Moraes-Costa and Schwamborn *Helgol Mar Res (2018) 72:1*
https://doi.org/10.1186/s10152-017-0504-0

Helgoland Marine Research

ORIGINAL ARTICLE

Site fidelity and population structure of blue land crabs (*Cardisoma guanhumi* Latreille, 1825) in a restricted-access mangrove area, analyzed using PIT tags

Denise Moraes-Costa[1] and Ralf Schwamborn[2*]

Abstract

Understanding the patterns of displacement and site fidelity in blue land crabs (*Cardisoma guanhumi* Latreille, 1825) has important implications for their conservation and management. The central objective of this study was to analyze seasonal variations in site fidelity in *C. guanhumi*, a species that is intensively exploited in Brazil, in spite of being part of the Official National List of Critically Endangered Species. This species currently suffers multiple severe threats, such as overharvesting and habitat destruction. *C. guanhumi* were sampled monthly at four fixed sectors that were delimited at the upper fringe of a restricted-access mangrove at Itamaracá Island between April 2015 and March 2016. One thousand and seventy-eight individuals were captured, measured, sexed, weighed, and their color patterns registered. Of these, 291 individuals were tagged with PIT (Passive Integrated Transponder) tags. Ninety-seven individuals (size range 27.0–62.6 mm carapace width) were successfully recaptured, totaling 135 recapture events. The largest interval between marking and recapture was 331 days. Through the use of mark-recapture-based models, it was possible to estimate the local population as being 1312 (± 417) individuals (mean density 2.23 ± 0.71 ind. m^{-2}). Considering the mean density of burrow openings and individuals, there were 3.4 burrow openings per individual. *C. guanhumi* showed a clear philopatric behavior. Seventy-seven percent of recaptured individuals were recaptured in their sector of origin, and the remainder in an adjacent sector. Site fidelity was higher in females. Males showed minimum site fidelity in October, which is most likely related to be the onset of the reproductive season. The present study opens new perspectives for the definition of reproductive seasons, based on seasonal changes in behavior, and thus to improve the conservation of exploited and severely threatened species.

Keywords: *Cardisoma guanhumi*, PIT tags, Mark-recapture, Philopatric behavior, Diel and seasonal activity patterns, Mangroves

Background

Many animals identify home ranges that they use for foraging, shelter [1, 2] and for reproduction [3]. Philopatric behavior, i.e., the tendency to prefer, stay in or return to a specific site, has consequences for many areas of biology and ecology, for example in population dynamics [4], sexual selection [5], orientation [6] and conservation [7].

*Correspondence: rs@ufpe.br
[2] Department of Oceanography, Federal University of Pernambuco (UFPE), Av. Arquitetura, s/no, CDU, Recife, PE 50670-901, Brazil
Full list of author information is available at the end of the article

Various species of decapod crustaceans clearly define a home range for foraging and shelter, the regularity and magnitude of dispersion being linked to the balance between the intensity of territorial and philopatric behavior, foraging ranges, reproductive migrations, and exploitation of new habitats [8]. Carnivorous crabs (*Carcinus maenas*) may affect the structure of local oyster beds through philopatric, site-specific predation [9]. Ocypodid ghost crabs [10, 11], lobsters [12] and tropical land crabs [13] have the ability to return to the same sites after foraging, thus showing a strong philopatric behavior.

Cardisoma guanhumi Latreille, 1825 (the blue land crab, locally known as guaiamum, goiamum or guaiamu), is a brachyuran belonging to the Gecarcinidae family, which inhabits the supralittoral upper fringes of mangroves, grass fields, shrubs and forests [14]. It occurs from Florida (USA), to the state of Santa Catarina, Brazil [15, 16].

Being considered a herbivore–detritivore, its diet has been reported to include insects, carrion, feces and even members of its own species [15, 17]. The blue land crab plays an important role as a source of income and food for local people in the Caribbean and Brazil [15, 18, 19] and has a high socio-economic and socio-cultural importance in the Brazilian northeast [20].

Cardisoma guanhumi is a gregarious species, where these crabs build deep burrows or galleries in sandy and muddy soils and does not usually share them [15]. The burrows are deep and tortuous [21, 22], always extending into the groundwater [14].

Individuals of *C. guanhumi* tolerate environments that are highly contaminated with household waste, sewage and chemical contaminants of water and soil [22]. Adult *C. guanhumi* can withstand high levels of acidity, salinity and hypoxia [23].

Despite the probable advantage over many other species regarding pollutant tolerance and soil type preference, this species is severely threatened by human interventions such as overharvesting and the destruction of its coastal and estuarine habitats.

Several studies have addressed specific aspects of the biology of *C. guanhumi* [14, 24, 25], as well as population aspects [26]. Yet, there are no studies on the seasonality of individual behavior or small-scale site fidelity for this important land crab. The hypothesis that C. *guanhumi* returns to its home site after foraging excursions is of great ecological and socio-economic interest. Is site fidelity equal between males and females? How are these crabs distributed in their home ranges? Are there seasonal variations in site fidelity, that may be related to climatic and reproductive cycles?

In recent years, there has been a sharp decline in the populations of these brachyurans in Brazil. Thus, in 2004, this species was included in the "Brazilian List of Aquatic Invertebrates and Overexploited or Threatened Fishes" [27]. Ten years later, *C. guanhumi* was listed in the "Official National List of Endangered Species" as a "Critically Endangered" species [28], remaining in this category until the present day.

In order to study animals in natural environments, it is often necessary to mark them individually. More recently, PIT (Passive Integrated Transponder) tagging was used for several crustacean species: *Macrobrachium rosenbergii* and *Cancer magister* [29]; *Paralithodes camtschaticus* [30, 31]; *Ucides cordatus* [32]; *Birgus latro* [33] and *Cardisoma guanhumi* [18, 34]. The latter studies investigated large-scale spatial displacement and abundance of individuals at different sites in Puerto Rico.

In this study, we investigated the small-scale site fidelity of *C. guanhumi* using PIT tags and tested the existence of seasonal patterns of site fidelity in these crustaceans, as well as possible differences between sexes. Also, we evaluated the size of the population and the relationship between crab densities and the density and size of burrow openings.

Methods

Study area

The study area (Fig. 1) is a well-preserved mangrove patch located inside the National Center for Research and Conservation of Aquatic Mammals of the Brazilian ICMBio agency (CMA/ICMBio), at Itamaracá Island, Pernambuco State, Brazil (07°48′36″S, 034°50′26″W at 07°48′31″S, 034°50′15″W).

The vegetation inside the mangrove patch is characterized by *Rhizophora mangle* and *Conocarpus erectus.* Four sampling sectors (A, B, C and D) were defined at the upper fringe of the mangrove, where *Cardisoma guanhumi* burrows were observed (Fig. 1). Additionally to the mangrove tree species *R. mangle* and *C. erectus,* typical beach vegetation also occurred at the sampling sites, such as *Terminalia catappa* and *Syzygium cumini*, forming a line of dense shrubs at the upper margin of the mangrove.

According to the classification of Köppen [35], the climate of Itamaracá Island, Pernambuco, is of the wet tropical type Ams' [36]. The rainy season in this region reaches from March to August, the peak dry season from November to January. Monthly accumulated rainfall values at Itamaracá during peak rainy season, in June and July 2015, were 234.1 and 291.0 mm, respectively. During peak dry season, rainfall in Itamaracá was zero in November 2015, 88.5 mm in December 2015 and 65.2 mm in January 2016 [37].

Sampling strategy

Four sectors were established along the upper fringe of the CMA mangrove, designated A, B, C and D, with a total upper edge length of 189 m (Fig. 1). Crabs that were sampled in each sector were generally released at a fixed point located at the center of their home sector, except during a translocation experiment (Experiment II, see below). The four release points were 46 m (A–B), 66 m (B–C) and 59 m (C–D) apart from each other. The four sectors had the following approximate upper edge lengths: 29, 51, 61 and 48 m, respectively (Fig. 1).

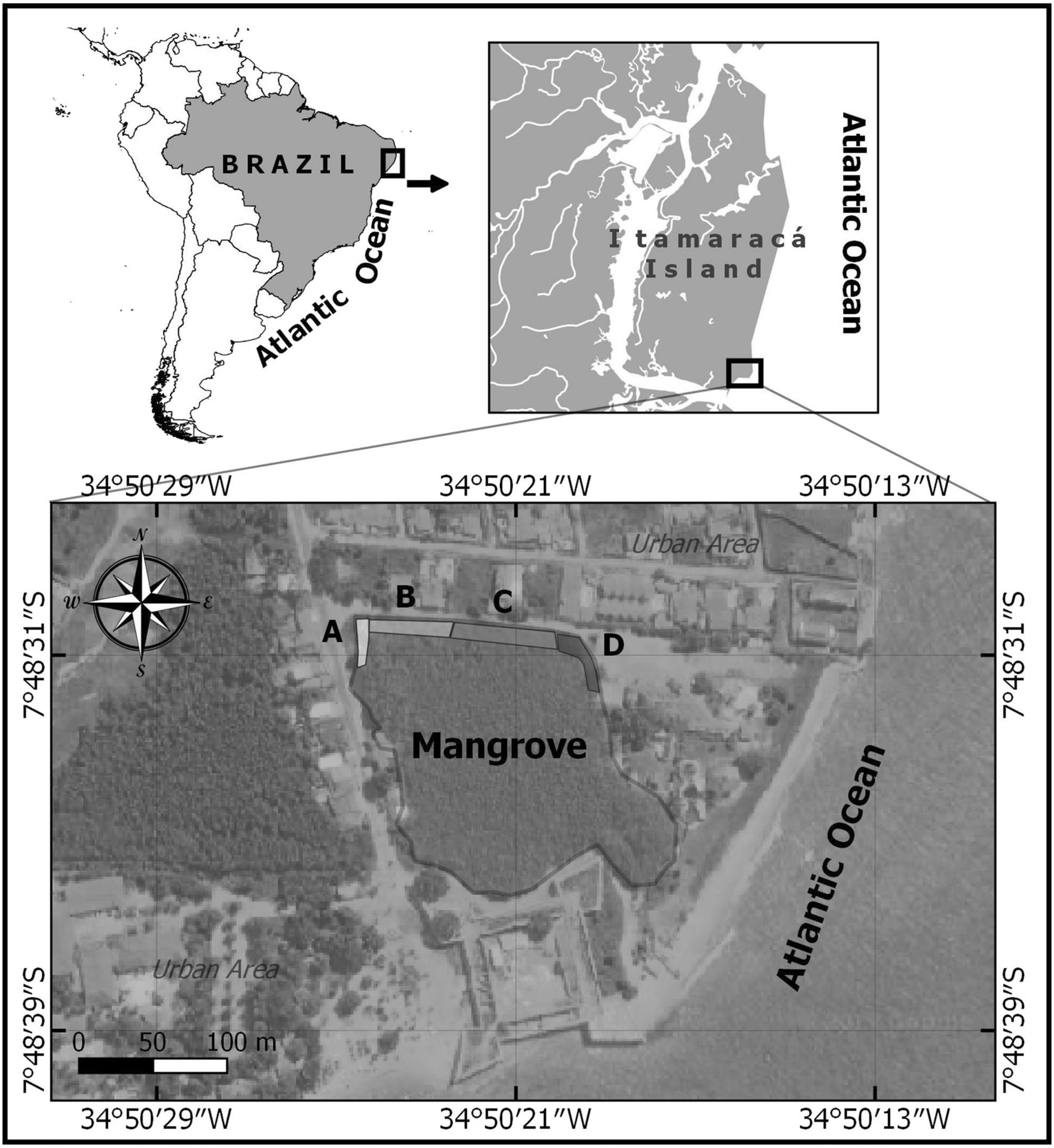

Fig. 1 Map of the study area showing sampling sectors A, B, C and D, at the upper fringe of the CMA mangrove at Itamaracá Island, Pernambuco State, Brazil

Within these four sectors, sixteen transects perpendicular to the upper margin of the mangrove (4 transects per sector) provided a framework for a detailed mapping of the distribution, bathymetry and relief of crab burrows, including the measurement of the diameters and densities of *C. guanhumi* burrows.

The maximum extent of recognizable *C. guanhumi* burrows into the vegetation at the upper edge of the mangrove was estimated to be on average three meters, resulting in a total area of 189 m × 3 m = 567 m^2, when adding up all four sectors. For the densities of the burrows, 65 squares (size 1 m × 1 m) were randomly arranged within each sector, and burrow openings were counted and measured along the year. Burrow openings were counted visually, when indications of the presence of living individuals were clearly visible. Diameters were measured only for burrows with the presence of dark fecal pellets at the exit of the burrows, characteristic of this species, or the presence of freshly excavated mud.

Sampling was performed monthly from February 2015 to March 2016. In each month, samplings and visual observations were made throughout 48 h, in 2-hour intervals. Cylindrical traps, identical to those used by artisanal fishermen, were built with plastic bottles and cans [38]. Inside each trap, a piece of pineapple was used as bait, as done in regular artisanal harvesting. A total of 70 artisanal traps were built for this study, with a diameter of 7.0–10.0 cm, and a length of 20.0–30.0 cm. Each trap was positioned at the entrance of a burrow for 48 h and evaluated every 2 h. Behavioral observations of active *C. guanhumi* (such as feeding habits) were also noted during these regular inspections.

The individuals captured in each sector were distributed into twelve plastic boxes of 70 × 30 cm and allocated by sector and size group (maximum: 15 individuals per box), prior to measuring and marking. These boxes were provided with approximately 200 ml of ambient estuarine water and lined with a shallow layer of leaves and branches of local bushes, to provide shelter and to reduce stress, aggressive behavior between crabs and desiccation. Maximum care was taken to reduce stress, e.g., by covering the crab's eyes with a dark wet towel during handling. All individuals were measured (carapace width, length and height, obtained by using a standard vernier caliper) weighed, sexed, and their color patterns registered prior to release.

Mark-recapture procedures

Of the 1078 individuals captured, 291 individuals (153 males and 138 females), or 27%, were tagged with PIT tags (Nanotransponder tags, Trovan, model ID 100 A, dimensions: 1.25 mm × 7.0 mm). The marked individuals had a carapace width of 24.4–59.5 mm.

PITs were always inserted into the ventral part of the carapace through the base of the fourth pereiopod, by injection with a specific syringe-type applicator (Fig. 6a). Each PIT has a unique numbering, which can only be obtained through a specific reader (Vantro Systems, model GR250).

As an aid for a long-range external visualization of tagged individuals, a heat mark (quick branding with a soldering iron) was made on the upper part of the carapace (Fig. 6b), which served as control at the time of recapture, indicating a marked individual. During the study period, all individuals (with or without visible heat scars) were examined with an electronic reader for the detection of PITs. Site fidelity was assessed by calculating the percentage of individuals that were recaptured in their home sector (i.e., in the sector of last capture), for each sex, expressed as percentage of all individuals recaptured in each month.

Study design

Two experiments were conducted to evaluate site fidelity in *C. guanhumi,* with specific objectives and designs:

Experiment I (monthly time series): From April 2015 to March 2016 monthly mark-recapture experiments were carried out to verify the dispersion rate of the blue land crabs. All individuals were released at the center of their home sectors (no translocation).

Experiment II (translocation experiment): During the onset of the reproduction period of *C. guanhumi*, in November 2015, a translocation experiment was carried out. Thirty-three tagged individuals were used (16 individuals captured and tagged in this month and 17 recaptured individuals, 17 males and 16 females), measuring from 25.5 to 57.0 mm (mean 38.6 mm). All crabs were translocated, i.e., released in the center of sectors other than their origin. Individuals captured in sector A were released in sector C, individuals caught in sector B were released in sector D, individuals caught in sector C were released in sector A, individuals captured in sector D were released in sector B. Distribution patterns of these individuals were investigated in the subsequent 4 months.

To evaluate if there were statistically significant differences ($p < 0.05$) in relation to site fidelity between males and females, a Wilcoxon paired rank test was performed [39].

Estimates of population size and density of *C. guanhumi*

Monthly estimates of population size were made using mark-recapture data, by applying three types models: (1) Simple linear dilution ("Linear method", see equation below), (2) "Bias-Corrected Petersen", [40, 41] and (3) "Bailey" [40, 41].

Simple linear dilution model:

$$\mathrm{Npop}_i = (\mathrm{Ntot}_i/\mathrm{Nmark}_i) * \mathrm{Nprevious\ release}_i$$

Npop_i: Estimated population size for the month i.
$\mathrm{Nprevious\ release}_i$: Total individuals tagged and released in the months prior to the month i.
Ntot_i: Total number of individuals caught in the month i.
Nmark_i: Total of marked individuals found in the sample of the month i.

Population size estimates using the Bias-Corrected Petersen and Bailey methods [40, 41] were obtained for each month with their respective 95% confidence intervals using the same monthly input data as in the linear method described above, applying the *mrN.single* function in "R" [42] for each month. This function outputs the population size estimates with these two methods and their respective 95% confidence intervals. The *mrN.single* function is inserted in the *fishmethods* package [42], within the "R" programming environment (version 3.2.4, "R Foundation for Statistical Computing", Vienna, Austria).

For an integrated estimate of population size, the mean of the estimates obtained with the three methods were calculated for all months and all recaptures (with readable PITs or with heat scars only, in case of PIT loss). This average value of the population size (ind.), divided by the total area (m^2) of the study area (sum of sectors A + B + C + D, in m^2) was used to estimate the mean population density (ind. m^{-2}).

Loss of PIT tags

A quantification of the loss rate of PIT tags was done by counting individuals with heat marks only (without the presence of PITs). The presence of other relevant features, such as tag extrusion scars and openings in the cuticle (in the middle of the abdomen or at the base of the pereiopod) were also verified in these individuals (Fig. 6d).

Results

A total of 1078 individuals of *Cardisoma guanhumi* (572 males and 506 females) were captured and measured. Most of the individuals captured were adults, with less than 1% juveniles (individuals who had the abdomen completely joined to the carapace = 14 individuals, i.e., 0.8% of the sampled individuals). Carapace width (CW) ranged from 20.9 to 70.0 mm, with a mean of 43.5 mm (median 44.05 mm; Fig. 2). As for weights, there was a variation between 0.04 and 162.0 g, with a mean of 45.9 g (median: 44.0 g).

Burrow density and diameter

There were no significant differences in densities of *C. guanhumi* burrows between months and between the four sectors. Mean density of burrows was 7.5 burrows m^{-2} (median: 7; range 4–12 burrows m^{-2}, n: 65 quadrates). *C. guanhumi* burrow diameters (BD) ranged from 19.05 mm to 152.4 mm. Mean and median diameter were identical at 63.4 mm (n: 106 burrows; Fig. 3).

Diameters of *C. guanhumi* burrows were considerably larger than carapace widths. In contrast to the carapace widths of the individuals of *C. guanhumi* (largest individual: 70 mm CW), the diameters of the burrows of this species showed a very large number of values above 70 mm (34% of the total), with highest peak (principal mode) between 50 and 55 mm diameter (carapace widths: principal mode between 44 and 46 mm).

On average, *C. guanhumi* burrows were 20 mm larger than carapace widths (Table 1). Extremely small *C. guanhumi* burrows, with less than 30 mm diameter, were very rare (only 4%, n = 4, one 19 mm burrow, and three burrows with 25 mm diameter). Only three burrows had extremely large diameters, much larger than expected (diameters: two with 127 mm and one with 152 mm diameters).

During this study, we did not observe cohabited burrows (two or more ind. in one burrow). All individuals were allocated each in its own burrow and in specific strata along the fringe of the mangrove, according to their size. At the upper fringe of the mangrove, the burrows were inhabited by larger individuals, the medium-sized *C. guanhumi* burrows were concentrated at

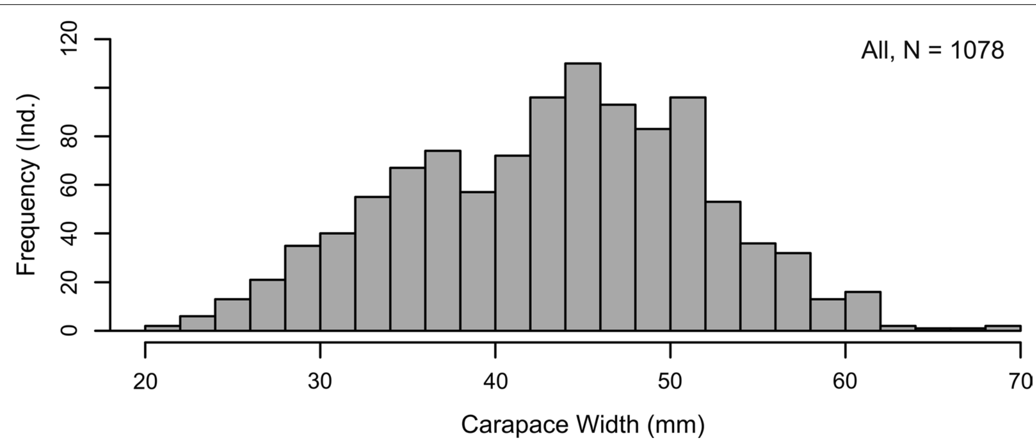

Fig. 2 *Cardisoma guanhumi*. Frequency distribution of carapace width of the sampled population at the upper margin of the CMA mangrove at Itamaracá Island, Brazil

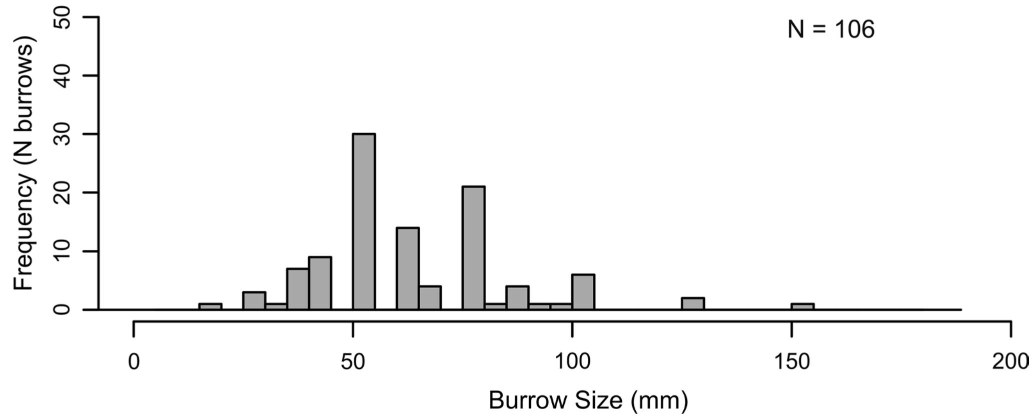

Fig. 3 *Cardisoma guanhumi*. Frequency distribution of burrow opening diameters at the upper margin of the CMA mangrove at Itamaracá Island, Brazil, in May and November 2015

Table 1 *Cardisoma guanhumi*. Comparison of carapace width (CW) and burrow opening diameter (BD)

	Min.	Max.	Mean	Median	Mode
CW (mm)	20.9	70.0	43.5	44.0	44–46
BD (mm)	19	152	63.5	63.5	50–55
BD/CW Ratio			1.46	1.44	

Carapace width (mm) of 1078 individuals (males and females). Diameters (mm) of 106 burrow openings of *C. guanhumi* measured at the upper margin of the CMA mangrove, Itamaracá Island, Pernambuco State, Brazil. Diameters were measured in May, August and November 2015 and in February 2016

mid-slope of the mangrove fringe and the smaller ones in the lower, wet and flat part of the mangrove fringe, where the smaller individuals of *C. guanhumi* occurred.

Foraging activity occurred mainly at dawn and at dusk. The individuals of *C. guanhumi* that were active outside their burrows, were always observed collecting freshly fallen leaves or fresh green leaves of mangroves and local shrubs, that were in reach of the crabs, prior to pulling then into their burrows. Also, direct feeding on freshly fallen fruits of *Terminalia catappa* was regularly observed. Leaves were also regularly placed loosely on top of the burrow, acting as a loose roof, thus providing shade during the hottest hours of the day. No insectivorous or any other non-herbivorous feeding activities were observed. A known predator of *C. guanhumi*, the crab-eating raccoon (*Procyon cancrivorus*) was sighted during two nights in the studied area, during the study period.

Summary of all recaptures (Experiments I and II)

In this study, a total 97 individuals *of C. guanhumi* were recaptured with a PIT tag and a visible heat scar (33% of the 291 marked individuals). The longest interval between tagging and recapture was 331 days and the shortest was 22 days (mean 107 days).

Among all the recaptured individuals (*Experiments I and II*), more than three-fourths (75 individuals, 77.3%) were found in the same sector of release, showing that this population has an overall low mobility across sectors. Twenty individuals (20.6%) were found in sectors immediately adjacent to their sector of release, and only two individuals (2.1%) were recaptured in sectors that were not adjacent to their release (Table 2).

Among the 97 recaptured individuals, 29 were recaptured multiple times in subsequent months, while 68 were recaptured only once. The highest frequency of multiple recaptures for a single individual with PIT and heat scar was 4 times (one individual). Six individuals were recaptured three times, while 22 individuals were recaptured twice. Considering multiple recaptures and both experiments, there was a total of 135 recapture events in the present study.

Seasonal patterns (Experiment I)

Experiment I yielded 127 recapture events. The number of recaptures (with PIT tags and heat scars) of males (81 ind.) was higher than for females (46 ind.) throughout the study period. Considering the individuals recaptured in their home sector as a percentage of the total recaptured, in the vast majority of recapture events (83% of all events,

Table 2 *Cardisoma guanhumi*. Numbers of individuals marked and recovered in the study area (Experiments I and II)

	Tagged	Recap.	Same Sec.	Adj. Sec.	Dist. Sec.
Males	153	61	42	17	2
Females	138	36	33	3	0
Total	291	97	75	20	2

both sexes) individuals were captured in their home sector, showing an overall high degree of site fidelity during Experiment I (Table 3). Site fidelity in females was overall considerably higher (93%) that for males (77%). Females showed 100% site fidelity in 9 months: April, May, June, July, August, September and November 2015, as well as in January and February 2016, when all recaptured females were found in their home sectors (Fig. 4). Males showed 100% site fidelity only in 3 months: April, June and August. The observed difference in site fidelity between sexes was significant, with higher site fidelity for females ($p = 0.01$, Wilcoxon test, $n = 11$ months).

Site fidelity showed a clear seasonal pattern (Fig. 4). Site fidelity was lower from October to December, at the onset of the reproductive season (October to March), especially for males. Male site fidelity showed a clear minimum in October, with only 44% of the individuals recaptured in their home sector (Fig. 4).

Response to translocation (Experiment II)

In Experiment II, among the 33 individuals (17 males and 16 females) that were initially released in November 2015, eight individuals (four males and four females), were recaptured with a PIT tag and a heat scar in the subsequent months of December 2015 and January 2016 (Fig. 5, Table 3). Two males and four females returned to their home sector and two males were captured in sectors adjacent to their home sector, between the catch area and the home sector, and were possibly still in the process of returning. All the recovered females returned to their home sectors. The largest interval between release and recapture for this experiment was 60 days and the smallest interval was 30 days.

Population size and density

With 291 tagged individuals, it was possible to assess the population size in the sampling area, albeit within a very wide range of estimates. The different estimates of the size of this population, obtained through marking and recapture, ranged from 599 ind. (Bailey's method, 95% Conf. Int: 390–998 ind.) in May 2015–2675 ind. (linear model) in July 2015 (Table 4). The arithmetic mean of the 33 estimates (3 methods, 11 months, recaptures with PIT and heat scar) of the population size was 1312 individuals (standard deviation: 417 ind., $N = 33$ estimates). Considering the size of the study area (sectors $A + B + C + D$) as 567 m^2, the mean population density was estimated as 2.23 ind. m^{-2} (standard deviation: 0.71 ind. m^{-2}).

Table 3 ***Cardisoma guanhumi*. Number of recapture events during Experiments I and II**

Exp I	Total recapture events	Same-area recap.	Other-area recap.
Total	127	105 (83%)	22 (17%)
Males	81	62 (77%)	19 (23%)
Females	46	43 (93%)	3 (7%)
Exp II	**Total recaptures**	**Returned to origin**	**Recaptured in between**
Total	8	6	2
Males	4	2	2
Females	4	4	0

Assessment of tag and scar loss

During the study period, 30 tag loss events were observed, where it was not possible to locate a PIT tag, although a heat scar was clearly visible (Fig. 6c, Table 5). Additional characteristics, such as openings in the cuticle, in the middle of the abdomen or at the base of the pereiopod (Fig. 6d) indicated that there was an active elimination of PITs, probably during ecdysis. The estimated percentage of tag loss was 18% [$18.0\% = 30$ losses/(135 PIT recaptures $+ 30$ losses) $\times 100$].

All individuals that were recaptured with PIT tags also showed a clearly visible heat scar (i.e., there was zero scar loss due to molting), showing that heat-branding is a reliable marking method for this species. Fresh heat scars were visible with a bright orange color (Fig. 6b), while older (post-moult) scars were visible due to changes in surface smoothness (undulated or raised scars, with a strong gloss) and had the same color as the surrounding carapace or a pale grey-blue color (Fig. 6c).

Discussion

This study demonstrated a clear seasonal pattern of varying site fidelity in *C. guanhumi*, that is most likely related to its reproduction cycle. Site fidelity is a key strategy for land crabs, where using the same site can reduce the risk of predation due to the optimized use and taking permanently possession of burrows and other shelters, and enhance the efficient long-term use of food resources in their territories. In contrast, migrating animals can completely extinguish local resources, such as in insects and herding mammals. Many fish and invertebrates define a constant home range except for seasonal reproductive migrations [43]. The existence of seasonal migrations was observed in this study, for the first time, for this species, based on mark-recapture data.

Population size and density

This study estimated that there is a population of *C. guanhumi* in the study area that consists of only 1312 (± 417) individuals. Such a small, isolated, slow-growing population could be fully exterminated by fishermen within a few days if there was any failure or deactivation

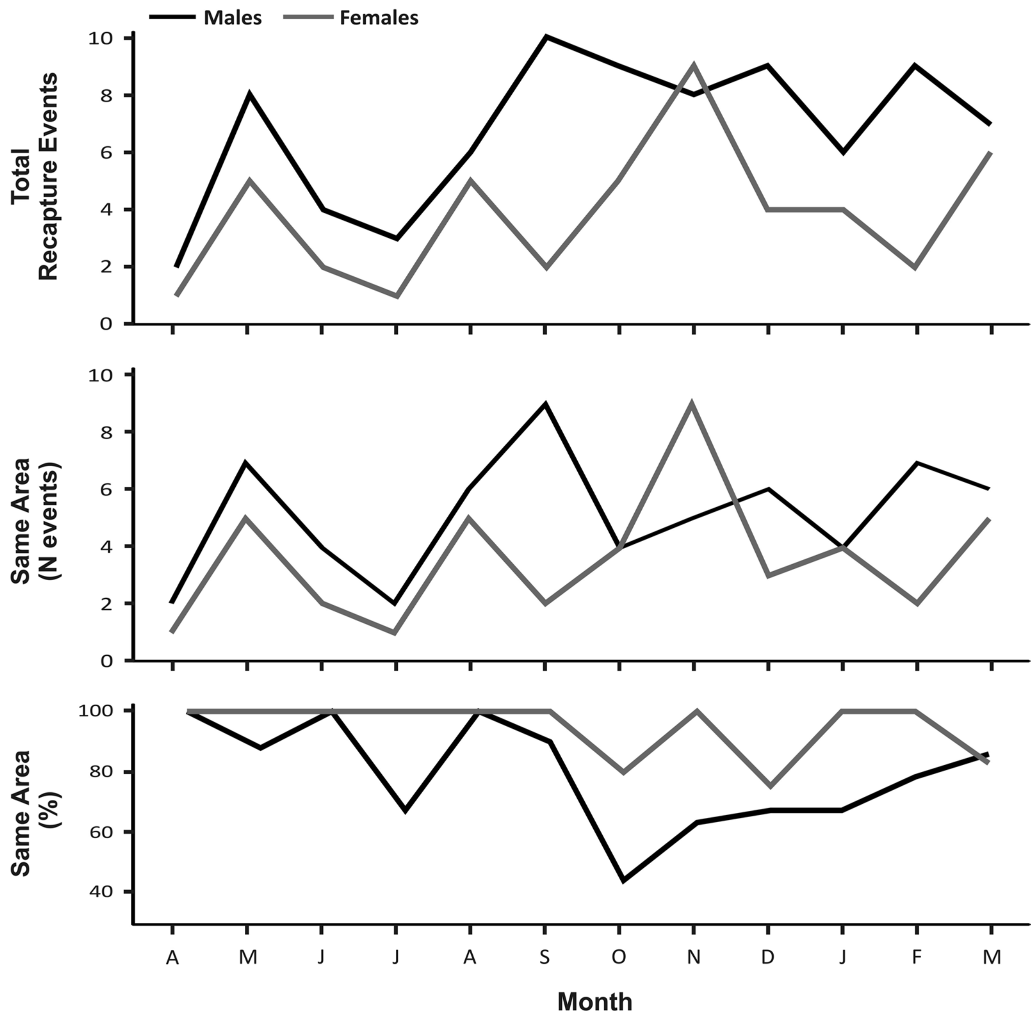

Fig. 4 *Cardisoma guanhumi*. Seasonal variation in site fidelity for males and females. Total recapture events with PIT tags and heat scars and recapture at the home sector (same area), from April 2015 to March 2016 (Experiment I)

in the CMA surveillance system. As this mangrove is a restricted area, artisanal catch as a means of subsistence is currently close to zero, but natural mortality due to predation may be considerable.

Natural predation was also referred to by Gifford [14], citing raccoons as important predators of *C. guanhumi*.

On the other hand, in the middle of the mangroves and shrubs, there are refuges for this species which could reduce their vulnerability. Diele [44] observed that the low vulnerability of the mangrove crab (*Ucides cordatus*) to overfishing in the mangroves of Pará is due to these refuges in the middle of the extensive tangle of roots of *Rhizophora mangle*.

In Brazil, the National Management Plan for sustainable use of crabs pointed to a dramatic decline in the nationwide catch of *C. guanhumi*. In 1994, yearly catch of this species was 685 tons, while in 2007, total nationwide catch was 89.5 tons only [45].

One of the major threats besides overfishing is the devastation of refuges at the upper edge of mangroves by deforestation and landfills, pollution and eutrophication of the ecosystem. All these factors led this species to be recently included in the Brazilian "Official National List of Threatened Species of Endangered Species" as a "Critically Endangered" species [28], which was subsequently revoked after widespread protests, mainly from artisanal fishermen.

Mean densities of 2.23 ind. m^{-2} and 7.5 active openings m^{-2} found in this study are among the highest ever reported for this species or similar sized crabs, probably due to the protection from artisanal fishermen in this small, closed area. For instance, in the extensive, open-access mangroves of the Imburana peninsula, Northern Brazil, mean density of *C. guanhumi* was only 0.39 ind. m^{-2} [46].

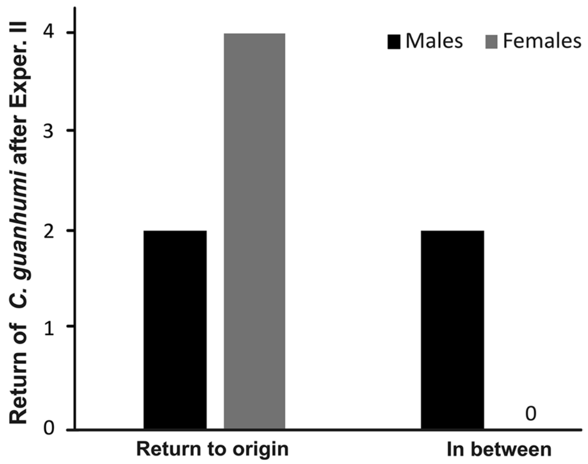

Fig. 5 Results of the translocation experiment (Exp. II). Each bar shows the numbers of blue land crabs (*C. guanhumi*) that returned to their home sectors ("Return to origin") or were caught in a sector between home and release sectors ("in between") after translocation (in November 2015), caught in the months of December 2015 and January 2016

Experiments I and II, seasonality and response of *C. guanhumi* to translocation

With experiments I and II, it was possible to conduct detailed investigations on the site fidelity of this species. In experiment I, 83% of the individuals were recaptured in the same sector of origin, similarly to experiment II, with 75% of the individuals recaptured in their home sector. It may seem trivial that in experiment II, most crabs returned to their home ranges, but moving through the territories of other aggressive crabs is far from simple, since they may actively hinder such movements. There are many other challenges for a crab that is trying to return to its home range, such as those related to the orientation through the complex labyrinth of prop roots and bushes and to the avoidance of common predators, such as humans, opossums, raccoons, monkeys, stray dogs and cats.

There was a significant difference between males and females regarding site fidelity. The number of recaptured males was 28% higher than that of females, but females presented on average 96% of fidelity to the home sector in the two experiments. These data indicate that males are more active and more prone to capture away from their home sector. Males are probably actively exploring new areas and competing for females, as observed in other land crabs. Sex-specific differences in behavior, such as habitat choice and food preference, have been described for *Armases cinereum*, another semi-terrestrial crab species, in coastal forests and saltmarshes on Sapelo Island, U.S.A. [47].

The seasonal pattern observed, with less site fidelity in October, is probably related to the beginning of the reproductive period of *C. guanhumi*, with the increase of temperature and the decrease of the winter rains, where the individuals begin their migration looking for mating partners. Previous studies [48, 49], which used tags in fish, found different movement patterns between species and between individuals of the same species, where some individuals of exploited species showed fidelity to the site, while others traveled long distances.

Gifford [14] observed greater activity in *C. guanhumi* in the reproductive period, in the months of October and November. In the state of Ceará (Brazil), Shinozaki-Mendes [50] did not find any reproductive activity in March for *C. guanhumi* similarly to the result found in this study, if we consider the decrease of migration events for this month.

Many decapod crustaceans use different habitat types throughout their life cycle [51, 52]. Different processes can influence the choice of a site. Few studies have tracked decapods for long periods in order to observe changes in land use.

However, some studies that used a marking method, such as Rodríguez-Fourquet and Sabat [53] that evaluated the impact of capture on the abundance, survival and demographics of *C. guanhumi* and Forsee and Albrecht [34], who estimated the population of *C. guanhumi*, both in Puerto Rico, reported at least one recapture event at the same first catch location. In this work, fidelity to the sites was evident, 77% of the individuals were recaptured in their area of origin, and the remaining individuals were recaptured in adjacent areas.

Table 4 Estimates of *C. guanhumi* population size in the study area

Method	Linear	Bias-corrected Petersen	95% Conf. Int. (B.C. Petersen)	Bailey	95% Conf. Int (Bailey)	Overall mean (ind.)
Min.	634	604	422–987	599	390–998	
Max.	2675	2183	1188–10,697	2168	1084–5420	
Mean	1422	1318		1312		1312
Std. dev. (N)	519 (11)	418 (11)		416 (11)		417 (33)

Summary of estimates (number of ind.) based on 11 months of recaptures with PIT tags and heat scars (N = 97 individuals), from May 2015 to March 2016. N = 1078 ind. captured and released and 135 recapture events

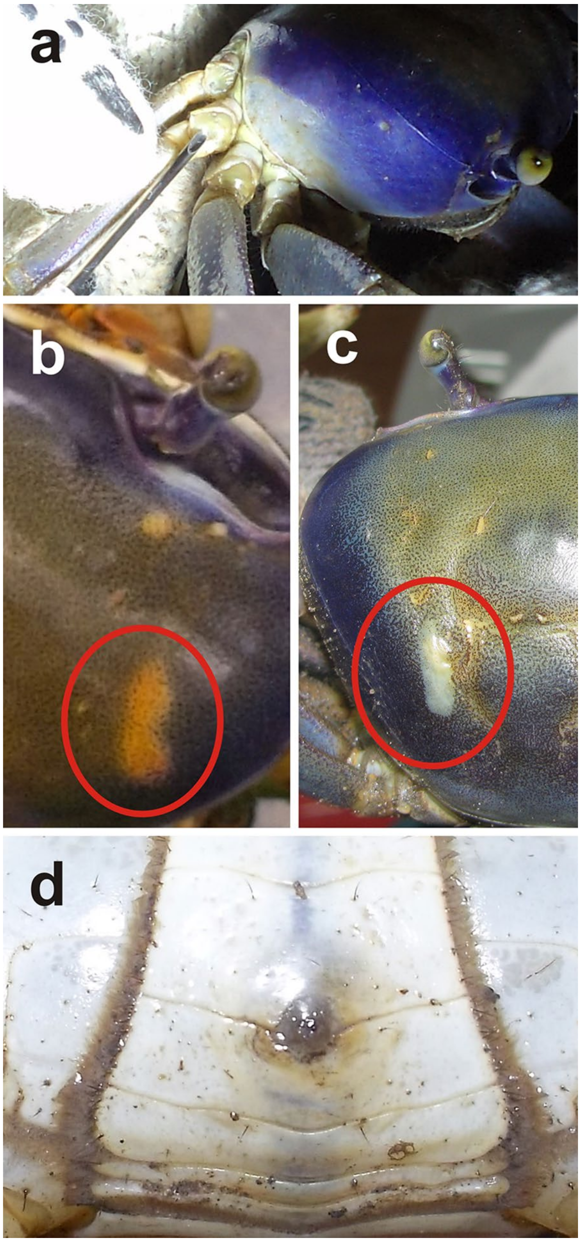

Fig. 6 Photographs of *Cardisoma guanhumi* during mark and recapture; **a** Procedure that was used to inject a PIT tag into the base of the fourth pereiopod; **b** Fresh heat scar made with a soldering nozzle at the time of marking; **c** pale heat scar after ecdysis; **d** evidence of tag loss, extrusion scar at the abdomen, indicating the site of PIT elimination

Diel cycle and behavior

The level of low activity of *C. guanhumi* during the night period observed in this study agrees well with previous studies [18, 53, 54] that indicated the prevalence of *C. guanhumi* individuals collected mainly during the hours of the early morning and near sunset. The dietary habits of this species observed in this study agree with the observations made by Herreid [17]. In Florida, he noted that *C. guanhumi* fed on 35 different plant species. They collected the vegetation near the burrows and carried them inside, as observed in the present study. He also observed that in shaded places and away from human presence, feeding activity spread throughout the day, but in places exposed to direct sunlight, individuals became active at dawn and dusk only.

In the present study, blue land crabs were seen feeding only on leaves and fruits. No carnivorous or insectivorous feeding behaviour was observed, in contrast to Herreid [17], where such non-herbivorous feeding was described. High rainfall coincided with the period of smaller catches in the cooler months of the year (June and July 2015). Our data indicate that rainfall can inhibit the migration of *C. guanhumi*, since activity was reduced during the rainy months.

Size classes

Capture and visualization of juveniles was very rare, probably since juveniles of this population shelter themselves in less accessible areas, in the low-lying core of the mangrove, where they are protected by mangrove roots.

Juveniles may be less active outside their burrows than adults and less prone to be captured. In *Neohelice granulata* the displacement of small individuals of was less intense than those of adult individuals due to the vulnerability to cannibalization by larger individuals [55].

The largest and smallest size classes were represented by males. This was also observed by Bozada and Páez [56], Silva and Oshiro [57], Shinozaki-Mendes et al. [25], Silva et al. [58] and Gil [59]. Males of this species tend to be larger than females [34, 50, 56, 59, 60].

In Brazil, current legislation regulates the appropriate size for the capture of male *C. guanhumi* individuals in each state. For instance, the Normative Instruction no. 90 02/02/2006 [61] allows only catches of individuals larger than 60.0 mm CW in the state of Pernambuco, and the capture of males only. The months from December to March are closed to capture, considered to be the reproductive period of this species. Since 2002, capture of *C. guanhumi*

Table 5 Loss of PIT tags in *Cardisoma guanhumi*

	PIT and scar (N)	Heat scar only (N)	Total N	Heat scar only (%)
Males	85	18	103	17
Females	50	12	62	19
Total	135	30	165	18

Numbers of recapture events where crabs were caught with/without PIT tags and heat scars females is forbidden in the states of Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia.

Carapace width of the largest individual captured in the CMA mangrove was 70.0 mm, much smaller than that found by Shinozaki-Mendes et al. [25] in the estuary of the Jaguaribe river, Ceará State (92.2 mm) and by Silva et al. [58] in the Potengi estuary (94.0 mm). Overfishing has probably affected stocks of *C. guanhumi* in Itamaracá Island, decreasing the size of crabs on this nearshore costal island. The small average CW of 43.4 mm indicates a population unfit for capture and consumption.

During the year of study, an occurrence of ovigerous females at some moment could have been expected, but none were collected nor observed. Silva [62] made similar observations, with absence or rarity of ovigerous females of this species, possibly due to behavioral changes of females after the extrusion of the egg mass. Shinozaki-Mendes [50] obtained very few specimens of ovigerous females, attributing this rarity to a form of predator protection and energy saving. Increased timidity and reduction of activity in ovigerous females is a common feature in land crabs. For example, in *N. granulata*, ovigerous females were almost inactive, suggesting that activity patterns are strongly correlated with the reproductive period [63].

Probably, these females, once they extrude the egg mass, become more timid and less active, and thus less propitious to be captured, or possibly, there is a migration to spawning areas that are closer to the river mouths.

Sex ratio

In brachyurans, sex ratio generally tends to be 1:1. Diele and Koch [64] report that for well-preserved populations, the relative abundance of males tends to be higher than of females. Hernández-Maldonado and Campos [65] found a sex ratio of 3:1 (males:females) of *C. guanhumi* at San Andrés Island. According to these authors, this island is a refuge for this species due to the lack of natural predators and there is little catch for consumption. The same was observed by Sato et al. [33], which found a ratio of 3:1 for males in *B. latro*.

In this study, sex ratio seemed to be in balance over the months, since the number of males of *C. guanhumi* was only slightly higher than that of females (males:females = 1.13:1). Several studies also obtained sex ratios close to unity for *C. guanhumi*, e.g., in Pernambuco, [26], Ceará [50], Mexico [56], Rio de Janeiro [57], Rio Grande do Norte [58] and São Paulo [59].

Patterns of burrow distribution and burrow density

Considering the density of individuals (2.43 ± 0.71 ind. m^{-2}) and the density of burrow openings obtained in this study (7.49 ± 1.8 openings/m^2), the ratio of openings/individuals estimated was 3.4:1. This would indicate that on average there are 3.4 actively maintained and inhabited burrow openings for each individual of *C. guanhumi*. Several authors already suggested that this species may dig burrows with various openings [14, 15, 17, 66].

In local artisanal crab harvesting, two openings that are very close to each other are sought, one is sealed with surrounding sediment and the other one is used to place the trap. This harvesting strategy also hints at the existence of multiple openings for one burrow. It was also possible to observe some abandoned burrows (absence of feces and mud) and many closed burrows, probably in the period in which these individuals perform their molt. These results clearly indicate that the ratio openings/individuals is considerably above 1:1. However, one must consider such ratios with caution, especially when obtained with different methods and temporal and spatial and scales.

The diameters of the burrows showed a distribution pattern quite different from the size distribution of *C. guanhumi*. There were 4 extremely small burrows, less than 30 mm in diameter, which formed only 4% of the burrows found. The occurrence of these small burrows may indicate the presence (in very low numbers) of small, cryptic *C. guanhumi* individuals (which would be absent in the samples due to selectivity of the traps), or possible identification errors, leading to counting burrows of other cryptic small crab species, such as *Sesarma* sp., *Armases* sp., or *Uca* spp. Gifford [14] also found several other crab species in the habitat of *C. guanhumi*, such as *Uca* spp. and *Ocypode albicans* (= *Ocypode quadrata*).

The presence of some very large burrows (even in very small numbers, N = 3 very large burrows) could be due to the existence of few, large, cryptic individuals. This is a real possibility if we consider the possibility that the diameter of the largest measure (max. burrow diameter = 152 mm), converted to the size of the individual (BD/CW = 1.46), would result in an estimated carapace width of $BD_{max}/1.46 = 104$ mm. This size would be well above the maximum crab size ($CW_{max} = 70$ mm) found, but still within the size range reported in the literature for this species.

On the other hand, several other factors, such as burrows more widely excavated than usual, or enlarged by predators (mammals) in search of food, or eroded by rainfall, can lead to erroneous measurements with exaggeratedly large burrows openings with much larger diameters than CW * 1.46. Therefore, caution is advised in the interpretation of these data, especially for unusually large burrows.

Due to the problems mentioned above and the difficulty of associating the burrows with absolute certainty to a particular species, the usefulness of this method for the study of population dynamics should be carefully evaluated, and ideally restricted to areas with a single species of brachyurans, such as the sand banks inhabited by *Uca leptodactyla* [67].

In contrast, burrow diameter data can be obtained very easily and with low impact, and may lead to new approaches and hypotheses, especially if compared with data from captured and properly identified individuals.

Other studies have already used the approach of analyzing burrow openings of *C. guanhumi* [66]. In an area of environmental preservation on the coast of São Paulo, Gil [59] found burrow diameters between 36.4 and 155.0 mm and Oliveira-Neto et al. [68] found burrow diameters ranging from 12.0 to 165.0 mm and a population density of 0.43 ind. m^{-2}, in coastal forest areas adjacent to an estuary in southern Brazil. In these two studies, *C. guanhumi* burrows with larger diameters were found in protected mangrove environments, suggesting that in this kind of habitat, this species can reach larger sizes.

The burrows found in the Itamaracá mangrove were usually inhabited only by a single individual of *C. guanhumi*, in contrast to the results Schmidt and Diele [69] for the mangrove crab *Ucides cordatus,* where burrows with up to four cohabitants were reported.

Usefulness of PIT tags

Recently, tagging with PTs was used for several species of crustaceans, such as *M. rosenbergii* and *C. magister* [29], *P. camtschaticus* [30, 31], *U. cordatus* [32], *B. latro* [33] and *C. guanhumi* [18, 34], but studies using this method for land crabs are still scarce. The loss of PIT tags observed in some individuals in this study did not influence our population size calculations, since all animals with heat scars were considered, and loss of heat scars was considered to be zero for this study period.

The mark-recapture approach applied in this study proved to be effective and appropriate for *C. guanhumi*, considering the difficulty of marking land crabs using other methods.

Conclusions and outlook for the conservation of blue land crabs

The scarcity of studies on the biology and population dynamics of *C. guanhumi* may hinder the implementation of important measures for the conservation and management of this resource. The maintenance of protected areas and refuges for this species are essential, especially considering their fidelity to specific sites.

Technological advances, such as marking devices, allow us to contribute to the knowledge on activity patterns of these animals. The data obtained with PIT tagging offer a robust approach to evaluate site fidelity in adults of *C. guanhumi.* Juveniles and individuals smaller than 20.0 mm are rare, and remain a major challenge to capture.

This study was the first to use PIT tags in *C. guanhumi* to show seasonal changes in behavior, that are related to the reproductive cycle. Evaluations of the reproductive cycle are usually based on the examination of gonads only [25, 62, 70] and not on changes in behavior, which is what actually affects the vulnerability of a species to overharvesting.

Mature males and females were found from November to February by Silva [62], while Shinozaki-Mendes et al. [25], observed maturation of females in August, but females and males during the reproductive period between November and December. These gonad-based studies only showed detectable changes in the gonads of *C. guanhumi* in November, 1 month later than the behavioral changes detected in the present study.

For the sympatric mangrove crab *Ucides cordatus*, the closure period is defined considering the well-known and easily observed reproductive mass migration (known as "*andada*" or "*andança*"), in addition to analyses of the gonads [71]. To date, there are no conclusive data on a possible "*andada*" events for *Cardisoma guanhumi*, except for anecdotal accounts from interviewed fishermen [72]. The present study cannot conclusively determine whether there is such a yearly mass migration event in *C. guanhumi*, but has contributed with new impulses on the study of seasonal behavior of this species.

According to the present results, male individuals showed less site fidelity (i.e., more motility) in October, which makes them more vulnerable to overharvesting during this month. Motile animals that are wandering around far from their burrows are much easier to catch, as observed during the "andada" of the sympatric mangrove crab *Ucides cordatus.*

It is suggested, thus, to adjust the current legislation to such seasonal activity patterns, e.g. by changing the period of closure from December to March for October to March. To implement additional months of closure, exactly at the peak activity and thus vulnerability, would greatly enhance the efficiency of protection of this species.

The approach used in this study opens new perspectives for the definition of reproductive seasons, based on seasonal changes in behavior and not through the analysis of gonads only, and thus to improve the conservation and management of stocks of exploited and severely threatened species.

Abbreviations

PIT: passive Integrated Transponder; CW: carapace width; BD: burrow diameter.

Authors' contributions

This study is part of the M.Sc. thesis of the first author, who collected the samples, conducted the analyses, interpreted the data and wrote the manuscript. RS assisted with the analyzes, figures and the writing of the manuscript. Both authors read and approved the final manuscript.

Author details

[1] Programa de Pós-Graduação em Biologia Animal, Federal University of Pernambuco (UFPE), Av. Professor Moraes Rego, s/no, CDU, Recife, PE 50670-420, Brazil. [2] Department of Oceanography, Federal University of Pernambuco (UFPE), Av. Arquitetura, s/no, CDU, Recife, PE 50670-901, Brazil.

Acknowledgements

The authors thank the Center for Aquatic Mammals (CMA/CEPENE/ICMBio) for local support and for the authorization to perform this study in their mangrove patch, especially to Fernanda Niemeyer, Gláucia Sousa and Fábia Luna. To the Brazilian System of Authorization and Information in Biodiversity - SISBIO for the permit no. 43255-1. Special thanks to the people who are part of UFPE's Zooplankton Laboratory for their help during fieldwork and to all who have somehow helped in this work.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The data supporting the conclusions of this paper are available in the mainpaper.

Consent for publication

The authors declare that they agree to publish in this journal.

Ethics approval and consent to participate

All samples were collected in compliance with Brazilian state and federal environmental laws (Permit MMA/ICMBio/SISBIO No. 43255-1).

Funding

This project received financial support from the National Council for Scientific and Technological Development - CNPq through project 471038/2012-1 (ST- ESPLAN-Tropic). The Foundation for Support to Science and Technology of Pernambuco - FACEPE provided a scholarship for DFMC, RS received a productivity fellowship from CNPq.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Received: 7 August 2017 Accepted: 20 December 2017
Published online: 04 January 2018

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