

*JOHNGARTHIA LAGOSTOMA* (H. MILNE EDWARDS, 1837) ON  
ASCENSION ISLAND: A VERY ISOLATED LAND CRAB POPULATION

BY

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ABSTRACT

A study was made of the land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837) on Ascension Island in the central South Atlantic: aspects of its distribution, population structure, and reproduction are described. On Ascension it is normally limited to altitudes >200 m, the only parts of the island with substantial vegetation. The population comprised predominantly pale colour morphs, and few immature specimens were sampled. The significance of both factors is examined. The breeding migration to the shore was observed. Migrations occurred in February to April, varied in intensity between years, and were dominated by females. Migrants had to cross the bare arid lowlands, resulting in mortality. There are no recent records of the return of the juvenile crabs after the planktonic larval phase.

RÉSUMÉ

Une étude a été menée chez le crabe terrestre *Johngarthia lagostoma* (H. Milne Edwards, 1837) sur l'île d'Ascension, dans l'Atlantique sud central : les aspects de sa répartition, la structure de sa population et sa reproduction ont été décrites. Sur l'île de l'Ascension, sa présence est limitée normalement aux altitudes >200 m, les seules parties de l'île avec une végétation substantielle. La population comprend des formes de couleur pâle et quelques spécimens immatures ont été échantillonnés. La signification de ces deux facteurs a été examinée. La migration de reproduction vers la mer a été observée. Les migrations ont lieu de février à avril, varient en intensité suivant les années, et sont dominées par les femelles. Les migrateurs ont à traverser les parties basses, dénudées et arides, qui sont cause de mortalité. Il n'y a pas de données récentes sur le retour des crabes juvéniles après la phase larvaire planctonique.

INTRODUCTION

Ascension Island is small, remote, and located in the middle of the South Atlantic Ocean. It has an area of 97 km<sup>2</sup>, is some 1500 km from the Liberian coast

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in West Africa, and over 2000 km from the coast of Brazil. It is of relatively recent (~1 million years) volcanic origin, effectively lacks running or standing water, and the lower areas are largely barren. Yet it supports a substantial population of the land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837) in what would appear a most inhospitable environment. The population of this crab on Ascension Island has not been previously studied in any detail (see Manning & Chace, 1990, and Ashmole & Ashmole, 2000, for notes on the minimal information available), other than for a study of its susceptibility for the poison used to eradicate feral cats (Pain et al., 2000). There are some studies of the species on the Brazilian islands. Fimpel (1975) carried out a study on Trinidad Island (not to be confused with Trinidad, West Indies, see below). The study focussed upon respiratory adaptations of the species. Texeira (1996) made a general study on the Atol das Rocas. The present paper presents the results of an investigation on Ascension of its distribution, population structure, and reproduction. The format of the paper is to combine methods, results, and discussion under each heading.

#### TAXONOMY AND GEOGRAPHICAL DISTRIBUTION

The nomenclature of the species has undergone various changes. It was initially known as *Gecarcinus lagostoma* H. Milne Edwards, 1837. *Gecarcinus* was a genus with species occurring on both coasts of the American mainland, as well as on a variety of Atlantic and West American Islands. Türkay (1970) divided the genus into two subgenera, *Gecarcinus* and *Johngarthia*. *G. lagostoma* was included in the latter, together with the Pacific species *G. planatus* Stimpson, 1860 and *G. malpilensis* Faxon, 1893. All three species are mainly restricted to small oceanic islands. Türkay (1973) subsequently separated *G. lagostoma* and *G. weileri* (Sendler, 1912), in the central and west Atlantic, and east Atlantic, respectively, making four species in the subgenus. Finally Türkay (1987) elevated *Johngarthia* to generic status, giving the species its current name of *Johngarthia lagostoma* (H. Milne Edwards, 1837). Nevertheless, it has still generally been referred to as *Gecarcinus lagostoma*, as in the review of Ascension Island biology by Ashmole & Ashmole (2000), and the abovementioned study by Pain et al. (2000). However, Ng & Guinot (2001), in their comprehensive listing of all gecarcinid species, confirm the generic status of *Johngarthia*. This would seem the route to follow.

There have also been changes in its reported geographical distribution, in part due to some imprecise or erroneous earlier locations, and also in response to the narrowing of the bounds of the species. Thus the type locality of *G. lagostoma* was given by H. Milne Edwards (1837) as "Australasie", which must be considered an

error. The true type locality is in doubt, though Manning & Chace (1990) present a fairly convincing case for Ascension Island. In her major review, Rathbun (1918) provides the following distribution. "Range.- Trinidad, West Indies; Fernando de Noronha, Brazil. Also recorded from Australasia; Mauritius; Madagascar; South and West Africa, including Ascension Island, South Trinidad island, South Atlantic Ocean, and from Bermuda with doubt." There is a footnote, referring to Calman (1909), stating that there is no trustworthy evidence for occurrence outside the Atlantic area. The 'Trinidad, West Indies' specimen was correctly identified, but was only mailed from that location, its collection site being unknown (see Manning & Chace, 1990). 'South Trinidad' Island presumably refers to Trindade, Brazil. Chace & Hobbs (1969) list the distribution as "Trinidad, Ilha Fernando de Noronha, Ascension I., Cameroon, and islands in the Gulf of Guinea". Trinidad is either a misprint for Trindade, or a repetition of Rathbun's observation (a mistake repeated by Hartnoll, 1988), and at that time *J. weileri* had not been separated, hence the African locations. They correctly omit the non-Atlantic records, which do not appear in subsequent publications. Türkay (1970) lists the distribution as Trinidad to North Brazil, and West Africa. His distribution map (Verbreitungskarte 1) indicates occurrences at Trinidad (West Indies), Fernando de Noronha, and the South American mainland from Georgetown to Natal. Subsequently Türkay (1973) revised the distribution as "Trindade, Fernando da Nohora (= Fernando de Noronha), Ascension." The first two are islands off Brazil, to which must be added Atol das Rocas, near to Fernando de Noronha (Coelho, 1965). The African locations Türkay (1973) attributed to *J. weileri*, and the locations on mainland Brazil and Trinidad West Indies he considered erroneous, a result of ambiguous references in the earlier literature (M. Türkay, 1973, pers. comm.). So the definitive distribution of *J. lagostoma* is currently regarded as the three islands off Brazil (Trindade, Fernando de Noronha, Atol das Rocas), and Ascension Island (for example, see Manning & Chace, 1990; Ashmole & Ashmole, 2000). These locations are shown in fig. 1, together with those for *J. weileri*: the latter are relevant to the discussion.

#### DISTRIBUTION ON ASCENSION ISLAND

This section covers the pattern of distribution outside the breeding season. In the breeding season there are migrations to other areas along the shore, as discussed below.

The basic requirements for land crabs include substrate into which they can burrow, moisture, and vegetation (which provides both shade and food). On Ascension Island these occur together mainly only in the higher areas, centred

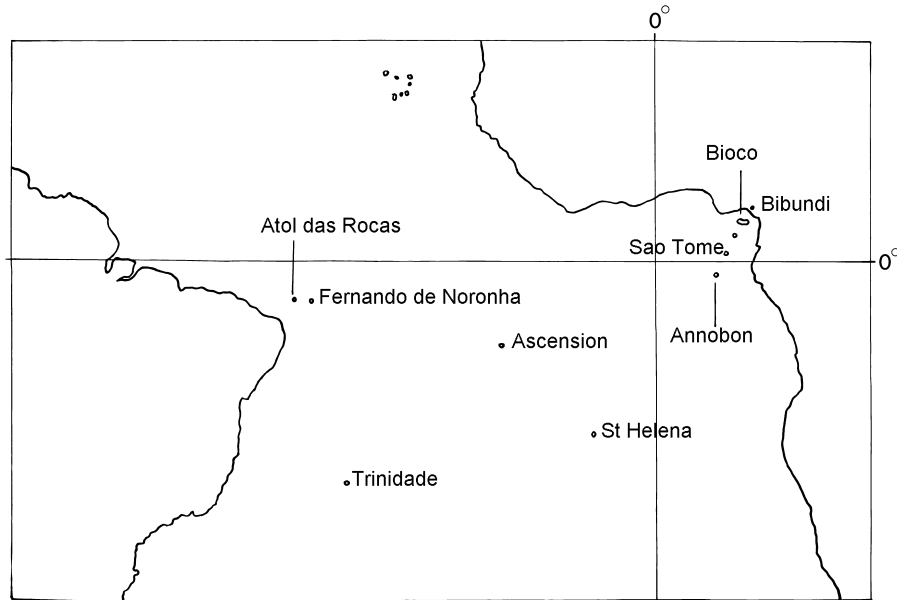


Fig. 1. Map to show the geographical distribution of *John garthia lagostoma* (H. Milne Edwards, 1837): Ascension, Atol das Rocas, Fernando de Noronha, and Trinidad. Also of *J. weileri* (Sendler, 1912): Annobon, Sao Tome, Bioco (= Fernando Poo), and Bibundi.

around Green Mountain in the SE sector of the island (fig. 2). This is due to a combination of greater rainfall, and older volcanic origin, which have allowed the development of substantial vegetation. Much of the rest of the island consists of very arid and barren terrain, some of relatively recent volcanic origin. See Ashmole & Ashmole (2000, Chapter 10) for an outline of the geological history, and detailed references thereto. Anecdotal reports from various sources indicated that the main distribution was above 200 m, and this was confirmed by observations in April 2005 (see fig. 2). The records were obtained by observing live crabs, noting roadkills and crabs dead from other causes, and obtaining first hand reports from reliable observers. All of the areas above 400 m can be regarded as crab habitat, and most of those above 200 m. The crabs were mainly active by night, so records are concentrated along the access roads. They were, however, also active by day after rain, which generated some off road observations. There are also some records from lower altitudes where conditions are suitable. Thus they are recorded from gardens in Georgetown (elevation <30 m) where the ground is regularly watered, and vegetation is maintained. They are also recorded from the Wideawake Fairs area when the sooty terns are breeding (elevation ~50 m), the eggs and chicks providing an abundant source of food. Land crabs have been suggested as a major factor limiting the breeding of open- or burrow-nesting petrels (Olsen, 1981): they

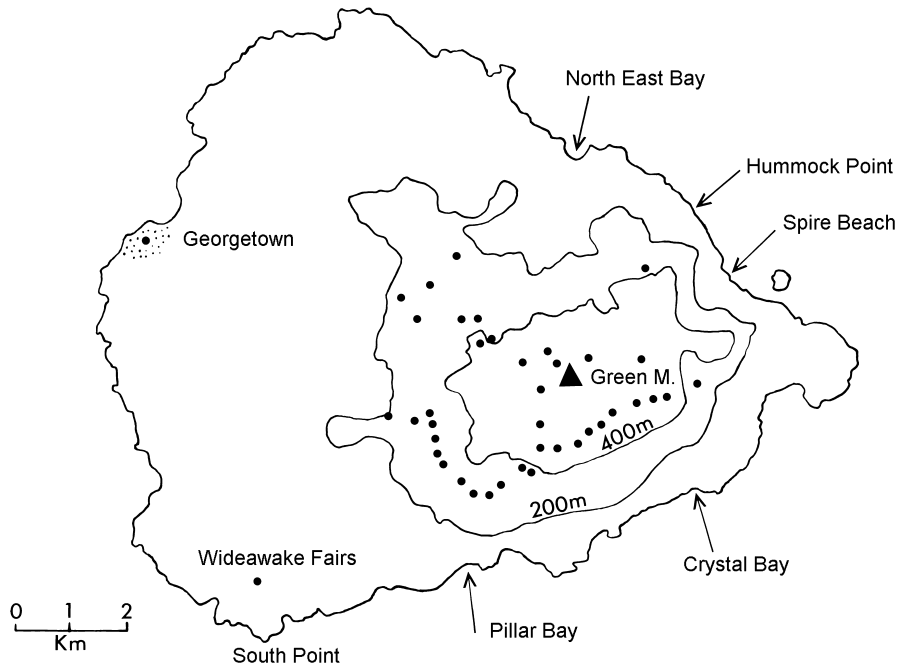


Fig. 2. Map of Ascension Island, to show areas of >200 m and >400 m altitude. The solid circles indicate non-breeding locations of *Johngarthia lagostoma* (H. Milne Edwards, 1837) confirmed in April/May 2005. The arrows indicate known sites of breeding activity at the shore.

are certainly limited on Ascension, though feral cats (recently eradicated, we hope) may have presented a greater problem.

#### POPULATION STRUCTURE AND SIZE AT MATURITY

The majority of specimens encountered were examined for colour (see below), sex, size (maximum carapace width in mm), and in the case of females for the presence of eggs. A number of specimens were numbered with felt pen, so that they could be subsequently recognized. For some analyses samples were separated into 'resident' populations, recorded on the higher grounds, and 'breeding' populations, recorded close to the shore.

There is a striking variation in colour (fig. 3). The majority of specimens are a bright yellow/orange in colour, with no dark coloration, and white areas on the ventral side of the chelar carpus and distal merus, and near the articulations of the walking legs. Other specimens are dark purple, but with white areas in the same positions as above. There are also a few intermediates, which are predominantly yellow/orange, but have large purple patches on the carapace. The coloration is not



sex specific: specimens of all colour morphs are found in both sexes. The following is a breakdown of a small sample of adult crabs.

	Purple	Intermediate	Yellow
Male	9	2	30
Female	10	2	59

This is adequate to show the predominance of the yellow/orange morphs, and the relative scarcity of the intermediates. However, a larger sample is needed to clarify whether there is any difference in colour distribution between the sexes. Manning & Chace (1990) stated “all of the smaller specimens . . . are red, and most of the larger specimens are yellow.” Ashmole & Ashmole (2000) state “Two colour phases are present: smaller individuals are normally red or purple . . . the largest individuals are normally yellow or orange”. The latter point is clearly not so — some of our largest specimens were purple. The colour of small specimens needs to be confirmed, as does whether any colour change occurs during growth: one small specimen we examined (45 mm CW) was indeed purple, but more records are needed, and of smaller size classes. One can only speculate on the biological basis of the colour variation. The yellow/orange morphs are strikingly more visible, both by day, and by artificial light at night (though this is hardly relevant in evolutionary terms). Since the crabs are largely nocturnal, colour would not seem a very important variable. However, they are at times active by day, particularly during the breeding season, when they can be exposed to heat and desiccation in the barren lowlands. Predation is probably not very important for adult crabs, but heat stress is, and many were found dead near the shore (see below). It has been shown for the tropical littorinid snail, *Littoraria pallescens* (Philippi, 1846) that light colour can reduce heat stress (Cook & Freeman, 1986), and that in the fiddler crab, *Uca pugilator* (Bosc, 1801-02) pale specimens heat up more slowly (Wilkins & Fingerman, 1965). This benefit may be a factor in the maintenance of the yellow morph in *Johngarthia lagostoma*.

On the Atol das Rocas there is a very different distribution of colours (Teixeira, 1996). In a sample of 1550 crabs, 56% were purple, and 44% yellow or orange. The two islands in the atoll are both small, and the crabs do not need to undertake long exposed migrations, perhaps reducing any physiological advantage of pale coloration. In the West Indies the similar sized *Gecarcinus ruricola*

Fig. 3. *Johngarthia lagostoma* (H. Milne Edwards, 1837). A, the two main colour morphs, males in dorsal view; purple morph on left, yellow/orange morph on right; B, yellow-orange male and purple female in the ‘guarding’ position.



(Linnaeus, 1758), which seldom needs to leave the shelter of its forest environment that extends close to the sea, has only a very few pale morphs (RGH, unpubl.).

Population structure was also examined in terms of sex ratio, and size frequency distribution. Separate analyses were carried out for the 'resident' population on the higher ground, and for the 'breeding' population near to the shoreline. The sex ratio distribution was as follows:

	Male	Female
Resident	73	61
Breeding	20	98

In the resident population there was a small surplus of males. However, in the breeding population females far outnumbered males. The ratio in the resident population could have been biased because it was determined in the breeding season, when a greater proportion of females had migrated towards the shore.

The size frequency distribution is shown in table I. There are several interesting features. One is the dearth of small specimens — few crabs of <70 mm CW were

TABLE I

*Johngarthia lagostoma* (H. Milne Edwards). Carapace width frequency distribution of specimens collected on Ascension Island in April/May 2005. 'Resident' specimens were collected from 200 m or higher. 'Breeding' specimens were collected from the shore. Also for specimens from Atol das Rocas (from Teixeira, 1996)

Carapace width (mm)	Resident		Breeding			Atol das Rocas	
	Male	Female	Male	Female (all)	Female (ovig.)	Male	Female
10-19	1						
20-29						6	
30-39	1					11	1
40-49	1					27	4
50-59						113	23
60-69		1		2	2	338	63
70-79	3	4		12	4	123	280
80-89	8	18	2	34	16	157	234
90-99	30	35	9	39	12	146	40
100-109	29	3	9	11	5	26	
110-119	2						
Total	73	61	20	98	39	947	645
Mean (mm)	97.6	90.7	98.5	89.6	88.6	84.3	78.4



collected. This may be because they are genuinely scarce, or possibly because they are more cryptic in habit. Land crabs are notoriously cannibalistic, and when adults are abundant, juveniles tend to be marginalized to peripheral habitats (Hartnoll et al., in press). In each sample the distributions are unimodal, with no evidence of year classes or cohorts. This is to be expected in a species which is slow growing and long lived (see Hartnoll et al., in press, for a discussion of age and growth in land crabs). Males reach a larger size than females, exceeding them by about 8 mm in mean carapace width. For both sexes the size distributions and mean sizes are very similar between resident and breeding populations. This suggests that only the sexually mature specimens were being sampled: for females this is supported by the size distribution of ovigerous females being similar to that of the overall female sample. The abundance and distribution of juveniles needs to be clarified, as it has major implications for population maintenance and conservation.

The only other data on size distribution on Ascension Island are in Manning & Chace (1990), based on relatively small samples of 19 males and 14 females (their measurements of carapace length have been converted to carapace width). Males had a size range of 29-106 mm CW, with one specimen below 50 mm, and a further 5 below 70 mm CW. Females also had a size range of 29-106 mm CW, with two specimens below 50 mm, and a further 6 below 70 mm CW. There was one ovigerous female of 58 mm CW. Despite the small sample sizes, and the diversity of collectors, locations, and dates, the size distributions in both sexes were generally smaller than in the current study (see table I), where few specimens were <70 mm CW. This could suggest that the current population is aging, and that recruitment has been limited in recent years.

The only other study of the size of *J. lagostoma* was on Atol das Rocas, where Teixeira (1996) measured large samples. The maximum size was similar, but the size distribution included many more smaller crabs than on Ascension for both sexes (table I). The greater numbers in the smaller size classes are striking, but it is not known whether these reflect a real population difference, or are artefacts of variation in environment or collecting protocols affecting the catchability of different size classes. Taken at face value they reinforce the idea that the current Ascension Island population is aging. The smallest female seen mating was 80 mm CW, and the smallest ovigerous female 75 mm CW. This suggests that the size at maturity is similar to that on Ascension Island.

Land crabs in the family Gecarcinidae are generally large species (other than *Epigrapsus*, at <40 mm CW, see Liu & Jeng, 2005). Species of *Cardisoma* are the largest, the Caribbean *C. guanhumi* Latreille, 1828 reaching 130 mm CW (Türkay, 1970). *Gecarcoidea natalis* (Pocock, 1888) exceeds 120 mm CW (Green, 1997), and *Gecarcinus ruricola* can reach 123 mm CW (Hoeven & Walters, 1998). So

with a recorded CW of 110 mm *Johngarthia lagostoma* is close to this upper size range. There is limited information on the size of other *Johngarthia* spp. Ehrhardt & Niaussat (1970) measured a sample of 200 *J. planatus* (Stimpson, 1860) from Clipperton Island, with a maximum 65 mm CW, though from a smaller sample Garth (1965) listed a maximum of 78 mm CW. On Socorro Island, in a sample of 269 crabs, the maximum was 88 mm CW (Alicia Perez, pers. comm.). However, Türkay (1970) lists a CW of 93 mm for this species, location unspecified, and Rathbun (1918) a CW of 104 mm for the Tres Marias Islands — the variation is considerable. Türkay (1970) lists a CW of 76 mm for *J. malpilensis* (Faxon, 1893) (presumably the same specimen listed as *G. planatus* by Garth, 1948), and of 43 mm for *J. weileri* (see Türkay, 1973): there seem to be no other data for these species. On current evidence, *J. lagostoma* would seem to be the largest of the genus.

#### BREEDING BEHAVIOUR

Land crabs of the family Gecarcinidae may spend virtually all their adult life on land, but the females must visit the sea for the eggs to hatch, and the larvae to be released. The larvae then undergo a planktotrophic pelagic development, lasting about 20 days, before the megalopa returns to the coast and the juvenile crabs recolonize the land. The migration of adult females to the sea is normally a major annual event, in many cases being the most spectacular aspect of the life cycle (e.g., Hicks, 1985, for *Gecarcoidea natalis*). The return of the juveniles to the land is less predictable, and in most years may not occur in any numbers (Hartnoll & Clark, in press).

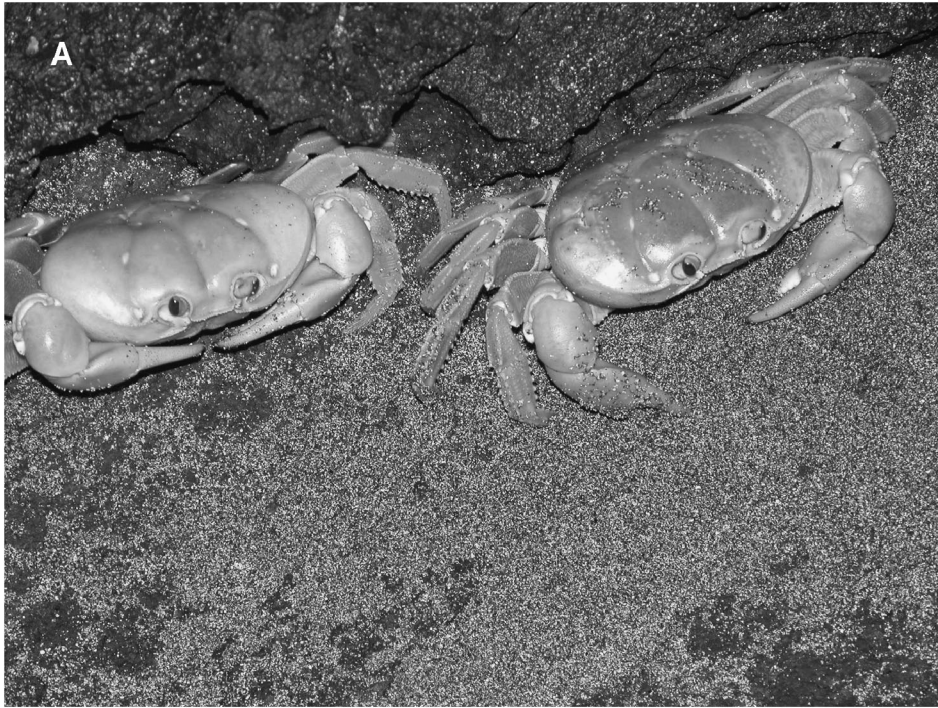
For most land crab species the migration to the sea involves a measure of risk and stress, since the crabs must leave their refuges and travel considerable distances, involving exposure to predators (including man), environmental stress, and in modern times traffic. This migration can normally occur in the shelter of vegetation, which extends close to the sea. On Ascension Island this is not so, however, and the crabs must cross several kilometres of bare dry volcanic rock in order to reach the sea, greatly increasing the risks. There are indications that substantial breeding migrations do not occur every year on Ascension, perhaps being limited by the incidence of rainfall (Ashmole & Ashmole, 2000), but no long term systematic records have been kept. The scattered data note breeding migrations from late January to March.

In recent years there were records of very extensive migrations in 2003: “Thousands on the beach at North East Bay in Feb-March time” (Graeme Hays, pers. comm.). In contrast, in 2004 there were no extensive migrations (TJP, unpubl.

obs.). The rainfall in the January to March period totalled 98 mm in 2003, but only 24 mm in 2004, suggesting a correlation. In 2005 regular observations were made at North East Bay. Crabs were observed in large numbers in early March: ~150 on 1 March, and “too many to count” on 3 March, with ovigerous females predominating. They were fewer on 10 March, when a sample comprised 3 males, 9 non-ovigerous females, and 56 ovigerous females. Breeding activity continued, with smaller numbers, through March and April, the last being seen in the first week of May. Rainfall records were again examined, to see if they could explain the large migration in the first week of March 2005, but there was no substantial rainfall at that time, nor in the preceding fortnight. The rainfall in January to March 2005 totalled only 6.1 mm (amongst the smallest totals for that period): thus the level of activity observed in March 2005 was surprising, and factors controlling the breeding migration require further examination. The activity on the 1-3 March was just before the last quarter of the moon, but more data are needed to examine any lunar rhythm. There are clearly major variations in breeding migrations between years, both in abundance and timing, and the season can be quite extensive.

The above records relate to North East Bay beach, but ‘beach’ is somewhat misleading. The crabs were normally concentrated on the rocky areas at each end of the beach. By day some crabs were seen in crevices in the rocks, or under rocks on the damp sand where they met the beach (fig. 4A). At night they were crawling over the rocks, down to the splash zone where they were wetted by the waves (including males, and females with and without eggs), and where ovigerous females were releasing their larvae. Few crabs were seen on the sand — a dangerous area for them given the persistent strong surf. The following points emerged from the observations of breeding activity in April 2005.

1. The ‘breeding’ population was dominated by females, but some males were present, and mating was observed on the shore. Crabs were observed in the ‘guarding’ position (male standing over and holding female) (fig. 3B), and also mating sternum to sternum (fig. 4B). Mating was seen between purple and yellow morphs.
2. Activity on the shore was mainly nocturnal, and occurred on rock rather than sand. Sometimes by day very few crabs were seen, but they were quite abundant the following night. There were presumably refuges in the supratidal rock, and those visible by day were only an outlier of the population.
3. No ovigerous females were observed away from the shore. At the shore, of those eggs that were staged, there were only 2 females with early eggs, but 24 with late stage eggs (in most cases very close to hatching). It would seem



that the females laid eggs only when close to the shore. They then sheltered during incubation, and emerged only when near to hatching.

4. Numbers of moribund and dead crabs were found on the sand above high water mark on North East Bay: males, and females with and without eggs. These may have been specimens migrating to the shore by night, but which failed to reach the shelter of the rocks before being caught in the sun. Alternatively, and more probably, they were specimens that entered the sea at night to re-hydrate, but which subsequently strayed onto the sand, rather than back to refuges in the rocks. Crabs were observed wandering over the sand by night.
5. In April 2005 the ovary condition was examined in small samples (at this stage the programme was designed to be basically non-sacrificial). All females examined in the 'resident' sites had small ovaries (these were females of 'mature' size). This was quite late in the breeding season, and they were either spent females that had returned from the shore, or females not breeding that season. At the shore a few females were found with maturing ovaries early in April: these were presumably about to lay. All ovigerous females with ripe eggs had small ovaries: there was no evidence of re-maturation, suggesting the production of only one batch per season. Later in April all the non-ovigerous females had small ovaries. They had presumably already hatched their eggs (in some cases this was confirmed from marked specimens), but had not immediately migrated back to higher ground.
6. A more comprehensive analysis of the reproductive cycle will require an intensive marking and recording exercise, starting before the breeding season. If acceptable, regular sacrificial samples will need to be examined for ovary and spermathecal condition.

All of the above details relate to observations at North East Bay, implying that this is the only important breeding site. This is very unlikely, but it is the only easily accessible breeding site, and it has been regularly visited at night by personnel studying the green turtle who have reported crab activity. An examination of fig. 2 indicates that many of the resident sites, along the southern and eastern sides of Green Mountain, are distant from North East Bay, but closer to the rocky shores in the sector from Spire Beach clockwise round to South Point. We have seen above that hatching and larval release occur from rocks, rather than sand, and at night, rather than by day. There are occasional records of mating crabs west of

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Fig. 4. *Johngarthia lagostoma* (H. Milne Edwards, 1837). A, crabs at NE Bay sheltering on damp sand at top of shore; B, crabs mating at NE Bay, female on top.

Pillar Bay, ovigerous females at Crystal Bay, crabs on the shore at Spire Beach, and crabs near Hummock Point (Conservation Centre staff). However, these areas are all difficult of access from both land and sea, and are not normally visited at night when breeding activity predominates. No breeding activity has been recorded in the sector from North East Bay anti-clockwise to South Point, many parts of which are easily accessible. The extent of the breeding area needs to be clarified: the activity observed at North East Bay may not be typical of the population as a whole.

The breeding pattern described above conforms in outline to those described for other land crabs: *Gecarcoidea natalis* (cf. Hicks, 1985), *Gecarcinus ruricola* (cf. RGH, unpubl.), *Gecarcinus lateralis* (De Fréminville, 1835) (see Klaassen, 1975; Bliss et al., 1978; Wolcott & Wolcott, 1982), *Epigrapsus notatus* (Heller, 1865) (see Liu & Jeng, 2005), *Cardisoma guanhumi* (see Gifford, 1962; Henning, 1975) and *Discoplax longipes* A. Milne-Edwards, 1867 (see Ng & Guinot, 2001). Migration is linked to the rainy season, but is highly variable between years. The statement in Liu & Jeng (2005) that in land crabs “The breeding season is . . . easily predictable” does not apply generally. The shoreward migration is not predictable. The larval release, subsequent to the shoreward migration, may be more predictable on a lunar basis. Activity is mainly nocturnal, except for the diurnally active *G. natalis*. Both sexes migrate towards the shore, though there are variable accounts as to the extent to which males participate, and how close to the sea mating occurs. There is general agreement that females predominate close to the shore (either because fewer males migrate, or females spend longer at the shore, or a combination of both). In all cases incubating females hide in burrows or other refuges, presumably to protect the developing eggs from desiccation (see Bliss et al., 1978), emerging only when the eggs are near to hatching. There are reports of lunar rhythms of hatching (as distinct from migration) for most species (the necessary detailed studies have not been made for *Johngarthia lagostoma*). There is uncertainty as to whether a female produces more than one batch of eggs within a breeding season, but this seems unlikely for *J. lagostoma*. There may be several successive breeding migrations during a year in most species (e.g., Hicks, 1985), but there is no firm evidence that individual females participate more than once. On the basis of ovary condition Gifford (1962) suggested that *Cardisoma guanhumi* females may spawn more than once per season. In captivity females of *Gecarcinus lateralis* produced up to three batches of eggs over the duration of the breeding season (Klaassen, 1975), but it is not certain that this occurs in the wild. Marking experiments suggest that *Epigrapsus notatus* breeds only once per season (Liu & Jeng, 2005). This point needs further study.

## RECRUITMENT

For populations on small oceanic islands the successful return of the postlarval crabs, which have spent some 3 weeks drifting in the plankton, is always going to be problematic. It will depend upon a fortuitous combination of winds and currents. For *Johngarthia lagostoma* on Ascension, there is only one record of returning juveniles, in March 1963! This is reported by Packer (1968), "In March, 1963, Georgetown was over-run with thousands of the minute young crabs going inland from the beaches, but residents of 12 years or more whom I questioned at the time could not remember seeing the phenomenon before, and I have heard of no subsequent observations." Regarding this event, Ashmole & Ashmole (2000) state that "Young crabs were still present near the settlement in May 1963, when Arthur Loveridge collected juveniles with carapace length 3.5 mm" (= 4.7 mm CW). It is not feasible that there has been no recruitment since 1963: even for land crabs, 40 years must be regarded as an improbable life span. The few small specimens in table I are evidence of more recent recruitment. The smallest specimen, 13 mm CW, was collected in May 2005: this was probably a recruit from settlement in 2004. Two points can be made. Firstly Georgetown is a most unsuitable location for juvenile recruitment — it is some 5 km from any regular source of food and shelter (see fig. 2), making survival of the small recruits doubtful. Hence the 1963 event must be considered anomalous. The more likely recruitment locations along the south and east coasts are rarely visited, and recruitment events could be easily missed. There may be regular trickle recruitment, with the occasional mass recruitment being an exceptional event. On Old Providence in the western Caribbean mass recruitment of *Gecarcinus ruricola* was observed only every six years or so, despite there being a continuous coast road to facilitate comprehensive observation (Hartnoll & Clark, in press).

## THE ORIGIN OF ASCENSION ISLAND LAND CRABS

The presence of land crabs on this oceanic island requires some explanation. Although they have a pelagic larval phase, the distances from the nearest recruitment reservoirs are very large. One possibility can be discounted—that they arrived on Ascension at a time when the Atlantic was much narrower. Such an explanation has been given for the occurrence of the freshwater crab, *Seychellum alluaudi* (A. Milne-Edwards & Bouvier, 1893) on the Seychelles: that it is a relict of the time when the Seychelles were joined to the African/Asian land mass some 35 mya (Ng et al., 1995). Since Ascension Island arose only 1-1.5 mya (Atkins et al., 1964), when the Atlantic Ocean was at roughly its current width, such an argument is untenable.



So there are three possibilities. Colonization from West Africa, colonization from the East American region, or colonization from some now disappeared central Atlantic islands. They could have arrived by pelagic larval dispersal, or by rafting. The latter is a feasible proposition for marine crabs, but from what we know of the physiology of land crabs, it would seem an unlikely method. Manning & Chace (1990) discuss the origin of the decapod fauna of Ascension Island in some detail, and make three important points. (1) They outline the complex current patterns, and show how these could facilitate the transport of larvae from either the east or west Atlantic. (2) Transport from either side to Ascension might just be possible within the 20+ days of the larval development of *Johngarthia lagostoma*. (3) Of the 74 decapods on Ascension, 41 occur in the western Atlantic, and 36 in the eastern Atlantic. These points leave the options open. Ashmole & Ashmole (2000) suggest "a possible scenario for the origin of the South Atlantic Island populations (of land crabs) would be colonisation of Ascension from the western coasts of Africa, and of Brazilian islands from Ascension." However, this is based on the assumption of only a prevailing westerly current, which is not the case: also, it does not follow intuitively from the distribution of related species (see below). The concept of a series of now-submerged mid-Atlantic islands was developed by Wilson (1963), and is discussed in Chace & Manning (1972). It would simplify the colonization of Ascension Island, but does not clarify the origin of the land crab stock. Briggs (1974) examined the relationships of the Ascension Island marine fauna, especially the fish. He identified on that basis that the strongest ties were with the west Atlantic. Although Ascension Island is normally considered to lie within the westerly flowing northern limb of the South Atlantic Gyre, he considered that it must intermittently come under the influence of the easterly flowing Equatorial Countercurrent.

The geographical distribution of the related species (*Gecarcinus* spp. and *Johngarthia* spp.) may provide further clues. *Gecarcinus* is restricted to the American Pacific and Atlantic coasts, and to Caribbean Islands and Bermuda (Türkay, 1970). *Johngarthia malpilensis* and *J. planatus* occur on islands off the Pacific coast of central America, *J. lagostoma* is found on the Atlantic islands described above, and *J. weileri* on west African islands in the Gulf of Guinea (Türkay, 1970, 1973). The parsimonious conclusion is that separation of *Gecarcinus* and *Johngarthia* occurred in the central American region. *Johngarthia* subsequently dispersed westward into the Pacific islands, and eastwards across the Atlantic. The concept of a single eastward migration is difficult to sustain: Ascension Island is geologically recent, and its population of *J. lagostoma* is still conspecific with the west Atlantic populations. However, *J. weileri* has diverged further, suggesting an earlier eastward migration, presumably predating the emergence of Ascension Island, but possibly involving mid-Atlantic islands

now lost (Wilson, 1963). It is hoped that planned genetic studies may provide more evidence. Garth (1967) provided a convincing argument for the eastward transport of crab larvae in the Pacific, counter to the obvious current systems: his arguments are equally relevant to the Atlantic.

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