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Population ecology

Short-term climate change and the extinction of the snail *Rhachistia aldabrae* (Gastropoda: Pulmonata)

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The only known population of the Aldabra banded snail *Rhachistia aldabrae* declined through the late twentieth century, leading to its extinction in the late 1990s. This occurred within a stable habitat and its extinction is attributable to decreasing rainfall on Aldabra atoll, associated with regional changes in rainfall patterns in the late twentieth and early twenty-first century. It is proposed that the extinction of this species is a direct result of decreasing rainfall leading to increased mortality of juvenile snails.

Keywords: Mollusca; extinction; Aldabra atoll; rainfall

1. INTRODUCTION

Island populations have long been of particular interest to evolutionary biologists due to their role in the development of the theory of evolution (providing important data for both Darwin and Wallace) and magnifying general processes of colonization, extinction and scaling in classic island biogeography theory (Simberloff 1974; Lomolino 2000). Numerous studies have demonstrated that rates of colonization and extinction can be high in some islands, depending on size and location (Johnson *et al.* 2000; Woolfit & Bromham 2005). This may lead to a rapid rate of species turnover in these cases, although more isolated or larger islands may have comparatively stable systems (Hunt & Hunt 1974; Drake *et al.* 2002). Although this is apparent in the available data on rates of colonization and species diversity, there are few datasets showing long-term changes in species abundance. These data are needed in order to understand the process of extinction in these small populations.

Research into island ecosystems has largely comprised occasional observations, manipulations and monitoring of threatened species. Few islands have been the focus of research interest for long enough for the accumulation of useful datasets for long-term monitoring (notable exceptions being Barro Colorado and the Galapagos Islands). Aldabra atoll in the Seychelles group has been one of the most intensively studied small islands over the last 100 years, with particularly intensive research since 1968. This includes long-term monitoring of giant tortoises *Dipsochelys dussumieri* (Bourn *et al.* 1999), habitats and invasive coccid insects. These studies have been focused on the recovery of the tortoise populations and their impact on the atoll's habitats and the impact of invasive species. No monitoring has been carried out on indigenous invertebrates. Most invertebrate collections on the atoll date back to 1970s, with the exception of terrestrial molluscs. Land snail collections on Aldabra were first made in 1895, with occasional collections since then and extensive surveys in 1997, 2000 and 2005. Examination of collection material allows the evaluation of distribution and abundance change for the largest and most distinctive Aldabran snail species, the banded snail *Rhachistia aldabrae*.

Rhachistia aldabrae is endemic to Aldabra atoll where it has been recorded from the islands of Picard, Malabar, Polymnie, Esprit and Grande Terre (Gerlach 2006). *Rhachistia* is a widespread genus in Africa and Asia, particularly in coastal woodlands (Mordan 1992), and little is known about the ecology of the genus itself; closely related taxa are algal grazers with high reproductive rates and relatively long lifespans (2–3 years; Gerlach 2006). No detailed studies of *R. aldabrae* have been carried out, but several visitors to the atoll since 1895 have collected specimens deliberately or incidentally in general invertebrate sampling. The last specimen was collected in 1997, since then extensive searches have been made for this species in many parts of the atoll (including all localities where the species had been recorded previously) in 2005 and 2006 but only old shells (estimated to date back at least 5 years) could be located. Climatic and habitat variables are known to affect the stability of some snail populations (Baur & Baur 1993) and the aim of this paper is to investigate the possible factors contributing to the apparent decline of *R. aldabrae*, including habitat change and climate.

2. MATERIAL AND METHODS

Collections containing specimens of *R. aldabrae* were examined and the data collated to investigate the pattern of change in distribution, abundance and demography of the species from 16 collections spread over 102 years (table 1 and figure 1*a*). This covers all collections from Aldabra (both institutional and private) known to the author. The probability of population survival was evaluated using Solon's (1993) Bayesian estimation, which is sensitive to absence records towards the end of runs of data (Burgman *et al.* 1995), as in the present case. Shells were measured with dial callipers accurate to 0.1 mm. Individuals were assigned to four size or age categories: neonatal (no more than a single whorl in addition to the protoconch), juvenile (2–7 mm: from one whorl to one-half adult shell length), subadult (7–14 mm: adult shell length but lacking any development of a lip) and adult (greater than 14 mm, with a slight lip). The effects of annual temperature extremes and rainfall on the number of specimens collected were investigated using data from Aldabra Research Station (available data cover the periods 1950, 1958–1959, 1968–1983 and 1994–2006) and by comparing changes in vegetation cover between 1988 (data from T. Scoones *et al.* 1989, unpublished data) and 2005 when no specimens could be located. In 2005, vegetation data were collected by identifying all individual plants over 1 m tall along 4 m wide transects on Malabar Island where diverse vegetation types were recorded in 1988. The 1050 m transect was divided into 50 m sections; this is the same method employed in the previous studies.

3. RESULTS

Recent shells of live snails were recorded on the main islands of Picard, Malabar and Grande Terre during 1907–1976; after that only two isolated fresh specimens have been found (1989 and 1997), both on Picard. In 1907, the species was noted as being particularly abundant in the 'Coroupa' area of

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Table 1. Collection data for *R. aldabrae* and Bayesian estimation of survival probability.

year	no. of snails		probability of survival
	recent shells	live snails	
1895	3	0	1
1907	1	0	1
1908	1	2	1
1909	0	2	1
1966	2	8	1
1972	0	3	1
1975	0	12	1
1976	0	10	1
1977	0	1	1
1989	1	0	1
1996	0	0	1
1997	0	1	1
1998	0	0	0.881
2000	0	0	0.666
2005	0	0	0.322
2006	0	0	0.258

Grande Terre (Fryer 1911). This locality was visited in 2000 and no evidence of any recent survival of the species was found. Probability of population survival is shown in table 1, indicating that there would be no significant probability of survival ($p<0.05$) by 2012. These calculations indicate that the species is probably already extinct as a 95% probability of extinction is attained when the critical value of the last sighting (Solon 1993) is exceeded; this is calculated in 2006 (critical value of 102 years from the first record). This analysis assumes that all surveys are comparable; however, the pre-1997 collections are incidental and probably indicate high levels of abundance of the species. Post-1997 surveys have been more systematic and in 2005 and 2006 comprised exhaustive surveys focused specifically on locating *R. aldabrae*. The absence of any recent shells or live specimens in those surveys further supports the view that this species is extinct.

Significant correlations were found with annual rainfall; while the relationship between snail numbers and rainfall may not be expected to be linear or normally distributed, simple linear regression provides a statistically significant result applicable to the limited data available ($y=0.0394x-40.318$, $R^2=0.788$, $n=7$, $p=0.008$; where y is the number of shells and x is the annual rainfall in millimetres). No *R. aldabrae* were recorded in years where rainfall fell below 966 mm (1023 mm predicted from regression; figure 1*b*). The vegetation survey methods of 1988 and 2005 are directly comparable. No significant differences were found between the samples for any plant species using a two-factor ANOVA (excluding species found only as single individuals, treating abundance of each species as a dependent variable and 50 m sections as replication units, overall $F_{1,210}=3.88$, $p=0.09$, all individual species $p>0.05$), indicating that habitat change is unlikely to be a significant contributor to *R. aldabrae* population decline. Of 30 years of rainfall data, 17 were below 1023 mm. Such years occurred as isolated dry years or two consecutive dry years until 1999; since then all 6 years for which data are available have been dry. Both the frequency of low-rainfall years and the length of dry periods have increased (figure 1*c*); during 1970–1980, there were three low-rainfall years compared with seven during 1994–2003, and this is statistically significant (for frequency of low-rainfall years runs test $p_{13,15(1)}=0.01$; for length of dry period mean square successive difference test (Bennett & Franklin 1954) $C_{1,8}=0.855$, $p=0.0002$; isolated years 1950, 1959–1960 excluded).

Changes in the proportions of adult and juvenile size categories of shell were detected (figure 1*b*); these do not follow a regular pattern and the non-systematic early collections may be assumed to be biased towards the conspicuous adults. No juveniles have been collected since 1976.

4. DISCUSSION

No specimens of *R. aldabrae* have been located since 1997 despite extensive searching and as the most recent remains appear to date from approximately 2000, this species is considered to be extinct. No general changes in vegetation cover or structure have been identified on Aldabra and the algal browsing diet of this family of snails (Gerlach 2006) would imply that habitat and food availability are unlikely to have changed significantly over the past 100 years. The species was recorded in mixed scrub on Picard (R. Prys-Jones 2006, personal communication) and in areas of 'mixed vegetation, partly of 'open country' plants but mainly of 'shore-zone' forms' (Fryer 1911) suggesting that it did not have any special association with any restricted habitat. The decline in abundance correlates with increasing prolonged dry periods. During periods of drought, *R. aldabrae* aestivated on the branches of shrubs (Gerlach 2006). Decreases in rainfall would have reduced the length of activity periods. This may not have been a major additional cause of mortality to adults, but the small juveniles would be less able to tolerate the desiccation. Consequently, long dry periods would be expected to reduce reproductive success, with complete failure in prolonged dry periods. This is supported by the demographic change in the population, from a high proportion of juveniles and neonates during 1974–1976 to only adults after 1976. Shell fragments found in 2000 and 2005 are all assignable to the adult size categories. From this, it seems probable that decreasing rainfall over 1980s and 1990s led to high juvenile mortality, and consequently an ageing population. Senescence may have led to the complete extinction of all populations between 1997 and 2000. This pattern may be analogous to the increased embryonic mortality associated with raised temperatures seen in other snail species (Baur & Baur 1993) although no correlation with temperature was detected in *R. aldabrae*.

This may be one of the few cases of extinction that cannot be attributed to a change in habitat, predators or diet, but may plausibly result from the direct impacts of climate on survival. Climate change has

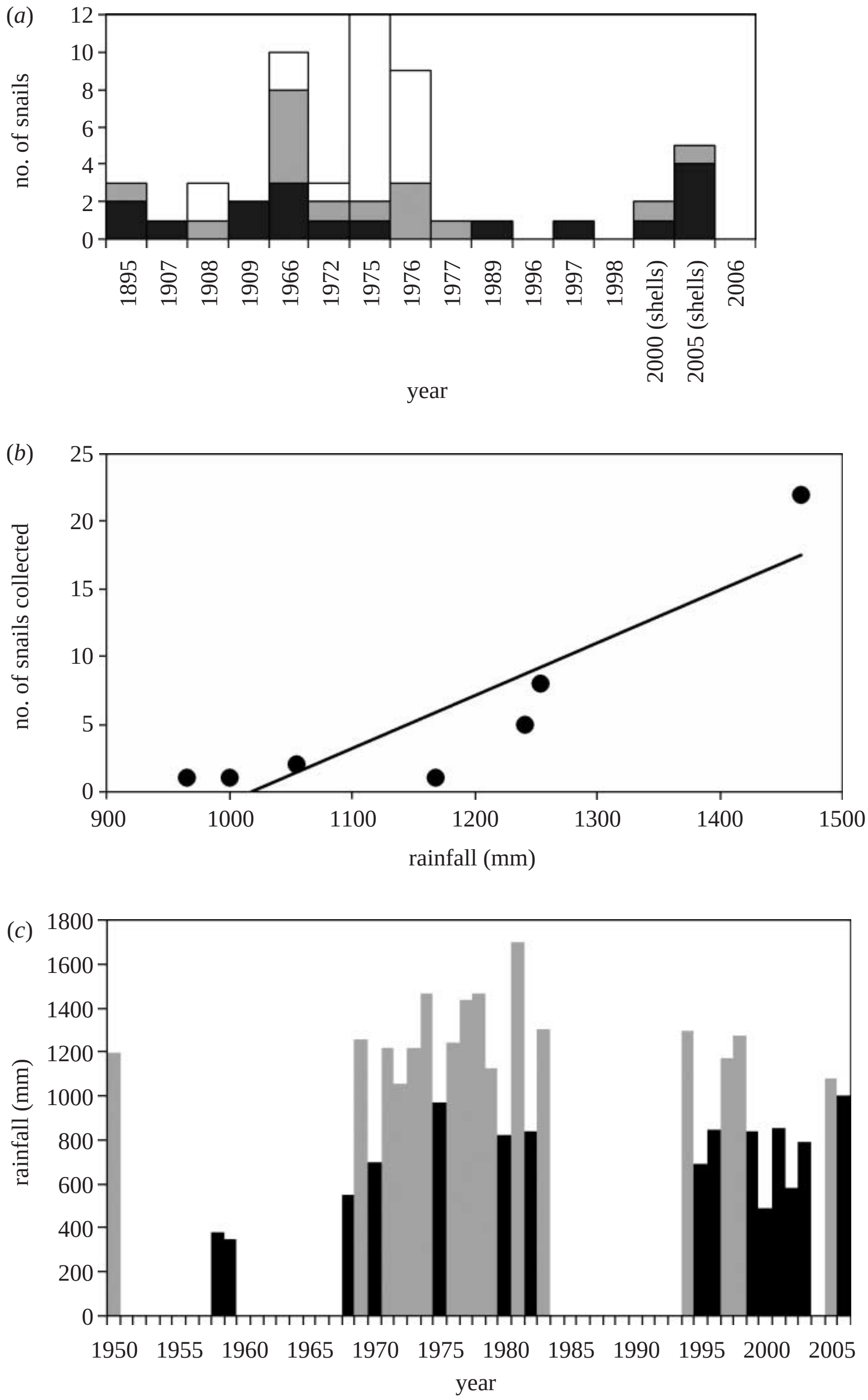

Figure 1. (*a*) Population structure of *R. aldabrae* collections (open bars, juvenile; grey bars, subadult; black bars, adult). (*b*) Correlation between rainfall and number of *R. aldabrae* fresh shells and live snails collected on Aldabra atoll (1966–1997; data from subsequent years are not used because no recent *R. aldabrae* shells were located). (*c*) Frequency of low-rainfall years (black bars, under 1023 mm; grey bars, over 1023 mm). No data for 1951–1957, 1960–1967 and 1984–1993.

been proposed as a factor leading to the decline of many species (Thomas *et al.* 2004), either directly or through indirect associations, such as host–parasite dynamics (Mouritsen *et al.* 2005). There are few cases where this has been demonstrated directly (the golden toad *Bufo periglenes*; Pounds & Crump 1994; Pounds *et al.* 1999), although indirect effects are reported for a large number of amphibian species (Stuart *et al.* 2004; Pounds *et al.* 2006). Cyclical patterns in rainfall have been reported from Aldabra (Stoddart & Walsh 1979), but the decrease in rainfall described here appears to be distinct from those and closely matches patterns from East and Southern Africa (Hoerling *et al.* 2006). At present, the data from Aldabra are too limited to confirm that the climate change pattern is part of the drying trend of Southern Africa and not merely a local or short-term phenomenon. However, it is to be expected that the impacts of the changes reported here will be detected in more species in the future as rainfall patterns change.

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NOTICE OF CORRECTION

The genus name is now correct.

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biology letters