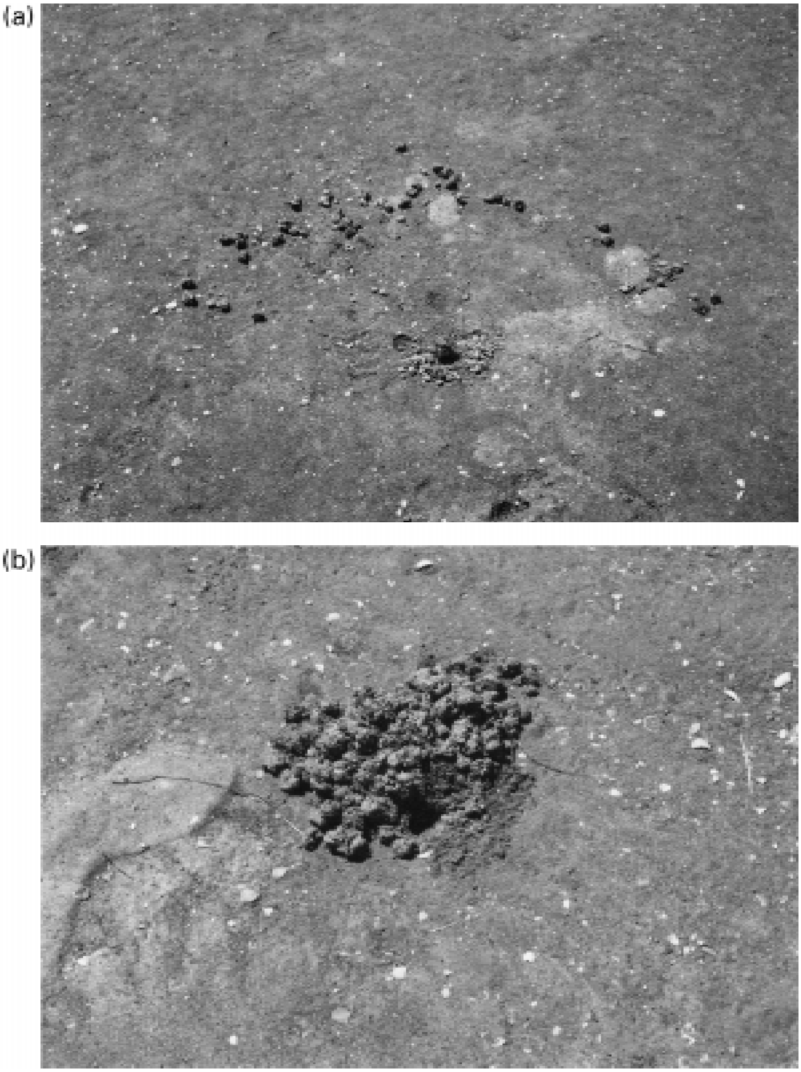

Figure 3. Photographs of typical male (a) and female (b) burrows with mudballs.

contact in stimulating waving behaviour and that the absence of visually apparent neighbouring crabs does not reduce mudballing. The increase in time spent feeding and mudballing by fully enclosed males suggests that crabs normally trade-off time spent waving with time spent feeding and mudballing.

Experiment 2: Effects of Mudball Removal

The effects on agonistic interactions of removing mudballs were striking. The numbers of aggressive interactions between focal males and both neighbours and intruders increased by 300–400% when mudballs were absent (i.e. after mudballs had been removed). After the mudballs were replaced in their original positions, agonistic interactions returned to the levels seen before mudball removal (Table III). The level of aggression noted in interactions between focal males and neighbours was highest in the period when mudballs were absent and a similar, but less marked, effect was seen for interactions between focal males and intruders (Table IV).

Table II. The mean proportions of mudballs and neighbours (±SE) in each 90° section of a circle radius 1.8 m around the burrow of 25 males and 24 females

Section	Mudballs	Neighbours
Males		
Front	0.65±0.046	0.34±0.042
Back	0.04±0.040	0.18±0.029
Large claw	0.11±0.051	0.30±0.013
Small claw	0.16±0.030	0.14±0.031
Females		
Front	0.50±0.058	0.21±0.045
Back	0.09±0.027	0.39±0.061
Right claw	0.26±0.049	0.18±0.038
Left claw	0.15±0.039	0.23±0.054

Table III. The number of aggressive interactions between 30 focal males and their neighbours or intruders when the mudballs were removed

	Stage of mudball removal			
Interactions with	Before	During	After	*P*
Neighbours	15	59	8	<0.001
Intruders	5	17	8	0.06

P is derived from Friedman ANOVA.

Experiment 3: Effects of Male Mudballs on Female Choice

Isolated females placed in an enclosure with two dummy males, only one of which was surrounded by mudballs, showed a significant tendency to approach the male with mudballs first and to do so with significantly shorter latency (Table V). The females also spent significantly more time near the male with mudballs and were significantly more likely to enter its burrow (Table V). When both males were surrounded by mudballs, females showed a significant tendency to approach the male with more mudballs first and to do so with significantly shorter latency, but although they tended to spend more time near the male with more mudballs, this difference was not significant and almost equal numbers of females entered each burrow (Table V). These results suggest that females more readily detected burrows surrounded by mudballs and that more mudballs were more readily detected.

DISCUSSION

Uca tangeri spent approximately one-third of their time at each low tide forming and placing mudballs. In the process males displaced an average of 250 cm^3 of substratum. Females moved about 20% of this volume, yet males are only about 12% larger than females (Table I). This difference in total mudball volume is related to differences between the sexes in burrow volume in this species (R. F. Oliveira & C. Latruffe, personal observation) and in other fiddler crabs (e.g. *U. annulipes*: Backwell & Passmore 1996). However, the fact that females placed mudballs significantly closer to the burrow suggests that the deposition of mudballs is the result of digging out the burrow for females whereas it has evolved to fulfil additional functions in males.

Although there was no significant difference in the number of neighbours surrounding male and female burrows, females' neighbours were significantly closer than those of males (Table I). This difference may indicate that mudballs function in male spacing, perhaps by marking territorial boundaries. The role of mudballs in reducing aggression was clearly shown by the effect of removing mudballs: both the number and intensity of aggressive interactions increased markedly

Table IV. The frequency of the highest level of aggression (see Methods) reached in interactions occurring in each trial (*N*=30) before, during and after mudball removal

Level of aggression	Focal versus neighbours			Focal versus intruders		
	Before	During	After	Before	During	After
1	1	1	7	3	1	6
2	4	8	1	2	8	2
3	1	4	0	0	2	0
4	2	2	0	0	1	0
5	1	8	0	0	0	0

Table V. The responses of visually isolated female *U. tangeri* to artificial burrows with dummy crabs surrounded by different numbers of mudballs

Response	Number of mudballs		N	P
	20 mudballs	No mudballs		
First approach	19	5	24	0.004
Latency to first approach	74.9 ± 23.93	366.8 ± 90.13	24	0.004
Time spent near	77.29 ± 40.79	22.0 ± 38.52	24	0.004
Entered	11	2	13	0.013
	30 mudballs	20 mudballs		
First approach	14	7	21	0.026
Latency to first approach	66.42 ± 36.14	153.57 ± 63.31	21	0.017
Time spent near	57.38 ± 25.95	117.17 ± 76.73	21	0.566
Entered	7	8	13	0.705

The response ‘first approach’ noted the zone first entered by a female (P derived from chi-square test) and ‘latency to first approach’ was the time (s; $\bar{X}\pm$ SE) taken to do so (P derived from Mann–Whitney U-test). The time (s; $\bar{X}\pm$ SE) spent in each zone was the response ‘time spent near’ (P derived from Wilcoxon signed-ranks test). Some females ‘entered’ and remained in one or other of the burrows (P derived from chi-square test).

(Tables III and IV). Zucker (1981) found that in two species of hood-constructing fiddler crabs, males responded to the removal of hoods with an increased frequency of combats; when artificial hoods were replaced the number of combats fell to a level similar to that found in areas with undisturbed hoods. Similar behaviour has been described in other animal groups. For example, mudskippers, *Boleophthalamus boddarti*, build mud walls to define their territory, creating polygonal areas in which they live and feed and removal of these walls led to a significant increase in the number of interactions between neighbouring males (Clayton 1987). Removing the territorial boundaries of a colonial swallow *Petrochelidon pyrrhonota* produced similar results: the birds responded with an increase in aggression and reconstruction of the boundaries (Emlen 1952). The mudballs of *U. tangeri* cannot act as visual barriers between waving males because during waving the claw is extended well above the average height of the mudballs.

The video-recordings showed that where males placed mudballs in the short term was influenced by the behaviour of surrounding males at moderate distances (i.e. within 90 cm). A radius of 30 cm approximates the detection distance for other crabs of the smaller but closely related species *U. pugilator* (Land & Layne 1995) and it seems reasonable to assume that a similar radius applies to *U. tangeri* in the absence of data to the contrary. The relationships between where males placed mudballs and the behaviour of surrounding males were still apparent within a 30-cm radius but failed to reach significance because of the small numbers of surrounding males within 30 cm. Also, general observations found that within this 30-cm radius males placed mudballs in less than 10% of sectors that contained neighbours and in over 50% of sectors without neighbours. These findings may be explained by the relative importance for visual communication of an uninterrupted area (i.e. without mudballs) in the 30-cm radius within which visual acuity is highest, versus any territorial boundary function of mudballs. The tendency to place fewer mudballs in the large claw sector (which was significant within 90 cm and approached significance within 30 cm), if more fights between neighbours have occurred there, could be related to the role of the large claw as a weapon. Males may prefer opponents to approach from this direction and leaving this sector relatively free of mudballs may channel such approaches towards the large claw as well as making it less likely that mudballs will physically impede fighting. The tendency could also be explained by the focal crabs maximizing the chances of observing fighting between surrounding males. Fights between neighbours and/or intruders can provide information on the relative fighting ability of future opponents (McGregor & Dabelsteen 1996). Fights probably generate significant amounts of substratum-borne vibrations, providing a composite cue and extending the distance at which they can be detected over that for purely visual signals. Certainly our impression from watching the videos was that focal crabs oriented very rapidly towards fighting males and passing females at greater distances than would be expected from a consideration of the acuity of *U. pugilator* visual systems.

An intriguing possibility is that mudballs may exploit a feature of crabs' visual acuity to act as an early warning system of intruders. Fiddler crabs have a sensitive predator detection area of the visual field that is not stimulated by crabs at ground level (Land & Layne 1995; Layne et al. 1997); however, a crab climbing over a mudball would be elevated into this area and therefore be detected much more readily. The distance at which males place most mudballs (28 cm, Table I) is close to the 30 cm reported as being the limit of the range of best visual acuity for *U. pugilator* (Land & Layne 1995) and therefore may be the furthest distance at which such an early warning system could operate.

One of the effects of experimentally visually isolating males was to increase the amount of mudballing, showing that visual contact with neighbouring crabs is not a necessary stimulus for mudballing behaviour. In fact, visual contact seemed to limit the time for mudballing by increasing the time spent waving. However, we cannot conclude that mudballing occurs in the absence of apparent neighbours because the isolated crabs could still have detected neighbours from signals such as substratum-borne vibrations (Aicher & Tautz 1990) or air-borne sounds (Salmon & Atsaides 1968).

The experiments with isolated females and dummy males provided evidence for a mate attraction function of mudballs: females more readily approached males surrounded with mudballs than those without and more mudballs were approached more readily than fewer. The difference in numbers of mudballs presented to females (20 versus 0; 30 versus 20) was considerably smaller than the difference between the sexes found in the study population (30, Table I). The magnitude of difference and the lack of any clue from the number of mudballs to the sex of the burrow owner may account for the lack of significant results in some measures in these experiments (Table V).

Mudballs could function to indicate to females that the general area contains a burrow. Such passive attractors (sensu Andersson 1982) could play an important role in mate attraction in *U. tangeri* as males are invisible when inside the burrow. A similar function has been proposed for the bones placed at some distance from the bowers of spotted bowerbirds, *Chlamydera maculata*, a species with widely spaced display sites (Borgia 1995).

Females could use mudballs to assess male quality. The significant positive correlation between mudball diameter and numbers made by a male may be one such indication of male quality. It has been suggested that the pillars constructed by *U. beebei* indicate male vigour and females prefer males with pillars to those with none (Backwell et al. 1995). Similarly, the overall vigour of male satin bowerbirds, *Ptilonorhynchus violaceus*, may be indicated by the number of bower decorations and bower quality (Borgia et al. 1985). The mudballing behaviour of male *U. tangeri* is more directly comparable to the stone piles built by male black wheatears, *Oenanthe leucura*, during the breeding season (Moreno et al. 1994). This stone-carrying behaviour can be considered a post-mating sexual display which allows females to adjust their reproductive effort according to the quality of the males, as clutch size varies with the number of stones (Soler et al. 1996).

Female *U. tangeri* could also assess the quality of the burrow as a brood chamber from features of mudballs. The volume of the male's burrow and therefore its quality as a brood chamber is likely to be related to the number of surrounding mudballs excavated from it. Females may also be able to determine the micro-environment of the burrow (e.g. oxygen content) from features of the excavated material used to make mudballs.

In the context of a broader understanding of multi-modal signals and inter-sexual displays, it is interesting to note that display functions of *U. tangeri* mudballs, black wheatear stone carrying and bowerbird bowers have all originated from nest-building behaviour.

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