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ARTICLE

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Male-like mudballing behavior of some female fiddler crabs (*Uca tangeri*)

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Abstract At each low tide, male and female *Uca tangeri* remove mudballs from inside their burrows and place them on the surface. Previous studies have shown clear intersexual differences in mudball arrangements. However, we noticed that some females placed their mudballs in an arrangement similar to that of males. In this study, we investigated several factors that may have been responsible for this change in female mudballing behavior. We found no significant effect of the lunar cycle, female size and reproductive state, or burrow features. We briefly discuss the avoidance of sexual coercion or parasite modification of host behavior as possible factors. Our study shows that intersexual differences in mudballing behavior are more complex than previously thought.

Key words Fiddler crab · *Uca tangeri* · Mudballing · Male-style behavior · Sexual harassment · Parasites

Introduction

At least 14 species of fiddler crab (genus *Uca*, Ocypodidae) form constructions from mud or sand each low tide (Christy 1988a). There are different types of structures that fulfill various functions. The shelters formed by *Uca terpsichores* reduce territory size in high-density populations (Zucker 1974), whereas the hoods constructed by *U. latimanus* play a role in courtship (Zucker 1981) and the pillars made by *U. beebei* act as guideposts to burrow entrances (Christy 1988a,b). Several species of *Uca* form mudballs (P. Backwell, personal communication), but this behavior has been little studied, perhaps because a key reference for fiddler crabs dismisses mudballing as simply being a means of burrow excavation at each low tide (Crane 1975). Recently, however, the mudballing behavior of *U. tangeri* has been the focus of several investigations (Oliveira et al. 1998; Latruffe et al. 1999; Burford et al. 2001), which have shown that mudballing in this species is more interesting and complex than mere excavation behavior.

Uca tangeri occurs along the Iberian peninsula and the West African coast; it is the only species of *Uca* in Europe (Crane 1975). Both males and females maintain burrows that provide protection from predators during low tide periods and a secure refuge during tidal inundation. Males attract females to their burrows using a waving display of their hypertrophied chelae. Copulation occurs inside the male burrow, which the female then takes over as an incubation site, while the male leaves to either take over another crab's burrow or dig a new one (Crane 1975).

Each low tide, males and females may spend up to 2h forming and placing mudballs. These mudballs are carried from within the burrow to the mudflat surface and placed in the area surrounding the burrow opening. There are several intersexual differences in the mudball arrangements of males and females, which have been well documented by Oliveira et al. (1998). Males place a significantly greater number of significantly larger mudballs than females (Oliveira et al. 1998), although this may be a result of differences in burrow volume, as males tend to have longer and deeper burrows than females (C. Latruffe, unpublished data). However, there are also obvious differences in the placement of mudballs by males and females. Males tend to place their mudballs significantly further than females, forming a wide arc in front of the burrow, whereas females tend to deposit their mudballs in a small pile directly outside the burrow opening (see Oliveira et al. 1998, fig. 3). Removing male mudballs led to a 400% increase in the number of male–male aggressive interactions (Oliveira et al. 1998), thus suggesting that male mudballs reduce intermale aggression by forming territorial boundaries around the burrow. In contrast, it seems that females only

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place mudballs as a means of clearing out the burrow (Oliveira et al. 1998).

These obvious differences in the mudball arrangements enable human observers and, possibly, conspecific *U. tangeri* to determine the sex of a burrow occupant when it is not on the surface. This distriction might enable females to avoid approaching male burrows too closely, where they may suffer sexual harassment, and allow males in search of a new burrow to discriminate male burrows (a potential takeover opportunity) from female burrows (a potential mating opportunity). However, in 1999 we noticed for the first time that several females placed their mudballs in a broad semicircle resembling the male mudball arrangement. We therefore compared these male-style female arrangements (hereafter referred to as male-style arrangements) with both male arrangements and typical female arrangements (hereafter referred to as female arrangements), with the aim of identifying factors that may have influenced this change in female mudballing behavior.

Materials and methods

Study site

All fieldwork was conducted at the Ria Formosa Natural Park, Algarve, Portugal. Preliminary measures were taken during June 1999, and a more detailed investigation was conducted throughout May and June 2000. The population of crabs studied inhabits intertidal mudflats that are exposed for approximately 6 h each low tide.

Mudflat zonation

In 1999, we took measures from females distributed throughout the mudflat, and the average burrow density was 2.6 burrows/m^2. In 2000, we divided the mudflat into three main zones, depending on the type of substratum in each. At the lowest point of low tide, we measured the area of each zone that contained fiddler crab burrows, and the density of crabs active on the surface in each zone, using 10 random 1-m^2 quadrats per zone. The overall mudflat burrow density in 2000, corrected for different zone sizes, was 1.6 burrows/m^2.

Zone 1 was close to the tide line, measured 33 m^2, with an average density of 2.6 burrows/m^2. The substrate was muddy clay with a small amount of algal cover, but there were many large rocks, stones, and pebbles, both on the mudflat surface and underground. Zone 2 was adjacent to zone 1, also along the water's edge, but was much larger, 124 m^2; this was the most densely populated zone with an average of 3.1 burrows/m^2. Zone 2 consisted of sandy clay with extensive algal cover in some areas, and few stones and pebbles. Zone 3 was the largest zone, lying away from the tide line above zone 2. This zone was the first zone to be uncovered as the tide receded and the last to be covered as high tide approached; it measured 255-m^2, with a density of only 0.7 burrows/m^2. The sandy substrate had no algal cover or pebbles.

Mudball arrangement measures

In 1999, measures were taken from 30 male, 20 male-style, and 17 female mudball arrangements. In 2000 we measured 73 male, 90 male-style, and 63 female mudball arrangements. Males and females were easily distinguished by the white male major chela, which is obvious even on males with small regenerating chelae. Also, males were waving during the period of low tide when mudball arrangement measures were taken.

In 1999, all crabs were marked and released immediately after the measures were taken to avoid reuse. Due to time constraints, we did not mark crabs used in 2000, and therefore it is likely that the mudball arrangements of some crabs were measured at more than one low tide. Using the areas covered by the three zones and the average burrow density in each, we calculated the average number of crabs present in each zone. These estimates are conservative because we took all density measures during one low tide 2 days before a full moon (when the crabs are less active; C. Latruffe, unpublished data) and because crabs do not necessarily come out of their burrows each low tide (Burford et al. 2001). We sampled 78 crabs in zone 1 from an estimated total of 86 crabs, 90 crabs in zone 2 from an estimated total of 384, and 58 crabs in zone 3 from an estimated total of 179. Using resampling statistics (Manly 1997) with 100 repetitions, in the three zones we found that 63.2%, 89.9%, and 86.5% of crabs, respectively, were used only once. Therefore, we can be confident that the possibility of having remeasured mudball arrangements of some crabs should have a negligible effect on our results in zones 2 and 3. The higher percentage of resampled crabs in zone 1 suggests that we should interpret the results for this zone with care.

From each mudball arrangement measured, we noted the total number of mudballs, the diameter of eight randomly selected mudballs measured to the nearest millimeter using calipers (from which an average was calculated), and the distance to the nearest and furthest mudballs, as well as the distance to the center of the mudball aggregation. In 1999 we took several more measures that we did not use in 2000: the distance from the focal burrow to the burrow of the nearest neighbor, the length and depth of female burrows (measured to the nearest centimeter), and the carapace width of the resident females (measured to the nearest millimeter). All distances were measured to the nearest centimeter. In both years we noted whether the resident females were ovigerous (carrying eggs) and measured the burrow entrance of all subjects as a representation of crab size [Lourenço (1995) found that burrow entrance diameter is highly correlated with the carapace width of the resident crab in *U. tangeri*].

As *U. tangeri* behavior is strongly influenced by the lunar cycle (C. Latruffe, unpublished data), in 2000 we took measures every third tide over a period of 30 days, to cover an entire moon phase, giving a total of 10 tides. During each of these tides we observed a random sample of 20 burrows in each of the three zones, noting whether they were occupied by males or females and, for females, the style in which the mudballs were arranged. We then took measures (as already listed), when possible, from three male, three male-style, and three female mudball arrangements in each zone.

Statistical analyses

All the measures taken from mudball arrangements in both 1999 and 2000 were significantly correlated (r_s, 0.27–0.92; $n = 293$). Therefore, we used a principal components analysis to combine the measures into composite scores (McGregor 1992), on which statistical analyses were then conducted. We also performed two discriminant function analyses, the first to identify measures distinguishing the three mudball arrangement styles, and the second to identify measures distinguishing the mudball arrangements of ovigerous and nonovigerous females (regardless of mudball arrangement style). The measures of the burrows and crabs that were taken only in 1999 were analyzed separately.

Results

Mudball arrangement styles

Male arrangements are characterized by a greater total number of mudballs and a greater distance to the nearest, central, and furthest mudballs. Female mudball arrangements contain fewer mudballs and are closer to the burrow opening. Male-style mudball arrangements are intermediate to male arrangements and female arrangements, more closely resembling male arrangements in the distances at which the mudballs are placed and more similar to female arrangements in the number of mudballs placed (Fig. 1).

The mudball arrangements differed significantly (two-way ANOVA: $F_{2,282} = 113.7$, $P < 0.001$; Fig. 2) with significant differences between all three arrangement styles (Scheffe post hoc tests, $P < 0.001$ in all cases). There was also a significant difference between years ($F_{1,282} = 29.6$, $P < 0.001$), but there was no interaction between these two factors ($F_{2,282} = 1.2$, $P = 0.29$).

Discriminant function analysis (DFA) supported our interpretation that male-style arrangements are more similar to male arrangements (Fig. 2). The overall success rate for correctly classifying male, male-style, and female arrangements was 71.2% (Table 1). However, the success rate for correctly classifying female arrangements was 94.9%, whereas male and male-style arrangements were classified with success rates of 58.8% and 65.4%, respectively. The majority of misclassified male arrangements were placed in the male-style arrangement category (83.3%) and, similarly, most misclassified male-style arrangements were placed in the male arrangement category (75.7%).

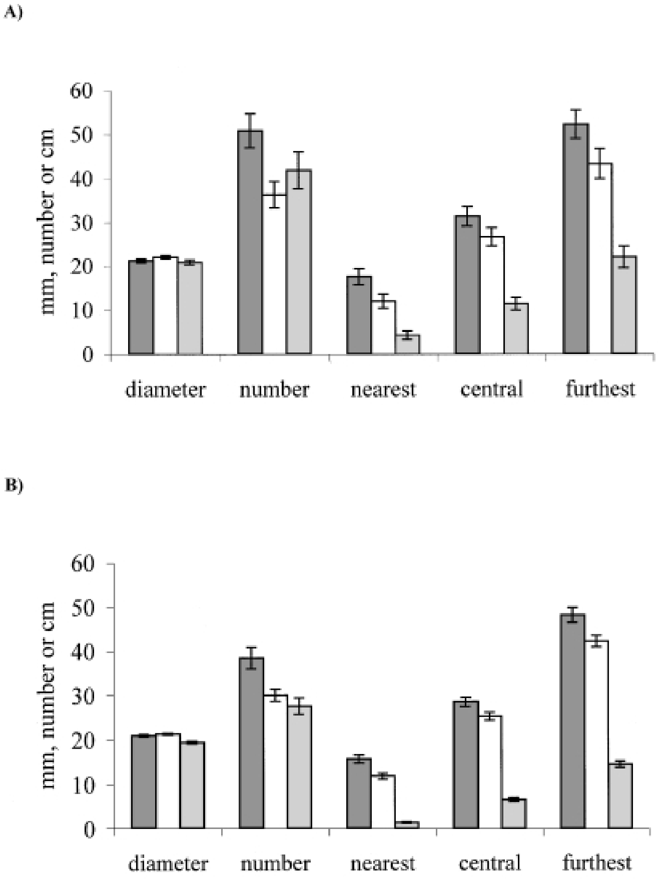

Fig. 1. Mudball arrangement measures (mean ± SE) from 1999 (**A**) and 2000 (**B**). Measures were taken from male (*black bars*), male-style (*white bars*), and female (*gray bars*) arrangements. Measures are mudball diameter, in millimeters (*diameter*), total number of mudballs made (*number*), and the distances, in centimeters, to the nearest mudball (*nearest*), the central mudball (*central*), and the furthest mudball (*furthest*). Sample sizes for male, male-style, and female arrangements are 30, 20, and 17, respectively, in 1999, and 73, 90, and 63, respectively, in 2000 [except for mudball diameter measures of female arrangements in 1999 ($n = 16$), male in 2000 ($n = 72$), and male-style in 2000 ($n = 87$)]

Effect of female reproductive state

We classified the mudball arrangements according to whether they were made by ovigerous or nonovigerous females, regardless of their arrangement style (i.e., male-style or female) and investigated whether a DFA could separate females in these different reproductive states on the basis of their mudball arrangements. DFA had an overall success rate of 68.1% for correctly classifying females into the two categories (Table 2), which is similar to the 50% success rate expected by chance alone.

Interzone comparisons

The data collected in 2000 can be separated according to the zone of the mudflat in which they were collected. There are several differences in the male and male-style mudball arrangements among the three zones (Tables 3 and 4, respectively), although there were no significant differences

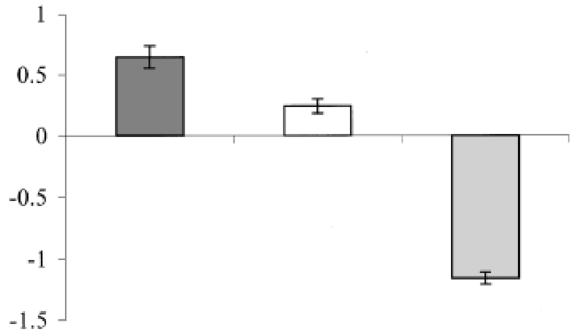

Fig. 2. Means ± SE for the first principal component scores of the three mudball arrangement styles: male (*black bar*), male-style (*white bar*), and female (*gray bars*). The first principal component (PC1) obtained from these individual measures accounted for 58.9% of the variance. The variables are weighted as follows: distance to the central mudball (0.95), distance to the furthest mudball (0.93), distance to the nearest mudball (0.86), average mudball diameter (0.52), and total number of mudballs (0.43)

Table 1. Classification results of discriminant function analysis of variables measured from the mudball arrangements of males and two arrangement styles of females: 1999 and 2000

Actual style of arrangement	Styles into which arrangements were classified			
	Male (%)	Male-style (%)	Female (%)	*n*
Male	59.2	34.0	6.8	103
Male-style	26.2	65.4	8.4	107
Female	2.5	2.5	95.0	79

Two discriminant functions were used in the analysis, with function 1 accounting for 91.4% of the variance (overall significance of the analysis: chi-square, 10 df = 279.9, $P < 0.001$). The variable weightings of function 1 were distance to the central mudball (0.97), distance to the furthest mudball (0.91), distance to the nearest mudball (0.73), average mudball diameter (0.24), and total number of mudballs (0.18). The variable weightings of function 2 were total number of mudballs (0.59), average mudball diameter (−0.44), distance to the nearest mudball (0.27), distance to the central mudball (−0.10) and distance to the furthest mudball (0.02)

Table 2. Classification of ovigerous and nonovigerous females using features of their mudball arrangements: 1999 and 2000 ($n = 182$)

Actual reproductive state	Reproductive state as classified by discriminant analysis		
	Ovigerous (%)	Nonovigerous (%)	*n*
Ovigerous	60.6	39.4	66
Nonovigerous	27.6	72.4	116

A single discriminant function was used in the analysis (overall significance: chi-square, 3 df = 37.0, $P < 0.001$) based on the following variable weightings: total number of mudballs (0.63), distance to the nearest mudball (−0.45), distance to the furthest mudball (−0.42), distance to the central mudball (−0.42), and average mudball diameter (0.32)

among the zones in female mudball arrangements (Kruskal–Wallis; $P > 0.05$ for all variables). There were no significant differences between the zones in the sizes of the crabs making any of the three mudball arrangement styles (as measured by the diameter of the burrow opening). However, males in zone 3 made significantly larger mudballs than males in zones 1 and 2 and more mudballs than males in zone 1 (see Table 3). Furthermore, males in zone 3 placed their mudballs significantly further from the burrow (in all three distance measures) than males in zones 1 and 2 (Table 3). Male-style mudball arrangements in zone 3 had their nearest, central, and furthest mudballs significantly further than those in zone 1 (see Table 4). There were also significant differences in the distances to the central mudballs between zones 3 and 2 and in distances to the furthest mudballs between zones 2 and 1 (Table 4).

There was a clear sex ratio bias toward females in each of the zones observed in the random scans (zone 1, 2.5 ± 0.7 males, 14.7 ± 1.0 females; zone 2, 8.0 ± 0.5 males, 12.0 ± 0.5 females; zone 3, 3.2 ± 0.7 males, 16.8 ± 0.7 females). However, there was a significantly higher proportion of males in zone 2 than in zone 3 [$n = 10$, means ± SE: zone 2, 0.35 ± 0.04; zone 3, 0.31 ± 0.03; Kruskal–Wallis $\chi^2 = 14.76$, $P < 0.01$; significant post hoc Mann–Whitney *U* tests (*P* adjusted to 0.02 to reduce the chances of committing a type I error), $P < 0.001$]. Furthermore, there was a significantly higher proportion of male-style arrangements in zone 3 compared to zones 1 and 2 [$n = 10$, means ± SE: zone 1, 0.59 ± 0.04; zone 2, 0.59 ± 0.06; zone 3, 0.99 ± 0.009; Kruskall–Wallis $\chi^2 = 19.73$, $P < 0.001$; significant post hoc Mann–Whitney *U* tests (*P* adjusted to 0.02 to reduce the chances of committing a type I error), zone 1 vs. zone 3, $P < 0.001$; zone 2 vs. zone 3, $P < 0.001$).

There was a significant tendency for a lower proportion of ovigerous females to occur in zone 3 than in zones 1 and 2 [$n = 10$, mean ± SE: zone 1, 0.44 ± 0.08; zone 2, 0.34 ± 0.07; zone 3, 0.15 ± 0.08; Kruskall–Wallis $\chi^2 = 7.04$, $P = 0.03$; post hoc Mann–Whitney *U* tests (*P* adjusted to 0.02 to reduce the chances of committing a type I error), zone 1 vs. zone 3, $P = 0.03$; zone 2 vs. zone 3, $P = 0.04$]. There were significantly more nonovigerous than ovigerous females in zone 2 (20 ovigerous females, 40 nonovigerous females; $\chi^2 = 6.7$, $P < 0.01$) and zone 3 (5 ovigerous females, 29 nonovigerous females; $\chi^2 = 16.9$, $P < 0.001$), but there was no significant difference in zone 1 (26 ovigerous females, 33 nonovigerous females).

Intrazone comparisons

There were significantly more male-style arrangements than female arrangements observed in the random scans in zone 3 (166 male-style, 2 female; $\chi^2 = 160.0$, $P < 0.001$), but there were no significant differences in zones 1 (84 male-style, 63 female) and 2 (69 male-style, 51 female).

Effect of lunar cycle, neighbors, crab size, and burrow

There was no obvious pattern of change in the proportion of male-style and female mudball arrangements during the lunar cycle (Fig. 3). The distance from the focal burrow to that of the nearest neighbor did not differ significantly between male-style and female arrangements (mean ± SE:

Table 3. Comparison of male mudball arrangements among the three zones

	Zone 1	Zone 2	Zone 3	Kruskal–Wallis χ^2	Post hoc <0.02*
Diameter	20 ± 1	21 ± 0	22 ± 1	11.59	1 vs. 3
	(19)	(30)	(23)	P < 0.01	2 vs. 3
Number	29.4 ± 2.9	36.3 ± 3.1	49.0 ± 5.3	11.92	1 vs. 3
	(19)	(30)	(24)	P < 0.01	
Nearest	12.9 ± 1.6	13.9 ± 1.2	20.8 ± 1.7	21.33	1 vs. 3
	(19)	(30)	(24)	P < 0.001	2 vs. 3
Central	22.9 ± 1.5	27.9 ± 1.4	34.3 ± 1.5	19.80	1 vs. 3
	(19)	(30)	(24)	P < 0.001	2 vs. 3
Furthest	38.4 ± 2.0	48.5 ± 2.8	55.9 ± 2.4	6.87	1 vs. 3
	(19)	(30)	(24)	P < 0.05	2 vs. 3

Values are means ± SE of the five measures taken from male mudball arrangements (with sample sizes given in brackets), in the three zones defined in 2000. The measures are average mudball diameter measured to the nearest millimeter ("diameter"), total number of mudballs made ("number"), and the distances to the nearest ("nearest"), central ("central"), and furthest ("furthest") mudballs, measured to the nearest millimeter

*The significance level for the post hoc Mann–Whitney tests was adjusted to 0.02 to reduce the chances of committing a type I error

Table 4. Comparison of male-style mudball arrangements among the three zones

	Zone 1	Zone 2	Zone 3	Kruskal–Wallis χ^2	Post hoc <0.02*
Diameter	21 ± 0	22 ± 0	22 ± 0	ns	
	(30)	(30)	(27)		
Number	28.5 ± 2.3	31.6 ± 2.5	30.5 ± 2.6	ns	
	(30)	(30)	(30)		
Nearest	9.5 ± 0.8	11.9 ± 1.1	14.6 ± 1.4	8.69	1 vs. 3
	(30)	(30)	(30)	$P < 0.05$	
Central	21.2 ± 1.2	24.4 ± 1.3	30.7 ± 1.4	23.40	1 vs. 3
	(30)	(30)	(30)	$P < 0.001$	2 vs. 3
Furthest	35.5 ± 1.5	42.3 ± 2.1	49.6 ± 2.6	20.1	1 vs. 2
	(30)	(30)	(30)	$P < 0.001$	

Values are means ± SE of the five measures taken from male-style mudball arrangements (with sample sizes given in brackets), in the three zones defined in 2000. The measures are average mudball diameter measured to the nearest millimeter ("diameter"), total number of mudballs made ("number"), and the distances to the nearest ("nearest"), central ("central"), and furthest ("furthest") mudballs, measured to the nearest millimeter

*The significance level for the post hoc Mann–Whitney tests was adjusted to 0.02 to reduce the chances of committing a type I error

male-style, 97.7 ± 11.6 cm, $n = 20$; female, 72.4 ± 8.9, $n = 17$). Furthermore, the sex of the nearest neighbor had no significant effect on female mudball arrangements (Mann–Whitney *U* tests: all $P > 0.05$). There was no difference in the carapace width of the females making the two styles of mudball arrangement measured in 1999 (mean ± SE: male-style, 27.1 ± 0.28 mm, $n = 18$; female, 27.8 ± 0.4 cm, $n = 15$). However, there was a significant difference in the burrow diameters of the crabs measured in 1999 and 2000 (Fig. 4) (Kruskal–Wallis $\chi^2 = 12.5$, $P < 0.05$). We adjusted the significance level to $P < 0.008$ for the Mann–Whitney post hoc tests to reduce the chances are committing a type I error; therefore, the only significant difference in burrow sizes was that male-style females in 1999 had significantly larger burrow entrances than males in 2000. There were no differences in the length (mean ± SE: male-style, 31.5 ± 1.5 cm, $n = 12$; female, 28.2 ± 2.0 cm, $n = 13$) or depth (mean ± SE: male-style, 21.1 ± 1.7 cm, $n = 12$; female, 25.9

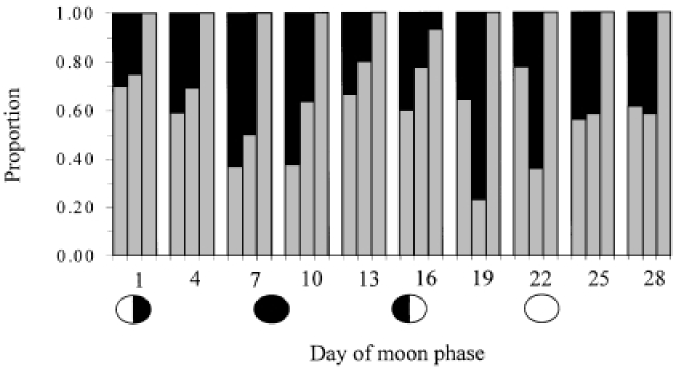

Fig. 3. Proportion of male-style (*gray bars*) and female (*black bars*) mudball arrangements over an entire moon phase (times of new moon, half moon, and full moon are indicated). For each day there are three bars, representing, *left* to *right*, zones 1, 2, and 3, respectively

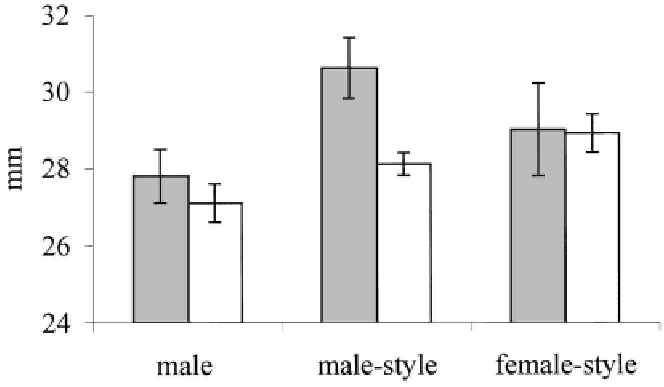

Fig. 4. Means ± SE of burrow diameters for male, male-style, and female arrangements in 1999 (*gray bars*) and 2000 (*white bars*). Sample sizes for 1999 and 2000, respectively, are male, 30 and 73; male-style, 20 and 90; and female, 17 and 63

± 1.8 cm, $n = 13$) of the burrows inhabited by females making the different mudball arrangement styles.

Discussion

Male-style mudball arrangements showed a strong similarity to male arrangements in the distance at which mudballs are placed, but they were more similar to female arrangements in the number of mudballs. The distance at which the mudballs were placed from the burrow was the key feature that we used to distinguish male-style and female arrangements, and DFA could not successfully separate male and male-style arrangements. It is possible that *U. tangeri* would have similar difficulties in distinguishing male from male-style mudball arrangements. Unsurprisingly, mudball diameters were very similar across the three mudball arrangement styles, probably because mudball size is constrained by the morphology of the crabs ambulatories that carry the completed mudballs.

We looked for differences between the styles of female mudballing and several factors. We found no evidence that the lunar cycle, length and depth of the burrow, female size, or reproductive state of the female affected mudball style. We think that burrow density can be excluded as a factor affecting mudball style. Although the total number of mudballs placed by females was smaller in 2000 (when burrow density was 1.6/m^2) than 1999 (burrow density, 2.6/m^2), zone 3 had the lowest burrow density (0.7 burrows/m^2) yet contained the highest proportion of male-style arrangements. We also think it unlikely that substratum type affected mudball style, because although it could conceivably affect the number of mudballs placed (by making it easier to excavate and form them), it should not affect the distance at which mudballs were placed. (We only rarely observed mudballs disintegrate when being carried.)

The literature on the avoidance of sexual harassment and the behavioral effects of parasitic infestation suggests explanations that merit initial consideration. Sexual coercion inhibits free choice of mates by females (McLain and Pratt 1999) and can often lead to females evolving traits to reduce the costs of harassment (Clutton-Brock and Parker 1995), including resembling males or adopting male behavior. For example, in the damselfly, *Ischnura ramburi*, some females have a malelike color morph that reduces the amount of male harassment they receive (Robertson 1985). Male *Uca* spp. have, on occasion, been described as herding or carrying females into their burrow for copulation (Crane 1941; Altevogt 1969; Zucker 1983, 1986). Male-style displays may therefore represent an attempt by females to avoid such harassment. We do not have the data to assess this idea directly, but the lack of an association between whether a female was ovigerous and mudball style makes it unlikely.

Parasites are known to affect host behavior in many ways (Moore 1995) and at least one rhizocephalan parasitic castrator of a decapod crustacean can induce masculinization of female morphology (Attrill 1989). Therefore, the possibility that masculinization of female *Uca tangeri* mudball arrangements to male style is a result of a parasite deserves direct investigation.

In summary, we cannot offer a definitive explanation of the differences in female mudballing styles we observed. Further progress in understanding variation in patterns of female mudballing behavior requires physiological and parasitological investigations together with experimental manipulations.

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