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## Mating strategies of the endangered insular land crab *Johngarthia lagostoma* (H. Milne Edwards, 1837)

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### ABSTRACT

Hard-shell-mating is the typical way that semi-terrestrial and terrestrial crabs copulate, when females reproduce with a hard carapace during the intermoult period and the couples have a brief or absent pre- and post-copulatory behaviour. For Gecarcinidae crabs there are few studies on reproductive behaviour, and are especially rare for isolated species, as in the genus *Johngarthia*. Here, we describe the mating behaviour of the endangered insular crab *J. lagostoma* endemic of the South Atlantic Ocean, with a focus on pre-, copulatory, and post-copulatory behaviours. Observations were made on 20 pairs in the field, with every female in intermoult. Accessory behaviours were absent, with copulation beginning after sexual recognition. After mating, there were no records of males guarding or embracing females. All couples had the female in an upper position and passive males, which do not react when other males are near the mating site. The size of the chelipeds and males were random and not determinant to mating. However, yellow crabs predominated (95%) in mating pairs and the linkage of colouration to sexual selection needs to be more elucidated because purple crabs are less frequent in the population and the lower representation in the couples can be an effect of this. Experimental studies are required to investigate sexual selection and the occurrence of the behaviour described herein at other locations.

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## Introduction

In natural populations, each species shows specific behavioural strategies to obtain a partner to achieve reproductive success. This framework of strategies is known as ‘mating system’ (Emlen and Oring 1977). In brachyuran crabs, the selective pressures act differently on males and females. Males ensure their fitness by fertilizing the largest number of target female gametes, while females mate with the highest possible number of males to maximize the genetic variability and ensure the success of the offspring (McLay and López Greco 2011; Sal Moyano et al. 2014). According to these authors, in some species female crabs have advantages related to their reproductive anatomy (e.g. sperm storage in seminal receptacles) and a greater opportunity to pair with other males, resulting in a greater genetic and taxonomic diversity.

Eubrachyura has a wide range of reproductive behaviours, especially copulatory or associated behaviour (Brockhoff and McLay 2005). The female moulting stage of each taxonomic group directly regulates these

behaviours in two evolutionarily selected forms: soft- and hard-shell-mating. Soft-shell-mating, which is particular to aquatic crabs, occurs when the female copulates immediately after ecdysis (exoskeleton not yet calcified); males are attracted by pheromones released in the female’s urine, which reverberate over a long behaviour period (copulatory, pre- and post-copulatory) (Hartnoll 1969; Gleenson 1991; Pinheiro and Fransozo 1999; Waiho et al. 2015). In contrast, hard-shell-mating is characteristic of semi-terrestrial and terrestrial crabs. The female copulates in intermoult (calcified exoskeleton) and has a shorter-time copulatory behaviour, as well as the accessory reproductive behaviour (pre or post-copulatory), which in some cases may not occur (Brockhoff and McLay 2005; Hartnoll 2015; Baker et al. 2018). However, there are some species that are exceptions to the basic patterns described above, such as aquatic crabs that copulate in intermoult (e.g. the portunid *Charybdis japonica* – Baker et al. 2018) and other semi-terrestrial/terrestrial species, whose copulation can or not depend on the female moulting (e.g. the

grapsid *Pachygrapsus crassipes* – Bovbjerg 1960). From a phylogenetic perspective, soft-shell-mating behaviour appeared earlier than hard-shell-mating (McLay and López Greco 2011), systematizing several reproductive aspects shared by species of the same group, corroborating previous studies (Hartnoll 1969, 1998; Sainte-Marie et al. 1999; McLay and López Greco 2011; McLay and Becker 2015; Nascimento et al. 2020). Little is known about the mating of terrestrial crabs, since most of the studies were focused on species of economic interest, especially aquatic crabs (Sainte-Marie et al. 1999; Brockerhoff et al. 2005; González Pisani and López Greco 2020).

Most of the reproductive literature on land crabs of the Gecarcinidae MacLeay, 1838 focuses on migratory behaviours (Bliss et al. 1978; Hicks 1985; Hartnoll et al. 2006; López-Victoria and Werding 2008; Doi et al. 2019), and few studies focus on copulatory behaviour (Quinn 1981; Ameyaw-Akumfi 1987). In studies focusing on migratory behaviours, information on how copulations occur is scarce, without any details of these behaviours. *Johngarthia lagostoma* (H. Milne Edwards, 1837) is a land crab that occurs only on four oceanic islands in the South Atlantic: Fernando de Noronha, Rocas Atoll, Ascension, and Trindade. In Brazil, an evaluation carried out in 2010–2014 categorized this species as 'Endangered (EN)' due to its endemism, reduced area of occupation, and habitat quality, as well as the threat of predation by exotic domestic species (Pinheiro et al. 2016). In Ascension Island, this species has infrequent recruitment, with a declining and ageing population (Ascension Island Government 2015). There are studies on *J. lagostoma* only for Ascension Island's population. Male size on average is slightly larger than female size (96.3 and 89.1 mm, respectively), as well as maximum size (120 and 110 mm, respectively) (Hartnoll et al. 2009). Phenotypical variation manifests in the different colour patterns (yellow to purple) and in peculiar chelar polymorphism, where adult males can be homochelous (equal chelipeds) or heterochelous (different chelipeds) (Hartnoll et al. 2009, 2017). In the Ascension population, different colours are supposed to indicate population variants where the yellow morph is the majority in larger crabs perhaps because the light colour is most adapted to resist heat stress and dehydration (Hartnoll et al. 2009). However, such studies present speculations about the function of these morphological characters and do not yet explain whether they are related to the reproductive process or not.

The present study, therefore, aims to describe the reproductive behaviour of *J. lagostoma* focusing on those related to copulation and accessory behaviour (pre- and post-copulatory) based on observations

carried out in the field on Trindade Island (South Atlantic Ocean). In addition, we evaluate whether morphological characters of both sexes, such as size (body and chela) and the chromatic variation of the exoskeleton shapes couple arrangement. Finally, we discuss the linkage of mating behaviour to the *Brachyura* terrestriatization, to verify the occurrence of a pattern among terrestrial and semi-terrestrial crabs.

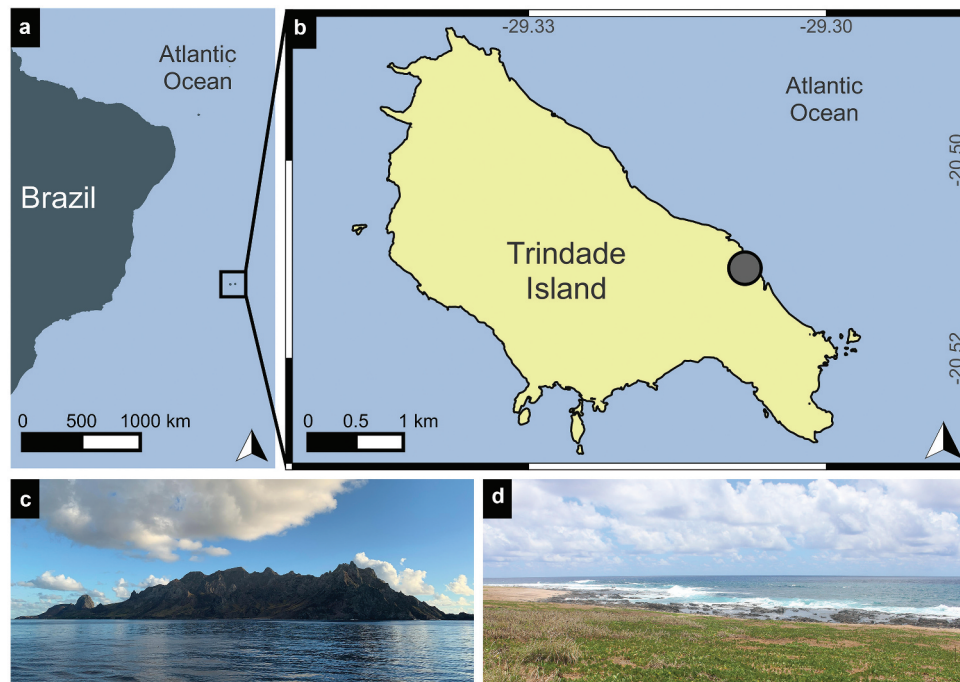
## Material and methods

### Study area, sampling and mating description

Trindade Island (20°51'09.44' S, 29°30'82.34' W – Figure 1 (a, b)) has a volcanic origin, is 3.7 million years old and located 1,200 km off the coast of Brazil (Marques et al. 1999). With the Martins-Vaz Archipelago, it comprises the two emerged areas that make up the Vitória-Trindade submarine chain, which are categorized as an environmental protection area (Clemente et al. 2018). Trindade Island (Figure 1(c)) is small (10 km<sup>2</sup>) with a varied topography, ranging from beaches to promontories measuring about 600 m in height. The island is permanently inhabited by researchers and military personnel (~40 people) and has permanent sources of freshwater (Marques et al. 1999), providing independence and greater diversity for on-site organisms. Among them, the crab *J. lagostoma* is still abundant and distributed in several habitats, especially in the sandhill vegetation and adjacent sandy beaches. It is also recorded on the hillsides and on the largest promontories.

Sampling of *J. lagostoma* was carried out between December 2019 and February 2020 during the reproductive season, which is from December to May for Ascension Island and Rocas Atoll (Teixeira 1996; Hartnoll et al. 2010). For 12 days, copulatory and accessory behaviours (pre- and post-copulatory) were recorded at Praia dos Andradas and the adjacent sandhill vegetation (Figure 1(d)), inside of an area with 1,000 m<sup>2</sup>, during the day and night. The behavioural displays were photographed at such a distance as to allow greater details, but without interruption or obstruction to the verified patterns. In night-time activities, headlamps with a red lamp were used due to the low sensitivity of crustaceans to this wavelength (Cronin 1986).

The records of copulatory behaviour, as well as those related to pre- and post-copula, were duly detailed and qualitative information related to the places and periods of greatest activity were recorded (day or night). For each couple found in a reproductive behaviour the following was recorded: (1) position between the partners



**Figure 1.** Geographic location of the study area showing Trindade Island and Andradas Beach. a) Southeast Brazilian coast showing the distance between the islands from the Brazil coast, b) general view of Trindade Island; Andradas Beach (grey dot), c) general view of Trindade Island, and d) study area view showing vegetation in Andradas Beach.

and between them and the substratum, (2) position of locomotor appendages and abdomen of both partners, (3) locomotor situation of each partner (active or passive), (4) social interaction of the couple with other crabs in their surroundings (agonistic or indifferent), and (5) description of behaviours accessory to copulation (pre- and post-copulation), if any.

### **Biometry, moult condition, and statistics**

Immediately after the mating, each partner was assessed as for their moulting stage using the characters described by Drach and Tchernigovtzeff (1967). In particular, the consistency and flexibility of some regions of the cephalothorax (e.g. branchial and epimeral lines) were confirmed. The specimens were classified according to three stages: post-moult ( $A_1$ - $B_2$ ); intermoult ( $C_1$ - $C_4$ ); and pre-moult ( $D_0$ - $D_4$ ). Then, whenever possible, both partners underwent biometrics, recording body size (CW, largest carapace width) and chelipeds (PL, largest propodus length), which were measured with a precision calliper (0.05 mm) (measurements in millimetres). The CW measurements of the couples were plotted on a scatter plot and subjected to regression analysis using a simple linear equation ( $Y = bX + a$ ), with its adjustment indicated by the coefficient of determination ( $R^2$ ), being considered a good fit if  $R^2 \geq 0.70$ . The association between partner sizes was assessed using

Pearson's linear correlation coefficient ( $r$ ), verifying that it is positive or negative and its significance is higher or lower than 5%. The CW means of the copulated partners were also compared by  $t$  test to confirm a possible difference between the sexes during the formation of couples in copulation.

The partners of each couple were also evaluated for biometric comparison of the cheliped (right vs. left), which is associated with the predominant colour/shade (>70%) of the specimen's cephalothorax (yellow/light, and purple/dark) to ascertain whether such associations are explanatory of the sexual selection process in the species. In the analysis of heterochely, the length of the cheliped propodus (PL) of the right and left chelae were measured for each specimen, expressed as  $PL_{major}$  (major chela) and  $PL_{minor}$  (minor chela), as well as calculating the heterochely ratio ( $HR = PL_{major}/PL_{minor}$ ), characterizing, therefore, if crabs presented heterochely (HT: when  $HR > 1.10$ ) or homochely (HM: when  $1.00 \leq HR \leq 1.10$ ). Possible differences between the proportions of homochelous/heterochelous individuals, as well as between light/dark chromatic morphotypes, were evaluated by the Chi-square test, separately for each sex, always considering the restrictions imposed by the test, namely the observed frequencies ( $fo$ ) always >20, expected frequencies ( $fe$ )  $\geq 1$ , and  $fe > 5$  when  $20 \leq fo \leq 40$ . In all cases, the statistical analyses were based on the tests and procedures established by Sokal



and Rohlf (1995), with the significance always considering a level of 5% or less. All statistical analyses described above were conducted in 'R' environment (R Core Team 2020).

## Results

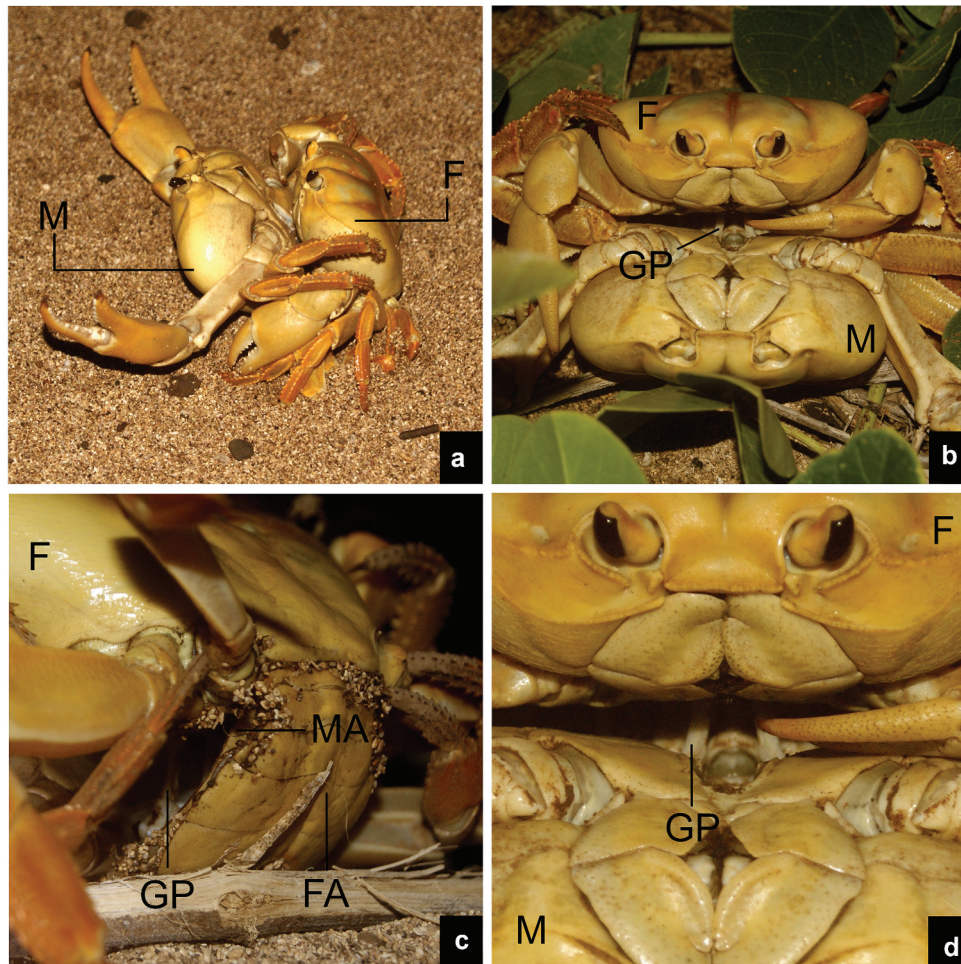
### Mating description

During the period of behavioural observations, 20 couples were already paired. They were used to describe copulatory behaviour and other accessory behaviours (pre- and post-copulatory). Of the copulated couples, 75% ( $n = 15$ ) were spotted during dusk or night, while the remaining 25% ( $n = 5$ ) were recorded at dawn or daytime.

Copulating couples were always observed on open terrains away from burrows or other shelters (e.g. shrub/

undergrowth, between rocks etc.), with both partners in intermoult (hard-shell-mating) and no record of exuviae in the immediate vicinity. All copulations were recorded from the beginning of sexual pairing, with no pre-copulatory behaviours (e.g. courtship or embracing) nor agonistic behaviours among males when they were close in the moments before mating.

The copulatory behaviour of *J. lagostoma* was similar in all observed couples. In the beginning, after sexual recognition, the partners positioned themselves face to face and then assumed a posture perpendicular to the ground. The male fitted between the female's abdomen and the thoracic sternites (Figure 2(a)). At this time, both sexes were extremely active; the male partner kept its chelipeds arched and the other pereopods held the female close to it, while the female was receptive to the male, making no movement to refuse copulation. After coupling, the males remained immobile,



**Figure 2.** Mating behaviour of *Johngarthia lagostoma*. a) Initial position of the copula with both sexes at a perpendicular position in relation to the ground and face to face position, b) Copula position with the female on top and male without activity, with chelipeds down and closed ocular peduncles, c) Conformation of abdomen of both sexes, with the female abdomen touching the ground, and d) Gonopods of the male showing the apical portion inserted in the gonopore of the female. M, male; F, female; GP, gonopod; FA, female abdomen; and MA, male abdomen.

presenting copulation and sperm pumping. On this occasion, the couple assumed a position parallel to the substratum (male: lower; and female: upper – Figure 2(b)), with the male immobile and its chelipeds extended in a lateral position to the body supported on the substratum, in addition to ocular peduncles remaining housed in their respective orbits. Meanwhile, females had a reduced motor activity, but their peduncles were erect and away from their sockets, allowing for a greater perception of the surroundings. During copulation, the partners' thoracic sternites did not fully touch; there was a gap that made it possible to observe the insertion of the male's first pair of pleopods (gonopods) into the female's gonopores (vaginas). During copulation, the female's abdomen involved the male's back, keeping close to the substratum (Figure 2(c)), while the male's abdomen folded and its gonopods were positioned laterally (Figure 2(d)). The gonopods had only their apical portion inserted into the gonopores of the female, with the basal and median portions positioned externally, which can be easily observed (Figure 2(d)).

The couples of *J. lagostoma* commonly share the environments spatially with other adult individuals of the same species, an aspect that did not cause variations to the behavioural pattern previously described (Figure 3(a)). On the same night, up to four copulating couples were recorded within an approximate distance of ten metres between them. Interactions of adult males with copulated couples occurred in only 15% ( $n = 3$ ) of cases; only one of them interrupted the copulatory behaviour of the partners

(Figure 3(b)), although there was no later interaction whatsoever between them.

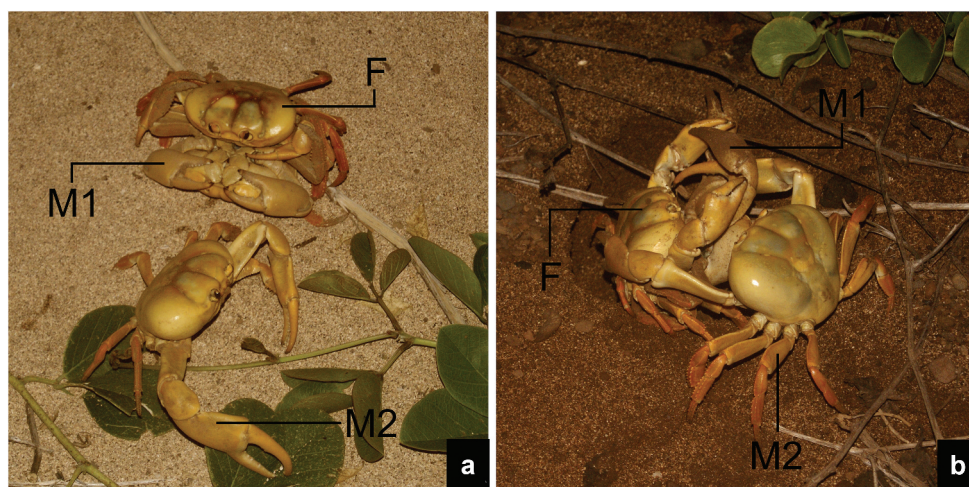
There was no post-copulatory behaviour; the partners drew away at the end of the copulation, without showing any other interaction between partners.

### Biometry, moult condition, and statistics

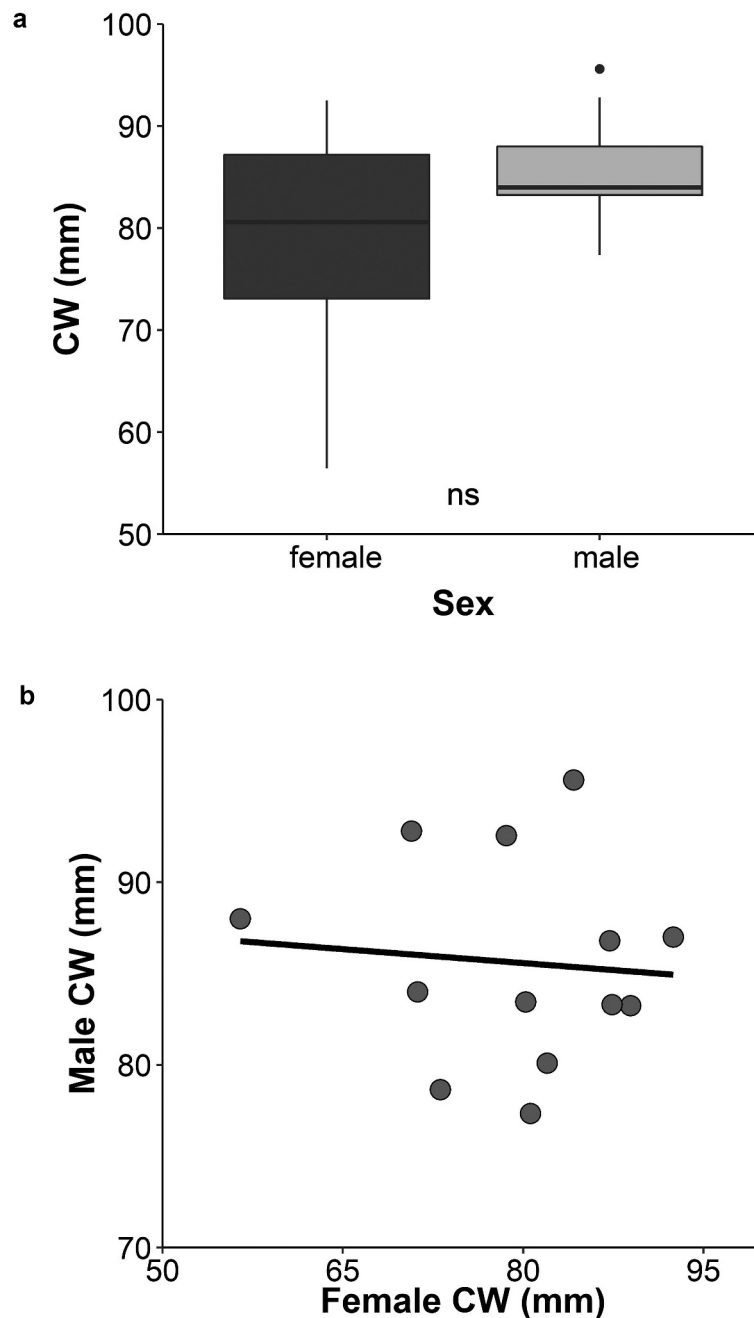
Biometrics were performed for 65% ( $n = 13$ ) of couples in copulation, with some similarity in the variation in body size (CW) of males (77.4 to 95.6 mm; mean  $\pm$  standard deviation:  $85.6 \pm 5.6$  mm) in relation to females (56.5 to 92.5 mm;  $79.5 \pm 9.7$  mm). There was no significant difference between the CW means of copulated partners (Figure 4(a)) ( $t = -1.98$ ,  $P = 0.06$ ). The relationship of size between sexual partners in copulation (Figure 4(b)) did not have a significant association between the body sizes of males and females ( $r = -0.088$ ,  $P = 0.77$ ), resulting in a poor adjustment by the simple linear equation to the empirical points ( $Y = -0.05x + 89.7$ ,  $R^2 = 0.008$ ).

After the couple's separation, some individuals quickly runaway and the measurement of cheliped size was possible in only six females and eleven males. The females showed homochely in all cases ( $n = 6$ ), making it impossible to use the Chi-square test and suggesting homochely as the standard for this sex. Among males, 45.5% ( $n = 5$ ) were homochelous and the remaining 54.5% ( $n = 6$ ) were heterochelous, percentages which did not differ significantly from each other ( $\chi^2 = 0.091$ ,  $P > 0.05$ ).

As for the colour patterns, 100% of the males ( $n = 20$ ) belonged to the yellow/light morphotype,



**Figure 3.** Mating pairs of *Johngarthia lagostoma* reacting in the presence of other mature males. a) Passive posture of both sexes interacting with mature male near the mating site, and b) Agonistic behaviour between the couple and external male near the mating site. F, female; M1, male in the mating; and M2, external male of mating.



**Figure 4.** Relationship between carapace width (CW, mm) of females and males of *Johngarthia lagostoma*. a) Boxplot of each sex with comparison of CW (*ns*, not significant =  $P > 0,05$ ). b) Linear relation between female CW (independent variable) and male CW (dependent variable) without correlation.

which made it impossible to apply the Chi-square test, while 95% ( $n = 19$ ) of females had this same morphotype, with only 5% ( $n = 1$ ) presenting the purple/dark morphotype ( $\chi^2 = 16.2$ ,  $P < 0.05$ ). It is important to highlight that the only female with a purple/dark morphotype was the smallest partner observed in copulation (56.5 mm CW). The yellow/

light morphotype was the most frequent in sexual partners (70.7 to 95.6 mm CW).

## Discussion

Here, we systematically describe the copulatory behaviour of *J. lagostoma* for the first time on one of the



South Atlantic islands. The data showed that mating is of the hard-shell-mating type, preferably occurs at night, and there are no pre- or post-copulatory behaviours. Copulation partners did not differ in size, and there was no significant association between the size of partners. Although there are homochelous and heterochelous males in the population, pairing and copulation did not imply a predominance of one of these chela morphotypes for this sex. However, there was a predominance of yellow/light colour in males and females of couples, with a single female record of lesser size with a purple/dark colouration. The time of the mating process was not evaluated here, needing to be investigated in future studies.

The hard-shell-mating recorded for *J. lagostoma* on Trindade Island confirms the pattern of copulation with the female for most terrestrial brachyurans (see Hartnoll 1969). However, pre-copulatory behaviours may vary according to the degree of terrestriality (Table 1), which may be short-lived or suppressed in these species (McLay and López Greco 2011). This fact is confirmed for *J. lagostoma* in the present study, where there was no behavioural performance prior to copulation. Despite this, it should be noted that behavioural displays that precede copulation are generally very brief, especially for semi-terrestrial and terrestrial crabs, which further minimize their duration, avoiding greater exposure to predation and cannibalism (Koga et al. 1998; Brouckerhoff and McLay 2005). When these pressures are present, males can be extremely violent both in chasing away predators/competitors and immobilizing females during pre-copula (Fukui 1994; Romero 2003; Brouckerhoff et al. 2005), a fact reported for some grapsid and varunid species (e.g. *Grapsus grapsus* and *Gaetice depressus*, respectively). For Gecarcinidae, there is no description of complex courtship behaviours, although some authors mention that males use their chelipeds to touch the female carapace possibly aimed at sexual recognition (i.e. *Johngarthia malpilensis*, *G. natalis*, and *Cardisoma armatum*). In the remainder of studies, including the present study, the pre-copulatory behaviour tends to be suppressed (i.e. *Gecarcinus lateralis* and *Cardisoma carnifex* – Bliss et al. 1978; Quinn 1981).

Pre-copulatory behaviours may show some plasticity, varying according to the peculiar characteristics of each partner of the couple, as well as the social and ecological context that evolves the place where copulation occurs. For example, the fiddler crab *Leptuca beebei* can drastically reduce their waving when exposed to a high probability of predation (Koga et al. 1998). This is evident too for the gecarcinid *J. malpilensis*, which may present two reproductive variants regarding pre-copulatory behaviour: (1) no behaviour, when large males pair

themselves with ovigerous females close to the sea, and (2) abbreviated behaviour, as that of males and non-ovigerous females in places farther from the coast (López-Victoria and Werding 2008). In the case of *J. lagostoma*, Hartnoll et al. (2006) found that males assume a pre-copulatory embracing position, although the authors do not provide a detailed description of this behaviour. In the present study, none of the couples presented such behaviour, which indicates that *J. lagostoma* has a certain plasticity in pre-copulatory behaviours. Possibly, this behavioural plasticity of *J. lagostoma* is due to the environmental contrast between Ascension Island (greater urban influence and human density) and Trindade Island (pristine environment with a low human density). In pristine island environments, species of the genus *Johngarthia* do not suffer frequent predation, but it may occasionally occur (López-Victoria and Werding 2008). Thus, possibly the pre-copulatory embrace record for *J. lagostoma* by Hartnoll et al. (2006) is the result of the increase in risks resulting from anthropization, as the introduction of alien species on Ascension Island (Ascension Island Government 2015).

During the copulation of *J. lagostoma*, there was no variation in the position between the partners of each couple; females always occupy a higher position than males. This is the usual arrangement for hard-shell-mating crabs (Hartnoll 1969), as well as for semi- and terrestrial species (Table 1). This behavioural pattern is prevalent in the Grapsidae, Varunidae and Gecarcinidae, but it is not confirmed for species of Ocypodidae (Table 1). Regardless of the position assumed by partners during copulation, the different patterns of behavioural activity presented by males of the different terrestrial crabs already studied shows an effect of the ecological contexts that each species are involved. Females of Grapsidae and Varunidae occupy a higher position than males during copulation, while the males have an aggressive posture in relation to their partner and other surrounding individuals (Fukui 1994; Romero 2003; Brouckerhoff et al. 2005). There are also reports of aggressiveness of males of ocypodids that are copulated in relation to other males and/or predators although their position in copulas is always superior to that of females (Salmon 1984; Linhares and Silva 2012). The predominant position of Gecarcinidae is that the male is positioned inferiorly to the female although in two other species the coupling is the inverse (*J. malpilensis*, according to López-Victoria and Werding 2008; and *C. armatum*, according to; Ameyaw-Akumfi 1987). In such inverse cases, the females present a passive posture during copulation, contrasting with the greater activity of the male (e.g. males of *J. malpilensis*, who use the



**Table 1.** Summary of literature data on mating behaviour in semi-terrestrial and terrestrial crabs during the intermoult period, with peculiarities in relation to couple position and other behaviours associated with copulatory, pre- and post-copulatory phases. Note that not all families are included because of lack of data.

Family	Species	Couple position	Pre-copulatory or courtship behaviour	Copulatory behaviour	Post-copulatory behaviour
Sesamidae	<i>Aratus pisonii</i> <sup>1</sup>	male on top	-	alert male embraces female with ambulatory legs	-
Grapsidae	<i>Sesarma cinereum</i> <sup>2</sup>	-	brief, male strokes the female's carapace with its cheliped	males produce bubbles	-
	<i>Grapsus grapsus</i> <sup>3</sup>	female on top	present, aggressive behaviour of male or embracing female with its chelipeds	alert male embraces female with ambulatory legs and occludes her eyes with the chelipeds	absent
	<i>Pachygrapsus crassipes</i> <sup>4</sup>	female on top	brief, male extended chelipeds followed by a courtship dance	both sexes passive and without agonistic behaviour	absent
	<i>Cyclograpsus lavauxi</i> <sup>5</sup>	-	present, male embracing female with its chelipeds	alert male embraces female with ambulatory legs and attacks other males	absent
Varunidae	<i>Gaetice depressus</i> <sup>6</sup>	female on top	present, aggressive behaviour of male or embracing the female with its chelipeds	alert male embraces female with ambulatory legs and attacks other males	absent/present, when occur in shelter
	<i>Helice crassa</i> <sup>7</sup>	female on top	absent	alert male embraces female with ambulatory legs	absent
	<i>Hemigrapsus sexdentatus</i> <sup>8</sup>	female on top	absent	alert male embraces female with ambulatory legs	present, guarding until the oviposition
	<i>Neohelice granulata</i> <sup>9</sup>	female on top	present, male embraces female with pereopods and chelipeds or blocks entrance to the burrow	alert male embraces female with ambulatory legs and occludes her eyes with the chelipeds	present, when other males are near
Gecarcinidae	<i>Cardisoma armatum</i> <sup>10</sup>	male on top	brief, male strokes the female's carapace with his cheliped and performs feed movements	passive female and alert male embracing her with ambulatory legs	absent
	<i>Cardisoma camifex</i> <sup>11</sup>	-	-	both sexes passive and without agonistic behaviour	absent
	<i>Gecarcinus lateralis</i> <sup>12</sup>	female on top	absent	alert male embraces female with ambulatory legs	absent
	<i>Gecarcoidea natalis</i> <sup>13</sup>	female on top	brief/absent, male strokes the female's carapace with his cheliped	alert male embraces female with ambulatory legs	-
	<i>Johngarthia malpensis</i> <sup>14</sup>	male on top	brief/absent, male strokes the female's carapace with his cheliped	passive female and alert male embraces female with ambulatory legs and stays with extended chelipeds	-
	<i>Johngarthia lagostoma</i> <sup>15</sup>	female on top	brief, male can guard female	passive male embraces female with ambulatory legs	-
	<i>Johngarthia lagostoma</i> <sup>16</sup>	female on top	absent	passive male embraces female with ambulatory legs	absent
	<i>Gelasimus vocans</i> <sup>17</sup>	-	present, male doing wave movements	alert male embraces female with ambulatory legs	absent
	<i>Ucidus cordatus</i> <sup>18</sup>	male on top	brief, male extend pereopods around the female	alert male embraces female and stay with extended chelipeds	absent
	<i>Ocypode quadrata</i> <sup>19</sup>	male on top	absent/brief, male grasps the female	passive female and alert male, embracing her with ambulatory legs	-

Footnote: (-) Without information about this subject. Citations: <sup>1</sup>Warner (1967), <sup>2</sup>Seiple and Salmon (1982), <sup>3</sup>Romero (2003), <sup>4</sup>Bovbjerg (1960), <sup>5</sup>Brocknerhoff et al. (2005), <sup>6</sup>Fukui (1994), <sup>7</sup>Nye (1977), <sup>8</sup>Brocknerhoff and McLay (2005), <sup>9</sup>Sal Moyano et al. (2014), <sup>10</sup>Ameyaw-Akumfi (1987), <sup>11</sup>Bliss et al. (1978), <sup>12</sup>Quinn (1981), <sup>13</sup>Hicks (1985), <sup>14</sup>López-Victoria and Werding (2008), <sup>15</sup>Hartnoll et al. (2006), p. <sup>16</sup>Present study, <sup>17</sup>Salmon (1984), <sup>18</sup>Linhares and Silva (2012), <sup>19</sup>Hughes (1971).

chelipeds to occlude the female's eyes and to ward off other males and predators – López-Victoria and Werding 2008). In gecarcinids whose females are in a higher position than males during copulation, males are passive or not very active, with rare episodes of male–male combats (Bliss et al. 1978; Hicks 1985; Hartnoll et al. 2006).

Post-copulatory behaviours (e.g. guard embracing) are not a common trait of crabs with a higher degree of terrestriality (McLay and López Greco 2011), a fact confirmed for *J. lagostoma* in the present study. Table 1 shows that post-copulatory behaviour occurs in 10.5% of the terrestrial species, but is a behaviour exclusive of the Varunidae species (Fukui 1994; Bockerhoff and McLay 2005; Sal Moyano et al. 2014). For example, males of *Hemigrapsus sexdentatus* embrace females until the laying of eggs, which ensures paternity (Bockerhoff and McLay 2005). However, post-copulatory behaviour can have some plasticity in varunides as in *Neohelice granulata*, whose guard embracing occurs depending on the number of male competitors (Sal Moyano et al. 2014). In all other species described in the table, even for Ocypodidae, which copulate in or near their galleries (Hughes 1971; Linhares and Silva 2012), the animals separate quickly after the end of copulation.

In the present study, in 53.8% of the couples of *J. lagostoma* mating, males were larger than females, while in the remaining 46.2% the males' size was smaller than or equal to that of females, with such variation not showing any significant correlation between the size of the sexes and being statistically similar. The probability value of size comparison ( $P = 0.06$ ) is nearly significant, indicating a tendency to sex difference, which is recorded as the tendency of male specimens being larger than females at a population level (e.g. on Ascension Island – Hartnoll et al. 2006; Atol das Rocas – Teixeira 1996). However, the absence of assortative-mating suggests that bigger males are not an obligatory factor for sexual selection. There is a tendency for larger males to have a greater reproductive success, especially in species where this sex manipulates, protects, and/or carries females during mating (Pinheiro and Fransozo 1999). In *Helice crassa*, due to the intense confrontation between males for the possession of receptive females, the partners that are recorded in copulation usually correlate positively with size (Bockerhoff et al. 2005). Another example occurs with *Austruca mjobergi*, where there is a strong positive correlation between the size of copulated partners and a highly biased sexual proportion for males, which increases the likelihood of disputes (Clark and Backwell 2016). This confirms the dependence on the size of males in copulation systems characterized by intense male–male competition for partners, a fact that

is not evident for *J. lagostoma*. Size differences at the population level can result from the risks provided by seasonal migrations, which may reduce gecarcinid females' longevity and, thus, generate males larger than females (López-Victoria and Werding 2008; Turner et al. 2011).

The size of chelipeds also do not prove to be a determining factor in the pairing of *J. lagostoma* on Trindade Island, since the proportion between homochelous and heterochelous males was similar. In general, homochely is highly frequent in juvenile males of *J. lagostoma* on Trindade Island but, after reaching maturity size, the occurrence of the two male types are similar (João et al. unpublished data). This confirms the indications of Hartnoll et al. (2017), who addressed the existence of chelar polymorphism for this species on Ascension Island and the absence of relationships with sexual selection and pairing. After all, individuals who invest heavily in weapons (i.e. chelipeds) have a marked and constant chelated sexual dimorphism, especially males (Shuster and Wade 2003), and, when the opposite happens, it corroborates the absence of agonistic conflict between males. In this case, the competition can be discreet and related to other factors, including a greater availability of receptive females, when males save energy in direct confrontations by targeting the copulation with a higher number of partners (Baeza and Asorey 2012). On Ascension Island, the sex ratio (male: female) of *J. lagostoma* is similar between the sexes (1:1, Hartnoll et al. 2009), favouring sexual encounters. This needs to be better evaluated for Trindade Island but, on the Andradas Beach, the sexual proportion has a slight bias towards males (1:0.8, João et al. unpublished data). However, it is one of the traits of the *pure searching and interception* mating system, where males copulate with several females, disputes between males for partners are rare, and pre- and post-copulatory behaviours are minimized or non-existent (Christy 1987; Shuster and Wade 2003). Bockerhoff et al. (2005) identified several Grapsidae and Varunidae with this copulation system. However, there are still no evaluations in this context for the family Gecarcinidae.

For sexual selection, there are indications of the influence of the chromatic pattern, as the prevalence of the colour of couples in copulation was yellow/light. However, this may be an effect of the occurrence of colour patterns at a population level. For the individuals of *J. lagostoma* on Ascension Island, there is a low percentage of purple/dark individuals (13.7%) in relation to yellow/clear (86.3%) (Hartnoll et al. 2009). For Trindade, the same ratio occurs: yellow/light crabs predominate by more than 83% in both sexes (83.5% in males and 89.3%

in females, João et al. unpublished data). Future studies should verify if there is any selection favouring the light colour of the breeding couple or if its related to the colour rate in the crab population.

The copulation and sexual selection strategies for *J. lagostoma* addressed in the present study lead to new questions for a more holistic understanding of this reproductive process. The number of studies adopting this perspective is low for brachyurans, especially for terrestrial crab species, which are listed in Table 1. According to McLay and López Greco (2011), there is a lack of studies on post-copulatory sexual selection, sperm competition, and paternity considering the spermatophoric contents stored in the seminal receptacles. In this sense, the few studies on semi-terrestrial and terrestrial crabs show that the content stored by the same female may comprise a gene pool of several males, with randomness in the advantage of that males neglected in the generation of offspring (Jennings et al. 2000). In Gecarcinidae, in particular, energy expenditure on reproductive migration is extremely high, being one of the most stressful events in the history life of these crabs (Hartnoll et al. 2006, Sanvicent-Añorve et al. 2007). Thus, the absence of agonistic confrontations and complex copulatory behaviours, added to the equalization in the advantage of fertilizing the eggs of females, may represent an intriguing energy trade-off in the reproductive biology of these crabs. None of these perspectives have been evaluated for *J. lagostoma*. It is necessary to fill some gaps raised in the present study about the mating system of this species, including experimental designs, to confirm whether sexual selection occurs principally pre- or post-copula.

In general, all behavioural characteristics presented and discussed here show some content for semiterrestrial and terrestrial crabs. Families with low degree of terrestriality (Sesamididae, Grapsidae, Varunidae and Ocypodidae) have the most aggressive behaviours, mainly in males, in relation to most terrestrial species (Gecarcinidae). We believe that this may be related with the ecological differences of the site where each group inhabits, for example between supralittoral continental and insular environments, where predation pressure is different. The isolation of oceanic islands leads fewer species to settle down in these communities, and land crabs may thus occupy niches in almost all places on the island (Lindquist et al. 2009). In this less competitive reality, insular land crabs can be selected to have less 'cautious' mating behaviours. However, there were behaviour variations for semi-terrestrial species (i.e. Varunidae) in environments with more or less predation pressure (Sal Moyano et al. 2014). In gecarcinid species, this plasticity was not recorded and is

a worrisome aspect, mainly due to the growing urbanization in oceanic islands, which exposes land crabs to alien species and creates confirmed impacts (Paulay and Starmer 2011; Perger 2019). The presence of predators or human intervention can promote changes in the reproductive behaviour (Sainte-Marie et al. 2008). For *J. lagostoma*, it is crucial compare the behaviours described here between the different islands as a function of the distinct adverse effects, among them 1) predation of the crab by exotic species (e.g. Fernando de Noronha Island), 2) anthropic impact (e.g. Ascension Island and Fernando de Noronha), and 3) food, spatial, and freshwater limitation (e.g. Rocas Atoll).

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