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Population biology of the endangered land crab *Johngarthia lagostoma* (H. Milne Edwards, 1837) in the Trindade Island, Brazil: Identifying crucial areas for future conservation strategies

Marcio Camargo Araujo João[1,2] | **Rafael Campos Duarte**[3,4] | **Andrea Santarosa Freire**[5] | **Nicholas Kriegler**[1,2] | **Marcelo Antonio Amaro Pinheiro**[1,2]

[1]Departamento de Ciências Biológicas e Ambientais—Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), Instituto de Biociências, Campus do Litoral Paulista (IB/CLP), Universidade Estadual Paulista (UNESP), São Vicente, São Paulo, Brasil

[2]Programa de Pós-Graduação em Ecologia, Evolução e Biodiversidade—UNESP, Instituto de Biociências, Rio Claro, São Paulo, Brasil

[3]Centro de Ciências Naturais e Humanas, Universidade Federal do ABC (UFABC), São Bernardo do Campo, São Paulo, Brasil

[4]Centre for Ecology and Conservation, University of Exeter, Exeter, UK

[5]Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina (UFSC), Florianópolis, Santa Catarina, Brasil

Correspondence
Marcio Camargo Araujo João, Departamento de Ciências Biológicas e Ambientais—Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), Instituto de Biociências, Campus do Litoral Paulista (IB/CLP), Universidade Estadual Paulista (UNESP), São Vicente, São Paulo, Brasil.
Email: marcio.joao@unesp.br

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Abstract

The life history of insular gecarcinid crabs is divided into a marine larval and an adult phase, adapted to the terrestrial environment. As adults, individuals migrate seasonally to locations near the sea, engaging in reproductive behaviors. Therefore, identifying breeding and recruitment areas is crucial for the conservation of insular gecarcinids, especially for those endangered, such as *Johngarthia lagostoma* (H. Milne Edwards, 1837). We used sex ratio and sexual dimorphism analyses (body and cheliped size) as well as records of juveniles and adults to describe the population structure of *J. lagostoma* in the Trindade Island, Brazil. During the reproductive period, several population parameters were compared among sites with different altitudes, comprising two beaches (Andradas and Tartarugas) and two hills (Príncipe, 136 m; and Desejado, 612 m). Overall, males predominated in the population and invested more in body and cheliped growth than females. However, at Andradas Beach, it was observed a similar frequency of adult males and females as well as a small difference in the body size between the sexes. In comparison, the smallest crabs were found at Príncipe Hill. The analyzed population presented a predominance of adults, especially at Andradas Beach (93.1%). Compared to the other sites sampled, Príncipe Hill showed the highest abundance of juveniles (males: 22.2%; females: 40.8%). Thus, Andradas Beach was considered a reproductive site, while Príncipe Hill had the highest density of juveniles, which makes them priority areas for the conservation of *J. lagostoma* in Trindade Island.

KEYWORDS
Gecarcinidae, migration, oceanic island, population structure, sexual dimorphism

1 | INTRODUCTION

Gecarcinidae crabs, popularly known as land crabs, are animals extremely adapted to living in the terrestrial environment (Burggren & McMahon, 1988; Hartnoll, 1998), with juveniles and adults inhabiting areas with low-water dependence, while the larval stages develop entirely at the sea (Hartnoll & Clark, 2006). The success of land crabs depends on the perfect integration between the phases of their life cycle, overcoming specific requirements of the species, which varies according to their degree of terrestriality (Doi et al., 2019). Gecarcinidae species can be classified into those of lower terrestriality, which inhabit coastal and supralittoral regions (i.e., genera *Cardisoma*, *Tuerkayana*, and *Epigrapsus*; Doi et al., 2019; Guinot et al., 2018; Naruse et al., 2018), and those of higher terrestriality, which inhabit insular environments (i.e., genera *Johngarthia*, *Gecarcinus*, and *Gecarcoidea*; Burggren & McMahon, 1988; Hartnoll, Baine, et al., 2006).

Insular gecarcinids have a unique life history and can occupy diverse niches and stand as keystone species in island communities (Green et al., 1997; Lindquist et al., 2009; Paulay & Starmer, 2011). This is probably due to the reduced establishment of predators in island environments, where land crabs occupy vacant niches (Andrades et al., 2019). In addition, insular crabs can travel large distances on the land-sea gradient (Perger, 2014; Vermeij & Dudley, 2000), with adults residing in higher altitude areas (>1000 m) and migrating over great distances in the scale of kilometers to reach the coast for breeding (Hartnoll et al., 2006a, 2009; Hicks, 1985). The migration of the Christmas Island red crabs (*Gecarcoidea natalis*) is a classic example; the adults move in large numbers from the forests where they live to the beaches where they engage in reproductive behavior, and then the recruits move back to their parent's habitat (Adamczewska & Morris, 2001; Hicks, 1985). This expressive migration makes it possible to delimit the travel route more intuitively and define the crabs' breeding and residential areas on the island, an information that has been used in management strategies such as the closure of roads in areas used by crabs to avoid them being hit by cars (Ryu & Kim, 2021). However, delimiting the travel route becomes a major challenge for other terrestrial crab species that migrate less intensively (as *Johngarthia malpilensis*—according to López-Victoria & Werding, 2008) and inhabit locations of difficult access (as *Gecarcinus ruricola*—according to Hartnoll et al., 2006a, 2007; and Hartnoll & Clark, 2006).

Oceanic islands have distinct evolutionary histories (Paulay & Starmer, 2011; Walter, 2004), and each one has a particular community composition. However, several island crab species share a population decline due to increasing anthropogenic threats arising from growing human density, including the introduction of exotic species and the capture of crabs for consumption (Ascension Island Government, 2015; Baine et al., 2007; O'Dowd et al., 2003; Perger, 2019; Pinheiro et al., 2016). Therefore, applying management measures for insular land crabs is urgent, although difficult due to incipient and fragmented studies for most species (Hartnoll et al., 2006a). Based on that, it is necessary to intensify studies toward basic aspects of species biology, especially aiming to identify residential, breeding, and recruitment areas (Pinheiro et al., 2016).

In the South Atlantic, *Johngarthia lagostoma* (H. Milne Edwards, 1837) inhabits four oceanic islands (Fernando de Noronha, Rocas Atoll, Ascension, and Trindade), which have distinct degrees of human occupation and genetic structuring of the species (Rodríguez-Rey et al., 2016). Most of the studies on *J. lagostoma* are restricted to Ascension Island, which has an area of 97 km^2, about 1000 inhabitants, and a declining population of crabs (Ascension Island Government, 2015). On the contrary, Trindade Island has an area of 13 km^2, approximately 40 inhabitants (comprising military personnel and researchers—SECIRM, 2018) and sparse information about any eventual capture of crabs for consumption. From December to May, there has been described a seasonal reproduction for *J. lagostoma* in Ascension Island, when adults of each sex migrate to beaches in similar sex proportions (Hartnoll et al., 2009). In addition, phenotypic variation in the chelar size and shape (homochely and heterochely in adult males—Hartnoll et al., 2017) were registered, with no apparent connection to reproduction. Particularly Trindade Island, copulation between *J. lagostoma* individuals occurs close to the beach (e.g., sand hill vegetation), where sexual partners have similar sizes and males exhibit homochelous and heterochelous morphotypes in equal frequencies (João et al., 2021).

Throughout their occurrence range, *J. lagostoma* populations are genetically divided into three evolutionary units: Ascension Island, Atol das Rocas/Fernando de Noronha, and Trindade (Rodríguez-Rey et al., 2016), the latter being the most distinct and isolated from the others. Because of the large distance among islands, these different units are in a very unlikely population connectivity scenario, especially for terrestrial and semi-terrestrial Brachyuran crabs (Freire et al., 2021). The endangered category for *J. lagostoma* has not yet been established at the global level by the IUCN Red List of Endangered Species (2021), but in Brazil (ICMBio, 2018) the species was already assessed and categorized as endangered, according to the IUCN's criteria. According to the Brazilian assessment, the species fits the criteria of the "Endangered" (EN) category, considering that the islands' area is less than 5000 km^2 and the species occurs in less than five sites, in addition to the species being endangered by the introduction of invasive species (e.g., rats, cats, dogs, among others), and the reduction of habitat area and quality (Pinheiro et al., 2016).

Here, we evaluated the populational aspects of *J. lagostoma* during its reproductive period in Trindade Island, using morphological and reproductive parameters to define possible breeding, residential, and juvenile occupation areas. For that, we sampled crabs at different sites of varying altitude (beaches and hills) to evaluate: (i) population sex ratio, (ii) record of ovigerous females, (iii) the relative frequency of two ontogenetic phases (juvenile and adult), and (iv) sexual dimorphism based on body size and chelar growth as well as chelar types (homochelous and heterochelous). With these results, we can propose areas to improve conservation actions and protect the reproduction of this endangered species, including the closure of the main breeding areas to guarantee the mating and larval dispersion of *J. lagostoma* in Trindade Island.

2 | METHODS

2.1 | Study area, sampling, and biometry

Johngarthia lagostoma individuals were collected in the Trindade Island (20° 51″ 09.4′ S—29° 30″ 82.3′ W) in two expeditions, lasting two months each (March–April/2019 and January–February/2020). These periods encompassed the reproductive season of *J. lagostoma*, which is from December to April (5 months) for Ascension Island (Hartnoll et al., 2010) and Rocas Atoll (Teixeira, 1996). Trindade is an island in the South Atlantic Ocean, considered the southern limit of *J. lagostoma* distribution (Melo, 1996). The island is 1200 km off the South American coast (Figure 1a), with a volcanic origin dated at 3.9 million years, and is one of the emersed points of the Vitória-Trindade submarine chain (Clemente et al., 2018). It also has a rugged relief, although there are well-structured mountain plateaus, with a maximum altitude of 612 m (Figure 1b).

Crabs were manually and randomly captured at four sites, with different altitudes, being two beaches (Andradas and Tartarugas: 0 m) and two hills (Príncipe: 136 m; and Desejado: 612 m). Six sampling transects per site were established, measuring 30 m × 2 m ($60\,\text{m}^2$), summing up $3600\,\text{m}^2$ of sampling area per site, except for Desejado Peak, where sampling occurred in three transects, totaling $1800\,\text{m}^2$ due to the smaller area available in this site. Crabs of all sites were sampled at night with the aid of red-light frontal headlamps in the same moon phase (crescent moon) and on subsequent days. Each sampled crab was maintained in bags until sunrise to avoid resampling, being further sexed based on the abdominal dimorphism (subtriangular in males and semi-oval in females) and the number of pleopods (two pairs in males and four pairs in females). Next, we used a mechanical caliper (precision 0.05 mm) to measure the carapace width (CW, greatest width) and the right and left chelar propodus length (PL, length from the end of the fixed finger to the propodial tooth of the propodus-carpal joint) of each crab. All procedures were performed in the field, with the animals being further released to their original sites, following the guidelines of the Biodiversity Authorization and Information System (SISBIO).

2.2 | Sex ratio, size structure, and sexual dimorphism

First, chi-square tests (Wilson & Hardy, 2002) were used to assess whether the sex ratio of the studied *J. lagostoma* population was consistent with the null hypothesis of balance between males and females (1:1, Fisher, 1930) and evaluate whether this parameter varied as a function of body size, considering 10 mm CW classes with a minimum of 10 individuals per class (Wenner, 1972). Frequency histograms were built for each sex based on the same size classes, from which we calculated the Fisher asymmetry coefficient (skewness—*SK*, according to Sokal & Rohlf, 2012). A symmetric distribution occurs when *SK* values are between −0.5 and 0.5, indicating a population equally composed of juveniles and adults. On the other hand, a positive or negative asymmetric distribution occurs when *SK* is estimated outside this range, specifying a population represented mostly by juveniles and adults, respectively. Asymmetry can also be classified as moderate (positive, $0.5 < SK < 1$; or negative, $-1 < SK < -0.5$) or high (positive, $SK \geq 1$; or negative, $SK \leq -1$) (Wegner, 2010).

Sexual dimorphism was evaluated by comparing the crab's body size (CW) between sexes using a *t*-test ($\alpha = .05$). The normality of residuals was visually checked using a histogram and q-q plot, while the homogeneity of variances tested through an *F*-test. The CW was therefore log-transformed to meet test assumptions. We used the length of both major (PL_{major}) and minor (PL_{minor}) propodus to calculate the heterochely ratio ($HR = PL_{major}/PL_{minor}$) for all crabs as a way to identify them as homochelous (HM: chelae with similar size, where $1.00 \leq HR \leq 1.10$) or heterochelous (HT: chelae with distinct sizes, where $HR > 1.10$), as described by previous studies with gecarcinid crabs (Doi et al., 2019; Hartnoll et al., 2017). The HM:HT ratio was calculated across different size classes (CW) to assess whether the chelar polymorphism occurs progressively or it is peculiar only in larger individuals. Considering only heterochelous crabs, we also quantified whether individuals were primarily right-handed (i.e., when the major claw is on the right side

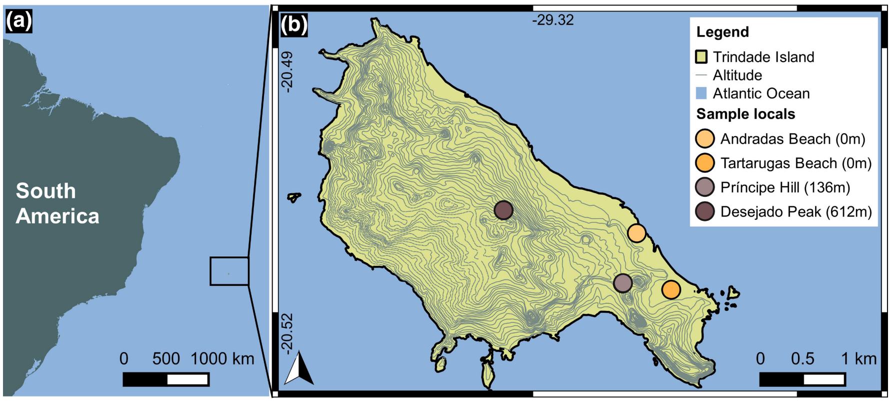

FIGURE 1 Geographical location of the Trindade Island (Brazil), including the four sampling sites with different altitudes within the island. (a), Southeast Brazilian coast showing the position of the island (within the rectangle); (b), general view of the Trindade Island including the altitudinal variation (lines) and the study sites (dots), being two beaches (Andradas and Tartarugas, 0 m) and two hills (Príncipe Hill, 136 m; and Desejado Peak, 612 m).

of the body—right heterochely, RHT) or left-handed (i.e., when the major claw is on the left side of the body—left heterochely, LHT) to assess for the existence of laterality in the species. The proportion of individuals of each chelar morphotype was calculated for the overall population, as well as by the different size classes and types of laterality (RHT and LHT), with the results being analyzed by chi-square tests (Sokal & Rohlf, 2012). Individuals with broken or missing chelipeds were excluded from the analyses.

Simple linear regression analysis, using the log-transformed version of the power function ($\ln Y = \ln a + b * \ln X$), was performed to assess the relationship between body (CW) and chelipod (PL, here defined as the major cheliped) size for each sex and chelar morphotype (Hartnoll, 1982). Thus, the relative growth of the cheliped in function of body size was evaluated according to the value of slope *b*, being defined as isometric ($b = 1$), positive allometric ($b > 1$), or negative allometric ($b < 1$). Departure from isometry ($b = 1$) was tested through a *t*-test (Sokal & Rohlf, 2012). Finally, we tested whether the relationship between the dependent variable (PL) and the covariate (CW) is influenced by the factors of sex (males or females) and chelar morphotype (HM or HT) through three different models of analysis of covariance (ANCOVA, Sokal & Rohlf, 2012) in R (R Core Team, 2020). The first model compared such relationship between sex levels (males × females), while the second and third models compared between chelar morphotype levels, separately for males (HM males × HT males) and females (HM females × HT females). When the interaction between the covariate and the factor is significant, the slopes (*b*) of the fitted regression lines differ between the levels of the respective factor.

2.3 | Structure of *J. lagostoma* population in different altitudes

Aiming to investigate whether there is a differential structure of the *J. lagostoma* population in Trindade Island during the reproductive period, we evaluated different population parameters in the four sampling sites (two beaches: Andradas and Tartarugas; and two hills: Príncipe Hill and Desejado Peak). This procedure was employed to identify potential breeding, residential, and juvenile concentration areas. First, we compared the size (CW) of both male and female crabs among the four sites using a two-way analysis of variance (ANOVA), considering ‘sex’ (males and females) and ‘sites’ (Andradas Beach, Tartarugas Beach, Príncipe Hill and Desejado Peak) as fixed factors (Sokal & Rohlf, 2012). In case of significant effects, the Tukey test was used for a posteriori comparison between factor levels. Analyses were performed in R (R Core Team, 2020), using the functions “aov” to build the ANOVA model and “emmeans” for a posteriori comparison (Lenth, 2020). CW was log-transformed to meet model assumptions, but the variances remained heterogeneous even after the transformation. Therefore, we decided to use raw data since our sample size was sufficiently large, providing robustness to the ANOVA test (Underwood, 1997).

The sexual maturity size values of *J. lagostoma* (males: 56.4 mm CW; and females: 56.6 mm CW, according to João et al., 2022) were used to calculate the operational sex ratio (OSR) and the ontogenetic phase ratio (OPR) for each sampling site. For the OSR, the sex ratio was established only by counting adult females and males (Emlen & Oring, 1977), while for the OPR, the proportion of juvenile and adult individuals was considered. The chelar morphotype ratio (CMR) was also established for adult males at each site to test whether any morphotype predominates in the reproductive area. We used only adult males to calculate this ratio because a similar proportion of both morphotypes was registered only for this sex (see Results). This was calculated as the ratio between the frequency of HM individuals and the total of crabs sampled (HM + HT), with a value of 0.5 representing equal proportions of HM and HT crabs in the population (1:1). We used chi-square tests (Wilson & Hardy, 2002) to assess departures from the evenness of all measured ratios (OSR, OPR, and CMR). We predicted that in reproductive areas, the OSR will be close to 1:1, with a predominance of adults (Hartnoll et al., 2009), and the CMR will be biased toward heterochelous crabs, in case this is a sexually selected trait.

3 | RESULTS

3.1 | Sex ratio, size structure, and sexual dimorphism

We collected a total of 1251 *J. lagostoma* individuals (758 males and 493 females) at the different sampling sites in Trindade Island, with a significant predominance of males over females (male:female = 1:0.7; $\chi^2 = 54.7$; $p < .001$). The size of males ranged from 21.0 to 105.5 mm CW (mean ± standard deviation: 75.3 ± 15.9 mm CW) and was on average larger than the size of females (12.9 to 100.1 mm CW; 69.6 ± 15.5 mm CW) ($t_{1078} = 7.50$; $p < .0001$). The size of ovigerous females ($N = 69$) ranged from 50.4 to 100.1 mm CW (74.9 ± 11.8 mm CW). Size frequency histograms indicate a moderate negative asymmetry for both males ($SK = -0.7$; Figure 2a) and females ($SK = -0.5$; Figure 2b). Although males were numerically predominant in the overall population, the OSR was significantly biased toward males only in animals larger than 70 mm, while in the smallest size classes (20–70 mm CW), the proportion of males and females was similar (Figure 2c).

Individuals with similarly sized (HM, homochelous) and distinctly sized (HT, heterochelous) chelipeds were recorded for both sexes, indicating the existence of a chelar polymorphism in the species, with HM being the predominant morphotype in the population. In males, HM crabs represented 60.5% ($N = 447$; $\chi^2 = 33.4$; $p < .0001$), with the frequency of HT individuals significantly increasing after the maturity size, attaining a 1:1 (HM:HT) ratio in size classes larger than 70 mm CW (Figure 3a). In addition, the size of HT males (79.3 ± 12.8 mm CW) was significantly larger than that of HM males (71.8 ± 19.2 mm CW) ($t_{712} = 7.30$; $p < .0001$). In the case of females, the frequency of HM individuals in the population was 87.8% ($N = 400$; $\chi^2 = 279.2$; $p < .0001$), but, differently from males, this morphotype was predominant throughout ontogeny (Figure 3a). Moreover, the size of females from both morphotypes was similar (HM: 70.5 ± 17.8 mm CW; HT: 67.7 ± 12.2 mm CW; $t_{167} = 1.90$;

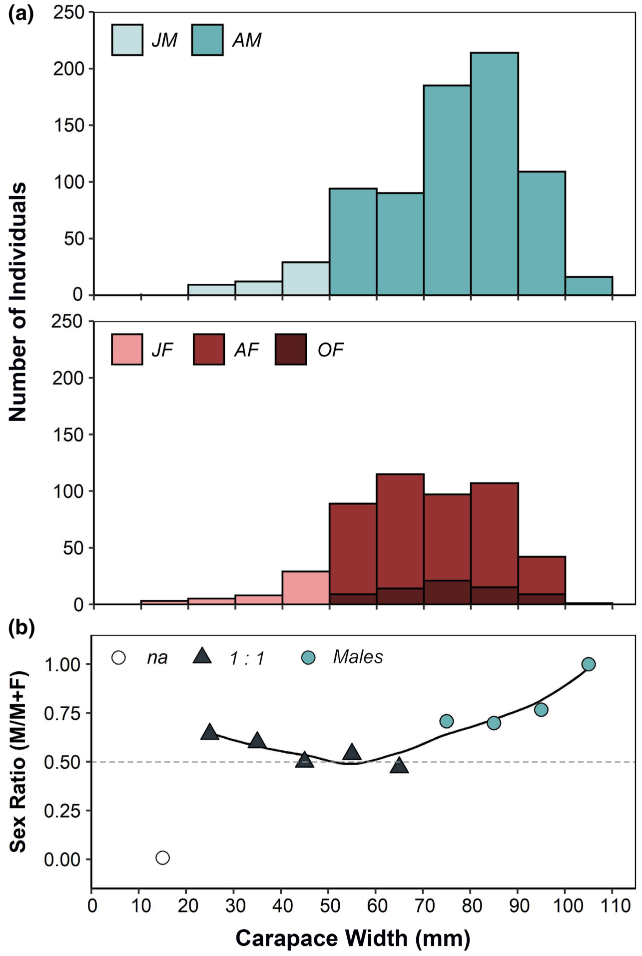

FIGURE 2 Population structure of *Johngarthia lagostoma* from Trindade Island, Brazil. (a) size-frequency histograms of males (blue) and females (red), separately for juveniles (light colors) and adults (dark colors), where: AF, non-ovigerous adult female; AM, adult male; JF, juvenile female; JM, juvenile male; and OF, ovigerous female. (b) dot dispersion showing the variation of sex ratio (number of males divided by the total of individuals) along 10 mm (carapace width, CW, in mm), where the blue dots indicate sex ratios biased toward males ($p < .05$); dark gray triangles show similar proportion between each sex (1:1, $p > .05$); and white dot refers to non-applicable (*na*) data for chi-square tests due to the small number of observations.

$p = .06$). Heterochelous crabs exhibited a similar ratio of right-handed and left-handed individuals in both males (RHT:LHT = 1:0.9; $\chi^2 = 1.70$; $p = .20$) and females (RHT:LHT = 1:1; $\chi^2 = 0$; $p = 1$), indicating the absence of laterality in the species (Figure 3b).

Regardless of the sex of the individuals, the relationship between PL and CW exhibited positive allometry (Table 1), but the degree of allometry was higher in males ($b_{\text{males}} = 1.61$) than in females ($b_{\text{females}} = 1.22$) (Table 2). In addition, the slopes of the fitted models significantly differed between male chelar morphotypes, being larger for HT ($b_{\text{male HT}} = 1.84$, $b_{\text{male HM}} = 1.56$), but not between female morphotypes, with both HM ($b_{\text{female HM}} = 1.21$) and HT ($b_{\text{female HT}} = 1.29$) crabs exhibiting similar degree of positive allometry (Table 2).

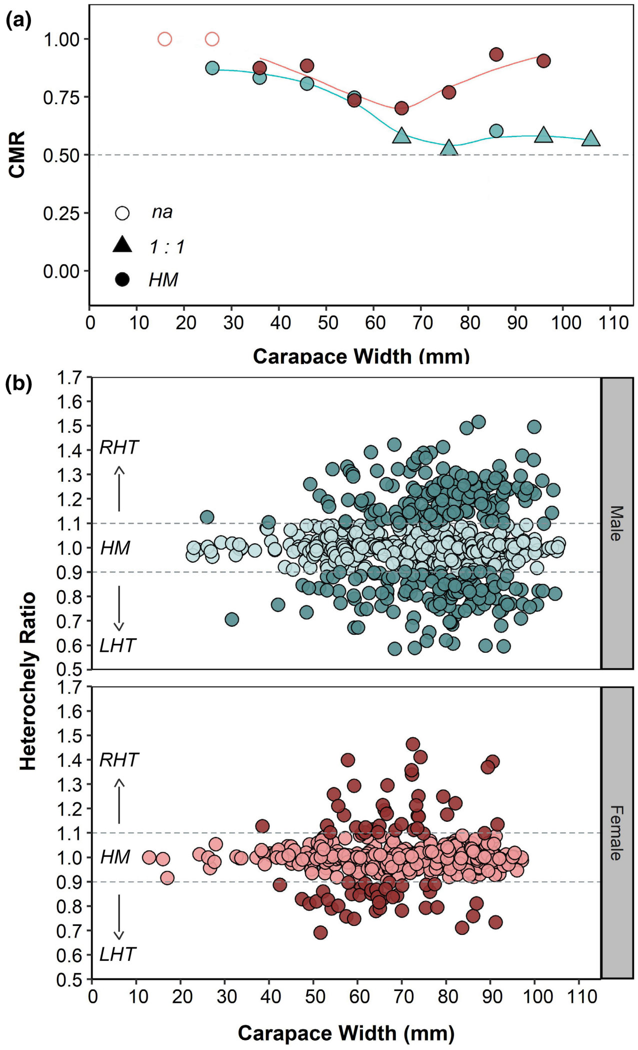

FIGURE 3 Chelar polymorphism of males and females of *Johngarthia lagostoma* from Trindade Island, Brazil. (a) dot dispersion showing the variation of the chelar morphotype ratio (CMR, calculated as the number of homochelous divided by the total of individuals) along the 10 mm size classes of carapace width (CW, mm), where the blue and red dots indicate proportions biased toward homochelous ($p < .05$) in males and females, respectively; the blue and red triangles indicate similar proportion between morphotypes (1:1, $p > .05$) in males and females, respectively, and the white dots refer to non-applicable (*na*) data for chi-square tests due to the small number of observations. (b) dot dispersion showing the relationship between the heterochely ratio and CW of males (blue) and females (red), premising the visualization of homochelous (light colors) and heterochelous (dark colors) of each sex along the ontogeny, where: HM, homochelous; LHT, left heterochely; and RHT, right heterochely.

3.2 | Structure of *J. lagostoma* population in different altitudes

The size of *J. lagostoma* crabs differed between sexes but the magnitude of this difference depended on the sampling site as indicated by the significant interaction between main factors (sex × sites: $F_{3,\,1246} = 4.67$; $p = .003$). Although males were larger than females

TABLE 1 Relative growth of chelipeds of *Johngarthia lagostoma* individuals from the Trindade Island (Brazil).

Sex	Morphotype	$\ln y = b \ln x + \ln a$	N	R^2	t	Allometry
Male	Total	$\ln y = 1.61 \ln x - 3.00$	739	0.91	35.82*	+
	Homochelous	$\ln y = 1.56 \ln x - 2.82$	447	0.95	31.62*	+
	Heterochelous	$\ln y = 1.84 \ln x - 3.96$	292	0.90	23.66*	+
Female	Total	$\ln y = 1.22 \ln x - 1.52$	400	0.95	17.53*	+
	Homochelous	$\ln y = 1.21 \ln x - 1.49$	322	0.97	18.62*	+
	Heterochelous	$\ln y = 1.29 \ln x - 1.82$	78	0.85	5.54*	+

Note: The log-transformed version of the power function was adjusted to the relationship between the major propodus length (*y*) and the carapace width (*x*) of male and female crabs, separately for each chelar morphotype (HM, homochelous; and HT, heterochelous).

Abbreviations: R^2, coefficient of determination; *t*, value of the *t*-test evaluating departure from isometry ($b = 1$).

*$p < .05$, indicative of significant positive allometry (+).

TABLE 2 Summary results of three different models of analysis of covariance (ANCOVA) testing changes in the relative growth of the major propodus length (PL) of *Johngarthia lagostoma* crabs from the Trindade Island in relation to body size (CW—covariate) according to the factors (i) sex (male and female) and chelar morphotype (homochelous, HM; and heterochelous, HT), separately for (ii) males and (iii) females.

Models	Source of variation	df	MS	F	p
(i) Male × female	Carapace width (CW)	1	174.5	15437.6	<.0001*
	Sex	1	8.0	705.1	<.0001*
	CW × Sex	1	2.7	242.4	<.0001*
	Residuals	1131	0.01		
(ii) HM male × HT male	Carapace width (CW)	1	113.7	8266.1	<.0001*
	Morphotype	1	0.7	53.1	<.0001*
	CW × Morphotype	1	0.1	7.8	.005*
	Residuals	735			
(iii) HM female × HT female	Carapace width (CW)	1	45.4	9689.9	<.0001*
	Morphotype	1	0.02	3.4	.07
	CW × Morphotype	1	0.01	2.6	.1
	Residuals	396	0.0		

Abbreviations: *df*, degrees of freedom; *F*, *F-value*; *MS*, mean-squares.

*$p < .05$.

in all sites (Table 3; Figure 4), the difference between the average size of males (mean ± standard deviation: 80.4 ± 13.4 mm CW) and females (76.5 ± 12.4 mm CW) was smaller at Andradas Beach (4 mm) than at the other sites (Desejado Peak, 12.8 mm; Tartarugas Beach, 10 mm; and Príncipe Hill, 7.9 mm). Regardless of sex, Andradas Beach and Príncipe Hill were the sites where the largest and smallest individuals on average were observed, respectively, with crabs from Tartarugas Beach and Desejado Peak exhibiting an intermediate size (Table 3; Figure 4).

Ovigerous females were observed only at Andradas Beach ($N = 69$), comprising 25% of the females collected at this site (Figure 5). Moreover, this was the only site where the OSR was close to evenness, indicating similar frequency of males and females (1:1; $\chi^2 = 0.02$; $p = .98$), and where over 93% of the sampled individuals were adults (OPR: $\chi^2 \geq 204.3$; $p < .001$, Table 3). In the other sites, there was a predominance of males and a significant increase in the number of juveniles, mainly females, attaining an OPR close to evenness, especially at Príncipe Hill (1:0.7; $\chi^2 = 3.5$; $p = .061$). Finally, there was a predominance of homochelous crabs in the population regardless of the sampling sites and the sex of individuals (Table 3). Although the frequency of heterochelous males increased after maturity, there was little variation in the proportion of this morphotype among the four collection sites (Tartarugas Beach, 41.2%; Desejado Peak, 42.5%; Príncipe Hill, 43.6%; and Andradas Beach, 44.1%; Figure 5).

4 | DISCUSSION

Our results shed light on crucial aspects of the population structure and reproductive patterns of the land crab *J. lagostoma* both in a general context for understanding the species life history and on local processes particular to Trindade Island (Brazil). Overall, there was a predominance of males in the population, with the sex ratio varying among the different sites, being equal (1:1) only at Andradas Beach. Males were on average larger than females and exhibited higher chelae growth, although there was no evidence that this differential investment is related to any sexual selection process. Adults predominated in the island population, mainly at Andradas Beach ("reproductive place"), while juveniles were more abundant in

TABLE 3 Population structure of *Johngarthia lagostoma* from Trindade Island (Brazil), including comparisons of population parameters among sites with different altitudes, namely: Andradas Beach (0 m), Tartarugas Beach (0 m), Príncipe Hill (136 m) and Desejado Peak (612 m).

Site	Sex	*N*	CW (mean ± SD)	OSR (M:F)	OPR (A:J)	CMR (HM:HT)
Andradas Beach	M	278	80.4 ± 13.4	1:1$^{n.s.}$	1:0.1*	1:0.7*
	F	206	76.5 ± 12.2		1:0.1*	1:0.1*
	OF	69	74.9 ± 11.8			
Tartarugas Beach	M	206	74.4 ± 19.1	1:0.2*	1:0.3*	1:0.7*
	F	45	64.4 ± 19.2		1:0.6$^{n.s.}$	1:0.3*
Príncipe Hill	M	135	68.5 ± 16.0	1:0.6*	1:0.3*	1:0.8$^{n.s.}$
	F	103	60.6 ± 15.7		1:0.7$^{n.s.}$	1:0.5*
Desejado Peak	M	142	73.2 ± 11.5	1:0.4*	1:0.1*	1:0.7*
	F	70	60.4 ± 10.7		1:0.5*	1:0.4*
Trindade Island	M	758	74.4 ± 17.4	1:0.7*	1:0.2*	1:0.7*
	F	562	69.6 ± 16.9		1:0.3*	1:0.2*

Note: For each site and sex, we calculated the mean carapace width (CW), operational sex ratio (OSR), ontogenetical phase ratio (OPR) and chelar morphotypes ratio (CMR). Where: A, adult; F, non-ovigerous female; HM, homochelous; HT, heterochelous; J, juvenile; M, male; and OF, ovigerous female. * and n.s. indicate significant ($p < .05$) and non-significant ($p > .05$) departures from evenness (1:1 ratio), respectively, of different population parameters assessed by chi-square tests.

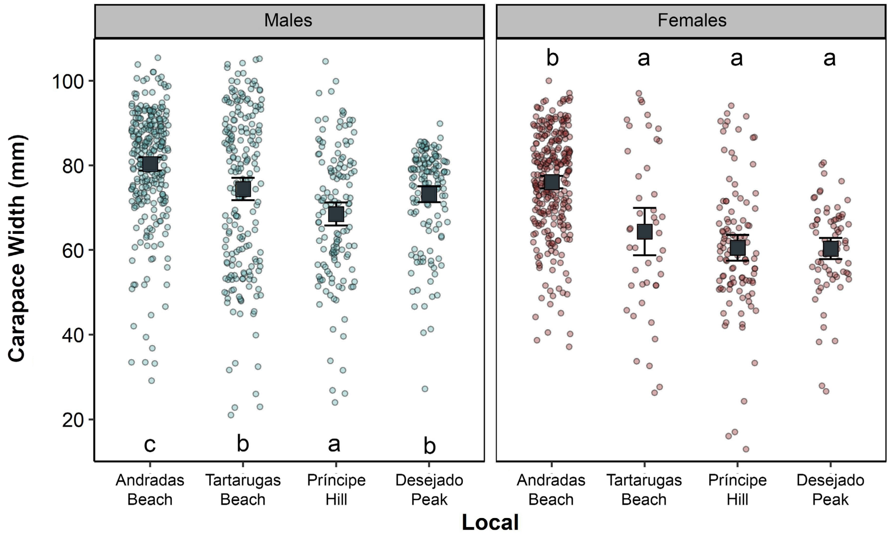

FIGURE 4 Carapace width (CW, mm) variation of males and females of *Johngarthia lagostoma* in sites with different altitudes (Andradas and Tartarugas Beach, 0 m; Príncipe Hill, 136 m; and Desejado Peak, 612 m) in the Trindade Island, Brazil. Where: square dot, mean; circle dot, original CW data on which a random noise was added to avoid overlap; error line, mean confidence interval at 95%. Distinct letters indicate significant differences of CW between crabs of the different sampling sites ($p < .05$) within each sex.

Príncipe Hill ("growing place"). Our results expand the knowledge on the life history of *J. lagostoma* that was previously restricted to the Ascension Island (Hartnoll et al., 2009), providing crucial information to be used in species management. In Trindade Island, we suggest Andradas Beach and Principe Hill as relevant sites for future conservation and management programs.

Overall, *J. lagostoma* males were more frequent than females in Trindade Island, a similar pattern was observed for most gecarcinid crabs (Hartnoll et al., 2009; Liu & Jeng, 2005; Oyenekan, 1995; Turner et al., 2011). This bias toward males has been observed for other crab species, and several factors may be maintaining this pattern, including differential mortality between the sexes, as observed for fiddler crabs in which males are less predated than females due to their hypertrophied cheliped of the first (Johnson, 2003). The predominance of males in the *J. lagostoma* population in Trindade Island can also be a result of differential mortality between sexes, since such predominance is evident only for large individuals, with an unbiased sex ratio observed in small size classes. In most gecarcinid crabs, females perform extensive migrations with high-energy expenditure that also exposed crabs to other risks as the possibility of falling into the sea during larvae release (e.g., *Gecarcoidea natalis*, Hicks, 1985; and *T. hirtipes*, Turner et al., 2011), to be attacked by other crabs (e.g., *Gecarcoidea lalandii*, Liu & Jeng, 2007), or being captured by humans in islands where fishing is a common activity (e.g., *G. ruricola*, Hartnoll et al., 2006a). For *J. lagostoma*, we believe that the lower proportion of females in large size classes is probably due to thermal and energy stress that they are subjected to during migrations, which is increased by the lack of vegetation and/or shelter in the breeding areas. This would explain the record of several dead females on the Ascension Island beaches (see Hartnoll et al., 2010) as well as in the Trindade Island (João, *field observations*).

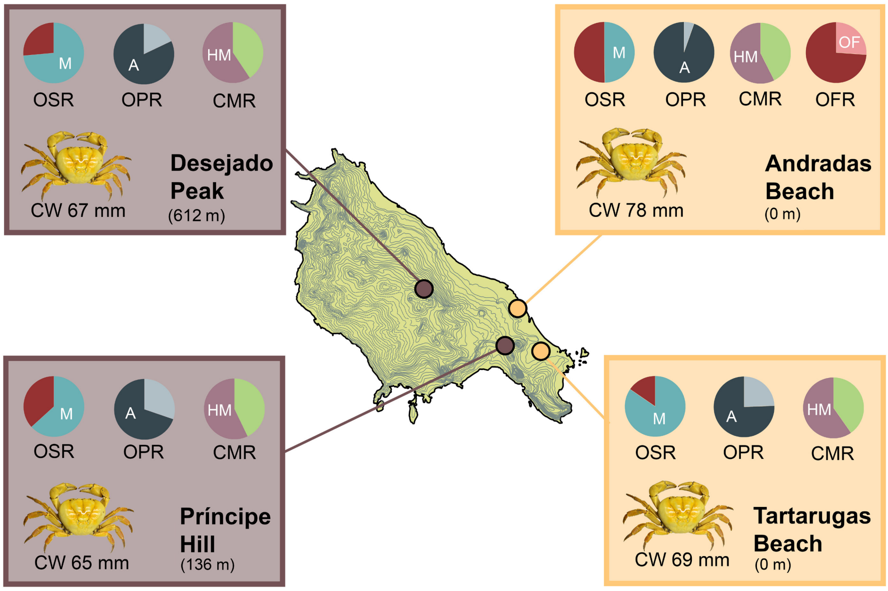

FIGURE 5 General view of all population parameters obtained for *Johngarthia lagostoma* from different sampling sites in the Trindade Island, Brazil. Where: A, adult; CMR, chelar morphotypes ratio; CW, carapace width (mm); F, non-ovigerous female; HM, homochelous; M, male; OFR, ovigerous female ratio; OPR, ontogenetical phase ratio; and OSR, operational sex ratio.

The sex ratio of the *J. lagostoma* population in Trindade Island differed between sites of different altitudes, a pattern already observed in Ascension Island where males were more frequent on the hills (residential areas) and female frequency increased progressively toward the beaches as the migration proceeds, reaching a 1:1 sex ratio at the spawning areas (Hartnoll et al., 2006b, 2009). In the Trindade Island, both the hill sites (Príncipe Hill and Desejado Peak) and the Tartarugas Beach, can be considered residential areas, where males predominate even during the reproductive period (Figure 5). On the other hand, Andradas Beach showed a similar ratio of adult males and females, being a site with higher breeding potential. In addition, many mating pairs (João et al., 2021) and ovigerous females, not included in this study, were observed near the sea in an adjacent area known as Calhetas Beach. Variation in sex ratios along the migratory route have been confirmed as a pattern for gecarcinids, particularly for species from oceanic islands that perform long reproductive migrations (Foale, 1999; Hartnoll et al., 2006a, 2009, 2010; Hicks, 1985). For *J. lagostoma*, it is remarkable how the sex ratio pattern we recorded for Trindade Island (this study) is similar to the observed on the Ascension Island (Hartnoll et al., 2009). Conversely, in Rocas Atoll (Brazil), males were also predominant, but there was no seasonal or spatial difference in sex ratio along the island, which makes it difficult to understand the processes and locations involved in migration (Teixeira, 1996), possibly because of the small territorial area (~4.4 km^2) of this site.

The size data recorded for *J. lagostoma* crabs in Trindade Island indicates that males achieved larger sizes and were larger on average than females. This sexual dimorphism in body size is a recurring aspect for several crab families (Hartnoll, 1982), being probably the result of high investment in reproduction by females and in somatic growth by males (Hartnoll & Gould, 1988). In addition to this differential investment, other studies have defined sexual dimorphism in crab body size due to sexual selection because females prefer larger males, or males have an advantage in mating male–male competition (Baeza & Asorey, 2012). Sexual dimorphism in body size toward larger males has been confirmed for all gecarcinid species studied so far (Turner et al., 2011), including *J. lagostoma* in Ascension Island (Hartnoll et al., 2009). On the other hand, this difference also can be an effect of the high costs/risks associated with migratory behavior (Doi et al., 2019; Hartnoll et al., 2006a, 2009; López-Victoria & Werding, 2008; Turner et al., 2011). In Ascension Island, most of the dead individuals recorded were composed of large females, mainly at breeding beaches (Hartnoll et al., 2009). Based on that, it would be expected that females exhibit similar size to males if both sexes participate equally in migrations. We believe that the pattern observed in Ascension Island is also the case for *J. lagostoma* on Trindade Island, as the size difference between males and females is not linked to sexual selection, since at this site the size of couples during pairing was random (i.e., males and females may have larger sizes) and, on average, similar (João et al., 2021).

Chelar polymorphism was observed in both sexes of *J. lagostoma*, with homochelous and heterochelous crabs occurring in all size classes. Regardless of sex, there was no preferential laterality of the larger chela among heterochelous crabs, with similar frequency of right-handed and left-handed individuals, following the pattern described for other gecarcinids (Hartnoll et al., 2017). Overall, homochely was predominant in the population, being much more evident in females (80.5%) than in males (60.5%). Up to now, chelar polymorphism has been described for a few semi-terrestrial (e.g., the mangrove crab *Ucides cordatus*, study that is being conducted by our group) and terrestrial Brachyuran (e.g., *J. lagostoma* in the Ascension Island, Hartnoll et al., 2017; and *Epigrapsus politus*, Doi et al., 2019). A progressive polymorphism was reported in all examples above when a gradual increase and the predominance of one of the morphotypes (mainly heterochelous individuals) occurs after sexual maturity (Hartnoll, 2012). However, our results for *J. lagostoma* in the Trindade Island indicated equal frequencies of the chelar morphotypes in males after reaching the maturity size (> 56.4 mm CW), suggesting that males exhibit definitive polymorphism, with individuals maintaining their chelar type throughout adulthood (Hartnoll, 2012). This pattern was distinct from the recorded in Ascension Island (Hartnoll, 2012), although to explain such differences between populations it would be necessary to obtain records of molting throughout crab's ontogeny, an information that is still rare for gecarcinids and unknown for *J. lagostoma* (Hartnoll et al., 2006b).

Although heterochely occurred indistinctly in both sexes of *J. lagostoma*, the degree of chelae allometry in homochelous males was 17.6% lower than in heterochelous males, while no significant difference was observed between female morphotypes. This indicates that males present a higher energetic investment directed to the cheliped compared to females, a recurrent pattern in several gecarcinids species (e.g., *E. notatus*, Doi et al., 2019; *G. ruricola*, Hartnoll et al., 2006a; *C. guanhumi*, Shinozaki-Mendes et al., 2013; and *T. hirtipes*, Turner et al., 2011). Although the higher growth of male cheliped is usually derived from the selection of these appendages as a secondary sexual trait (Alencar et al., 2014; Baeza & Asorey, 2012; Spani et al., 2020), it is uncertain whether the high-energetic investment in this structure is related to reproduction in *J. lagostoma*. Previous studies indicated that homochelous and heterochelous males formed mating pairs in similar proportions, indicating randomness in the selection of this trait during mate choice (João et al., 2021). Furthermore, our results show that the frequency of heterochelous and homochelous adult males was similar in all sites, even at Andradas Beach, which was considered a reproductive area (Figure 5). Therefore, we support the hypothesis proposed by Hartnoll et al. (2017) that both male morphotypes of *J. lagostoma* in Ascension Island remain frequent because they have equal chances of reproductive success, an information that needs to be tested in future experimental studies.

The population of *J. lagostoma* in Trindade Island has a prevalence of adults ($N=1046=83.6\%$) over juveniles ($N=205=16.4\%$). Even though, the number of juveniles sampled on this island was significantly higher than those from Ascension Island and Atol das Rocas, which represented 0.7% (Hartnoll et al., 2009) and 4% (Teixeira, 1996) of the overall population, respectively. Such lower incidence of juveniles was also recorded for other gecarcinids (e.g., *T. hirtipes*: 8.5%, Turner et al., 2011; *G. ruricola*: 26%, Hartnoll et al., 2006a; and *E. notatus*: 36.4%, Doi et al., 2019) and can be probably explained by the rare and sparse events of recruitment described for some species (Hartnoll et al., 2009; Hartnoll & Clark, 2006; Hicks, 1985). However, in none of these cases, the record of juveniles was as low as that for *J. lagostoma* in Ascension Island by Hartnoll et al. (2009). Past studies have suggested that the crab populations of Ascension Island and Rocas Atoll may be undergoing an "aging process", making it crucial to conduct studies designed to map, define, and describe recruitment areas that are fundamental for the species conservation. Specifically, for Trindade Island, the aging of the *J. lagostoma* population is still not evident, but some strategies can already be taken to avoid future concerns. For example, 30.3% ($N=72$) of the crabs collected at Príncipe Hill were juveniles, and so far, this is the site with the highest density of juveniles on the island, indicating that after recruiting at the beaches, these animals go up to the hills. Despite this, no mass recruitment event has been recorded so far in the Trindade Island for *J. lagostoma*.

Basic information about the biology of land crabs from oceanic islands is still incipient, especially in the more isolated places, such as Trindade Island. Our results advance the understanding of the population biology and spatialization of *J. lagostoma* in Trindade Island, which has not yet undergone significant anthropogenic alterations. We highlight the need for management in two sites of the island (Figure 5), namely (i) Andradas Beach, due to the high reproductive potential, and (ii) Príncipe Hill, due to the high abundance of juveniles (12.9–56.6 mm CW). We also urgently recommend the development of studies to describe the population parameters of *J. lagostoma* in Fernando de Noronha, since this is an anthropized island, mostly by impacts caused by tourism and the introduction of exotic species, which can increase interspecific competition and predation especially over juvenile crabs. Understanding the ecology of land crabs in island environments can help in controlling and managing invasive species and, consequently, the conservation of local species (Griffiths et al., 2011; Misso & West, 2014; O'Dowd et al., 2003; Veitch et al., 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The original data of this manuscript are available in https://github.com/marcio-joao/j.lagostoma_population_biology.

ORCID

Marcio Camargo Araujo João https://orcid.org/0000-0002-6157-5030
Rafael Campos Duarte https://orcid.org/0000-0001-7059-3129
Andrea Santarosa Freire https://orcid.org/0000-0001-6280-7254
Nicholas Kriegler https://orcid.org/0000-0003-2387-1098
Marcelo Antonio Amaro Pinheiro https://orcid.org/0000-0003-0758-5526

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