

REPRODUCTION IN THE LAND CRAB *JOHNGARTHIA LAGOSTOMA* ON ASCENSION ISLAND

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ABSTRACT

Reproduction was studied in the land crab *Johngarthia lagostoma* on Ascension Island in the central South Atlantic from 2005 to 2008. Both sexes are mature by 60-70 mm carapace width (the sample > 4,000 crabs consisted almost entirely of mature specimens). Breeding occurs around the east and south shores of the island, but was studied predominantly at the only easily accessible site at North East Bay. The annual breeding migration extends from January to May, with peak migration in March in most years. The intensity of migration varies between years, and is not obviously related to rainfall. There is lunar entrainment, with increased numbers at the shore in the first quarter, but largest numbers in the last quarter. Both males and females migrate, but with females in greater numbers. At the shore 80% of the crabs are females. A few females mate and lay eggs in the upland residential areas, a greater number do so on the migration route, but the majority only after reaching the shore. Reproductive investment per brood averaged 5% on a dry weight basis, and fecundity averaged 72,000 eggs.

KEY WORDS: Ascension Island, *Johngarthia*, land crab, migration, reproduction

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INTRODUCTION

The land crab *Johngarthia lagostoma* (H. Milne Edwards, 1837) is found only on Ascension Island (U.K.) in the central South Atlantic, and on three small Brazilian islands (Fig. 1). The taxonomy, geographical distribution, and biology of the species on Ascension Island have been reviewed in Hartnoll et al. (2006). The population structure was examined in greater detail in Hartnoll et al. (2009). This 2006 paper described aspects of reproduction but was based only on short term observations in a single breeding season. This study is based on an extended set of data, spread over four breeding seasons, and including some season-long observations.

The reproductive pattern of *J. lagostoma* resembles that of most other gecarcinids. Gecarcinid crabs normally live inland both as juveniles (all of the time) and as adults (most of the time). However, they retain a marine planktonic larval phase, and adults (or at least the females) must undertake annual migrations to the shore for breeding and larval release. These migrations are often spectacular mass movements – the red land crab *Gecarcoidea natalis* (Pocock, 1888) on Christmas Island provides the best publicized example (Hicks, 1985). The migrations are a major focus of this study, including timing and participation of the sexes. Other topics covered are size at sexual maturity, mating activity, frequency of egg production, and reproductive investment.

MATERIALS AND METHODS

Data were collected during the breeding seasons from 2005 to 2008. KES worked on Ascension from March to June 2006 as part of her

M.Sc. programme and presented the results as a dissertation (Saunders, 2006).

Field Sampling

The majority of data were collected in the field. Specimens were hand collected, and most sampling was by night, when the crabs were most active. Other specimens were collected by day, either after rain, or on the shore where they congregate during the breeding season. Date, time, location and rainfall were logged. The following were recorded for selected samples: sex, colour, and maximum carapace width (to 0.1 mm, using dial callipers). In females the presence of eggs was recorded, and (in sub-samples) whether the eggs were early stage (without eye spots) or late stage (with eye spots). Other samples were only sexed and counted. After examination specimens were normally released unharmed. A few females were retained for dissection to determine ovarian status and presence of stored sperm in the spermathecae, because large scale sacrificial sampling was considered inappropriate. This imposed a constraint on the data: without dissection it was not possible to discriminate immature specimens from mature, nor females with ripe ovaries preparing to lay from spent females where the egg mass had already hatched. Over 3,000 specimens were marked on the carapace with a unique number using a dry marker. Recaptures were recorded.

Surveys were conducted in many parts of the island, but they were focussed on three areas, selected essentially because they were both accessible by road (a logistic necessity for safe working by night), and had adequate concentrations of crabs. These three areas were surveyed on a regular basis, sometimes daily in periods of peak activity (Fig. 1).

1. The NASA Road (NASA), from where it reaches an altitude of 200 m to where it ends at the disused NASA tracking station (~ 8 km length). It reaches an altitude of 518 m. This is within the area where crabs live outside the breeding season, and is termed the 'resident' population.
2. The NE Bay Road (NEBR), from beyond Two Boats Village (200 m) to the track leaving it for NE Bay (100m), approximately 4 km length. The population here is predominantly in transit during the breeding season, and is termed the 'migrating' population.

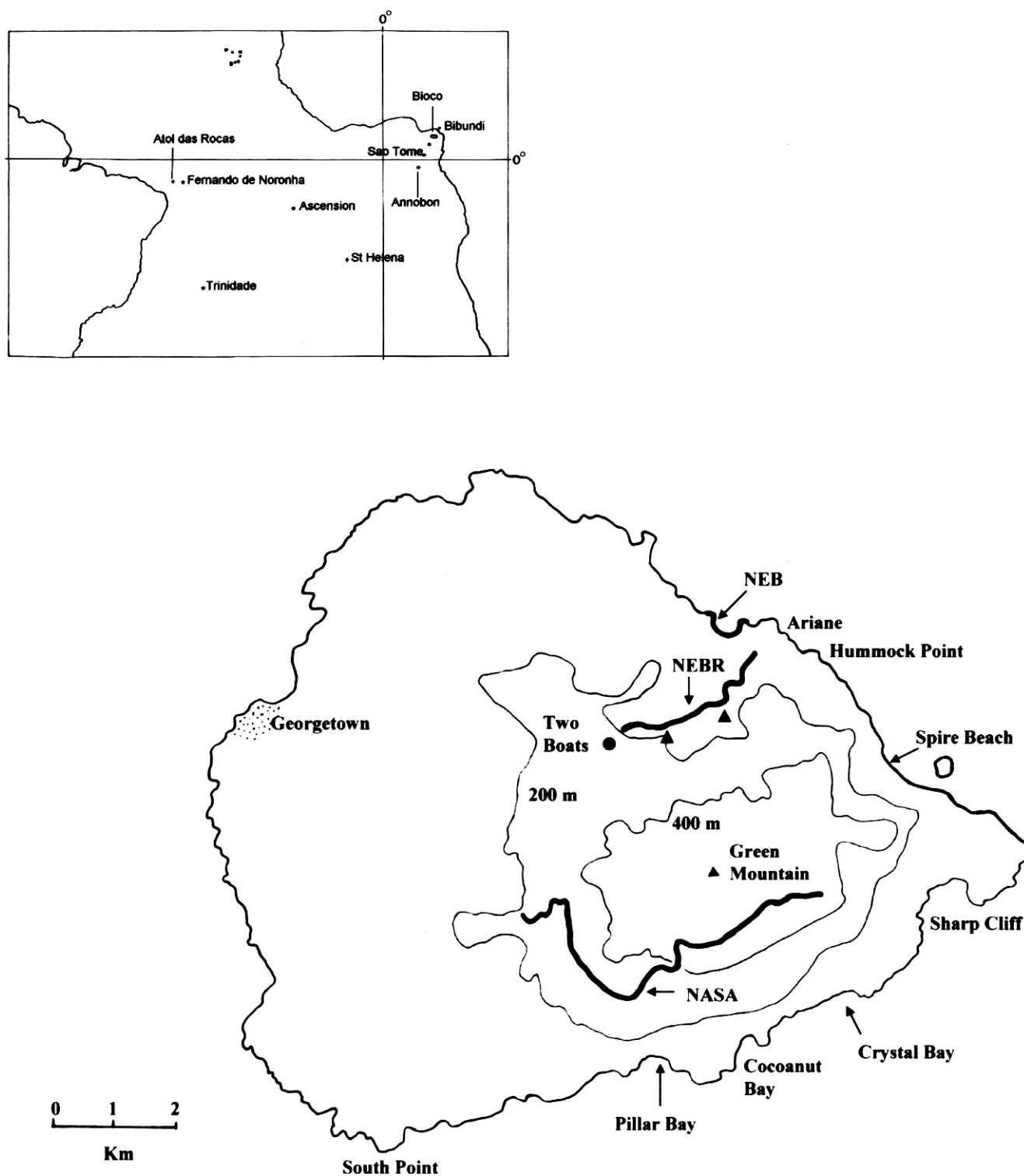


Fig. 1. Ascension Island. Upper map to show location in the South Atlantic. Main map to show topographic detail. The 200 m and 400 m contours are indicated, and the summit of Green Mountain. The three main sampling sites are shown as bold lines, Northeast Bay (NEB), Northeast Bay Road (NEBR), and NASA Road (NASA). The triangles on NEBR are the main 'transit camps'. Other locations mentioned in the text are shown.

3. The shore at NE Bay (NEB), consisting of the sandy beach, and the rocks at the north and south ends of the beach. Crabs occur here only in the reproductive season, and are termed the 'breeding' population. Live crabs were found predominantly among the rocks at each end of the beach. Numbers of dead crabs were found along the landward margins of the sandy beach: these were also recorded.

Evidence of migration on other routes, and activity on other shores, was sought during the breeding season by occasional visits to these less accessible areas. Other locations mentioned in the text are also shown on Figure 1. During each survey the areas were driven or walked as appropriate, and all crabs recorded. If crabs were very abundant, counts were estimated, and sub-samples examined.

Dissection

A small number of females (< 40) were dissected, supplemented wherever possible by the autopsy of road kills. Females were examined for ovarian condition and for the state of the spermathecae. Ovaries were divided into two categories. Unripened or spent (these cannot be discriminated macroscopically) ovaries are small, and pale or orange coloured. Ripening or ripe ovaries are medium or large, and brown or dark green colour.

Spermathecae were classed as unmated (small, flattened in shape), or mated (medium or large size, clearly rounded and swollen). Movement in the genital opercula was also assessed by gently pressing with a seeker.

Reproductive Investment and Fecundity

Reproductive investment and fecundity are preferably determined on early stage eggs (Hines, 1982). However, sufficient early stage eggs were not obtained, and determination was made on a mixture of early, mid and late stage eggs. Samples were alcohol preserved. The eggs were separated from the female, both were blotted dry, and weighed. They were then dried to constant weight at 80°C, and reweighed. Reproductive investment (RI%) was calculated from both wet and dry weights as

$$RI\% = \text{egg mass weight} \times 100 / \text{female weight (excluding egg mass)}.$$

From each of five females a counted sample of ~300 eggs was dried and weighed. The results were used to calculate mean dry weight per egg, and using this value fecundity was estimated from the dry weight of each egg mass.

RESULTS

Size at Sexual Maturity

There was only one observation of mating, so size at sexual maturity has had to be assessed from two other factors. One is participation in the breeding migration, which presupposes maturity. For females there is also the production of eggs, which proves maturity. Dissections supplemented these data.

Participation in the breeding migration was examined by comparing the size distributions of migrating and breeding crabs with the sizes of those in the resident population (Fig. 2). All size classes of both sexes in the resident population, including the smallest at 61-70 mm CW (smaller size classes are so poorly sampled as to provide no useful data), are represented in similar proportions in the migrating and breeding populations. The mean sizes of both migrating and breeding crabs are, surprisingly, smaller than for resident crabs in both sexes (Table 1). This indicates a lack of non-migrating juveniles in the resident population. This suggests that the populations sampled consist almost entirely of mature specimens, and that by 60-70 mm CW both sexes are mature. The data on ovigerous females supports this, since the 61-70 mm CW class has a high proportion of ovigerous females (Fig. 2), as do all larger classes. The smallest ovigerous female was 63 mm CW. The limited dissection data give supporting evidence. Of 43 females examined, 42 had swollen spermathecae to indicate they had mated: they ranged in size from 70 to 105 mm CW. Only one female, of 70 mm CW, was unmated: that was migrating on the NEB Road, had ripe ovaries, and would certainly mate and lay in that instar.

Migration Routes and Breeding Sites

The main collections indicate that there is a major migration route from Green Mountain down to North East

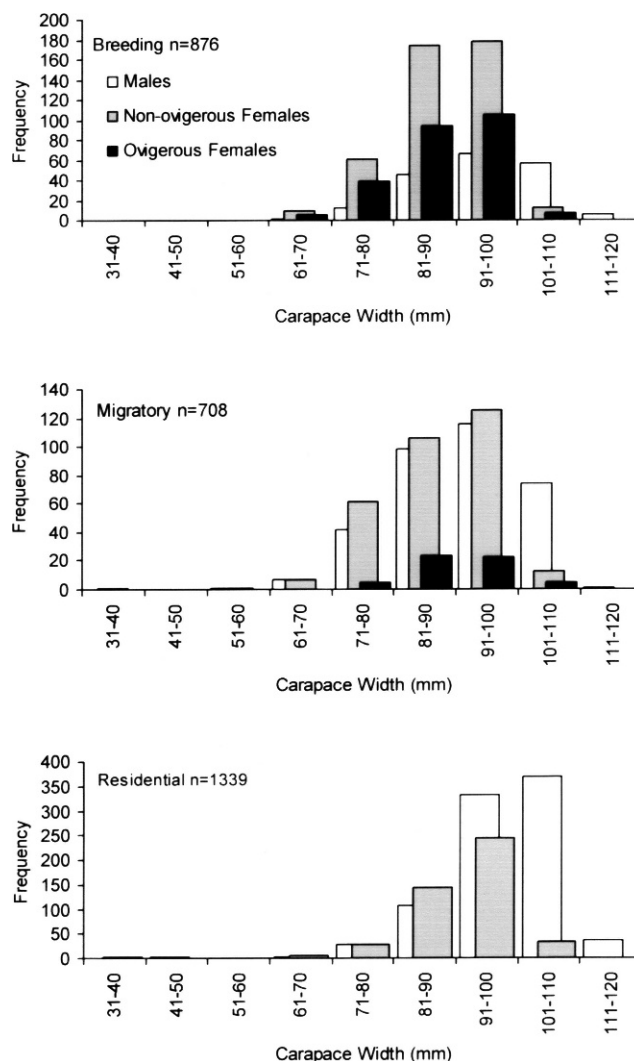


Fig. 2. *Johnngarthia lagostoma*. Size frequency distribution of crabs sampled in 2006 in the breeding, migrating, and resident populations.

Bay Road, and continuing on to North East Bay where there is an important breeding area. However, NE Bay is not the nearest potential breeding location for crabs resident on the southern and south-eastern slopes of Green Mountain, and other breeding sites were located.

Live and/or dead crabs were found at the shore in the following additional locations: Ariane, Hummock Point, Spire Beach, Sharp Cliff, Crystal Bay, Coconut Bay, Pillar Bay, and between Pillar Bay and South Point (Fig. 1). This indicates breeding activity around the sector of shore from NE Bay clockwise to South Point. The rest of the shoreline, from South Point clockwise to NE Bay is relatively easy to access in many places, but nevertheless no breeding activity was observed within that sector. There was evidence of migration routes along gullies down to several of the putative breeding sites in the form of occasional crabs, and the presence of many burrows (= transit burrows, see below): the routes to Spire Beach, Sharp Cliff and Pillar Bay were particularly evident. However, the presumption that crabs follow the shortest routes to the shore is not fully supported by mark/recapture data

Table 1. *Johngarthia lagostoma*. Within each population category (see Methods) the following are given for each sex: number collected (and percentage of each sex) and mean carapace width. Total collected for that category also given. Based on collections in 2006.

Category	Males		Females		Total No.
	No. (%)	Mean CW (mm)	No. (%)	Mean CW (mm)	
Resident	881 (66)	98.2	458 (34)	91.2	1339
Migrating	339 (48)	91.2	369 (52)	88.0	708
Breeding (live)	190 (22)	95.6	686 (78)	88.2	876
Breeding (dead)	37 (18)	94.0	166 (82)	90.1	203
Total	1,551 (47)	96.1	1,782 (53)	89.1	3333

(Table 3). Thus a female marked on NEB Road was recaptured 49 days later, 5 km away on NASA Road. Similarly a male marked on NASA Road was recaptured 8 days later, and 4 km distant, on NEB Road. Movement patterns are clearly complex.

During the migration season crabs of both sexes were found in burrows along the migration routes. Thus from March-May several areas along NEB Road had concentrations of burrows occupied by numbers of male and female crabs, but outside the breeding season (in July) these same burrows were deserted, with the entrances blocked by accumulations of debris (Fig. 3). We term these seasonal refuges 'transit burrows'. At the shore the majority of crabs sheltered in crevices in the rocks above high water, but a few were found in temporary burrows excavated in sand above high water. The considerable number of dead crabs observed at the shore (Tables 1 and 2) were found on the barren sandy areas behind the beach. It is presumed that these crabs, which included many ovigerous females (Table 2), were either migrating towards the shore, or had subsequently left the security of the rocky areas. In either case they had failed to find shelter at dawn, and had later died from heat and desiccation.

At NE Bay female crabs were observed releasing larvae at night. They descended the rocks into the splash zone, and shook the masses of hatching larvae into the water, where they often fell into the swash zone on the adjacent sand. Predation of the larval masses by mole crabs, *Hippa testudinaria* (Herbst, 1791), was observed in both 2007 and 2008 (Stroud, 2008). Large numbers of mole crabs congregated in the swash zone below the females, seizing the larval masses as soon as they were released.

Participation of Sexes in the Migration

The basic evidence for the participation of the sexes in the breeding migration is presented in Table 1. There is no reliable value for an unbiased overall sex ratio of the population (see Hartnoll et al., 2009), so the data for different sections of the population during the breeding season can only be compared with each other. The resident population has, during the breeding season, a predominance of ~ 65% males (chi-square, $P < 0.05$): in the absence of other evidence, it is assumed that this is due partly or entirely to the greater migration by females (see below). The migrating population has an equal sex ratio (chi-square, $P > 0.05$). The breeding population, at the shore,



Fig. 3. *Johngarthia lagostoma*. Entrances to burrows. A. Unused burrow, 'transit camp' on NEB Road, July 2007. B. Occupied burrow in the residential zone, July 2007.

has a predominance of ~80% females (chi-square, $P < 0.05$). The parsimonious conclusion is that females migrate in greater proportion than males (or migrate for longer periods), and that of the migrating crabs, more of the females migrate as far as the shore.

The interaction of the sexes during migration is clarified by the location of egg laying (mating is closely linked to laying, as explained in the discussion). A breakdown of the incidence of ovigerous females, and of the stage of eggs (in the subsamples examined) is given in Table 2. In the resident population very few ovigerous females were seen. In the

Table 2. *Johngarthia lagostoma*, females. Number sampled in 2006 for each population, number and percentage ovigerous, and for those examined, number and percentage with early and late eggs.

Location	Number	No. (%) ovig.	No. (%) early eggs	No. (%) late eggs
Resident	505	2 (0.4)	1	
Migrating	518	60 (12)	13 (43)	17 (57)
Breeding (live)	696	262 (38)	11 (13)	75 (87)
Breeding (dead)	180	83 (46)		

Table 3. *Johngarthia lagostoma*. Results of the mark and recapture observations, March to June 2006. NASA, NASA Road; NEBR, NE Bay Road; NEB, NE Bay shore.

Mark site	Recapture Site	Sex	Number	Interval (days)		
				Min	Max	Mean
NASA	NASA	M	34	3	57	18
NASA	NASA	F	9	3	45	20
NASA	NEBR	M	1	-	-	8
NEBR	NASA	F	1	-	-	49
NEBR	NEBR	M	11	7	59	16
NEBR	NEBR	F	1	-	-	49
NEBR	NEB	M	2	1	61	-
NEBR	NEB	F	3 ¹	2	39	15
NEB	NEBR	F	3 ²	3	16	7
NEB	NEB	M	8	1	40	24
NEB	NEB	F	4 ³	1	24	19

¹ One female with late eggs when marked, but had shed them on recapture after 3 days; another without eggs when marked, but late eggs on recapture after 39 days.

² Two with eggs when marked, but not when recaptured.

³ Three without eggs when marked, but had late stage eggs on recapture.

migrating population appreciable breeding was taking place, with 12% of females ovigerous. About half of these females had late stage eggs, so had either remained in the migrating zone during incubation, or had laid before reaching it. On the shore, in the 'breeding' population, 40% of females were ovigerous, the majority with late stage eggs.

Ovarian condition and mating status were recorded from the limited dissections and road kill autopsies. They are so restricted that no attempt has been made to break them down by time, other than to separate results in the breeding season (February–May) from the non-breeding season (July). In July, 5 females were dissected: all had unripened ovaries, and mated spermathecae. In the breeding season, samples were examined from the three main sites, and ovary condition (unripened/spent and ripening/ripe, respectively) was as follows: resident (7 and 19), migrating (8 and 10), and breeding (16 and 9).

All ovigerous females had spent ovaries: there was no sign of the ovaries re-ripening during incubation, even in females with very mature eggs. All females dissected had mated, except for one. This was a specimen of 70 mm CW, with empty spermathecae, but with ripe ovaries.

Mark and Recapture Data

Over 3,000 crabs were marked, and 77 were recaptured (a few more than once). Given the logistic limitations of the study, a recapture rate of 2.5% was considered good, and the results are informative. Of the total, 42 crabs were both marked and recaptured on the NASA Road, 12 on the NE Bay Road, and 12 on the shore at NE Bay. The remaining 10 observations involved movements between these three areas. The longest migrations were between the NASA and NEB roads: a male was marked on the NASA Road, and recaptured 8 days later ~ 4 km distant on the NEB Road; a female marked on NEB Road was recaptured 5 km away on the NASA Road 49 days later. Summaries of the observations are presented in Table 3. There are data on the time spent in different areas: clearly crabs are not merely making brief visits to the migration zone on NE Bay Road

Table 4. *Johngarthia lagostoma*. The date and number of crabs observed at peak abundance at North East Bay: the moon phase at that time is also given. The rainfall figures are the total rainfall for January to March at the Air Base.

Year	Date	Maximum abundance			Rainfall (mm)
		Number	Moon phase		
2003	8-9 Feb	>1000 ¹	last qu.		98
2004	-	v. few ²	-		24
2005	1-3 Mar	v. many ³	last qu.		6
2006	27 Mar	134	last qu.		15
2007	14-15 Mar	2300	last qu.		27
2008	5 Mar	620	new		41

¹ "Thousands on the beach" (Graeme Hays, personal communication).

² Very little migration that year (Tara Pelembe, personal communication).

³ "Too many to count" (Hartnoll et al., 2006).

(average stay > 16 days), nor to the shore at NE Bay (average stay > 19 days). The disparity in recaptures between the sexes on NE Bay Road (11 males, but only 1 female), despite an equal sex ratio there, suggests that males are spending much longer in the 'transit camps' than are females. The observations on presence and absence of eggs confirm that some females lay in the migration zone, but others only after reaching the shore.

Six of these recaptures provided minimum estimates for the speed of migration (minimum because they may not have moved directly, nor moved all of the time). Estimates ranged from 106 to 870 m day⁻¹, with a mean of ~ 450 m day⁻¹. Modest values for these large active crabs.

Temporal Patterns of Migration

The duration of migration during each year was examined by recording the presence and abundance of crabs on the shore at NE Bay as follows: 2005, (1 March to 5 May), 2006 (10 March to 27 May), 2007 (29 January to 3 June) and 2008 (8 January to 11 June). In 2005 and 2006 observations were not made before early March. The timing and intensity of the peak abundance in each year is outlined in Table 4, together with data on lunar phase at peak abundance, and rainfall over the early part of the year. Except in 2003, peak abundance was observed in March. The number observed at peak abundance at NE Bay varied considerably between years, but was not consistently related to rainfall.

There is evidence of lunar entrainment. In most years the time of peak abundance was in the last quarter (Table 4). Further analysis was made by calculating the mean number of crabs seen at NE Bay for each phase of the moon, using the data for 2006 to 2008. The mean values were: new moon, 87 crabs (n = 13); first quarter, 161 crabs (n = 16); full moon, 77 crabs (n = 15); last quarter, 442 crabs (n = 12): Kruskal Wallis test, Chi square = 12.3, d.f. 3, P < 0.007. Greatest abundance was in the last quarter, followed by the first quarter. This pattern is clearly illustrated by the data for 2006 at NE Bay (Fig. 4).

Reproductive Investment and Fecundity

Determinations were made on eight females (Table 5). RI% wet weight ranged from 4.2-15.1%, with a mean of

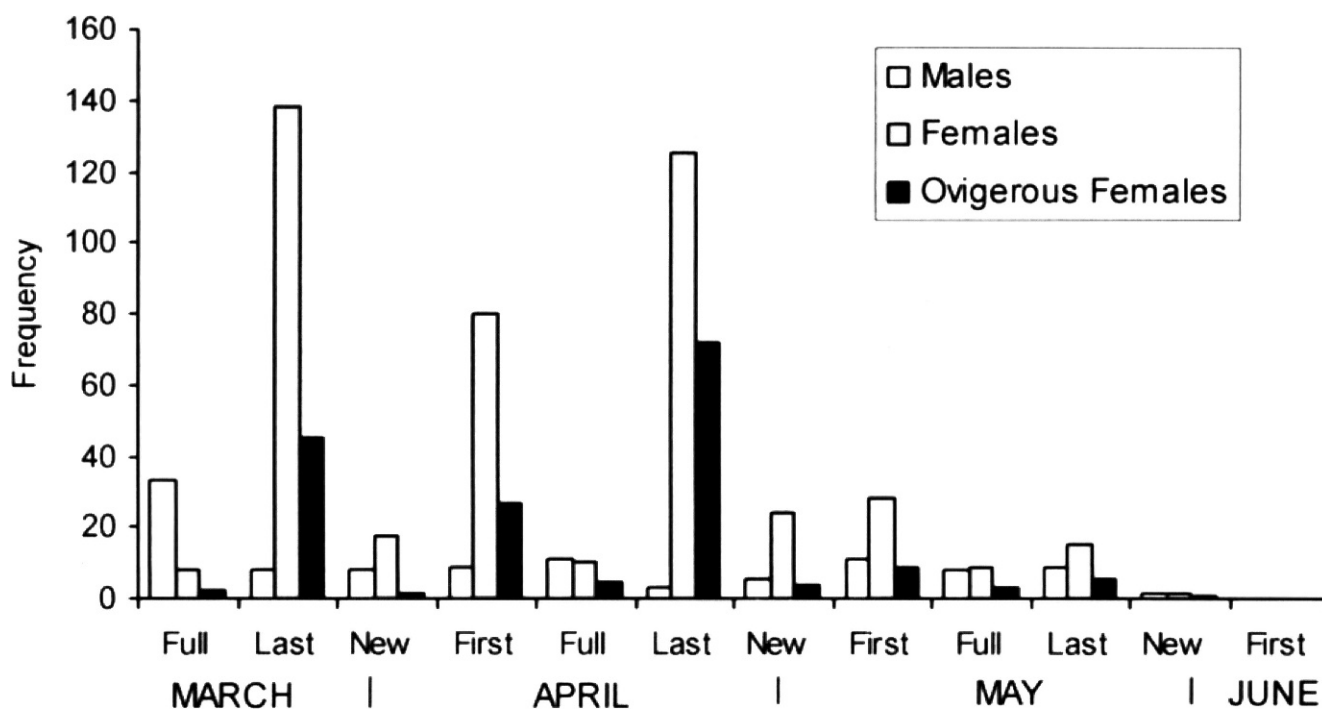


Fig. 4. *Johnngarthia lagostoma*. Number of crabs recorded per visit at NE Bay in 2006, by month, and by phase of the moon.

9.0%. RI% dry weight ranged from 3.1–7.3%, with a mean of 5.4%. Mean dry weight per egg was 6.02×10^{-5} g. Fecundity ranged from 35,900 to 109,100 with a mean of 71,800. Neither RI% nor fecundity varied consistently with egg stage – hence there is no indication of substantial egg loss during incubation. RI% did not show a significant relation to CW ($r^2 = 0.026$, $P > 0.05$). Log fecundity was regressed on log CW, and there was no significant relationship ($r^2 = 0.113$, $P > 0.05$).

DISCUSSION

Size at Sexual Maturity

Determination of the size of sexual maturity is made difficult by the lack of small specimens: of over 3,500 crabs measured, only 25 were < 60 mm CW (Hartnoll et al., 2009). Possible reasons for this were considered in the above paper, but no definitive conclusion was reached: such a skewed distribution is not observed in other populations of *J. lagostoma*, or in other gecarcinids (Hartnoll et al., 2009).

The evidence available, from migration participation, egg production, ovarian maturity, and evidence of mating, all indicates that sexual maturity in both sexes is attained by 60–70 mm CW. The paucity of smaller specimens meant that it could not be determined whether any specimens mature at a smaller size. Nevertheless, 60 mm CW is about half of the maximum observed size, and this is about the proportional size at which maturity occurs in several other species of gecarcinid, e.g., *Gecarcinus ruricola* (Linnaeus, 1758) (see Hartnoll et al., 2007), *Gecarcoidea natalis* (see Hicks, 1985), and *Epigrapsus notatus* (Heller, 1865) (see Liu and Jeng, 2005).

Migration Routes and Breeding Sites

Logistic constraints meant that this study focussed on the one accessible breeding site at NE Bay, and the migration route to that site where it crosses the NE Bay Road. Limited surveys indicated that breeding also occurred at a number of other relatively inaccessible sites from NE Bay clockwise around the north eastern and southern shores of Ascension Island, but it was impossible to evaluate the relative intensity of breeding at different sites. Outside the breeding season the distribution of the crabs is around the slopes on all sides of Green Mountain from about 200 m upwards, and the parsimonious assumption would be that crabs travel along the shortest migration route to the shore. On that basis crabs living along the NASA Road would be expected to migrate to the southern shores, but the evidence from limited mark/recapture data shows that there is some migration between the NASA Road and NE Bay Road, en route to the north-eastern shores. This raises the possibility that the NE Bay area is the major breeding site for all

Table 5. *Johnngarthia lagostoma*. Results for the determination of reproductive investment (RI%) from wet (WW) and dry (DW) weights, and fecundity.

CW (mm)	Egg stage	RI% WW	RI% DW	Fecundity
81	late	15.11	7.25	72,600
90	mid	10.13	6.61	66,400
93	mid	4.19	3.05	35,900
93	early	6.69	4.20	49,000
94	early	8.84	5.53	88,400
98	early	5.13	3.44	58,100
101	late	11.67	6.08	94,500
104	early	10.12	6.95	109,100
Mean values		8.98	5.39	71,800

sectors of the population, with consequent implications for conservation. NE Bay lies at the base of the major Island watershed, so the routes from Green Mountain to the Bay may provide a superior number of moist refugia.

Limitation of breeding to specific sectors of an island's shore, as on Ascension, does occur in other land crabs. In the San Andres Archipelago, breeding of *Gecarcinus ruricola* is restricted to western shore areas on both San Andres and Old Providence islands (Hartnoll et al., 2007). Conversely, on Christmas Island the breeding of *Gecarcoidea natalis* occurs on all sides of the island (Hicks, 1985). The migration paths on Ascension need further study.

The Timing of Migration

There is limited information on the annual seasonality of the breeding migration on Ascension: for earlier years there is only anecdotal information. There are references to very abundant migrations in March 1977 and January 1987 (John Packer, pers. comm.), and in February/March 2003 (Graeme Hays, pers. comm.). From earlier data the general consensus was that migration occurred mainly from late January to March (Ashmole and Ashmole, 2000). The present study, for 2005 to 2008, indicates migration from January into May or early June, with peak numbers in March. This confirms Ashmole and Ashmole (2000) in relation to migration starting in January, but indicates that in recent years at least, it extends well beyond March. There is variation between years in the intensity of migration: substantial migrations occurred in 2003, 2005, 2006, 2007 and 2008, whilst in 2004 the migration was limited.

There is a general trend in gecarcinids for the migration period to coincide with the rainy season, an obvious benefit in limiting desiccation stress. There are a number of examples: *Cardisoma hirtipes* Dana, 1851 (see Gibson-Hill, 1947; Shokita, 1971), *Cardisoma guanhumi* Latreille, 1825 (see Gifford, 1962), *E. notatus* (see Liu and Jeng, 2005), *Gecarcinus lateralis* (Fremenville, 1835) (see Klaasen, 1975; Wolcott and Wolcott, 1982), *Gecarcinus ruricola* (see Hartnoll et al., 2007), *Gecarcoidea lalandei* H. Milne Edwards, 1837 (see Liu and Jeng, 2007) and *Gecarcoidea natalis* (see Gibson-Hill, 1947; Hicks, 1985). On Ascension the heaviest rainfall is, on average, in the months March to May (Ashmole and Ashmole, 2000): so *J. lagostoma* matches the general trend of migrating during the wet season. However, rainfall on Ascension varies greatly from year to year, and there was no consistent correlation between amount of rainfall in the early part of the year and the intensity of migration. The very strong migration in 2003 did coincide with high rainfall, but the strong migration in 2005 coincided with the smallest January to March rainfall for many years. On a finer scale, correlations within years could not be found between the intensity of migration and rainfall in the immediately preceding period. One complication is that rainfall measurements are recorded at low altitudes at the Air Base, and may not reflect that experienced at the higher altitudes on Green Mountain.

Various gecarcinids exhibit lunar rhythmicity in migration and/or spawning. In *Gecarcinus ruricola*, the migration of females with ripe eggs was greater at the period around new moon, suggesting that larval release may be concen-

trated at such periods (Hartnoll et al., 2007). In *Gecarcoidea natalis*, it is concentrated in the last quarter (Hicks, 1985), as it is in the congener *G. lalandei* (see Liu and Jeng, 2007). There was greater larval release at full moon in Columbia for *Gecarcinus lateralis* (see Klaasen, 1975), and immediately after full moon in Bermuda (Wolcott and Wolcott, 1982). In *E. notatus*, larval release is in the period following full moon (Liu and Jeng, 2005). In *C. guanhumi*, spawning is concentrated near the full moon (Gifford, 1962). For *J. lagostoma* on Ascension peak activity was consistently during the last quarter, with smaller peaks in the first quarter, all on neap tides. There is clearly no consensus for the family, and the optimum lunar phase for larval release may depend upon the environment. For mangrove crabs, such as *Cardisoma*, highest spring tides (at new or full moon) may be optimal for ease of immersion and larval export (Skov et al, 2005), as in *C. guanhumi* above. For species spawning on exposed rocky shores the lesser wave action associated with neap high tides (in first and last quarters) may be the preferred option, as in *Gecarcoidea* and *Johngarthia*.

Migration, Mating and Spawning: an Integrated Pattern

In order to interpret and integrate the results on the participation of the sexes in migration, the location and incidence of laying, the condition of ovaries and evidence of mating, and the mark/recapture data, some basic reproductive facts need to be presented.

Mating and egg laying are closely linked in gecarcinids, since the female genital opening is normally occluded by a rigid calcified operculum, which decalcifies for only a short period to allow mating, followed quickly by egg laying (see Hartnoll, 1968; Hartnoll et al., 2007). Thus the incidence of egg laying also provides an index of the potential for mating, both being limited to this 'window of opportunity'. Throughout the study only one female was found with flexible opercula (however, such examination was not practicable in the field), one which had very recently laid eggs. It is not certain how long opercular decalcification lasts in *J. lagostoma*, but in some other species it is only a matter of days (Henmi and Murai, 1999; Brockerhoff and McLay, 2005). Female receptivity may be extended if males are unavailable (Brockerhoff and McLay, 2005).

Females do not necessarily need to mate each time before laying. If they have previously mated, the unused sperm are stored in the spermathecae and may fertilise further batches of eggs. Several batches may be fertilised, e.g., in *Rhithropanopeus harrisi* Gould, 1841 (see Morgan et al., 1983); in *Chionoecetes opilio* (O. Fabricius, 1788) (see Rondeau and Sainte-Marie, 2001), though the fertilisation rate may decline batch by batch (Paul, 1984; Rondeau and Sainte-Marie, 2001). In at least some crabs the stored sperm are not lost when the female moults (Cheung, 1968; Nagao and Munehara, 2007).

Thirdly, ovarian maturation tends to be slow in gecarcinids. There are a number of tropical crabs where ovarian maturation occurs within the brief duration of egg incubation, typically less than three weeks: examples include *Metapograpus messor* (Forskål, 1775) (see Sudha and Anilkumar, 1996) and *Grapsus adscensionis* (Osbeck,

1765) (see Hartnoll, 2009). In contrast, in the closely related gecarcinid *Gecarcinus ruricola* ovarian maturation takes about four months (Hartnoll et al., 2007), and *J. lagostoma* is presumably similar. Specimens of *J. lagostoma* with fully ripe eggs show no signs of ovarian re-ripening. Hence it is unlikely that individual females could lay more than once in a breeding season.

The sequence of reproductive events can now be evaluated. Before the start of the breeding season all mature females are present in the resident zone around Green Mountain. A sample examined in the third week of March comprised 19 with ripe ovaries, and 7 with either unripe or spent ovaries. However, the breeding season had then started, and these 7 females could have already migrated to the shore, and returned to the resident area after spawning: alternatively they were not breeding that year. A sample would need to be examined earlier in the year to determine whether all mature size females ripen ovaries and breed every year. All of the females with ripe ovaries had swollen spermathecae and had previously mated, so they would not necessarily have to mate again before laying. A very few females were found with eggs in the residential areas, only 0.4% of the total. This indicates that there is only limited opportunity for mating in these areas, unless a proportion of females decalcify and mate, and then quickly leave the area before laying. If there is indeed so little potential for mating, why do so many males remain in the residential area? The few females laying in the NASA Road area do so some 2 km or more from the shore: however, the average migration speed of $\sim 450 \text{ m day}^{-1}$ allows ample time to reach the shore within the incubation period of >14 days.

The 'transit camps' along the NE Bay Road, where the migrating population was sampled, are about midway between the residential areas on the north side of Green Mountain and the breeding areas at NE Bay: about 2 km from each. There are presumably further transit camp areas in less accessible spots along the migration route. Along NEBR the sexes were equally represented, but the recapture figures (11 males but only 1 female) suggest that males spend longer in that area, averaging >16 days. There are obviously mating opportunities in this zone, since 12% of females there were ovigerous, about half with early eggs, indicating recent receptivity. However, a proportion of females had late stage eggs: these had either laid during an earlier phase of their migration, or had remained at NEBR after laying (though recapture data suggests that this is not so). On dissection about half the females had ripe ovaries, and were yet to lay; the other half had spent ovaries, and were on their return migration from the shore.

At the shore in NE Bay about 80% of the crabs were female, and of these 40% were ovigerous. The ovigerous females had 87% late eggs, so either they had laid before reaching the shore, or the females with early stage eggs tended to remain hidden, as is the case in other gecarcinids, e.g., *E. notatus* (see Liu and Jeng, 2005), *Gecarcinus lateralis* (see Bliss et al., 1978), *Gecarcinus ruricola* (see Hartnoll et al., 2007), and *Gecarcoidea natalis* (see Hicks, 1985). Certainly, a proportion of females lay only after reaching the shore: about a third of those dissected still had

ripe ovaries, and others were shown to lay at the shore by mark/recapture data. Also both courtship and mating were observed at the shore (Hartnoll et al., 2006). So for those males which migrate as far as the shore there are opportunities for mating: on average they spent at least 24 days there. At the shore 696 live crabs were sampled, and 180 dead crabs were found at the top of the sandy beach: the composition of the two samples was generally similar. The dead crabs perhaps died at the end of migration, because they could not find refuges amongst the rocks. Alternatively they strayed away from the rocks by night and failed to return by dawn: the high proportion of ovigerous females suggests the latter. The black sand on NE Bay beach, the result of it being at the end of the major Island watershed, will tend to increase heat stress. The figures should not be taken to indicate that nearly a quarter of migrating crabs die at the shore: whilst the total of dead crabs is a fairly realistic seasonal total, the number of live crabs is a 'snapshot' view and a gross underestimate of the total throughput. Nevertheless, it does confirm the greater mortality imposed upon females by the requirement to migrate to the sea.

In terms of the overall pattern of gecarcinid breeding migrations, *J. lagostoma* has a median position, rather similar to *Gecarcinus ruricola* (see Hartnoll et al., 2007). The opposing ends of the spectrum are presented by *Discoplax longipes* (A. Milne-Edwards, 1867) and *Gecarcoidea natalis*. In the cavernicolous *Discoplax longipes* eggs are laid and incubated in the caves where the adults live, and the females with ripe eggs migrate directly to the sea, and no males migrate (Ng and Guinot, 2001). This contrasts with *Gecarcoidea natalis*, where males and females migrate to the sea in similar numbers, and only after both indulge in 'dipping' in the sea, does courtship and mating occur (Hicks, 1985). In *J. lagostoma* some mating and laying occurs at all phases of the migration, and males migrate towards the sea in decreasing proportion with distance. The statement by Fimpel (1975) that only females of *J. lagostoma* migrate to the shore may perhaps apply to the Trindade population, but is clearly not true for Ascension.

The pattern of migration of the males is presumably determined by the opportunities for mating provided by the receptivity of females (due to opercular decalcification) at different stages of their migration. Hence the rationale of the presence of males at the transit camps and on the shore is evident from the discussion above, but the large residual male population in the resident areas during the breeding season seems counter-productive. It may be that the mating opportunities in areas such as the NASA Road are greater than our surveys suggest, but it is not evident why. Another feature to consider is the size structure of the migrating males. Intuitively the larger males might be expected to preferentially migrate, but in fact the migrating and breeding males are both, on average, smaller than those remaining in the residential areas. The same was observed in *Gecarcinus ruricola* (see Hartnoll et al., 2007). The explanation offered then was that larger males are competitively superior, and dominate the earlier mating opportunities during migration: smaller males must migrate further to improve their chances. The same reasoning could apply to *J. lagostoma*.

Reproductive Investment and Fecundity

The sample size is small for this type of study, and as is usual the variability of fecundity (and of RI%) is high, so results must be interpreted with caution. The lack of relationship between fecundity and egg stage suggests that egg loss during incubation is not great: there are no data on incubatory egg loss in other gecarcinids. The range of CW was small, and given the above variability, this will explain the failure to find a significant regression of log fecundity on log CW. A significant regression with a slope of ~ 3.0 is usual, as for example in *Gecarcinus ruricola* (Hartnoll et al., 2007).

The mean fecundity was 71,800 eggs at 94 mm CW. In *G. ruricola*, by contrast, a crab of that size would have a calculated fecundity of 199,000 eggs (Hartnoll et al., 2007). This disparity is predominantly accounted for by the larger egg size in *J. lagostoma*, with a DW of 6.0×10^{-5} g egg⁻¹, compared to 3.5×10^{-5} g egg⁻¹ for *G. ruricola* (Hartnoll et al., 2007). The egg number for *J. lagostoma* is near the middle of the range of 12,000 to $> 600,000$ recorded for other gecarcinids (see details in Hartnoll et al., 2007). Despite the smaller egg number, the greater egg size results in a DW RI% value of 5.4%, very similar to the 5.0% of *G. ruricola* (see Hartnoll et al., 2007), the only other determination for a gecarcinid. It is also similar to the 5.5% found for the supratidal rock crab *Grapsus adscensionis* (see Hartnoll, 2009). These values are low in comparison to the mean value of 10% determined for 20 marine species by Hines (1982). The possible reasons for low values of RI in land crabs (if confirmed by further studies) include the difficulty of accumulating resources for ovarian maturation on a low-energy and low-nitrogen diet of predominantly plant material (see discussion and references in Nordhaus et al., 2006). Additionally, the size of the egg mass is constrained by provision of an adequate oxygen supply to the developing embryos in its interior. In marine crabs oxygen levels can fall within the egg mass, and the females show behaviour to detect and remedy the problem (see discussion and references in Baeza and Fernandez, 2002). No comparable studies have been made on terrestrial crabs, which cannot access free water during incubation. For them the problems of oxygenation could limit viable egg mass size.

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