Research Article

Amazon freshwater crab *Dilocarcinus pagei* (Decapoda: Trichodactylidae): a view about burrow construction behavior

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ABSTRACT. Crabs use burrows to prevent predation, environmental interference and shelter. The present study investigated the excavation behavior of the trichodactylid crab *Dilocarcinus pagei*, considering the biometric aspects of the burrows, the excavation time, the amount of bioturbation and the excavation behavior of the two sexes. The burrows of males had a mean diameter larger than the females, although the depth was similar for both sexes. Females had higher bioturbation than males, and showed enlargement in a camera format at the bottom, even closing the entrance of the burrows with a "plug" after their construction. Both the camera and the presence of the "plug" in the burrows of the females may be associated with reproduction. The presence of pellets observed at the entrance of burrows is associated with the cleaning of the pereiopods by crabs after the excavation. The sequence of behaviors for the construction of the burrows is described in detail, contributing to the knowledge about the biology and ecology of freshwater crabs of the Amazon.

Keywords: *Dilocarcinus pagei*; Decapoda; sediment; crab behavior; Neotropical region; Amazon basin

INTRODUCTION

Animals may present different behaviors during their life stages, among them the excavation behavior developed by crustaceans, mainly marine (Crane, 1975), mangrove (Nordhaus *et al.*, 2009; Pülmanns *et al.*, 2016) and freshwater crabs (Sinha & Pati, 2008). The excavation behavior allows the soil to movement, promoting bioturbation (Meysman *et al.*, 2006). This soil movement during the construction of the burrows influences directly the sediment texture (Botto & Iribarne, 2000; Kristensen, 2008), nutrient cycling (Wang *et al.*, 2010) and increases the contact of the soil surface with air, benefiting the growth of microorganisms (Bertness, 1985). In addition to facilitating soil water flow by providing nutrient transport (Ridd, 1996), chemicals such as oxygen, iron, sulfur (Ferreira *et al.*, 2007), carbon and nitrogen are available to plants in the mangrove environments (Botto *et al.*, 2005; Natálio *et al.*, 2017).

The crabs excavate burrows with different shapes and sizes (Gusmão-Junior *et al.*, 2012). These structures can be shaped like chimneys (Shih *et al.*, 2005), hoods (Christy *et al.*, 2001; Ribeiro *et al.*, 2006) or pillars (Mokhlesi *et al.*, 2011). The construction of the burrows may be influenced by the reproductive period (Christy, 1982; Christy *et al.*, 2001; Shih *et al.*, 2005), environmental interference (Chakrabarti, 1981; Christy, 1982) and predation (Koga *et al.*, 2001). The morphology of the burrows ranges from simple (Christy, 1982) to complex (Chakrabarti, 1981; Lim *et al.*, 2015). Also, the burrows are attributes that serve as criteria for choosing partners (Backwell & Passmore, 1996; Ribeiro *et al.*, 2006; Heatwole *et al.*, 2018).

The crab *Dilocarcinus pagei* is an important member of the trophic chain, acting as an omnivore, predator and opportunist (Williner & Collins, 2002). This crab forms part of the bird diet (Magalhães, 1990; Olmos *et al.*, 2006) and inhabits rivers, lakes, ravines, macrophytes (Magalhães, 2003; Taddei & Herrera, 2010) and burrows (Pinheiro & Taddei, 2005; Melchor *et al.*, 2010; Genise, 2017). Despite its ecological importance, information on the behavior of *D. pagei* is still limited. Sant'Anna *et al.* (2014) described

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the daily activity and substrate preference; Senkman *et al.* (2015) investigated the reproductive behavior of *D. pagei* in populations in Argentina. The present study investigated the excavation behavior of *D. pagei*, analyzing this aspect in a population from the Central Amazon region, taking into account biometric aspects of the burrows, the time of excavation, the amount of bioturbation and the excavation behavior of both sexes.

MATERIALS AND METHODS

Burrows built in the environment

For the investigations of the biometric characteristics of burrows constructed naturally by males and females of the freshwater crab *Dilocarcinus pagei*, 32 crabs were captured (15 males and 17 females). The crabs were collected between September and October 2015 around Poranga Lake in Itacoatiara, Amazonas, Brazil (03º07'12.9"S, 58º27'6.5"W). This region is a characteristic area of várzea of the Amazon floodplain, which is completely flooded during the rainy season and becomes dry during the dry season (Junk, 1984).

The collections were carried out by three people for two hours during both day and night. The animals were collected by hand under vegetation and within burrows. A machete was used to aid the excavation. Once captured, the crabs were placed individually in plastic boxes for 12 h (18:00 to 6:00 h). Six translucent plastic boxes (42×28×38 cm) with the bottoms removed were used as a bulkhead and fixed 3 cm deep in the sediment. Only crabs with all body appendages were used in the experiment.

The excavation behavior was recorded during the experiment that lasted 12 h. All excavated sediment, including balls formed at the entrance of the burrows, were carefully removed with the aid of tweezers, brushes and spoons to avoid deformations. Ten sediment pellets from each crab were randomly collected and brought carefully to the laboratory for measurement. All substrate resulting from the excavation was subjected to granulometric analysis: the sediments excavated from the burrows of males and females were dried in an oven at 105°C for three hours to remove moisture from the sediment until reaching a constant weight. The dry sediment was sieved in six sieves, with diameters ranging from 2.0 to 0.063 mm, according to the method described by Santos (2000). The sediment retained in each sieve was weighed (0.001 g) and quantified in percentage to obtain the granulometric fractions (coarse sand, medium sand, fine sand and silt/clay). Also, the diameter (BD) and the depth of the burrow (BDTH) were recorded using a ruler (mm) always perpendicular to the sediment. In the

laboratory, the diameter of the pellets (DBS) was measured with a precision caliper (0.01 mm). The dry weight of the substrate excavated from the burrows of males and females was recorded with a digital balance (0.001 g).

After the sediment was removed from the burrow entrance, they were filled with quick-drying cement for molds (Nassau CP-II-E-32RS), which were removed after 12 h. Then, the molds were transported to the laboratory to be benchmarked for depth (BDTH) (mm).

The animals that presented excavation activities were transported live to the laboratory and identified, according to Magalhães (2003). For these crabs we measured with the aid of a caliper (0.01 mm) the carapace width (CW), carapace length (CL) and the length of the left and right propodus chelar (LPCl and LPCr, respectively), as well as the wet weight (P) with the aid of a digital balance (0.001 g). In the laboratory, the crabs were kept individually in aquariums (40×40×30 cm) and conditioned with *Eichhornia crassipes* macrophytes until the start of the experiment.

Excavation behavior

Eight adult crabs (four males and four females) were selected and placed individually in plastic boxes (28×46×35 cm) to analyze the excavation behavior of *D. pagei* in the laboratory. At the bottom of each plastic box, 15 cm of sediment from the collection site (Poranga Lake) was added.

The experiment lasted 24 h, and during this period, the behavior of each crab was recorded. At the end of this period, the crab was removed from the box, a 2 cm surface layer sediment was scraped off, and a new 2 cm layer was added; the remainder of the sediment was maintained. This procedure was performed to avoid those excretions and marks on the sediment left by another individual, which may have affected the excavation behavior of the next crab.

Video cameras (1/4" CCTV, 480TVL, NSTC) connected to a stand positioned on top of the boxes were used to visualize crab activity during 24 h monitoring. Each camera was programmed to document the movements of the animals as well as to evaluate the excavation time of males and females in minutes. At the end of each experiment, the animals were returned to the collection site. The crabs were monitored daily, and 40 W red light bulbs were used during the night. The use of this method allowed recording the movement of the crabs and avoided influencing the behavior of these decapods (Hazlett, 1966).

Data analysis

The normality of the data was verified by the Shapiro-Wilk test. The Mann-Whitney test was used to compare the biometric variables (CW, LW, P, LPCr and LPCl) of male and female crabs that exhibited excavation behavior (burrows and pellets). The size of the sediment pellets removed in front of the burrows, the diameter (BD), the depth (BDTH), the amount of sediment removed during the excavation (SR), the size of the molds of the burrows and the excavation time of males and females were also compared by a Mann-Whitney test. Simple linear regression analysis was used to evaluate the relationship between carapace widths (CW) and burrow characteristics (BD, BDTH, SR and DSB). All analyses of the tests were conducted in Software R 3.4.3. (R Core Team, 2015) with a significance level of $P < 0.05$.

RESULTS

Burrows built in the environment

A total of 32 specimens (15 males and 17 females) were observed in their natural habitat. There was no difference between the CW of males and females ($W = 175$, $P = 0.0779$). The CW size of males varied from 38.92 to 48.89 mm, with a mean of 42.97 ± 3.19 mm, and in females from 35.62 to 50.43 mm (40.84 ± 3.79 mm). Males presented CL ranging from 28.31 to 38.61 (35.15 ± 2.75 mm), whereas females had CL varying between 28.07 and 42.76 mm (34.03 ± 3.61 mm), with no difference between the sexes ($W = 165.5$, $P = 0.1567$). The LPCf of males ranged from 10.67 to 97.00 mm with a mean of 31.08 ± 18.29 mm, and in females from 19.29 to 29.55 mm with a mean of 23.27 ± 2.93 mm; males presented higher LPCf ($W = 219$, $P = 0.0021$). Male LPCr fluctuated from 17.53 to 45.50 mm with a mean of 36.47 ± 6.57 mm, and this variable ranged in female LPCr from 19.93 to 31.69 mm with a mean of 24.07 ± 3.17 mm. The LPCr was significantly higher in males ($W = 235$, $P = 0.00001$).

The burrow built by *Dilocarcinus pagei* in Lake Poranga and a burrow under construction are shown in Figures 1a and 1b, respectively. In the field, burrows had a diameter varying between 41.10 and 55.81 mm (48.91 ± 4.63 mm) and a depth ranging from 31.66 to 145.30 mm (77.39 ± 32.90 mm). The diameter of sediment pellets produced by males ranged from 4.32 to 6.64 mm (5.85 ± 0.63 mm), and those by females varied between 4.83 and 6.83 mm (5.88 ± 0.61 mm). The weight of the entire substrate removed by all males and females was 1.058 and 1.926 kg, respectively (Table 1).

Male burrows had a mean diameter greater than that of females ($W = 180$, $P = 0.0480$), although there was no difference between both sexes neither in the depth of the burrows nor in pellet diameter ($W = 103$, $P = 0.2417$ and $W = 131.5$, $P = 0.8948$, respectively). On the other hand, females removed significantly more sediment than males ($W = 71$, $P = 0.0330$).

Burrows presented distinct characteristics and shapes between the sexes, with female burrows showing an enlargement at the bottom forming a chamber (Fig. 1c), which was not detected in male burrows (Fig. 1d). The entries of female burrows were closed at the end of the construction with a "plug"; these burrows were characterized by a smaller opening and greater depth, forming a chamber with a greater width at the bottom. Male burrows did not present this characteristic and consisted of a simple channel. The depth of the burrows obtained from the molds for both sexes ranged from 70 to 98 mm, with a mean of 89.12 ± 8.80 mm. Male burrows ranged in depth from 70 to 92 mm (83.75 ± 9.60 mm), and that of females varied between 90 to 98 mm (94.50 ± 3.31 mm), with no significant difference between sexes ($W = 1$, $P = 0.05907$). Concerning the relation between carapace width (CW) and biometric variables of the burrows: only the CW *vs*. DB ratio was significantly but with a low coefficient of determination (Table 2).

Excavation behavior

In the laboratory, male and female excavations presented the same movement patterns, independent of the nocturnal or diurnal period. The main difference in digging behavior between the sexes was the entrance of the burrow with a sediment plug carried out only by females. This process of building the burrows was characterized by three stages (Fig. 2); the first and second stages of excavation being common in both sexes and only the third stage, closing the burrow with a sediment plug, was observed exclusively in females.

In the beginning, crabs touched the sediment using the right and left pereiopods to drill and analyze the texture of the sediment. The later use of the claw indicated the beginning of excavation activities. Claws were only used when the excavation of the burrow was finished; this behavior of inserting the claw had the purpose of analyzing the compaction of the surface of the sediment. After the recognition of the physical structure of the sediment, sequential movements of the second, third, fourth, and fifth pereiopods were initiated, which repeatedly perforated the sediment, making the surface more pliable, allowing removal of the upper layer of the sediment (Fig. 2a). The sediment was carried to the ventral region of the center of the body by pairs of pereiopods on both sides, always in the

Table 1. Bioturbation values of males and females of *Dilocarcinus pagei*. SD: standard deviation, BDTH: burrow depth, BD: burrow diameter, DSB: diameter of sediment balls, SR: sediment removed.

Males	Minimum	Maximum	Mean ± SD
BDTH (mm)	31.66	118.5	71.19 ± 32.51
BD (mm)	43.04	55.81	50.44 ± 4.72
DSB (mm)	4.32	6.74	5.85 ± 0.63
SR (g)	10.40	169.47	70.57 ± 49.13
Females	Minimum	Maximum	Mean ± SD
BDTH (mm)	34.20	145.30	83.23 ± 33.14
BD (mm)	41.10	53.25	47.57 ± 4.24
DSB (mm)	4.83	6.83	5.88 ± 0.61
SR (g)	18.53	189.17	113.30 ± 52.55

Table 2. Regression analyses between carapace width (CW) and biometric variables of burrows of *Dilocarcinus pagei*. BDTH: burrow depth, BD: burrow diameter, DSB: diameter of sediment balls, SR: sediment removed, ns: not significant, *significant values $P < 0.05$, R^2: coefficient of determination, *P*-value, F: test value, n: individual number.

	CW *vs*. BDTH	CW *vs*. BD	CW *vs*. DSB	CW *vs*. SR
R^2	0.0017	0.3435	0.0011	0.0002
P	0.8193[ns]	0.0004*	0.8566[ns]	0.9356[ns]
F	0.0531	15.695	0.0332	0.0066
n	32	32	32	32

Figure 1. View of a burrow construction of *Dilocarcinus pagei*. a) Constructed burrow and sediment balls (setae), b) crab in the burrow excavation, c) burrow morphology of female, d) burrow morphology of male.

direction of the posterior towards the anterior region (Fig. 2b). The repetition of this synchronized movement of pereiopods and claws was responsible for the formation of the pellets present on the surface of the substrate and was typical for the beginning of burrow construction. The sediment pellets were not related to foraging activity and were related to the friction of one pereiopod to the other as a way of cleaning them.

After starting the burrow construction and forming a cavity in the sediment by sequencing, drilling, and removal with the pereiopods, crabs were positioned laterally at a 90º angle to the inside of the initiated burrow and continued with the sediment removal of the burrow. Instead of using the pereiopods on both sides simultaneously, crabs used only one side at a time (Fig. 2c). Except for the claws, crabs used all pereiopods facing to the inner side of the burrow. These pereiopods had the function of digging and transporting the sediment to be deposited around the opening of the burrow, while the opposite pereiopods (third, fourth and fifth) facing the outermost side of the burrow always remained inserted in the sediment to support the crab body. At this stage of excavation, the chelipeds and the second pair of pereiopods were used the most to increase the depth of the burrows and to facilitate the removal of the sediments. These claws and the second pair of pereiopods presented synchronous movements as a mechanical shovel to promote sediment removal; the third pair of pereiopods was rarely used (Fig. 2d).
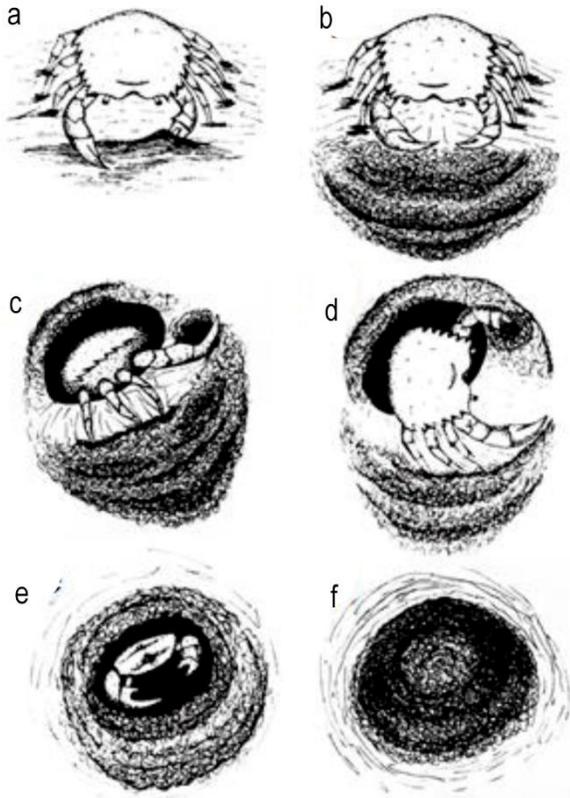
Figure 2. The process of burrow construction of *Dilocarcinus pagei*. a) Crab recognizes the sediment using the pereiopods (left and right), b) synchronized forward movement of pereiopods and chela in the sediment, c) crab is positioned laterally at the gallery entrance for sediment removal, d) removal and deposition of sediment around the burrow using only one of the chela in the form of a mechanical shovel, e) crab positioned at a 180° angle to promote the closure of the burrow, f) gallery closed with a sediment plug at the entrance.

Females of *D. pagei* closed the burrows with a sediment plug to block the entrance. To promote the closure of the burrow, females entered the deepest part of the burrow and positioned themselves parallel to the surface of the sediment. Inside the burrow, with the upper dorsal region facing the opening, they forced the carapace parallel to the sediment to promote the enlargement, beginning the construction of the chamber (Fig. 2e). After forcing the carapace, females used the pereiopods on both sides and moved small amounts of sediment from the bottom and sides of the burrow to reduce the aperture, initiating the closing process (Fig. 2f).

After 60 days of the experiment, females were dug up, and the presence of juveniles in their abdomens was verified. These females presented aggressive behavior when they were removed, and the ventral region was wet, different from the surface sediment that was completely dry and brittle.

The galling time ranged from 120 to 690 min, with a mean of 298.8 ± 204 min, with significant differences between both sexes ($W = 0$, $P = 0.0286$): males built burrows in less time (ranging from 120 to 185 min; mean 153 ± 32.27 min) than females (260 to 690 min; mean 445 ± 198.41 min). The sediment of the crab habitat used in the experiment was composed of coarse sand (45.6%), medium sand (24.2%), fine sand (17.4%) and silt/clay (12.7%).

DISCUSSION

The size of the claw of *Dilocarcinus pagei* did not influence the size of the burrow opening and the amount of sediment removed a pattern similar to that reported for *Uca annulipes* (Lim *et al*., 2015). The biometric relations between the size of *D. pagei* and the variables of the burrows did not present any significant difference. Only CW *vs*. BD was statistically significant, but also with a low coefficient of determination.

The beginning of the excavation process of *D. pagei* is different from that described for other crabs such as *Cancer magister* and *C. productus*; these species use the pereiopods simultaneously and claws to remove sediment (McGaw, 2005; Corcoran & Merz, 2014). *D. pagei* uses at the beginning of the excavation only the pereiopods (Genise, 2017); this behavior serves to explore and analyze the sediment hardness, because depending on the season, floodplain soils in the Amazon can retain different levels of water (Ferreira *et al*., 1999), and this may facilitate or hinder the excavation process.

The sediment deposition near the entrance of the burrow also differs from mangrove crabs (Gusmão-Junior *et al*., 2012), because the sediment is moister and fluid, due to the high presence of clay particles in it, which facilitates the withdrawal with only one of the dactyls and the second pair of pereiopods. During bioturbation, *D. pagei* rarely uses the claws, which are only used for the removal of larger amounts of sediment that form pellets under the sediment surface, which is different compared to observations from other crabs that simultaneously use pereiopods and claws for sediment removal (McLay & Osborne, 1985; Corcoran & Merz, 2014). Also, during the excavation, *D. pagei* uses only one side of the body for sediment removal, a pattern similar to that observed in *Uca thayeri* (Gusmão-Junior *et al*., 2012). This lateral position facilitates the removal of moist sediment from the interior of the burrow, promoting a lower energetic expenditure of the animal during this activity.

Males of *D. pagei* took less time than females to build the burrows, probably because their burrow was simpler than those of the females. The excavation time for *Uca pugilator* can vary from 15 to 60 min (Weis & Perlmutter, 1987). The excavation time of *Ovalipes catharus* is even shorter and is not different between individuals (McLay & Osborne, 1985). The excavation time of *D. pagei* is also longer than in mangrove crabs such as *Ucides cordatus* (Nordhaus *et al*., 2009). This difference in the time of excavation can be related to the type of habitat, because in mangroves, crabs tend to excavate burrows in a shorter time and deeper due to the influence of tidal effect (Nordhaus *et al*., 2009). The crab *D. pagei* does not need to excavate burrows in a short time or deeper because daily floods do not occur as in mangrove systems. In the study site (Amazonian floodplain), the soil presents a constant decomposition of organic matter, such as roots, leaves and sticks, with mostly fractions of sand. Areas like these receive nutrients from both aquatic and terrestrial origin (Junk, 1984). Due to this sediment composition, crabs need more time to excavate the burrow. On the other hand, energy investment in digging can be rewarded in the form of permanent shelters, differing from mangrove areas, where crabs periodically maintain burrows because of the tides (Micheli *et al*., 1991).

The excavation behavior of *D. pagei* resulted in small balls of sediment (pellets) left at the entrance of the burrow. These pellets were observed during the construction of the burrows, both in the field and in the laboratory, and for both sexes. They were formed during the cleaning process of the claws after digging the burrows. In *Ocypode quadrata*, this behavior is associated with foraging activities (Robertson & William, 1981), environmental orientation (Layne *et al*., 2003), reproductive strategy to attract females and marking of territory (Burford *et al*., 2001). Pellets formed by *D. pagei* are not associated with foraging activities, and they are a result of substrate removal during excavation, differing from what occurs with crabs of the genus *Uca* spp. (Crane, 1975).

The bioturbation of crabs is related to the size of the animal and the burrow constructed. Small species of the genus *Uca* promote less bioturbation than *D. pagei* (Penha-Lopes *et al*., 2009; Qureshi & Saher, 2012; Machado *et al*., 2013). On the other hand, larger estuarine crabs such as *U. cordatus* build deeper burrows with multiple openings (De Araújo & Calado, 2012; Pülmanns *et al*., 2016), and *Neohelice granulata* (previously *Chasmagnathus granulata*) (Iribarne *et al*., 1997; Botto & Iribarne, 2000) promotes considerably larger bioturbation than *D. pagei*.

The morphology of the *D. pagei* burrows includes a single chamber (Melchor *et al*., 2010), differing from the burrows of *Ocypode ceratophthalma*, which may present more than one chambers (Chan *et al*., 2006). The number of chambers within the burrow is associated with courting and mating behaviors (Christy & Salmon, 1984). The burrows excavated by female *D. pagei* are similar to those of *U. annulipes*, characterized by having a more elongated shape at the end of the burrow, which allows the movement of crabs within these structures (Lim, 2006). Another peculiarity attributed to the females of *D. pagei* is that they have the habit of closing the opening of the burrows with a sediment plug. Genise (2017) reported the presence of a closed dump of *D. pagei*, but the author did not identify the individual who closed the gallery.

The behavior of closing the burrow in *D. pagei* is similar to that observed in *Mictyris brevidactylus* (Vannini, 1980): this species uses pellets to camouflage the entrance (Takeda & Murai, 2004). Similar, *Cardisoma guanhumi* uses the background substrate to close the burrow entrance (Pinder & Smits, 1993). The closure of the burrow may be due to periodic flooding, as observed for *U. cordatus* (Nordhaus *et al*., 2009) or to avoid predation (Koga *et al*., 2001). In the case of *D. pagei*, the closure may be associated with the protection of the females concerning desiccation and predators at the time of oviposition and subsequent parental care with the juveniles, since all females carried juveniles in the abdomen when the burrows were opened in the laboratory. A similar pattern of this behavior of females remaining in the burrows to protect eggs or offspring has been recorded for other decapod species (Disney, 1971; Christy, 1982).

The site where the study was conducted is an Amazonian floodplain that is influenced by the seasonality of the Amazon River (Junk, 1984). Our study was carried out during the dry season, with a reduction in the level of water promoting greater exposure of organisms (Junk & Robertson, 1997). Also, during this field study, the presence of predatory birds was recorded, and the remains of exoskeletons of crabs were found. The sum of these effects (desiccation and predation) may have stimulated the adaptation of the excavation behavior of *D. pagei*, as reported in other crabs such as *Birgus lastro* (Burggren & McMahon, 1988) and *Chiromantes ortmanni* (Gillikin & Kamanu, 2005). Bishop (1963) found that freshwater crabs have difficulties in identifying and locating burrows, which are camou-flaged by the dry sediment of the environment, thus providing greater protection against environmental factors and predators.

The chambers in burrows of female *D. pagei* may also be an indication of reproductive behavior, since larger burrows, as reported in *Uca* spp. (Reaney & Backwell, 2007), can maintain a more stable tempe-

rature for egg development and influence the incubation period. The synchronization of these activities is important to ensure the survival of the crabs (Morgan & Christy, 1995). In our study site, the release of *D. pagei* juveniles from the burrow should coincide with the end of the dry period and the beginning of the flooding of the rivers (wet period), which is usually accompanied by rainfall, becoming a favorable condition for the dispersal and survival of *D. pagei* juveniles.

CONCLUSIONS

Females promote more bioturbation than males, due to the construction of a plug closing the entrance of the burrow, and an internal chamber associated with reproduction. The pellets found around the entrance of the burrows originate from the cleaning of the pereiopods and are not associated with foraging activities. The main difference in the digging behavior between the sexes was the entrance of the burrow sealed with a sediment plug produced only by females.

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