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POPULATION STRUCTURE OF THE LAND CRAB *JOHNGARTHIA LAGOSTOMA* ON ASCENSION ISLAND

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A B S T R A C T

The population structure of the land crab *Johngarthia lagostoma* was studied on Ascension Island from 2005-2007, predominantly during the period of the seaward breeding migrations; approximately 4000 crabs were examined. Sex ratio varied according to location of sampling. Males predominated in permanent residential areas on high ground. Sexes were equal along migration routes to the sea. Females predominated in the breeding sites on the shore. Very few immature crabs (< 60 mm CW) were found. Males had modal and maximum sizes of 100-109 mm and 120 mm CW, females of 90-99 mm and 110 mm, respectively. An aging population is indicated. Crabs < 40 mm CW were all dark coloured, and colour variation into yellow, purple and intermediate morphs developed between 40-50 mm CW. Overall colour distribution of the population was 85% yellow, 5% intermediate, and 10% purple. Yellow morphs were more abundant in females (89%) than males (81%). The predominance of yellow morphs may be an adaptation to reduce heat stress.

KEY WORDS: heat stress, *Johngarthia lagostoma*, land crabs, population structure

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INTRODUCTION

The land crab *Johngarthia lagostoma* (H. Milne Edwards, 1837) is found only on Ascension Island in the central South Atlantic and on three small Brazilian islands: Trindade, Fernando de Noronha, and Atol das Rocas. Ascension, at 97 km^2, is the largest of these islands but also the most remote. It is 1500 km from the West African coast, and over 2000 km from Brazil. Prior to its discovery (sixteenth century) and colonisation (early nineteenth century), *J. lagostoma* was the only large land animal, and it dominated the ecosystem. However, it now competes with introduced species, especially mice, rats, and rabbits (and formerly, goats). In addition, the indigenous vegetation has been largely supplanted by introduced species (see Ashmole and Ashmole, 2000 for details), a marked environmental change that is still ongoing. There are reasons for concern regarding the current status of the species on Ascension. Firstly, there is evidence of a decline in numbers over the years. In the late ninteenth century there was a bounty on the crabs because of their depredations on the farmed crops; as a result over 80,000 crabs were killed in 1879 alone (Ashmole and Ashmole, 2000). This number seems inconceivable at the present density. Secondly, there is a dearth of juveniles in the population, as detailed in this paper. Thirdly, recruitment from the planktonic larval stage has rarely been observed. A study of the population is timely on these grounds.

The taxonomy, geographical distribution, and distribution on Ascension Island of the species are described in Hartnoll et al. (2006a). Amongst other topics, that paper also examined the population structure of the species on Ascension Island, but on the basis of only a relatively small sample ($n = \sim 250$). Subsequently much larger samples have been examined ($n = 4137$), enabling the preliminary conclusions to be re-examined, and additional aspects to be investigated. This paper reports on the analysis of this enlarged sample, and concentrates on sex ratio, size frequency distribution, and colour pattern frequency.

MATERIALS AND METHODS

Data were collected by the authors in April 2005, March-June 2006, and July-August 2007 (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)). Other records were collected by staff and volunteers of the Ascension Island Conservation Office.

Surveys were conducted in many parts of the island, but they focussed on three areas, selected for accessibility by road (a logistic necessity for safe working by night), and concentrations of crabs. These three areas were surveyed on a regular basis, sometimes daily in periods of peak activity. The areas were driven along slowly, or walked over, as appropriate; all crabs encountered were recorded.

1. The NASA Road, 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 all within the area > 200 m where crabs live outside the breeding season, and is termed the 'resident' population. This elevated area has substantial vegetation, which provides both food and shelter for the crabs.
2. The NE Bay Road, from beyond Two Boats Village (200 m) to the track to NE Bay (100 m), approximately 4 km length. This area is barren, and the population here is predominantly in transit to the shore during the breeding season; it is termed the 'migrating' population. Some crabs occupied temporary burrows during migration.
3. The shore at NE Bay, consisting of the sandy beach, and of the rocks at the north and south ends of the beach. This is the only readily accessible

Table 1. *Johngarthia lagostoma*. Sex ratio of samples collected on Ascension Island, March to June 2006. The numbers collected are given, with the percentage of the total in parentheses.

Category	Males	Females	Total
Residential	881 (66%)	458 (34%)	1339
Migrating	339 (48%)	369 (52%)	708
Breeding (live)	190 (22%)	686 (78%)	876
Breeding (dead)	37 (18%)	166 (82%)	203
Total	1551 (47%)	1782 (53%)	3333

breeding site, and crabs occurred here only in the reproductive season; this is the 'breeding' population. Live crabs occurred predominantly among the rocks at each end of the beach; dead crabs were found along the landward margins of the sandy beach.

Specimens were hand collected. Most sampling was conducted by night, when the crabs were most active. Other specimens were collected by day after rain, and on the shore where they congregated during the breeding season (February-May). Particular efforts were made to find small specimens by searching under rocks and logs (known juvenile habitats in other land crab species) both within and outside the areas inhabited by adults. Specimens were examined at the point of capture, and released unharmed. The following were recorded: sex, colour, and maximum carapace width. Colour varied from yellow to deep purple. The majority of specimens were unambiguously categorised as either yellow or purple morphs, but there was a proportion of intermediates. Colour classification is to a degree subjective - a point discussed below.

Not all analyses were based on the same sample sizes, because not all variables were recorded for every specimen. Some samples were biased during collection and so ignored for certain purposes.

Results

Sex Ratio

The analysis of sex ratio was complicated because the studies were predominantly conducted during the breeding season. At that time, adult crabs migrate to the shore to breed, but more females than males congregate at the shore. Thus, the observed sex ratio will depend upon the location of sampling. The samples were categorised as resident (at $>$ 200 m), migrating (30-200 m), and breeding (adjacent to the shore) (Table 1). Breeding crabs included live crabs and those found dead close to the shore. Resident crabs were predominantly males. Sexes were approximately equal in migrating crabs. Both live and dead crabs at the shore were predominantly females. Except for the migrating crabs, each sample deviated significantly from a 1:1 ratio (χ^2 test, $P <$ 0.05). The total sample comprised 47% males and 53% females.

Size Distribution

The size frequency distribution (Fig. 1) for all samples measured from 2005-2007, totalling 3698 crabs (1726 males, 1974 females). There are several striking features. One is the paucity of small specimens, despite intensive effort to find them. The size of sexual maturity is 60 mm carapace width (CW) or more (Hartnoll et al., 2006a), but only 25 crabs of $<$ 60 mm CW were collected (0.7% of the total). Males reach a larger size than females as evidenced by the largest size classes, 110-129 mm CW, consisting almost entirely of males. The modal size class was 100-109 mm CW for males, and 90-99 mm CW for females. The mean sizes were 96.3 mm CW for males, and 89.1 mm CW for females, the maximum sizes 120 mm and 110 mm CW, respectively.

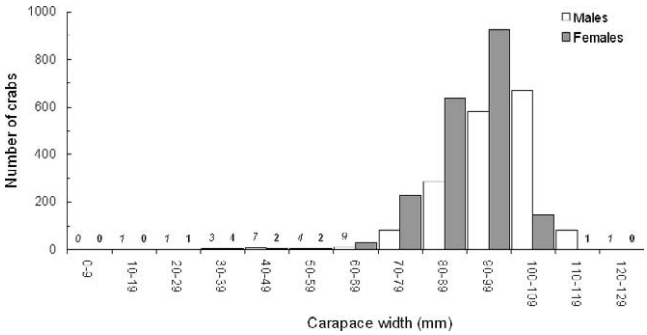

Fig. 1. *Johngarthia lagostoma*. Size frequency histogram of sample of 1726 males and 1974 females sampled on Ascension Island in 2005-2007. Where the sample size is $<$ 10 crabs in any category, the number sampled is indicated in italics for males, in bold for females.

Colour Patterns

Colour was recorded for each crab collected. The majority of specimens were unambiguously either 'yellow' (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) or 'purple' (dark purple all over, except for white areas in the same positions as above). These two morphs are shown in Hartnoll et al. (2006a: Fig. 3A). There are also some 'intermediates'. Typically these are predominantly yellow/orange, but have two large purple patches on the carapace. However, some specimens grade towards either yellow or purple morphs, and classification of these becomes subjective. The frequency of the morphs was examined, and analysed in relation to size and sex (Table 2).

Overall the yellow morph was dominant, comprising 85% of the population. The purple morph made up 10% and intermediate specimens 5%. There was no evidence of a size differential between morphs. In each sex the maximum and mean carapace widths were similar for the three colour patterns. However, there was a difference between the sexes in frequency of morphs ($\chi^2 = 57.9$, $P < 0.001$). The yellow morph made up 81% of males, but 89% of females. The purple and intermediate morphs were correspondingly less frequent in females. Although there was no size difference between morphs in the adult population, the same was not true of the juveniles of $<$ 50 mm CW. Only 21 crabs of this size were available, but there was a size-related pattern. All 13 specimens of $<$ 40 mm CW were dark in colour (dark brownish, rather than the purple of the adult morph). Of the 8 specimens of 40-49 mm CW, 50% were yellow, and 50% were purple: the smallest yellow morph was 40 mm CW. On the basis of this admittedly minimal sample, the variation in adult colour pattern would seem to start appearing only after 40 mm CW.

Discussion

Sex Ratio

The analysis of sex ratio confirms the results found in the breeding season of 2005 (Hartnoll et al., 2006a). The breeding population on the shore was heavily dominated by females, while the population in the 'residential' areas, where crabs occur outside the breeding season, had a surplus

Table 2. *Johngarthia lagostoma*. Frequency and size of each colour morph for all samples collected on Ascension Island. 2005-2007.

	Male			Female			Total
	n (%)	Max CW (mm)	Mean CW (mm)	*n* (%)	Max CW (mm)	Mean CW (mm)	*n* (%)
Yellow	1551 (80.7)	118	95.9	1973 (89.0)	108	89.2	3524 (85.2)
Intermediate	123 (6.4)	116	97.1	94 (4.2)	105	88.3	217 (5.2)
Purple	247 (12.9)	117	96.0	149 (6.7)	103	86.2	396 (9.6)

of males. The preferential migration of females out of these residential areas is the presumed cause of this. Only the migrating population had an equal sex ratio. The reasons for the different sex ratios in migrating and breeding populations is basically because not all males migrate as far as the shore. A proportion of females mate and lay during their migration, providing breeding opportunities for males at intermediate locations. These data do not enable the sex ratio within the whole population to be assessed without bias: although there is a surplus of females (53%) in the total sample, this could be an artefact of the substantial sampling of the female-dominated population at the shore. An unbiased estimate will require a major sampling effort outside the breeding season. The only other data on sex ratios in the species are from the Atol das Rocas (Teixeira, 1996). The environmental situation there is very different from Ascension, as the Atol comprises only two small (each $<$ 10 hectares) low-lying vegetated islands. The total sample had a substantial surplus of males (945:645), but the ratio varied between the two islands, and randomly with season. Samples were taken throughout the year at a number of stations around each island. Given the small size of the islands there is limited scope for confounding effects of breeding migrations, and the surplus of males appears real. In contrast, an unbiased sample of the black land crab *Gecarcinus ruricola* (Linnaeus, 1758), collected outside the breeding season on Old Providence (San Andres Archipelago), showed a surplus of females (Hartnoll et al., 2006b). The question of sex ratios in land crabs obviously needs further study. Intuitively a surplus of males might be expected, since the higher participation of females in the annual breeding migrations exposes them to greater risks.

Size Distribution

The most striking feature of the size frequency distribution was the dearth of small specimens of either sex: very few were collected below the size of sexual maturity. This disparity became clear early in the study, and subsequently intensive searches were made for small crabs in habitats known to be favoured by juveniles of other land crabs (under logs or stones), but with little success. There are two possible explanations: either the juveniles occur in some unexamined habitat, or they are genuinely very scarce. We can only offer one suggestion for the former possibility. In *Cardisoma carnifex* (Herbst, 1796), juveniles spend their early years within burrows of conspecific adults (Vannini et al., 2003): possibly *J. lagostoma* does likewise, though the generally dry upland habitat of adult *J. lagostoma* contrasts with the moist supratidal habitat of *C. carnifex*. As to the latter explanation, if they are genuinely so scarce, it indicates problems with recruitment. Island dwelling land crabs in general show irregular recruitment patterns due to the uncertainty of return to a small land mass after the planktonic larval phase (see Hartnoll and Clark, 2006). There is little information on recruitment of *J. lagostoma* on Ascension, possibly because most of the likely recruitment sites are inaccessible and rarely visited (Hartnoll et al., 2006a). On only two occasions has mass recruitment been observed, in both cases in the capital, Georgetown (the only inhabited coastal area). These were in March 1963 (Packer, 1968) and April 1977 (John Packer, personal information): both were incidentally around a new moon. Georgetown is an unsuitable recruitment area, due to its considerable distance from the normal upland residential areas of the crabs (see Hartnoll et al., 2006a). There must have been recruitment more recently than these observations, but where, when, and in what intensity is not known. A possible small recruitment was seen on NE Bay beach in March/April 1999 (ACB, unpublished).

Other land crab populations have potentially similar recruitment problems, but do not display the same extreme dearth of small specimens. Whilst the peak of abundance still lies in the mature size classes, immature size classes are more reasonably represented. This is so for *J. lagostoma* on the Atol das Rocas (Teixeira, 1996), with 4% $<$ 60 mm CW (still a low ratio), contrasted with 0.7% on Ascension. In *Gecarcinus ruricola* in the San Andres Archipelago (Hartnoll et al., 2006b), there were 26% of specimens below the size of maturity. The situation on Ascension is clearly atypical. Another anomaly of the distributions on Ascension is that in both sexes they are skewed to the largest sizes, with the modal classes close to the maximum size. This contrasts with the other studies cited above, where the modal size is near the middle of the mature size range. Thus, in several respects, the Ascension population of *J. lagostoma* shows characteristics of a markedly aging population, and implications for conservation need to be considered.

The larger size reached by males is a consistent feature not only of land crab demography, but indeed for many other crab species (Hartnoll, 1982). It is seen in *J. lagostoma* on the Atol das Rocas (Teixeira, 1996), *Gecarcinus ruricola* in the San Andres Archipelago (Hartnoll et al., 2006b) and Saba (Mulder and Stam, 1987), *Gecarcoidea natalis* (Pocock, 1888) on Christmas Island (Hicks, 1985) and *Epigrapsus notatus* (Heller, 1865) on Taiwan (Liu and Jeng, 2005). There are two possible reasons for males reaching a larger size. In crabs generally, females expend greater resources on reproduction, at the expense of growth. Specifically in land crabs females of most species play a greater part in the seaward breeding migrations, being thereby exposed to greater risk and increased mortality. The

dead specimens of *J. lagostoma* collected near the shore were predominantly females.

With a maximum size of 120 mm CW *J. lagostoma* is the largest member of the genus, and as large as (or larger than) most other land crabs (see Hartnoll et al., 2006a for references and discussion). Only species of *Cardisoma*, such as *C. guanhumi* Latreille, 1828 at 130 mm CW (Türkay, 1970), reach an appreciably larger size. For most land crabs, a major constraint on growth is the problem of obtaining water for post-moult expansion (Hartnoll, 1988; Green, 2004). Most *Cardisoma* spp. are supra-tidal species which avoid this constraint by burrowing down to the water table: this will facilitate a larger moult increment, helping them to reach a larger size.

Colour Patterns

The dominance of the yellow morph confirms the provisional conclusions from earlier small samples (Hartnoll et al., 2006a). Some earlier studies have suggested that the yellow morph is characteristic of the larger size classes. Manning and Chace (1990) stated "all of the smaller specimens ... are red, and most of the larger specimens are yellow." Ashmole and Ashmole (2000) state "Two colour phases are present: smaller individuals are normally red or purple ... the largest individuals are normally yellow or orange." Whilst it seems true that small individuals of < 40 mm CW are indeed all dark coloured, the yellow/purple colour variation becomes established by 50 mm CW, and there is no evidence that the darker morphs decrease in frequency at a large size: all three morphs are represented in the largest size classes, and have similar mean sizes. There is evidence that the yellow and purple morphs are variants of the same population. They have been observed mating together (Hartnoll et al., 2006a), and there is no genetic separation between the morphs (Antonio Sole Cava, unpublished, based on provisional studies).

There is a clear rationale for the juveniles to be dark coloured, as they are exposed to a variety of predators (including larger conspecifics), and will benefit from cryptic colour. A similar pattern of dark coloured juveniles and variously patterned adults is seen in *Cardisoma guanhumi* (Gifford, 1962). However, the reason for the highly visible yellow colour of the majority of larger *J. lagostoma* is less clear. This predominance of yellow morphs is not found in all populations of the species. On the Atol das Rocas only 46% of a sample of 1550 crabs were yellow (Teixeira, 1996). On Fernando de Noronha only 17% of an admittedly small sample of 23 crabs were yellow (RGH, unpublished). The situation on Trindade is unclear: the only two photos we can find are of yellow morphs, and there is a description of "caranguejo terrestre, de coloração amarelada (= land crab of yellowish colour)" (Gasparini and Floeter, website). So perhaps yellow morphs predominate there. It has been suggested that the yellow colour is an adaptation to resist heat stress on the barren lower areas of Ascension which must be crossed during the breeding migration (Hartnoll et al., 2006a). Both Atol das Rocas and Fernando de Noronha are heavily vegetated close to the sea, so migrating crabs will not be subjected to the same heat exposure. In contrast, Trindade is relatively barren. The correlation between abundance of yellow morphs and barren environment appears to hold up. On Ascension females migrate to a greater extent than males: this greater exposure could provide a reason for the higher incidence of yellow morphs in females.

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