# The sequence of mudball placement by male fiddler crabs, *Uca tangeri*

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**Abstract.** Male *Uca tangeri* place mudballs in the area surrounding their burrows each low tide to delineate territory boundaries. We investigated the sequence of mudball placement by noting the distance at which each mudball was placed and its location in one of eight sectors around the burrow. Ten of the 13 focal males placed their mudballs in a pattern that was significantly different from random. No relationship was found between mudball distance from burrow and order of placement in the mudball sequence. However, most males placed each mudball in the same or a nearby sector to that of the previous mudball.
**Key words:** fiddler crab, *Uca tangeri*, mudball.

**Resumen.** Los machos de *Uca tangeri* colocan bolas de barro en el área que rodea a sus madrigueras cada vez que baja la marea a fin de establecer los bordes de sus territorios. En el presente estudio se investigó la secuencia de colocación de las bolas de barro anotando la distancia a la que cada bola se colocaba y su localización respecto a cada uno de los ocho sectores alrededor de la madriguera. Diez de los 13 machos focales colocaron las bolas de barro en un patrón que difería significativamente del azar. No se encontró ninguna relación entre la distancia de las bolas de barro a la madriguera y el orden de secuencia en que estas bolas se colocaban. Sin embargo, la mayoría de machos colocaron cada bola en el mismo sector en el que habían colocado la bola anterior o en uno cercano.

## Introduction

At least 14 of the 80 species of fiddler crab (genus *Uca*, Ocypodidae) form sand or mud constructions on the mudflat surface near the opening to the burrows that the crabs maintain as refuges during high tide and for protection from predators (e.g. Christy, 1988a, b; Zucker, 1974, 1981; Salmon, 1987). Many species form mudballs from material excavated from within the burrow (P. Backwell, personal communication). These mudballs are then placed on the mudflat surface around the burrow entrance. Until recently, the formation and placement of mudballs was mostly overlooked as a construction behaviour, being regarded as merely a means of excavating and repairing the burrow (Crane, 1975). However, studies on *U. tangeri*, the only fiddler crab to occur in Europe, have shown that mudballing is more complex than previously thought.

Male *U. tangeri* tend to place their mudballs in a broad semi-circular pattern in front of their burrow opening, whereas most females tend to deposit their mudballs in a pile directly outside the burrow. Three pieces of evidence suggest that male mudballs form a territory boundary. First, removal of a male's mudball display leads to a 400% increase in the number of aggressive interactions with neighbouring males (Oliveira et al., 1998). Second, the distance at which individual males place the furthest mudballs each low tide has a low level of variation (CV of 18%) compared with their nearest mudballs (50%; Burford et al., in press), suggesting that the placement of more distant mudballs is more constrained or more critical. Finally, male *U. tangeri* re-position mudballs that are experimentally moved closer to the burrow (Burford et al., in press).

One aspect of the function of mudballs as a territory boundary is that we might expect the first mudballs placed by males to be the more distant, in order to delineate their territories early on in the low tide period. We investigated this idea by studying the sequence of mudball placement by male *U. tangeri*.

## Material and Methods

All fieldwork was carried out in May and June 2000, at the Ria Formosa Natural Park, Algarve, Portugal, where a population of *U. tangeri* inhabit the mudflats that are exposed each low tide. The crabs spent

Table 1. Associations between the sequence of mudball placement and mudball distance, and sector. Mantel tests were performed on 13 subjects. Values are the t-values from the Mantel tests and their associated significance levels.

| Male | Sequence v distance | | Sequence v sector | |
|---|---|---|---|---|
| | t-value | P | t-value | P |
| 1 | 1.473 | ns | 2.089 | < 0.05 |
| 2 | 4.486 | < 0.001 | -0.142 | ns |
| 3 | 0.958 | ns | -0.599 | ns |
| 4 | 4.546 | < 0.001 | 2.029 | < 0.05 |
| 5 | 4.095 | < 0.001 | 5.572 | < 0.001 |
| 6 | -0.073 | ns | -0.034 | ns |
| 7 | 1.842 | ns | 1.574 | ns |
| 8 | 3.796 | < 0.001 | 2.220 | < 0.05 |
| 9 | 5.428 | < 0.001 | 5.533 | < 0.001 |
| 10 | 6.104 | < 0.001 | 4.386 | < 0.001 |
| 11 | 2.470 | < 0.05 | 6.992 | < 0.001 |
| 12 | 1.857 | ns | 1.973 | < 0.05 |
| 13 | 3.815 | < 0.001 | -0.608 | ns |

Table 2. The distance mudballs were placed from the burrow was correlated with the order of their placement for the eight subjects that showed a non-random relationship between sequence and mudball distance. Values are the Spearman rank correlation coefficients ($r_s$) between distance and placement order, the associated significant one-tailed P values and the number of mudballs placed (n), ordered from strong negative correlations to strong positive correlations.

| $r_s$ | P (1-tailed) | n |
|---|---|---|
| -0.51 | 0.01 | 51 |
| -0.51 | 0.01 | 28 |
| -0.43 | 0.01 | 40 |
| -0.33 | 0.05 | 28 |
| -0.07 | ns | 51 |
| 0.43 | 0.01 | 78 |
| 0.44 | 0.01 | 58 |
| 0.63 | 0.01 | 30 |

approximately 1 to 1.5 hours mudballing each low tide. Focal males were chosen at random from the study area.

The area surrounding a focal male's burrow was divided into eight 45° sectors, numbered S1 to S8, clockwise from 12 o'clock (the direction of the sloped burrow opening). Males were observed while placing mudballs. The presence of an observer had no effect on the male subjects, as long as the observer remained still while the crabs were on the surface. After each mudball was placed and the crab had re-entered his burrow, we measured the distance from the burrow entrance to the mudball and noted which sector it was placed in. The observer could usually do this by reaching forward. If the observer needed to move, we timed the interval to re-emergence to detect disturbance, taking a longer re-emergence interval as evidence for disturbance. Only males that we considered to be undisturbed were included in the data set. We continued to take measures until the male ended his mudballing period. This was defined as occurring when entering his burrow and surfacing without a mudball three times consecutively, or when beginning to wave continuously. All subjects were measured and marked after the observation period.

To investigate whether the pattern of mudball placement by each male was significantly different from random, we compared matrices using a Mantel test. The first matrix contained the difference between the order in which mudballs were placed, for example the sequence difference between mudballs 1 and 10 is 9. The second matrix contained the differences in the distances between each mudball placed, for example, the difference between mudball 1 placed 61.5 cm from the burrow and mudball 10 placed 53.6 cm from the burrow is 7.9 cm. The third matrix contained the differences between the sectors each mudball was placed in. The shortest distances were always used, therefore if mudball 1 was placed in S7 and mudball 10 was placed in S8, then the difference shown in the matrix is 1. However, if mudball 20 was placed in S1, then the difference between mudballs 1 and 20 is 2. All measures were absolute distances (i.e. the sign of the differences were ignored). We then compared matrix 1 with matrices 2 and 3 and the resulting t-values showed whether or not there was a significant association between matrix 1 and each of matrices 2 and 3 (Schnell 1985).

## Results

Ten of the 13 males placed their mudballs in a sequence that was significantly different from random (Table 1). Of these 10 males, six showed non-random placement of mudballs in both distance and sector, while a further two males showed non-random placement in mudball distance only and the remaining two showed non-random placement according to sector only.

To investigate our hypothesis that males place their more distant mudballs first to quickly delineate their territory boundaries, we correlated mudball sequence and mudball distance for the eight males that showed a significantly non-random pattern of placement. Four of the males followed the pattern of placing distant mudballs early in the placement sequence (i.e. showed negative correlations between mudball distance and order of placement, Table 2). However, three males showed significant positive correlations (i.e. placed distant mudballs last) and one showed no significant correlation (Table 2).

The effect of mudball placement sequence on the sector in which mudballs were placed was investigated by looking at scatterplots of the data. Of the eight males that showed a significantly non-random relationship between mudball sequence and sector, all but one placed each mudball either in the same sector as the previous mudball, or up to two sectors away. For example, a male that placed his fifth mudball in S1, then placed his sixth mudball either in S1 again, or in S7, S8, S2 or S3. The exception was one male that placed each mudball up to four sectors away from the previous one.

Table 3. Features of males that place their distant mudballs early in the sequence (n = 4), males that place their distant mudballs later in the sequence (n = 3) and a male that showed no significant relationship between mudball sequence and distance (n = 1). For details see Table 2. Values are means ± se. All linear measures are in mm.

| | Distant mudballs earlier | Distant mudballs later | No relationship |
|---|---|---|---|
| Carapace width | 27 ± 1 | 28 ± 3 | 33 |
| Carapace length | 18 ± 1 | 19 ± 2 | 21 |
| Major chela length | 41 ± 3 | 33 ± 1 | 61 |
| Major chela height | 15 ± 1 | 13 ± 2 | 17 |
| Handedness | All right-handed | All left-handed | Left-handed |

Males that placed their distant mudballs early in the placement sequence were right-handed and tended to possess longer major chelae than the males (all left-handed) that placed their distant mudballs later in the placement sequence (Table 3). The male that showed no significant correlation between mudball placement order and mudball distance had a larger carapace and a considerably longer major chela than males that showed a significant correlation (either negative or positive).

## Discussion

Ten males showed significantly non-random sequences of mudball placement either in the distance at which the mudballs were placed, the sector they were placed in, or both. On the basis that rapid delineation of territory boundaries would be advantageous, we expected the sequence of mudball placement to begin with males placing their more distant mudballs. However, the evidence does not support this idea: four males placed their more distant mudballs early on in the sequence, but three males placed them towards the end of the sequence. This suggests that while rapid delineation of territory boundaries may have some effect on the distance at which mudballs are placed, there are probably other influencing factors. These factors are likely to differ between males as a consequence of conditions specific to each male (e.g. neighbour density and proximity, value of the burrow to the male or availability of females).

Eight males placed their mudballs non-randomly in the sectors around the burrow, usually either in the same sector or a sector nearby the one that the previous mudball was placed in. Such a pattern of placement could result in a semi-circular arrangement of mudballs in front of the burrow. The effect of sequence on the sector in which mudballs are placed is more apparent than its effect on the distance at which they are placed. There are also suggestions in our data that the morphology of individuals (handedness and major chela length) affect the sequence in which mudballs are placed (Table 3).

In summary, we have provided further evidence that mudballing is more complicated than first thought and should not be dismissed simply as a process of burrow excavation. Oliveira et al. (1998) concluded that females placed mudballs as a by-product of burrow excavation, but recently it has been shown that this is also an oversimplification as some females produce male-style patterns of placement (Burford et al., unpublished data). The non-random placement of male mudballs and the individual differences in the sequence of mudballing (e.g. whether a male begins by placing distant or closer mudballs) indicate that mudball placement and factors influencing it are worthy of further investigation.

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