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Burrows with Chimneys of the Fiddler Crab *Uca thayeri*: Construction, Occurrence, and Function

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João B. L. Gusmão-Junior, Glauco B. O. Machado, and Tânia M. Costa (2012) Burrows with chimneys of the fiddler crab *Uca thayeri*: construction, occurrence, and function. *Zoological Studies* **51**(5): 598-605. Building of soil structures is observed in a variety of semi-terrestrial crustaceans. In fiddler crabs (Genus *Uca*), this behavior occurs in several species, some of which build structures that are largely ornamental and others construct barriers that are apparently for defense. Although there is a relative abundance of studies on this type of behavior in *Uca*, the relationship between the social context and the occurrence of these structures remains poorly studied. Thus, this study attempted to analyze in detail the construction, occurrence, and function of mud chimneys built by the fiddler crab *Uca thayeri*; these sedimentary structures are possibly associated with burrow defense. Field investigations and laboratory experiments were conducted. Both sexes were often found in burrows with chimneys; however, laboratory experiments showed that only females actively built and maintained chimneys, with some difference in the morphology of these structures between sexes. The social context had little influence on the construction of chimneys, which showed that the stimulus for constructing chimneys could be endogenous. Our results suggest that burrows with chimney of *U. thayeri* may have functions other than defense, and may act in regulating the internal conditions of the burrow, as observed in other crustaceans with such building behavior. http://zoolstud.sinica.edu.tw/Journals/51.5/598.pdf

Key words: Construction behavior, Biogenic structure, Crab behavior.

Several species of semi-terrestrial crustaceans have a characteristic behavior of burrow building, which can be described as the stacking of sedimentary material in the vicinity of the burrow opening. Among taxonomic groups in which this behavior occurs, crayfish from the superfamily Astacoidea and crabs from the superfamily Ocypodoidea stand out (McManus 1960, Crane 1975, Takeda et al. 1996).

The genus *Uca* Leach 1814 (fiddler crabs) contains a large number of species with such construction behavior (Crane 1975). However, the morphology and possible functions of such structures built by these species vary, but there are 3 basic types: chimneys which are a sedimentary structure similar to a wall surrounding the entire edge of the burrow opening (Crane 1975, Slatyer et al. 2008); hoods which are a sedimentary structure of semicircular shape, forming a covering that protects part of the burrow opening (Zucker 1974, Crane 1975, Christy et al. 2001, Kim et al. 2004, Christy 2007, Mokhlesi et al. 2011), and pillars which are sedimentary structures piled next to the burrow opening (Crane 1975, Christy 1988, Mokhlesi et al. 2011).

In some species, only males construct hoods,

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which may act as an ornamental structure (Yamaguchi 1971, Christy et al. 2001, Kim et al. 2004) or be associated with territoriality (Zucker 1974, Christy 1988). In other species, as is the case of *U. thayeri* Rathbun 1900, apparently only females build chimneys that possibly protect the burrow from intruders (Crane 1975, Salmon 1987). There are also species in which both sexes build structures, as in the case of *U. arcuata* De Haan 1835 and *U. capricornis* Crane 1975, the chimneys of which also have a defensive function (Wada and Murata 2000, Slatyer et al. 2008).

Most studies evaluating the roles of chimneys did not consider how the social context could influence the construction of these structures. Chimneys are thought to act as barriers that give an advantage to the resident crab, and consequently it is expected that the investment in the construction of these structures increases when potential intruders are present.

This study attempted to investigate the construction, occurrence, and function of chimneys built by the fiddler crab *U. thayeri* through field investigations and laboratory experiments. The field investigations were performed to verify the occupants of burrows with chimneys, and to assess temporal variations in the occurrence and size of the structures. Laboratory experiments were conducted to examine how the chimneys are constructed and to test if the presence of potential conspecific intruders affects the construction of these structures.

MATERIALS AND METHODS

Study species

The species *Uca thayeri* occurs along the east coast of the Americas and in the Caribbean islands, and is mainly distributed between latitudes of 32°N and 28°S, where it is commonly found in muddy and shaded areas on the outer edge of mangrove forests (Crane 1975, Melo 1996). This species shows the behavior of building a sedimentary structure in the form of a chimney surrounding its burrow; these chimneys are apparently only built by females (Crane 1975, Salmon 1987).

Field sampling

Study site

The study site consisted of a mangrove forest in the municipality of Praia Grande, on the coast south of São Paulo, Brazil (23°59'15"S, 46°24'23"W). This forest is characterized by the presence of *Rhizophora mangle* on its margin next to the water line, and *Avicennia schaueriana* in its inner portion. Two sampling areas separated by about 80 m were established, each with dimensions of approximately 50 × 18 m, located 10 m from the water line (tide height = 0.0 m). The sediments predominantly consisted of silt and clay (with an average grain size of 5.3 ± 1.4 ϕ), an organic matter content of 16.5% ± 8.8%, and a moisture content of 24.7%.

Sampling techniques

Samples were obtained monthly from Nov. 2008 to Oct. 2009 using the quadrat technique. A quadrat size of 75 × 75 cm was determined in a previous pilot study, according to the method of Wiegert (Krebs 1989).

Each month, 9 quadrats were randomly sampled in each sampling area. The number of burrows with and without associated sedimentary structures and the dimensions of the structures, namely the width (W) and height (H) (Fig. 1), were recorded. The crabs were captured by excavation of each burrow using a garden shovel. This method was selected due to the fact that capturing the animals after they had come to the surface could take a long time and might introduce some deviations in the results because females (mostly ovigerous ones) may be less active and conspicuous than males. Sex and carapace width (CW) of the crabs were recorded, and they were

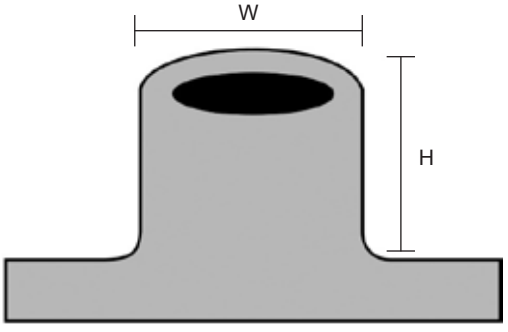

Fig. 1. Measurements of sedimentary structures of *U. thayeri*. H, height; W, width.

classified as adult (CW > 10 mm) and young crabs (≤ 10 mm CW) (based on Negreiros-Fransozo et al. 2003). Given that some burrows were apparently empty, we excluded burrows whose the occupants were not captured from the analysis in order to prevent deviations in the results.

Experiments in a controlled environment

Sampling site and experimentation

Specimens of *Uca thayeri* used in experiments were collected in the same mangrove forest where the field sampling was carried out. Adult crabs (with a CW > 13 mm) and young (with a CW of < 10 mm) with intact chelipeds and pereopods were used.

The experiments were conducted in the laboratory using matte plastic cylindrical terrarium containers with a diameter of 24 cm and a height of 26 cm, filled with a 15-cm layer of sediment (with an organic matter content of approximately 16%, a predominance of silt and clay, and a moisture content of ca. 24%) which had previously been sieved to remove the macrofauna. The temperature was maintained at 24-28°C.

Experimental design

To record and analyze the construction of the sedimentary structures, adult individuals of *U. thayeri* were videotaped. Male, female, and ovigerous female crabs were kept in individual terrariums (n = 4), where they were filmed for 3 d, from 08:00-18:00, totaling 30 h of film per replicate. After 3 d (72 h), we recorded and measured the height and width (Fig. 1) of the structures that had been built. The number of structures built by each individual was not computed because each crab build at least 1 burrow with a unique associated sedimentary structure during the experiment.

To investigate the function of chimneys as possible defensive structures, as proposed for other species of fiddler crabs (Wada and Murata 2000, Slatyer et al. 2008), we tested the influence of the social context (the presence or absence of potential conspecific intruders) on the construction of these sedimentary structures. To this end, ovigerous adult females in the intermediate stage of egg maturation (resident), which are individuals described as being active builders of chimneys (Salmon 1987), were subjected to different treatments (n = 12 replicates for each treatment): treatment A consisted of a resident and an adult male intruder; treatment B consisted of a resident and an ovigerous female intruder; treatment C consisted of a resident and a non-ovigerous adult female intruder; treatment D consisted of a resident and a young intruder (CW < 10 mm); and the control consisted of only a resident ovigerous female. After 72 h, each terrarium was analyzed for the presence of sedimentary structures associated with the burrows of resident ovigerous females, and their dimensions (height and width in mm) were measured.

Data analysis

The frequency data were compared by applying a Chi-squared test (χ^2), with α = 0.05. Continuous data were compared by a one-way analysis of variance (ANOVA), complemented by post-hoc Fisher's least significant difference, with α = 0.05. The homoscedasticity was verified by Cochran's test (α = 0.05), with the data transformed to a base 10 logarithm when necessary.

RESULTS

Field data

Three different morphotypes of burrows occupied by *Uca thayeri* were found: chimneys, irregular deposits, and burrows without a surface structure. Chimneys were sedimentary structures that surrounded the entire burrow opening with a cylindrical or conical shape and vertical walls. Irregular deposits of sediments were small deposits around the burrow opening that did not constitute a defined structure. Finally, burrows without associated structures had neither a chimney nor sediment deposits associated with the opening.

In total, 1518 burrows occupied by *U. thayeri* were recorded (377 in the summer, 331 in the fall, 391 in the winter, and 419 in the spring); among them, 462 had the chimney morphotype, 193 had irregular sediment deposition, and 863 had no associated sedimentary structures (Fig. 2). We collected 366 adult males, 386 young males, 388 adult females, 81 ovigerous females, and 297 young females.

Adult ovigerous and non-ovigerous females were more frequently found in burrows with chimneys than in burrows without structures (ovigerous: χ^2 = 127, $d.f.$ = 2, p < 0.001, non-ovigerous: χ^2 = 120.4, $d.f.$ = 2, p < 0.01) (Table

1). Adult males were more abundant in burrows with chimneys and those with irregular deposits than in burrows without associated structures (χ^2 = 55.7, *d.f.* = 2, $p < 0.01$). Young crabs of both sexes were more abundant in burrows without associated structures than in burrows with associated structures (young males: χ^2 = 694.8, *d.f.* = 2, $p < 0.01$; young females: χ^2 = 532, *d.f.* = 2, $p < 0.01$).

Considering only burrows with chimneys that were occupied by adult crabs, the dimensions of the chimney significantly differed among males, non-ovigerous females, and ovigerous females (ANOVA, height: $p < 0.001$, F = 21.8688, *d.f.* = 2; and width: $p < 0.01$, F = 5.0271, *d.f.* = 2). Structures associated with burrows of ovigerous females were significantly taller and narrower than those observed with burrows of males and non-ovigerous females (Fig. 3). Structures of burrows of non-ovigerous females, despite having a lower height than those of ovigerous females, were taller than those occupied by males (Fig. 3).

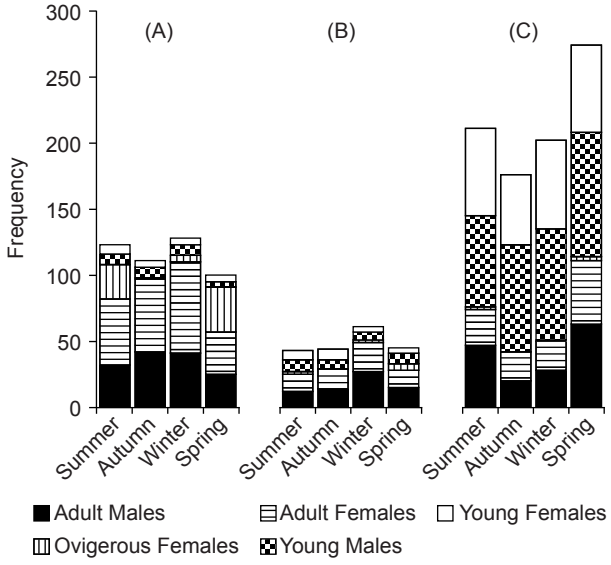

Fig. 2. Frequency of each demographic group (adult males and females, young males and females, and ovigerous females) of *U. thayeri* in burrows with a chimney (A), in burrows with sediment deposition (B), and in burrows with no associated sedimentary structures (C) per season.

Laboratory data

Adult males, non-ovigerous adult females, and ovigerous females constructed sedimentary

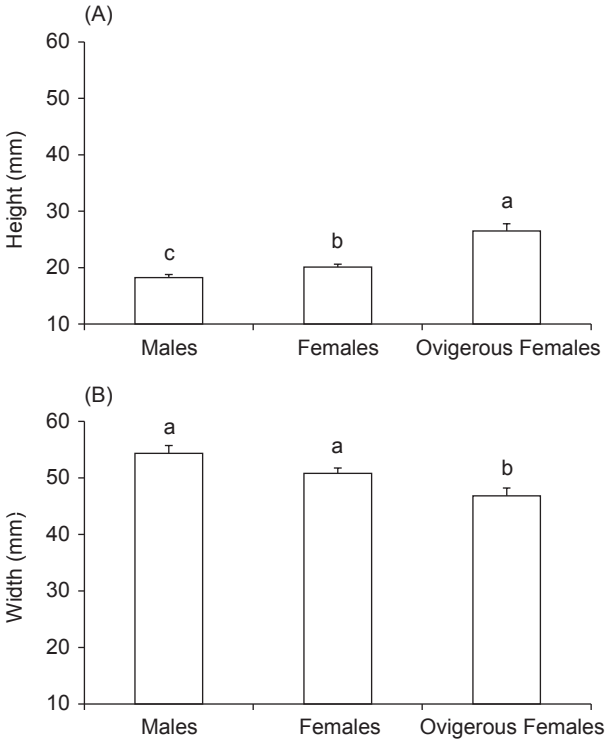

Fig. 3. Mean values (± standard error) of the height (H) and width (W) of sedimentary structures occupied by adult crabs (with a carapace width (CW) > 10 mm) sampled in the Portinho mangrove, Praia Grande, São Paulo (n = 412). Different letters indicate a significant difference ($p < 0.05$).

Table 1. Number and percent of each demographic group of *U. thayeri* in the different types of burrows

	All burrows		Chimneys		Irregular deposits		No structures	
	No.	Percent	No.	Percent	No.	Percent	No.	Percent
Adult males	366	24.1	140	30.3	68	35.2	158	18.3
Young males	386	25.4	28	6.1	30	15.5	328	38.0
Adult females	388	25.6	206	44.6	63	32.6	119	13.8
Ovigerous females	81	5.3	66	14.3	9	4.7	6	0.7
Young females	297	19.6	22	4.8	23	11.9	252	29.2
Total	1518	100	462	100	193	100	863	100

structures. The construction process was characterized by 3 behavioral acts, as illustrated in figure 4: (1) digging and depositing mud, in which the crab digs into the substratum using the 4 pereopods on 1 side of the body, removing sediment, and depositing it with the aid of the pereopods and chelipeds near the burrow opening; (2) dragging and stacking mud, in which the crab collects sediment from the surface surrounding the burrow and drags it with the pereopods to the edge of the burrow opening with the pereopods and chelipeds; and (3) modifying the structure, in which the crab stands on the sediment deposits (composed of pellets of excavation and sediments carried from the surroundings) and plasters them on the edge of the burrow opening using its pereopods and chelipeds. Of these 3 behavioral acts, it was found that adult males exhibited only 'digging and depositing mud', while ovigerous and non-ovigerous adult females performed all 3 behavioral acts. Only females invested in maintaining the built structures by reshaping their form and adding more sediment. All ovigerous females, 10 males (83.3%), and 10 non-ovigerous females (83.3%) built sedimentary structures. Average heights of the sedimentary structures built by males and non-ovigerous females were significantly lower ($p < 0.05$, $d.f. = 2$, $F = 5.4939$) than those of ovigerous females (Fig. 5A). The average width did not significantly differ among males, ovigerous females, and non-ovigerous females (Fig. 5B).

Resident ovigerous females, from both the experimental and control groups, constructed sedimentary structures. The average values of the height and width of the structures built by ovigerous females from the control group did not significantly differ from those built by resident ovigerous females from the other treatments (Table 2).

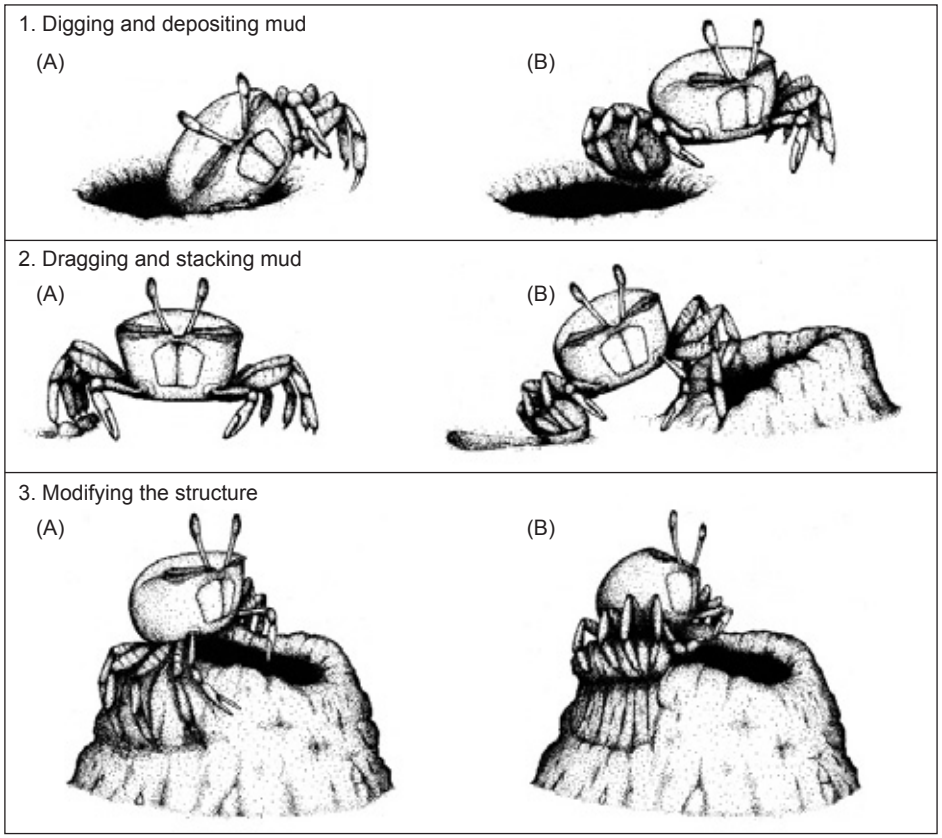

Fig. 4. Construction of chimneys by *U. thayeri*, an example of an adult female. (1) Digging and depositing mud: the crab digs into the substrate using the 4 pereiopods on 1 side of its body (1A), removing sediment and depositing it with the aid of the pereiopods and chelipeds near the edge of the burrow opening (1B). (2) Dragging and stacking the mud: the crab collects sediment from the surface surrounding the burrow (2A) and drags it with its pereiopods to the edge of the burrow opening with the pereiopods and chelipeds (2B). (3) Modifying the structure: the crab stands on the sediment deposits (3A) and modifies them at the edge of the burrow using its pereiopods and chelipeds (3B).

DISCUSSION

The construction of the sedimentary structures by *Uca thayeri* showed a pattern that was very similar to those described for *U. arcuata* (Wada and Murata 2000), *U. formosensis* Rathbun 1921 (Shih et al. 2005), *U. capricornis* (Slatyer et al. 2008), and *U. lactea* De Haan 1835 (Kim et al. 2004), although for the latter, the similarities were solely restricted to the behavioral acts. The building behavior of *U. thayeri* differed from those of *U. lactea*, *U. musica* Rathbun 1914, and other builders of hoods or pillars in several respects. The most notable was associated with the crab sex, in which only reproductively mature males build hoods (Crane 1975, Christy et al. 2001, Kim et al. 2004, Christy 2007), while in *U. thayeri* both sexes exhibited the construction behavior (as found in this study). The hoods apparently act as ornaments that assist in attracting females to the burrow of males (Christy et al. 2001, Kim et al. 2004, Christy 2007). This function does not apply to chimneys of *U. thayeri* because mating occurs in the burrow of females (Salmon 1987), and females, mainly ovigerous females, invest more in building the tallest structures (as found in this study).

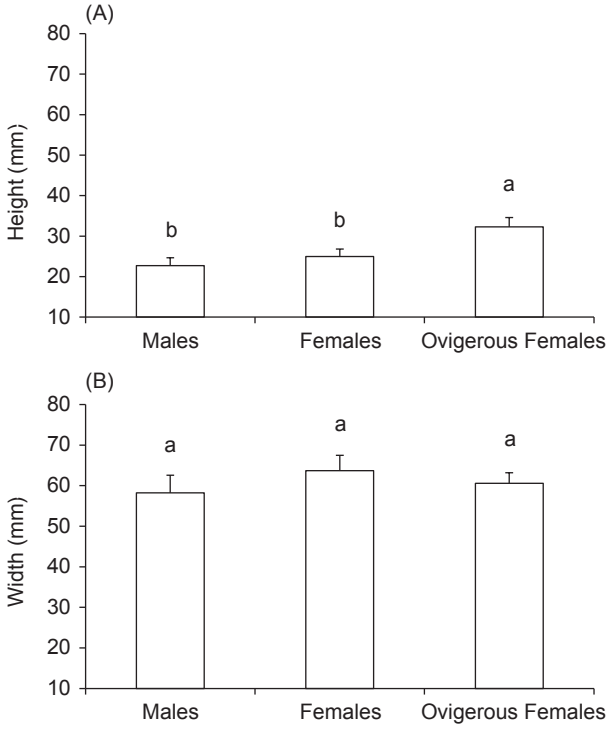

Fig. 5. Mean values (± standard error) of the height (H) and width (W) of sedimentary structures built by males and non-ovigerous and ovigerous females of *U. thayeri* in the laboratory (n = 32). Different letters indicate a statistical difference (p < 0.05).

Despite the high proportion of males occupying burrows with chimneys found in the field investigation, results of our laboratory research suggests that only females actively build chimneys (collecting material and shaping the structure), while the structures built by males are apparently the result of the deposition of excavation pellets during construction of the burrows. Our observations confirm what was described by Salmon (1987) about the behavior of this species. The behavioral differences between males and females possibly explain why there are morphological contrasts among the structure of burrows occupied by ovigerous females (taller and narrower than the others), adult females, and males (lower and wider).

The increased occurrence of adult females in burrows with chimneys, especially ovigerous females during spring and summer, apparently

Table 2. Experimental procedure: mean values (± standard error) of the resident and intruder size of each treatment (n = 12) with respective mean values of the height and width of the sedimentary structures built by the resident ovigerous female

	Crabs (CW)			Structures Built	
Treatments	Resident OF	Intruder	NSB	Height	Width
Control	17.58 ± 1.39	-	12	32.27 ± 2.30	60.61 ± 2.59
RE × OF	16.18 ± 1.76	15.82 ± 2.05	10	24.44 ± 2.00	53.38 ± 2.81
RE × F	17.79 ± 1.45	18.76 ± 2.21	11	35.95 ± 3.76	62.73 ± 3.63
RE × M	17.16 ± 1.36	19.02 ± 0.92	10	35.18 ± 3.37	64.27 ± 3.84
RE × Y	16.83 ± 1.48	7.6 ± 0.90	12	33.62 ± 3.49	51.83 ± 1.85

RE, resident crab; NSB, number of structures built; OF, ovigerous female; F, non-ovigerous adult female, M, adult male; Y, young crab; CW, carapace width.

confirms the observations of Crane (1975) and Salmon (1987), who reported a close relationship between these structures and the reproductive period of this species. Some authors described chimneys built by fiddler crabs as defensive structures, so that the walls play the role of barriers against conspecific intruders (Wada and Murata 2000, Slatyer et al. 2008) or hide the occupants from potential natural enemies (Shih et al. 2005). Considering that in *U. thayeri*, ovigerous females build structures that are taller than those built by other crabs, we suggest that they do this to enhance barriers against intruders and avoid agonistic interactions with conspecifics or at least to have an advantage in case of a confrontation. This possibly represents an advantage in the energy reserves of residents that own burrows with chimneys, given that the energy demand for reproduction is very costly.

Laboratory results revealed that the social context did not affect the construction of chimneys by ovigerous females of *U. thayeri*. This led us to suggest that the building behavior may be triggered by another stimulus or even an endogenous stimulus. Furthermore, the function of the chimney might not only be restricted to the defense of burrows and their occupants. In other groups of semi-terrestrial decapods that also build chimneys such as some species of crayfish (Cambaridae), the function of these structures is related to maintaining the internal conditions of the burrow, including regulating the evaporation of the internal water content (Williams et al. 1974, Trépanier and Dunham 1999). Chimneys built by female *U. thayeri* might also have a regulatory function (which does not exclude a possible defensive function), acting to maintain the internal conditions of the burrow, especially during the generation and incubation of egg masses, which could explain the greater investment by ovigerous females in constructing taller structures.

Our findings about the construction of chimneys by *U. thayeri* are summarized as follows: (1) the chimneys do not serve an ornamental function, as observed in other species; (2) both sexes build sedimentary structures, but apparently only females engage in developing and maintaining the chimneys, which explains the morphological contrast between structures associated with the burrows of males and females (especially ovigerous), found in both field and laboratory tests; (3) the social context does not influence the construction of chimneys by ovigerous females, which suggests that the stimulus triggering this behavior could be endogenous; and (4) it could be inferred that the defensive function might not be the only role of the chimney of *U. thayeri*, and the function of regulating certain internal conditions of the burrow, as observed in other crustacean chimney builders, could also be related to this behavior.

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