

MUDBALLING REVISITED: FURTHER INVESTIGATIONS INTO THE CONSTRUCTION BEHAVIOUR OF MALE *UCA TANGERI*

by

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Summary

Male and female *Uca tangeri* (the only fiddler crab species to inhabit Europe) construct mudballs from mud excavated from within their burrows. Individual males placed similar patterns of mudballs each low tide, suggesting that there is some degree of stereotypy. When mudballs were experimentally moved further from the burrow or closer to it, males only repositioned those that were moved closer, placing them further away again. However, males did not replace mudballs that had been experimentally destroyed at the end of the mudballing phase when they had started to court females. In binary presentation tests, females showed no significant differences in response to mudballs made from different types of mud, or different numbers of mudballs. These results are consistent with earlier findings that male mudballs function as territory boundaries. However, we provide evidence that male mudballs have no function in female attraction, contrasting with previous studies.

Introduction

Fiddler crabs (genus *Uca*) have been described as a highly visual genus because males wave their hypertrophied chelae in a display that attracts females and defends territories (Crane, 1975). However, at least 14 of the 80 *Uca*

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species also have another visual behaviour; they build a variety of structures from moist sand or mud (Christy, 1988a). Male *U. beebei* build pillars which act as guideposts for finding the burrow entrance and also attract females, but which appear to have no role in territory spacing or defence (Christy, 1988a, b). Male *U. terpsichores* form shelters over their burrow openings which reduce territory size in high density populations (Zucker, 1974), whereas the hoods built by *U. latimanus* play a role in courtship (Zucker, 1981). The closely related ghost crab, *Ocypode saratan*, builds large pyramids of sand to attract females (Linsenmair, 1967). Another ocypodid, *Ilyoplax pingi*, builds mounds of mud at the entrance of the burrow which prevent neighbouring conspecifics from approaching too closely (Wada *et al.*, 1994), while *I. dentimerosa* build barricades, fences and shelters, all of which reduce interference from neighbouring crabs (Wada, 1994).

Our study focused on the construction behaviour of male *U. tangeri* (Brachyura, Ocypodidae), the only fiddler crab species to occur in Europe (Crane, 1975). Both male and female *U. tangeri* form mudballs from substratum excavated from within the burrow each low tide, which they deposit in front of and around the burrow entrance (Oliveira *et al.*, 1998). However, males make a significantly greater number of larger mudballs than females and place them significantly further from the burrow opening (Oliveira *et al.*, 1998), suggesting that male mudballs have a signal function whereas those of females are simply a by-product of burrow excavation (Oliveira *et al.*, 1998).

Furthermore, Latruffe *et al.* (1999) found significant correlations between the length of the male's large chela and both the number of mudballs a male makes and the distance at which they are placed from the burrow. This, they conclude, could perhaps enable females to assess male quality (females prefer males with larger chelae (Backwell & Passmore, 1996; Oliveira & Custódio, 1998)) when the male is not on the surface.

We investigated the level of variability in the placement of mudballs by individual males over a series of tides. If the arrangement of male mudballs is related to male major chela size, as Latruffe *et al.*'s (1999) correlations suggest, then we would expect low variation in the number of mudballs and the distance at which they are placed over successive tides. Some visual displays such as the courtship head-throwing display of the male common goldeneye (*Bucephala clangula*, Dane *et al.*, 1959) have extreme levels of precision, giving a coefficient of variation of only 6.2%.

A consistent pattern of mudball placement, inferred from low levels of variation within an individual's displays, would lend more weight to the idea that male mudballs are a display. Displays are 'specially evolved' signals (Krebs & Davies, 1993) which, following Tinbergen's (1952) convention, should be exaggerated and conspicuous. Therefore, in order to be considered a display, male mudball arrangements need to be non-random and obvious to conspecifics. Furthermore, low variation in an individual male's display from tide to tide, but higher variation between males in the population would mean that females could use aspects of mudballs to discriminate between males. Mudballs could contain information about the male or the burrow quality or both.

If male mudballs are a display, we would expect males to react to experimental manipulations of their mudballs, all other things being equal. We investigated this in two experiments. First, we looked at the importance of the position of individual mudballs by moving them from their original locations as they were being placed. Then, to explore the value to a male of the mudball arrangement as a whole, we noted the reaction of males to our destruction of mudballs once mudballing was completed.

At present, it is not clear what information, if any, females gather from male mudball arrangements. Latruffe *et al.* (1999) found a significant positive correlation (albeit fairly weak: $r_s = 0.52$, $N = 31$, $p < 0.01$) between the depth of a male's burrow and the number of mudballs placed. This, the authors suggest, could allow females to assess burrow quality, without having to enter the burrow and risk forced copulations. In an experimental binary presentation (also called binary choice), Oliveira *et al.* (1998) found that females approached dummy males with a greater number of mudballs significantly faster and also spent a significantly greater amount of time in their proximity (comparing no mudballs versus 20 mudballs, and also 20 mudballs versus 30 mudballs). From this Oliveira *et al.* (1998) concluded that females prefer males with greater numbers of mudballs. However, when observing females in a natural setting, Latruffe *et al.* (1999) found no significant correlation between the number of mudballs placed by a male and whether or not females approached within 1 m of his burrow ($r_s = -0.06$, $N = 18$, $p = 0.85$).

We conducted three further binary presentation tests comparing female responses to male mudballs. Two of these experiments investigated whether

females respond to the composition of mudballs, and the third followed Oliveira *et al.* (1998), and presented females with different numbers of mudballs.

Methods

Study site

We studied a population of *U. tangeri* (male subjects' carapace width ranging from 23 mm to 33 mm) that inhabited the intertidal mudflats of Marim, in the Ria Formosa Natural Park, Algarve, Portugal. All fieldwork was carried out during May and June 1999.

Activity phases

The activity of *U. tangeri* falls into 3 phases over the 6-hour low tide period. Once the mudflat is exposed, the crabs emerge and feed intensively for approximately 1.5 hours (Wolfrath, 1993). In the following hour, they excavate their burrows and place mudballs on the mudflat surface. During the final phase, the males wave and court females while the females continue to feed or visit male burrows (Wolfrath, 1993). At the end of the low tide, the crabs enter their burrows and remain there, blocking the opening with a plug of mud, throughout the high tide period.

Mudballing patterns over successive tides

Twelve males were observed during the mudballing phase for three daylight low tides. Four of the 12 subjects came out of their burrows on three consecutive days, the other males were observed over the first three successive tides during which they emerged (the longest period of observation to gain three sets of measures was seven days, the mode was three days). The times at which each male began and finished mudballing were noted.

At the end of the mudballing phase, when all the males were waving, we took several measures from each mudball arrangement. We noted the total number of mudballs, the diameter of 8 randomly selected mudballs measured to the nearest mm using callipers (from which an average was calculated), and the distance to the nearest and furthest mudballs, as well as the distance to the centre of the mudball aggregation. We also measured the distance from the focal male's burrow to the burrow of his nearest neighbour. All distances were measured to the nearest cm. As the measures were not significantly different from a normal distribution (Kolmogorov-Smirnov one-sample test), a parametric repeated measures ANOVA was used to analyse the data.

The effect of moving mudballs

Subjects were males just starting to place mudballs. We were able to sit close enough to the burrow to manipulate the mudballs as they were placed. The presence of an observer had little effect on the behaviour of the crabs as long as the observer remained still while the subject was on the surface. We waited for the subject to place a mudball and when he had re-entered

his burrow to construct another mudball (a process which takes about 35 s (Oliveira *et al.*, 1998)), we moved the mudball, marking the new position with a natural marker such as a small shell or stone. This was repeated for 10 consecutive mudballs for each subject. The distance the mudballs were moved depended on the treatment group each crab was in. Eleven males had mudballs handled and then replaced in the original position (O); a further 11 had mudballs moved 5 cm further from the burrow (F); and a final group of 11 males had mudballs moved 5 cm closer to the burrow (C).

We noted whether the subject re-positioned the mudballs after they had been experimentally manipulated. If they had been re-positioned, we measured the distance the crab had moved each mudball from the experimental position.

The effect of destroying mudballs

At the end of the mudballing phase 20 males were selected and the same measures of their mudballs were taken as in the study of mudballing over successive tides.

The mudballs of 10 males were then removed, while those of another 10 males were handled and then immediately replaced in their original positions to act as controls. At the end of the waving phase, as the males were plugging their burrows, we again measured the mudball displays to see whether males whose mudballs had been destroyed had replaced them.

Female binary presentations

Following the procedure used by Oliveira *et al.* (1998), females were placed in the centre of a 1 m² arena made of 25 cm high opaque barriers, so that they were visually isolated. In two opposite corners of the test arena (labelled corners 1 and 3, with corner 1 always pointing towards the sea) a 20 × 20 cm² zone was defined by a fine line drawn in the substratum. Within each of these zones an artificial burrow, measuring 3 cm across and 8 cm deep, was made using a stick. Two resin-coated dead males, which were matched for both carapace width and major claw length, were placed beside the burrows. Mudballs were placed around the burrow openings according to the test being done and the treatment group allocated (see below). The males were swapped between zones after each trial and mudballs were changed between zones after every other trial, so that the different mudball treatments were presented to the females the same number of times in each location. We carried out three different tests with this set-up. In the first experiment we presented 47 artificial mudballs made from mud from inside a burrow vs 47 artificial mudballs made from mud from the surface. The second study compared female responses to 47 real mudballs taken from a nearby male's display vs 47 artificial mudballs made from mud taken from inside a burrow. We used 47 mudballs in these studies as Oliveira *et al.* (1998) found the mean number (\pm SE) of mudballs placed by male *U. tangeri* to be 47 (\pm 4.7, $N = 26$). In the final experiment we presented females with dummy males with 37 vs 57 mudballs (*i.e.* mean \pm 2 SE; cf 20 vs 30 used by Oliveira *et al.* (1998)).

The artificial mudballs were made using a melon scoop with a diameter of 25 mm, approximating the mean male mudball diameter (22.0 ± 1.0 mm, $N = 23$) reported by Oliveira *et al.* (1998). The two mudball zones were in corners 1 and 3, so the observer stood at corners 2 and 4 swapping every four trials, remaining still throughout the trial to avoid disturbing the subject. The females used were all taken from their burrows during the same

tide in which they were tested. Twenty non-ovigerous females were used in each of the three tests, and the same females were not re-used in different tests. Each trial began with the female being placed in the centre of the arena and lasted for a maximum of 20 minutes, unless the female remained still for 5 minutes (in which case the trial was abandoned) or until the female entered one of the two burrows and stayed there for 5 minutes (this was taken as meaning that the female had made a choice and the trial was ended). We measured the same four aspects of the females' behaviour as measured by Oliveira *et al.* (1998): the zone first approached by the female, the latency to the female first entering a zone, the time spent in each zone, and the burrow that the female entered and stayed in.

Results

Mudballing patterns over successive tides

We found no significant differences between any of the measures taken from the mudball displays over three tides within individual males (Table 1). The lowest coefficient of variation (CV) was for the mudball diameter (10.4%). The distances to the centre of the mudball aggregation and the furthest mudball had CVs of 22.1% and 17.8%, respectively. The CV for the distance to the nearest mudball was relatively high (50.0%) as was that of the total number of mudballs made (46.5%). There was only one significant difference between males sampled; some males spent significantly longer mudballing during each tide than other males (Table 1). However, there was no significant correlation between the amount of time spent mudballing and the total number of mudballs made ($r_s = 0.24$, $N = 36$, $p = 0.16$).

The effect of moving mudballs

We observed 33 subject males placing 10 mudballs each. The mean time from the male entering the burrow to surfacing carrying a mudball was 42 ± 2 s (\pm SE, $N = 33$). The males whose mudballs were moved further from the burrow (F) never re-positioned any of them. Ten of the 11 males whose mudballs were moved closer to the burrow (C) moved at least one of them further from the burrow again. Seven of the 11 males who acted as controls (O) repositioned their mudballs further from the burrow. None of the crabs moved any mudballs closer to the burrow. Males in group C repositioned significantly more mudballs and there was a non-significant tendency ($p = 0.03$, the level of significance for *post hoc* tests was reduced to $p < 0.02$ using a Bonferroni correction) to move them a greater distance

TABLE 1. *Measures relating to male mudballing behaviour over three tides*

	Tide 1	Tide 2	Tide 3	Between males	Within males
Mean burrow diameter (mm)	29 ± 1	28 ± 1	29 ± 1	$F = 0.29$ $p = 0.60$	$F = 1.06$ $p = 0.37$
Mean mudball diameter (mm)	22 ± 1	22 ± 1	21 ± 1	$F = 2.24$ $p = 0.17$	$F = 1.94$ $p = 0.17$
Distance to nearest mudball (cm)	17.2 ± 3.0	19.8 ± 3.0	19.0 ± 3.4	$F = 2.36$ $p = 0.16$	$F = 0.08$ $p = 0.92$
Distance to middle mudball (cm)	33.1 ± 3.3	37.6 ± 2.3	35.1 ± 3.1	$F = 0.74$ $p = 0.41$	$F = 2.09$ $p = 0.15$
Distance to furthest mudball (cm)	57.6 ± 4.8	59.6 ± 4.0	56.5 ± 4.3	$F = 0.001$ $p = 0.97$	$F = 1.95$ $p = 0.17$
Total number of mudballs	61.3 ± 6.3	43.0 ± 5.8	42.8 ± 5.8	$F = 2.29$ $p = 0.16$	$F = 0.34$ $p = 0.72$
Distance to nearest neighbour (cm)	66.7 ± 8.8	94.0 ± 21.6	79.2 ± 9.6	$F = 0.50$ $p = 0.50$	$F = 1.31$ $p = 0.29$
Time spent mudballing (mins)	65.1 ± 8.1	67.2 ± 7.6	54.3 ± 6.0	$F = 8.11$ $p = 0.02$	$F = 0.55$ $p = 0.59$

Values are means ± SE, $N = 12$ in each case. F ratios and p values are for the main effects (between males 1, 10 df; within males 2, 20 df) of the parametric repeated measures ANOVA. Measures were taken to the nearest mm for the length, and to the nearest 1/10 minute for time.

than either of the other two groups of males (Table 2). The males used in this study were all selected randomly, so we were surprised to find that males in group F had significantly larger major chelae (both in length and height) than did the males in group C (Table 2).

The effect of destroying mudballs

None of the 10 controls made any more mudballs during the waving phase of the tide. Two of the test group made more mudballs after their original displays were destroyed. Neither of these males replaced all the mudballs destroyed, one male which originally had 52 mudballs made two more, and the other male placed another six mudballs after his 10 original mudballs were destroyed.

TABLE 2. *Response of males (N = 11) to experimental re-positioning of their mudballs*

	O	F	C	χ^2	<i>Post hoc</i> < 0.02
Mean number of mudballs moved by each male	1.3 ± 0.4	0.0 ± 0.0	3.5 ± 0.7	18.75 <i>p</i> < 0.001	O vs F O vs C F vs C
Mean distance moved (mm)	5 ± 2	0 ± 0	15 ± 4	18.03 <i>p</i> < 0.001	O vs F F vs C
Mean major claw length (mm)	37 ± 5	48 ± 2	33 ± 2	11.57 <i>p</i> < 0.01	F vs C
Mean major claw height (mm)	13 ± 1	16 ± 1	13 ± 1	8.73 <i>p</i> < 0.05	F vs C

There were 3 treatment groups: mudballs left in original position (O), mudballs moved 5 cm further from the burrow (F) and mudballs moved 5cm closer to the burrow (C). Values are means ± SE, Kruskal-Wallis χ^2 values and significant Mann-Whitney *U*-test *post hoc* tests, with the significance level adjusted to *p* < 0.02 using a Bonferroni correction. Length measurements were made to the nearest mm.

Female binary presentations

We found no significant differences in the response of visually isolated females to the different types of mudballs in any of the three presentations (Table 3). In the two presentations comparing different mudball compositions, females entered both zones in similar proportions, took similar latencies to do so, spent similar amounts of time in each zone and entered the burrows in roughly equal proportions. However, when we compared female responses to different numbers of mudballs, there was a non-significant consistent pattern in the means, with females approaching the zone with 57 mudballs faster and spending more time in this zone than the zone with 37 mudballs.

There was no effect of where the observer stood (corner 2 or corner 4) or of mudball placement (corner 1 or corner 3) on the behaviour of the females in any of the three tests.

Discussion

There were no significant differences either within or between males in the patterns of mudballs placed over three successive tides. This result implies

TABLE 3. *The responses of females to artificial burrows with dummy males surrounded by different types or numbers of mudballs*

	Mudball type and number		<i>N</i>	<i>p</i>
	47 burrow mudballs	47 surface mudballs		
Mudballs 1 st approached	7	11	18	0.35
Latency to 1 st approach	53.71 ± 20.63	42.18 ± 21.90	18	0.22
Time spent in zone	155.39 ± 41.05	148.06 ± 42.32	18	0.83
Entered burrow	6	6	12	1.00
	47 burrow mudballs	47 real mudballs		
Mudballs 1 st approached	13	6	19	0.11
Latency to 1 st approach	38.31 ± 11.87	47.83 ± 20.46	19	0.73
Time spent in zone	192.74 ± 43.53	180.42 ± 46.34	19	0.81
Entered burrow	6	5	11	0.76
	37 real mudballs	57 real mudballs		
Mudballs 1 st approached	6	13	19	0.11
Latency to 1 st approach	160.83 ± 134.10	50.77 ± 15.52	19	0.93
Time spent in zone	96.32 ± 33.76	264.42 ± 46.31	19	0.053
Entered burrow	4	8	12	0.25

'Mudballs 1st approached' was the number of occasions on which each mudball zone was the first one entered (*p* derived from chi-square test). 'Latency to 1st approach' was the time (s, mean ± SE) taken for the first zone to be entered (*p* derived from Mann-Whitney *U*-test). The time spent in each zone was measured in seconds (mean ± SE, *p* derived from Wilcoxon signed ranks test). The number of females to enter and remain in the burrow of one particular mudball zone is the measure 'entered burrow' (*p* derived from chi-square test).

that mudballing is a stereotypical behaviour, as shown by the low coefficients of variation for most of the mudball placement measures (*e.g.* distance to the furthest mudball, CV of 17.8%). This stereotypy supports the display function of male mudballs, suggested by Oliveira *et al.* (1998).

We were not surprised that mudball diameter was the feature of the mudball arrangement with the lowest variation (10.4%), since it is probably constrained by the morphology of the crabs' ambulatories which carry completed mudballs. Burrow entrance diameter, which is constrained by crab size, has a similar level of variation (9.3%). The different levels of variation in the distances that mudballs are placed are more intriguing. The lowest coefficient of variation was for the distance to the furthest mudball (17.8%), and the distance to the centre of the mudball aggregation was also

fairly low (22.1%). However, the variation in the distance to the mudball nearest the burrow was more than twice that of the other distance measures (50.0%). This difference may be explained by the fact that the mudballs act as territory boundaries, therefore the further (boundary) mudballs should be more important in terms of placement than the ones nearer the burrow opening.

There was a surprisingly high level of variation in the total number of mudballs placed by males over three tides (CV of 46.5%). Latruffe *et al.* (1999) found that mudball number is positively (although weakly) correlated with the length of the male major chela ($r_s = 0.34$, $N = 32$, $p < 0.05$), so we would expect, all other things being equal, low levels of variation in the number of mudballs made by individuals. We suggest that our result could be due to varying levels of repair necessitated by high tide damage suffered by a burrow. Although, when we looked at the number of mudballs each of the subject males made during one of the tides in which he was observed, we found no correlation between mudball number and the difference between the peak water level of the preceding high tide and the lowest level of the low tide ($r_s = -0.31$, $N = 12$, $p = 0.33$). The change in tide level is not a particularly sensitive or direct indicator of the level of damage suffered by a burrow, so more direct observations are needed in order to rule out this possibility. As females only excavate mudballs to clear out the burrow (Oliveira *et al.*, 1998), variability in the number of mudballs females place could also give an idea of the amount of damage caused by the tide.

The only significant difference between males was the time spent mudballing, although individual males did not differ significantly over the series of tides. Whether a difference between the males, the burrows or an interaction between the two is responsible for this finding will require further data to establish.

Males re-positioned mudballs that were experimentally moved closer to the burrow. This result is further evidence of a display function of mudballs. Although they moved them further away again, the subjects never re-positioned the mudballs to their exact original location, unlike bowerbirds (*Amblyornis inornatus*) that either return experimentally moved bower decorations to their original position or discard them (Diamond, 1986). The crabs did not bring back the mudballs that were experimentally moved further away from the burrow, even though they frequently passed them when placing new mudballs. Oliveira *et al.* (1998) found that removing

mudballs leads to an increase in intermale aggression, implying that male mudballs are important in delimiting territories, and as larger territories should be preferable, we would not expect males to reduce their territory size from the experimentally enlarged territory.

Unfortunately the finding that males in group C re-positioned their mudballs while males in group F did not is confounded because males in the F treatment group had significantly larger chelae than those in the C treatment group, despite our attempt to randomly assign males to treatment groups. This means that we cannot distinguish between the effect of the experimental treatment and the size of the subjects. It is fairly common to see neighbouring males moving each others' mudballs, to increase their own territory size and decrease that of the neighbour (F. Burford, pers. obs.). However, males with larger chelae are more likely to win aggressive encounters (Jennions & Backwell, 1996), so they may be less prone to having their mudballs moved by neighbouring males. Therefore males in group F may not have moved their mudballs back to their original positions because their mudballs are rarely moved by neighbours. Males in group C, being smaller, are more likely to encounter neighbours interfering with their mudball arrangement and may therefore be more likely to re-position mudballs. It is an interesting possibility that the size of the male major chela could have such an effect on behaviour. In Algarve the male major chela is a local delicacy and is removed by fishermen, leaving the male to regenerate a new one. This claw-harvesting has implications for the stability of the population (Oliveira *et al.*, 2000). As well as the presence or absence of the major chela having an effect, the possibility that its size affects mudballing behaviour patterns (see also Latruffe *et al.*, 1999) indicates that these findings warrant further investigation.

To look at the importance of mudball arrangements as a whole, we destroyed them once they were complete. Males did not re-construct their mudball arrangements during the waving phase. However, as mudballs act as territory boundaries (Oliveira *et al.*, 1998) and as most aggressive interactions occur during the mudballing phase (Latruffe *et al.*, 1999) replacing mudballs during the waving phase probably does not have as high a priority as courting females. In natural conditions it is rare for mudballs to be destroyed by either conspecifics or humans (F. Burford, pers. obs.), so it is also possible that the crabs have not evolved behaviour patterns to effect mudball replacement. *U. beebei* males sometimes knocked down and then failed to repair the

pillars they had earlier constructed despite the fact that pillars attract females and females were actively sampling burrows (Christy, 1988b). In contrast, mudskippers (*Boleophthalmus boddarti*) build contiguous polygonal mudwalls around their burrows, which like the mudballs of *U. tangeri*, reduce inter-neighbour aggression by delineating territories (Clayton, 1987). When the walls were experimentally destroyed and replaced with clear perspex, the mudskippers rebuilt the visual barriers, but when they were replaced by hardboard no rebuilding occurred (Clayton, 1987).

In the three binary presentations conducted, females showed no significantly different responses to dummy males with different numbers or types of mudballs. There were no significant differences in response to mudballs made from mud from inside a burrow compared to mud collected from the mudflat surface. Similarly, there were no significant differences in response to artificial mudballs of mud taken from within a burrow when compared with real mudballs. Yet when we used real mudballs in quantities that represent a realistic level of natural variation encountered by females (*i.e.* 37 vs 57 mudballs), there was a non-significant tendency for females to approach faster and spend more time in close proximity with the male with the greater number of mudballs. These results are consistent with those found by Oliveira *et al.* (1998). The differences in statistical significance between this experiment and that of Oliveira *et al.* (1998) are not due to sample sizes, as we used only two individuals less.

Oliveira *et al.* (1998) concluded from their binary presentations that females prefer males with greater numbers of mudballs, contrasting with Latruffe *et al.*'s (1999) correlational results that females do not approach males based on the number of mudballs they have placed. All three results (*i.e.* Oliveira *et al.*, 1998; Latruffe *et al.*, 1999; this study) are consistent with females using mudballs to indicate the presence of a burrow into which she could retreat. In the artificial and stressful situation of a binary choice test it is likely that the females were primarily looking for a refuge, not selecting a potential mate. The mudballs indicated the presence of a burrow into which the female could retreat, and the larger number of mudballs could just have been more conspicuous.

It is possible that females do have preferences for different numbers or compositions of mudballs in the context of mating, but that they are not demonstrated in binary presentations such as we carried out. However, the lack of variation between males in their mudball arrangements (Table 1)

means that females have little potential to differentiate between males on this basis. Furthermore, if male mudball arrangements were an important source of information for females selecting mates, we would expect males to replace at least some of the destroyed mudballs during the waving and courtship phase of low tide. There could be a large amount of potential information about the microclimate of the burrow contained in mudballs (which should be important to females searching for suitable brood burrows), when mudballs are first placed on the mudflat surface, but by the courtship phase they would no longer accurately represent the internal state of the burrow.

Male and female mudball displays differ obviously (see Oliveira *et al.* (1998) for photographs) and we suggest that both males and females could use a mudball arrangement as an indication of the sex of the burrow-holder. In this way, a crab could discriminate whether a burrow belongs to a male or a female even when the resident is not on the mudflat surface. This is an important distinction to be able to make, as males may use the major chela to harass females (Altevogt, 1969; Zucker, 1986) and discriminating between male and female burrows would allow females to avoid approaching males too closely. It would also enable wandering males seeking new burrows to distinguish a male burrow (so posing a potential threat, but perhaps also an opportunity for taking over his burrow) from a female burrow (a potential mate).

In summary, we conclude that the male *U. tangeri* mudballs are a display that defines territory boundaries. Mudballing is a reasonably stereotypical behaviour and males respond to their mudballs being moved closer to the burrow by moving them further away, so preventing their territory being made smaller. However, once the courtship phase begins, waving to attract females seems to take a higher priority than replacing mudballs. Contrary to earlier studies, we suggest that male mudball displays contain little information suitable for use in female mate choice decisions. We suggest that at present there is only evidence for male mudballs functioning as territory markers in a male-male context.

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