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Space invaders? A search for patterns underlying the coexistence of alien black rats and Galápagos rice rats

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Abstract The introduction and spread of the black rat *Rattus rattus* is believed to have caused the worst decline of any vertebrate taxon in Galápagos. However, the "extinct" Santiago rice rat *Nesoryzomys swarthi* has recently been rediscovered in sympatry with *R. rattus* providing the first exception to this general pattern of displacement. We carried out an exploratory investigation of this novel system with the aim of identifying patterns that may facilitate the apparent coexistence of the two species. We carried out an extensive survey of Santiago Island to map the current distribution of the endemic rice rat and to explore broad scale distribution–habitat associations. We then used live-trapping, radio-tracking, and spool-and-line tracking to quantify abundance–habitat correlations and to test for evidence of interspecific spatial segregation, alteration of *N. swarthi* activity patterns (spatial and temporal), and microhabitat partitioning. We found that *N. swarthi* has disappeared from part of its historical range and appears to be restricted to a 14 km stretch of the north-central coast, characterised by high density of the cactus *Opuntia galapageia*. In contrast, the generalist *R. rattus* was found at all survey sites. We found no evidence of spatial segregation, and home range size, temporal activity and density of *N. swarthi* did not vary with local density of *R. rattus*. However, pre-dawn and post-dusk *N. swarthi* activity levels increased with *R. rattus* density perhaps reflecting an increase in foraging effort necessary to compensate for the costs of interspecific exploitation or interference competition. The distribution, microhabitat selection, and abundance–habitat relations of *N. swarthi* suggest that the endemic cactus *O. galapageia* may facilitate interspecific coexistence. Further research should include a comparison of inter-seasonal resource preference and foraging activity of the two species coupled with replicated field experiments to confirm and quantify competition and to elucidate the mechanism of competitive coexistence.

Keywords Cactus · Introduced species · Microhabitat · Spatial segregation

Introduction

The patterns underlying the coexistence of ecologically similar species have been a major focus of community ecologists for the last 40 years. Much of this research has concentrated on small mammal communities and there is now ample evidence to show that spatial, temporal and resource partitioning play crucial roles in the structuring of these natural communities (e.g. Schoener 1974; Price 1978; Abramsky et al. 1979; Bowers 1982; Morris 1987; Kotler and Brown 1988; Jorgensen and Demarais 1999; Jones et al. 2001). In contrast, the role of interspecific competition and coexistence in the restructuring of invaded communities has received relatively little attention. Although many authors postulate competition with exotic small mammals to explain the demise of native species (e.g. Brosset 1963; Alvarez and Gonzalez 1991; Stephenson 1993) much of this

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evidence is circumstantial and commendable studies of competitive processes in invaded systems remain rare (e.g. Gurnell et al. 2004). This is unfortunate considering the potential contribution of such research to the fields of community ecology and evolutionary biology (Yom-Tov et al. 1999; Shea and Chesson 2002; Courchamp et al. 2003) and the provision of information relevant to the conservation of endangered species (e.g. Ligtvoet and Van Wijngaarden 1994; Krupa and Haskins 1996; Macdonald et al. 2001; Zavaleta et al. 2001; Bryce et al. 2002; Courchamp et al. 2003).

An unexpected opportunity to explore such a system has arisen between endemic rodents and introduced black rats in the Galápagos Islands following the rediscovery, in 1997, of a population of the endangered rice rat *Nesoryzomys swarthi* on the north-central coast of Santiago Island (Dowler et al. 2000). This species had been presumed extinct since its initial collection at Sullivan Bay (Fig. 1) on the north-east coast of Santiago in 1906 (Orr 1938). It was believed that *N. swarthi* had met the same fate as at least half of the species of the once diverse assemblage of 12 endemic rodent species; the Galápagos rice rats (Orr 1938). This group had dominated the mammalian fauna of Galápagos but since the discovery of the archipelago in 1535, this group has experienced the highest extinction rate of any vertebrate taxon in Galápagos (Clark 1984; Dowler et al. 2000). Today, just four endemic species remain: *N. narboroughi* and *N. fernandinae* on Fernandina, *N. swarthi* on Santiago and *Oryzomys bauri* on Santa Fe (Dowler et al. 2000). Circumstantial spatio-temporal evidence suggests that the introduced black rat (*Rattus rattus*) played a leading role in the loss of the Galápagos *Nesoryzomys* and *Oryzomys* species (Brosset 1963; Niethammer 1964; Clark 1984). However, the rediscovery of *N. swarthi* in sympatry with *R. rattus* on Santiago Island is an exception to this rather clear pattern of alien arrival and native extinction. This is particularly intriguing when we consider the chronology and geography of the *R. rattus* invasion. Genetic analyses suggest that *R. rattus* first landed ashore at James Bay, Santiago in the late 1600s (Patton et al. 1975). Subsequent, separate introductions to the archipelago, resulting in the current colonisation of 33 islands (Charles Darwin Research Station (CDRS), unpublished data) and successful invasion of all Galápagos habitats, coincided with the loss of *Nesoryzomys* and *Oryzomys* species wherever the black rat became established (Clark 1984; Key and Muñoz Heredia 1994; Dowler et al. 2000). So, what conditions may foster the coexistence of *N. swarthi* and *R. rattus* on Santiago?

At the coarsest level, species coexistence may be facilitated by differential macro-habitat selection (e.g. Abramsky et al. 1990; Bryce et al. 2002). At a finer scale, where species are sympatric within the same habitat, spatial segregation may be maintained through interspecific territoriality (e.g. Lofgren 1995). Alternatively, microhabitat segregation may act to partition space (e.g. Bowers et al. 1987) and/or resources (e.g. Price and Waser 1985; Monamy and Fox 1999). A shift in temporal activity patterns may occur to minimise the probability of contact with the dominant species (e.g. Ziv et al. 1993; Jones et al. 2001).

In our introductory survey of this novel system we used a combination of radio-tracking, spool-and-line tracking and live-trapping to test two preliminary hypotheses: (1) Given the strong case for displacement of other Galápagos rice rat species following *R. rattus* establishment across the archipelago, we hypothesised that *R. rattus* and *N. swarthi* would exhibit segregation

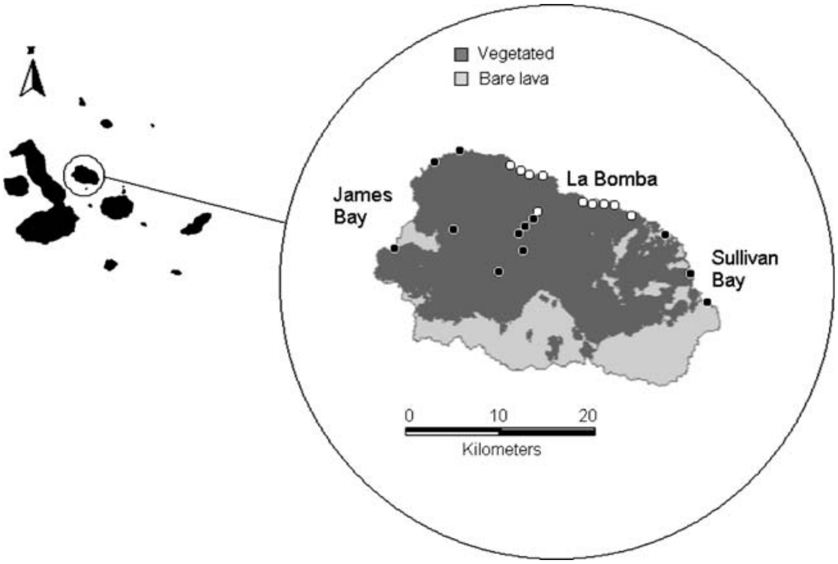

Fig. 1 Map of Santiago showing hair tube survey sites. *White symbols* indicate sites occupied by *N. swarthi* and *black symbols* indicate uninhabited sites. All sites were occupied by *R. rattus*

in macro- or micro-habitat or in space per se. (2) We hypothesised that *N. swarthi* would respond to increasing *R. rattus* density by adapting home range use or temporal activity pattern to minimise interspecific contact and/or maximise resource acquisition.

To validate the implications of our findings for the conservation status of this endangered, endemic species it was of paramount importance to begin by delineating the distribution of *N. swarthi* in relation to that of the exotic *R. rattus*. This was achieved through an extensive census of the previously unexplored parts of Santiago. The investigation then proceeded to focus down through progressively finer spatial scales from habitat associations to a detailed contrast of microhabitat selection and a brief exploration of activity patterns.

Materials and methods

Study site and species

The volcanic Galápagos Islands are situated 960 km west of mainland Ecuador in the Pacific Ocean. The uninhabited island of Santiago is the fourth largest Galápagos island at 585 km^2 with a maximum elevation of 907 m (Jackson 1993). The climate is strongly influenced by oceanic currents and there are two main seasons; the warm/wet season (January–May); characterised by warm temperatures with variable and often heavy rainfall at all altitudes, and the cool/dry season (June–December); characterised by cool temperatures with constant light rain and mist in many parts of the highlands but almost no precipitation in the lowlands (Mcmullen 1999). The mean annual rainfall in the Santa Cruz arid zone for the period 1965–2004 was 491.44 mm, notably higher than the median of 277.55 mm, ranging from 63.6 mm in 1985 to 2,768.7 mm during the El Niño of 1983. The temperature is comparatively stable with an annual mean of 23.95°C±0.14 SE ranging from 22.6 to 26.2°C (CDRS, unpublished data). The vegetation of the Galápagos islands has traditionally been classified by altitudinal zone. In order of increasing altitude these are the Littoral (Coastal) Zone, Arid Zone, Transition Zone, Scalesia Zone, Zanthoxylum Zone, Miconia Zone and Fern-Sedge (Pampa) Zone (McMullen 1999). The Santiago rice rat (*N. swarthi*) is currently known to exist as one localised population situated on the north-central coast of Santiago, in the Arid Zone. This region is composed of typical Arid Zone vegetation; the cactus *Opuntia galapageia* and primary tree species *Bursera graveolens*, *Cordea lutea* and *Croton scouleri* are distributed among a shrub layer that mostly consists of *Clerodendrum molle*, *Castela galapageia* and *Lantana peduncularis*. The area is exceptionally dry as it lies in the rain-shadow of the larger Santa Cruz Island and the highlands of Santiago. Past search efforts for *N. swarthi* have focused on southern and highland regions (Clark 1984; Dowler et al. 2000; CDRS, unpublished data) but have failed to find any *N. swarthi* in these areas. Previous research has demonstrated that *R. rattus* is nocturnal, exhibiting some activity in each hour of darkness, reaching an activity peak 2–3 h after the onset of darkness and that this pattern appears to be fairly general within the species (Barnett et al. 1975; Meehan 1984; Tobin et al. 1996; Innes 2005). Both Galápagos black rats and rice rats are omnivorous including a variety of fruits, seeds, invertebrate matter and carrion in their diet (Clark 1981; Jackson 1993). *R. rattus* is larger than *N. swarthi* (mean mass of male adult 183 and 115 g, respectively and female adult 141 and 91 g, respectively) (D.B. Harris, unpublished data). The data for this study were collected over 3 years from 2002 to 2004.

Current distribution

To delineate the current distribution of *N. swarthi*, baited hair tubes were used to survey for the presence or absence of *N. swarthi* and *R. rattus* at 22 sites predominantly located on the previously un-surveyed north coast (15 Arid Zone sites) of Santiago. We also sampled inland sites in the Arid Zone (3 and 4 km inland), the Transition Zone (5 and 6 km inland) and three highland sites (one Transition Zone, one Zanthoxylum Zone and one Fern-Sedge Zone). Each hair tube was constructed from a 30 cm length of 7.5 cm diameter PVC tubing that was bisected longitudinally. The bottom half was nested into the top and bound together with wire. The top and sides of the tube were lined with double sided carpet tape. The bait (peanut butter and oats) was twisted in a piece of muslin the ends of which were pinched between the two tube halves. Tubes were wedged between or tied to rocks and vegetation at ground level. Thirteen tubes were placed at each site in a T-shaped transect (7×7) at 30 m intervals (consistent with the trap spacing—see below). At the coastal sites, tubes were placed 100 m back from the shore to prevent bait consumption by hermit crabs. Tubes were collected after 1 week. The tubes were soaked in warm detergent solution overnight to loosen the hairs. Hairs were extracted with fine forceps and dried on tissue paper. PVC glue was smeared onto a microscope slide and hairs were laid carefully on to the wet glue. After the glue had dried, hairs were carefully extracted with fine forceps, discarded and the hair imprints were identified to species by individual cuticle patterns according to reference slides (Teerink 1991). As limited resources precluded repeat surveys at different times of year, tube visitation likelihood by *N. swarthi* was maximised by surveying in August (2004), a predictably dry time of year (Snell and Rea 1999) when *N. swarthi* are likely to be food limited and *R. rattus* numbers are in decline (Clark 1980).

Habitat associations

Habitat surveys were carried out at all of the coastal hair tube sites during the survey to determine the habitat type associated with the presence of *N. swarthi*. Abundance–habitat correlations were quantified by live-trapping on eight trap grids in the area of known occupancy, in the vicinity of a location locally known as La Bomba (0°11′10″S, 90°41′59″W). Four of these grids were located on the coast (100 m from the shoreline) and the other four were situated between 1 and 2 km inland. The T-square method (Greenwood 1996) was used to obtain an index of mature cactus density, tree density and shrub density for each hair tube site and for each grid. The species of trees and shrubs included in the density estimate were recorded. Cactus, tree and/or shrub density could not be recorded at sites where the point–plant and/or inter-plant distances exceeded 70 m as the rugged terrain precluded reliable judgement of the next nearest plant in many cases. Lava structure was coded within a 2 m radius plot at each of the survey points within which lava was classified as either predominantly flat or broken/cracked. Habitat surveys were conducted at five of the hair tube points (90 m spacing) and at 20 randomly selected grid points on each of eight trap grids. In addition, the relative proportions of dominant plant species (i.e. plant species composition) within the tree and shrub samples and the proportion of mature individuals within the cactus sample were calculated for each trap grid from the first 20 (point to nearest plant) trees, shrubs and cacti sampled.

Abundance data were based on estimates from 10 days of trapping on the eight grids. Each grid was composed of one collapsible Tomahawk trap (single door rat trap Model 201: 406.4×127×127 mm, Tomahawk Live Trap, Tomahawk, WI, USA) per point at 30 m spacing in a 7×7 array. Abundance was estimated using the Minimum Number Known Alive (MNKA) method of Krebs (Krebs 1966). MNKA was chosen as *N* (abundance) was less than 25 for some grids, failing criteria required by closed population estimators based on capture probabilities (Otis et al. 1978). The live-trapping was carried out from December 2002 to January 2003.

Spatio-temporal activity

Radio-tracking was used to investigate differences in *N. swarthi* home range parameters and activity patterns in relatively high and low *R. rattus* density areas. Preliminary live-trapping at multiple sites was first undertaken to identify two areas of similar *N. swarthi* density but one with low *R. rattus* density and the other area with a relatively high *R. rattus* density. The abundance data were based on estimates from 10 days of trapping on grids of 49 collapsible Tomahawk traps. Habitat surveys were conducted in each area and compared prior to the radio-tracking phase to test for underlying variation that may affect home range use. The densities of *C. molle* (the dominant shrub), shrubs (all species including *C. molle* if this was the nearest plant), trees (all species) and cacti (*O. galapageia*) were compared between grids by measuring to the nearest individual of each of the four plant types from 20 random points on each grid and comparing distances using *t* tests. Mean *C. molle* and mixed shrub size were compared by measuring the volume (maximum length × width × height) of each of the 20 plants in the sample and comparing volumes between grids using *t* tests. Mean tree size was compared by measuring the diameter at breast height (DBH) of the two dominant tree species—*B. graveolens* (*t* test) and *C. scouleri* (Mann Whitney *U* test). The species ratio was also compared using chi square analysis. Cactus size structure was similarly compared by classifying the 20 cacti according to the number of cladodes [0–25 (small), >25 (large)]. Other potential sources of environmental heterogeneity, for example, rainfall and sea spray, were minimised by the close proximity of the two grids (1.4 km apart) and the equal distance from the shore (100 m). Having established that the two sites were sufficiently homogeneous in microhabitat structure (see Results), 23 adult *N. swarthi* (11 females and 12 males) were radio-tracked between May and July 2002. Cable tie radio-collars (Biotrack Ltd, Dorset, UK), weighing less than 5% of each animal's body weight (Kenward 2001) were fitted under anaesthesia (halothane). Animals were tracked on foot using TR4 receivers (Telonics Inc. AZ, USA) and hand-held, flexible three-element Yagi antennas (Biotrack Ltd, Dorset, UK). Of this sample, 11 *N. swarthi* were tracked on the low density *R. rattus* grid and 12 *N. swarthi* were tracked on the high density *R. rattus* grid. Radio-tracking shifts alternated between 1600–0200 and 2200–0800 with a fix obtained for each of four animals every hour.

Only four animals were tracked in any one night and data were collected over a total of 26 nights. All analyses were carried out using programme Ranges6 (Kenward et al. 2003). Separate incremental analyses were carried out to check that the sample size (number of fixes) was sufficient for each animal. When delineating the home range, high use cores may be separable from peripheral areas that are seldom visited (Burt 1943; Kenward et al. 2001). To do this, we used cluster analysis with the single inclusive convex polygon method. Cluster analysis is a linkage method that clusters tracking fixes using nearest neighbour distances to form high use cores (Kenward et al. 2001). Inspection of area plots at increasing core percentages (5% increments) for each subject enabled selection of the high use core by the inflection in the curve of area versus percentage of locations. The 100% minimum convex polygon (MCP) estimate of home range area (i.e. the estimate before truncation) was also included. This estimate includes movements made by the animals out of the "home range" or high use core. The 100% MCP method was used to obtain the range span (R/span). All home range parameters were compared between high and low black rat areas. To assess temporal activity patterns, movement between subsequent hourly fixes indicted activity in that hour. To plot and analyse activity patterns on the high and low black rat areas the proportion of animals with at least one active fix at a particular time interval was calculated for each time interval between 1700 and 0800. Data were pooled across nights by classifying each individual as active for a particular time interval if there was movement between the two hourly fixes on any of the nights it was tracked. Not all individuals were tracked during all intervals. The proportion of active individuals was then calculated for each time interval. As the data for each time interval were therefore based on multiple animals tracked on multiple nights, the data were a mixture of repeated measures and independent data. Consequently, a separate 2×2 contingency table was analysed for each hour to compare activity between the high and low *R. rattus* areas. We also tested for correlation of nocturnal activity between the high and low *R. rattus* area and temporal variation in activity between these sites.

Spatial distribution

Data collected from the live-trapping in 2002 in May on the high and low density *R. rattus* grids described above and the later survey between December 2002 and January 2003 (the eight grids used to calculate the abundance–habitat correlations) were used to test for the presence of negative spatial association. Each trap (of 49 per grid) was assigned to one of four categories based on its history of occupancy: "*N. swarthi* only", "*R. rattus* only", "both species" or "neither species" over the 10 days. Fishers exact tests were used to test for interspecific spatial segregation as some expected values in the contingency tables were below 5 (Field 2000).

Microhabitat

Spool-and-line tracking was used to assess the microhabitat selection of *N. swarthi* and *R. rattus*. This method involves attaching a bobbin of thread (spool) to an animal the end of which is attached to vegetation or a rock at the release point. The spools unravel from the inside, so that as animals move through vegetation the thread plays out without resistance, attaching to vegetation and rocks or lava (Boonstra and Craine 1985). The trail can then be followed the next day and compared to the data from a control line oriented at a random angle from the start point to quantify microhabitat selection (Cox et al. 2000). This technique is simple, cheap and permits very fine scale analysis of behaviour that would not be possible using radiotelemetry or trapping (e.g. Boonstra and Craine 1985; Key and Woods 1996; Dennis 2002, 2003). In further support, a recent study has shown that the body mass, survival and trappability of kangaroo rats (*Dipodomys spectabilis*) is not biased by spool-and-line tracking and anecdotal observations suggest that behaviour is unaffected (Steinwald et al. 2006; M. Steinwald, personal communication). We conducted pilot trials to refine our technique and found that attaching the spools to the rump of *R. rattus* and between the shoulder blades of *N. swarthi* prevented them chewing them off. Allowing sufficient time for the adhesive to dry also minimised the probability of spool loss. Prompt return to the spooling site for spool line analysis minimised the likelihood of line breakage (probably caused by goats in most cases) which was distinguished from line termination by fraying of the cotton at the break point. In most cases the line reattached close to the break point (see also Key and Woods 1996).

Traps were set around dusk (1800) and checked between 2200 and 0200. Spools (quilting cocoons: Nm 140/2, Nylon size 7, 2.4 g, 155 m. Danfield Ltd., Leigh, Lancs., UK) were unravelled to an appropriate size and weight to fit each individual animal. Each spool was then wrapped in a casing of electrical tape to prevent snagging on vegetation. Final spool mass was checked to ensure that it did not exceed 5% of the body weight of the animal. This guideline is usually adhered to during radio-tracking studies to minimise the risk of affecting the animal's activity and behavioural patterns (Kenward 2001). Spools were attached to animals using cyanoacrylate glue (gel form). This adhesive has been tried and tested (Key and Woods 1996) and our pilot trials demonstrated that the spool case sloughs off shortly after the tracking without damage to the underlying skin. The end of the spool was tied to vegetation and the start position marked with flagging tape. Spool lines were analysed the following morning. Only lines of minimum length 30 m were analysed. The first 10 m was classified as a "flight response" and was not included in the analysis (Cox et al. 2000). Microhabitat variables were recorded over 5 m sections of line. The proportion of sections containing each of the following dominant shrub species; *C. molle*, *C. galapageia*, *L. peduncularis* and *Scutia spicata*, each of the two dominant tree species; *B. graveolens* and *C. scouleri*, and mature (>25 pads) and immature (0–25 pads) *O. galapageia* cactus were calculated. Trees and cacti were included in a given segment if the spool line passed under the canopy and/or within 2 m of the trunk. Finally, the proportional occurrence of broken lava was indexed by observation of 2 m radius plots at 10 m intervals within which the lava was coded as flat or broken/cracked. This analysis process was repeated along a straight line of equal length running in a random direction from the point of spool line attachment. This random line represented the microhabitat availability for that animal. Data were collected for 41 *N. swarthi* and 11 *R. rattus*. Data were screened for normality and microhabitat components extracted by factor analysis. A GLM (SPSS GLM > Univariate; SPSS v. 11) was then used to fit models to test if the difference between selected and random microhabitat on factor scores was statistically significant within and between species. The individual identity of rats was entered into these models as a blocking factor. These data were collected from six of the trapping grids throughout 2003.

Results

Current distribution

The hair tube survey identified ten sites that were inhabited by *N. swarthi* (Fig. 1). There was some initial uncertainty regarding hair classification at two sites (broken hairs) and hair tube tapes became damp and non-adhesive at a further two sites. However, post-hoc trapping at these sites as part of a study by CDRS personnel confirmed our predictions from the hair tube sampling (CDRS, unpublished data). The survey results confirm that *N. swarthi* is restricted to one population in *Opuntia* and *Bursera* thorn scrub habitat within the Arid Zone on the north-central coast of Santiago (Fig. 2). In contrast, *R. rattus* were present at all survey sites.

Habitat associations

The presence of *N. swarthi* at the hair tube survey sites was significantly correlated with the presence of mature cacti (*r*s(15)=0.577, *P*=0.024). All *N. swarthi*-occupied sites (nine of nine) contained mature cacti and cactus density was estimable at five of these sites [mean cactus density: 0.00239/m^2±0.000622 (1 SE)]. Individual cacti at the other sites were too wide-spaced for accurate measurement in the rugged terrain (see Materials and methods). Just two of the six unoccupied sites contained mature cacti and only one of these sites (north of James Bay) contained enough cacti for density estimation (0.000491/m^2). The density of shrubs and trees did not differ between occupied and unoccupied sites. However three of the unoccupied sites, those in the Sullivan Bay area, were mainly composed of barren lava with very little vegetation of any kind. As a result, shrub density was not measurable at any of these sites and tree density was estimable at just one of these sites (closest to La Bomba). The species composition of shrubs and trees on occupied and unoccupied sites was very different precluding statistical analysis. However,

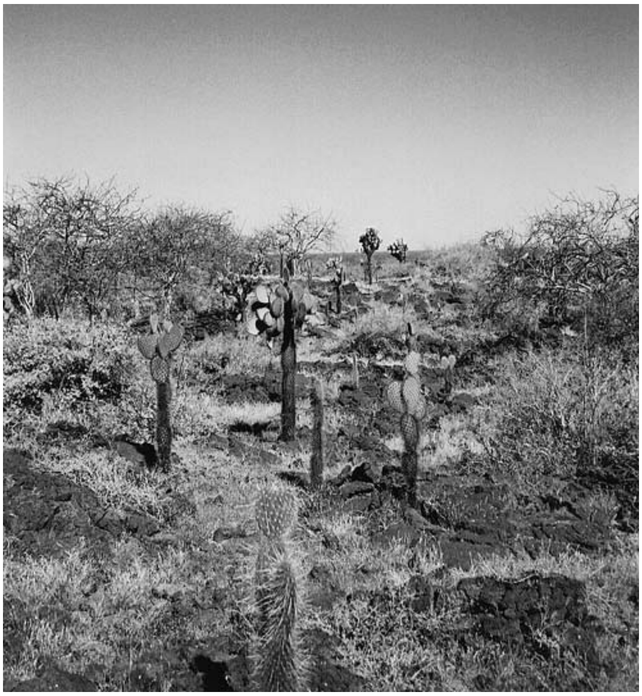

Fig. 2 *Opuntia* and *Bursera* thorn scrub habitat at La Bomba

the dominant shrub at occupied sites was *C. molle* (six of nine sites) and at unoccupied sites *C. galapageia* (two of four sites) with complete absence of *C. molle*. The tree species *B. graveolens* and *C. scouleri* were the dominant trees at seven of nine occupied sites and two of three unoccupied sites. At La Bomba the abundance of *N. swarthi* was positively correlated with cactus density ($r(6)=0.962$, $P=0.0001$) and the proportion of mature cacti ($r(6)=0.765$, $P=0.027$) but not with shrub density ($r(6)=0.689$, $P=0.059$). Of dominant plant species, *N. swarthi* abundance was positively correlated with *L. peduncularis* ($r(6)=0.880$, $P=0.004$) and negatively correlated with *C. galapageia* ($r(6) = -0.674$, $P=0.067$) and *B. graveolens* ($r(6) = -0.781$ $P=0.022$). A correlation matrix of the significant habitat variables showed that cactus density was strongly positively correlated with the proportion of mature cacti, shrub density and with proportion of *L. peduncularis* and strongly negatively correlated with *C. galapageia* and *B. graveolens* (all $r>0.7$). The abundance of *R. rattus* was not correlated with any of the microhabitat variables or with the abundance of *N. swarthi*. However, it was clear that the ratio of *N. swarthi* to *R. rattus* on the coastal grids (grids 1–4, Fig. 3), greatly exceeded the ratio inland which was closer to unity (grids 5–8, Fig. 3).

Spatio-temporal activity

The structure and composition of the habitat did not differ between the high (42 *R. rattus*:66 *N. swarthi*) and low (8 *R. rattus*:79 *N. swarthi*) black rat density areas confirming that the comparison of *N. swarthi* activity would not be biased by variation in measurable habitat variables. There was no significant difference in the index of *C. molle* ($P=0.234$), mixed shrub ($P=0.509$) tree ($P=0.380$) and *O. galapageia* ($P=0.677$) density. In addition, the mean size (volume) of individual *C. molle* plants ($P=0.224$) and mixed shrub plants ($P=0.460$) did not differ between grids. Mean tree size (DBH) did not differ between grids (*B. graveolens*: $P=0.147$ and *C. scouleri*: $P=0.550$) and tree species composition was similar ($P=0.686$). Cactus age composition was also comparable ($P=0.204$).

The home range area, MCP area and range span of males and females respectively (Table 1) were not significantly different on high versus low *R. rattus* grids ($P>0.1$ for all analyses using Mann Whitney U tests).

The proportion of active *N. swarthi* was significantly higher on the high *R. rattus* density grid at 0600 (sunrise) and marginally higher in the early evening, one hour prior to dusk, at 1700 ($\chi^2=7.213$, df=1, $P=0.007$ and $\chi^2=2.738$, df=1, $P=0.098$; Fig. 4). The variance structure of activity differed between grids (Levene's test: $F=5.640$, df=1, 30, $P=0.024$) and activity patterns were not correlated ($r(14)=0.493$, $P=0.053$). This appears to be due to the greater fluctuation in the proportion of active individuals during the latter half of the night/early morning on low *R. rattus* density grids compared with the higher, sustained proportion of

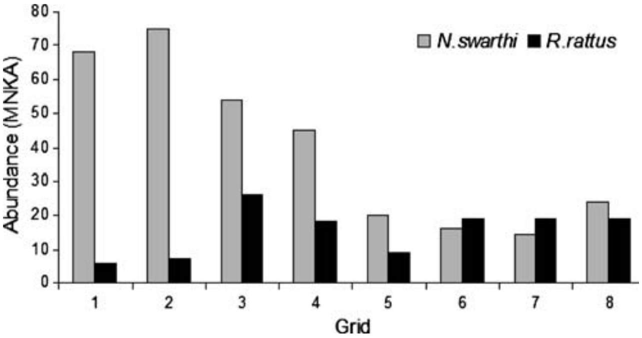

Fig. 3 Abundance (MNKA) of *N. swarthi* and *R. rattus* from live-trapping on four coastal (1–4) and four inland (5–8) grids at the start of the 2003 wet season (December 2002–January 2003)

Table 1 Home range area by mononuclear clusters truncated to % core (HR area), home range area by 100% minimum convex polygon method (MCP) and range span (R/span) of the 100% MCP for animals tracked on a low and high *R. rattus* density grid

R. rattus density	*N. swarthi* sex	*N*	% Core	HR area (ha)	MCP (ha)	R/span (m)
Low	Male	42	100	4.67	4.67	319
		18	100	1.5	1.5	173
		26	95	0.12	0.27	121
		33	95	0.63	1.12	129
		44	100	4.26	4.26	339
		42	90	1.57	4.07	376
		40	100	3.05	3.05	242
			Median	1.57	3.05	242
High	Male	31	100	1.97	1.97	223
		48	100	1.55	1.55	218
		58	95	3.12	9.56	528
		39	100	0.35	0.35	73
		32	95	0.58	1.13	144
			Median	1.55	1.55	218
Low	Female	27	95	0.22	0.97	236
		31	100	0.24	0.24	63
		43	95	0.65	2.13	229
		20	95	1.38	2.44	296
			Median	0.45	1.55	233
High	Female	41	95	0.19	0.31	90
		35	100	0.67	0.67	130
		35	95	0.34	0.68	111
		38	95	0.85	1.29	189
		28	100	0.53	0.53	100
		23	95	0.48	1.13	232
		16	100	0.41	0.41	79
			Median	0.48	0.67	111

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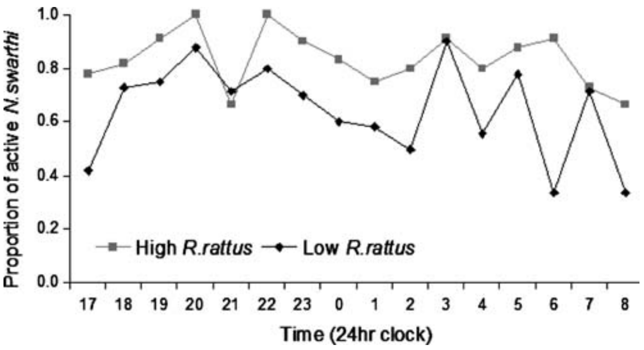

Fig. 4 The proportion of active individuals (*N. swarthi*) at hourly intervals (1700–0800)

active animals on high *R. rattus* grids throughout the night.

Microhabitat selection

Three components were extracted by factor analysis (eigenvalues > 1) which together explained 52.43% of the variation in the microhabitat dataset as revealed by spool-and-line analysis (Table 2).

Analysis of the paired (chosen versus random) data revealed that *N. swarthi* selected microhabitat type/component 2 (mature cacti and shrubs with broken lava) (F=31.274, df=1, 40, P<0.0001) and avoided microhabitat type/component 1 (trees and juvenile cacti) (F=8.652, df=1, 40, P=0.005). Use did not differ from availability for component 3 (mixed shrubs). Results are therefore consistent with the important plant species identified in the previous analyses. Similarly, *R. rattus* exhibited significant selection for microhabitat type/component 2 (F=14.078, df=1, 10, P=0.004) but use of the remaining microhabitat types was consistent with random. However, while it is likely that both rodent species use similar habitats, *R. rattus* is a subset (Fig. 5). This is probably due to the smaller sample of spooled *R. rattus*. The relative selection for each microhabitat did not differ between species (component 1: F=2.395, df=1, 50, P=0.128; component 2: F=0.060, df=1, 50, P=0.807; component 3: F=0.040, df=1, 50, P=0.843) and interspecific similarity in microhabitat use is evident upon inspection of the ordination plot (Fig. 5).

Table 2 Factor loadings for microhabitat variables within each component (eigenvalues > 1)

Plant species/lava type	Component		
	1	2	3
Bursera graveolens	0.671	−0.178	−0.075
Croton scouleri	0.721	0.159	0.303
Opuntia galapageia (juvenile)	0.595	−0.001	−0.531
Opuntia galapageia (adult)	0.381	0.543	−0.355
Clerodendrum molle	−0.046	0.483	0.545
Castela galapageia	0.470	−0.429	0.518
Lantana peduncularis	0.264	0.485	0.208
Scutia spicata	0.083	−0.409	0.370
Lava complexity	−0.103	0.690	0.204

Microhabitat types can be described as component 1, Trees (*B. graveolens* and *C. scouleri*) with *C. galapageia* and immature cacti; component 2, Shrubs (*C. molle* and *L. peduncularis*) with mature cacti and broken lava and component 3, Shrubs (*C. molle*, *C. galapageia* and *S. spicata*)

Spatial distribution

The distribution of species between trap types (*R. rattus* only, *N. swarthi* only, *R. rattus* and *N. swarthi* or neither species) in 2002 (two grids) and 2003 (seven grids) was not significantly different from random indicating that there was no significant negative (or positive) spatial association between individuals of the two species (Table 3).

Discussion

Our survey results reveal that the world population of *N. swarthi* is now restricted to a 14 km strip on the north-central coast of Santiago. There was no evidence

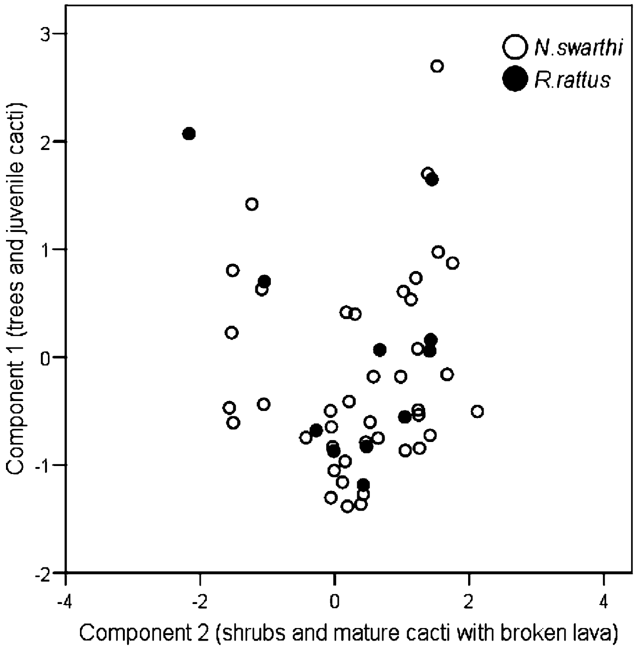

Fig. 5 Microhabitat use. Ordination plot of chosen spool route microhabitat data for the first two microhabitat components for *N. swarthi* (*open symbols*) and *R. rattus* (*closed symbols*)

Table 3 Contingency tables for trap occupancy in 2002 (two grids) and 2003 (eight grids)

2002, coast (grid 2)	*N. swarthi* +	*N. swarthi* −	*P*
R. rattus +	6	1	
R. rattus −	38	4	0.554
2002, coast (grid 4)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	27	8	
R. rattus −	9	5	0.476
2003, coast (grid 1)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	9	1	
R. rattus −	38	1	0.370
2003, coast (grid 2)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	5	1	
R. rattus −	42	1	0.232
2003, coast (grid 3)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	27	1	
R. rattus −	21	0	1.000
2003, coast (grid 4)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	34	0	
R. rattus −	15	0	Test invalid[a]
2003, inland (grid 5)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	13	6	
R. rattus −	20	10	1.000
2003, inland (grid 6)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	14	14	
R. rattus −	12	9	0.774
2003, inland (grid 7)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	9	20	
R. rattus −	7	13	1.000
2003, inland (grid 8)	*N. swarthi* +	*N. swarthi* −	
R. rattus +	17	7	
R. rattus −	20	5	0.520

[a] Grid 4, 2003 analysis was invalid as all traps were occupied by *N. swarthi*

of *N. swarthi* at, or in the vicinity of, Sullivan Bay, the area from which the type specimens were collected in 1906 (Orr 1938). In contrast, *R. rattus* has certainly colonised every Galápagos habitat from coastal desert to montane forest (Clark 1980) and our findings indicate that Santiago is no exception. These results therefore constitute the first evidence of *N. swarthi* range contraction since *R. rattus* introduction, substantiating the need to analyse the *N. swarthi*–*R. rattus* relationship at the last apparent stronghold.

Given that *R. rattus* is larger, more aggressive and behaviourally dominant to *N. swarthi* (D.B. Harris, unpublished data) it is surprising that interspecific densities were unrelated. Nevertheless, Hutchinson (1961) proposed that even under strong competition spatial and/or temporal heterogeneity could promote species coexistence. However, the investigation of interspecific spatial overlap demonstrated that the two species intermix freely in space. Under such conditions we may expect the home range size of the subordinate *N. swarthi* to vary with the density of *R. rattus*. For example, if interspecific competition is important then we may expect the home range to be larger where *R. rattus* density is lower (e.g. Trombulak 1985; Dickman 1986). Conversely, if resource competition predominates then we may expect home range to be smaller where *R. rattus* density is lower to reflect increased resource availability (e.g. Taitt 1981; Sullivan et al. 1983). However, home range delineation revealed no difference in the range size of *N. swarthi* in the high density *R. rattus* area compared to the low density *R. rattus* area.

Nevertheless, radio-tracking of *N. swarthi* on the high *R. rattus* density area revealed an intriguing trend towards increased activity levels and duration (including pre-dusk and post-dawn periods) compared to the low density *R. rattus* area. For comparison, a sample of 54 *R. rattus* radio-tracked in Hawaii showed peak activity between 2100 and 0300 (Tobin et al. 1996). As the activity pattern of *R. rattus* is believed to be fairly general it is likely that the species exhibits a similar activity pattern in the Galápagos (Barnett et al. 1975). *N. swarthi* on the low *R. rattus* grid show a comparable activity peak between approximately 2000 and 0300. However, on the high *R. rattus* grid they may be exploiting the low activity phase of *R. rattus* around dusk and dawn. This may reflect an increase in foraging effort necessary to compensate for the mutual exploitation of limited resources or may be a response to disturbance or interference by black rats in the vicinity. In natural desert rodent communities, the additional energy cost of extended foraging time has been shown to outweigh the benefits resulting in reduced foraging activity (Mitchell et al. 1990). The cost–benefit balance is uncertain here but there may be negative implications for the fitness of *N. swarthi* on high density *R. rattus* grids.

Finally, presuming that overlap in space and time correlates with the probability of encounter between the dominant *R. rattus* and subordinate *N. swarthi* we might expect there to be selection for microhabitat segregation. However, there were no interspecific differences in microhabitat use. In fact, both species strongly selected the same microhabitat type; areas containing large mature cacti, the typically expansive, dense shrub species *C. molle* and *L. peduncularis* and broken lava. This microhabitat type is found on the coast and is presumably ideal for rodents as it is composed of thick shrub cover and complex lava topography that together offer good protection from predators (hawks and owls) and relatively high food availability (shrubs and cacti).

Taken together these results suggest that the apparent coexistence of *N. swarthi* and *R. rattus* is not facilitated by spatial or temporal partitioning and that the two species have a high probability of encounter during normal activity. In other words, the data suggest that the species do not compete for space in the last stronghold where *N. swarthi* and *R. rattus* have been sympatric up to 400 years (Patton et al. 1975; Morris 1983). By comparison, *R. rattus* and *N. indefessus* were sympatric for just 4 years on Santa Cruz Island before the decline and extinction of the latter (Clark 1984). This anecdote, considered together with the apparent, and relatively recent (since 1906) loss of *N. swarthi* from Sullivan Bay, prompts us to ask: what is special about the final stronghold on the north-central coast of Santiago?

Our habitat investigations revealed a strong correlation between the occurrence of mature *Opuntia* cactus and the presence of *N. swarthi*. Indeed, the region occupied by rice rats appears to be unique in its habitat composition with a high density of mature *Opuntia* cactus. Furthermore, within this region, the abundance of *N. swarthi* was correlated with cactus density and the proportion of mature cacti. This may reflect a positive relationship between consumer (*N. swarthi*) and preferred resources in this chosen habitat (Rosenzweig 1991). The importance of *Opuntia* cactus to *N. swarthi* is further supported by a lack of *N. swarthi* reproduction on inland Arid Zone (low cactus) compared with coastal Arid Zone (high cactus) grids during a dry year (D.B. Harris, unpublished data). In contrast to the emerging *N. swarthi–Opuntia* relationship, *R. rattus* population density did not correlate with any of the main habitat components identified at La Bomba. The black rat is renowned for ecological flexibility which at least partly explains its success as a widespread invader (Clark 1980, 1981; Lehtonen et al. 2001; Courchamp et al. 2003; Russell and Clout 2004). This ecological plasticity coupled with behavioural dominance over *N. swarthi* may have given the black rat the competitive edge in the Sullivan Bay area which is composed almost entirely of lava with very little vegetation. It is feasible that competition is intensified in such habitat where interspecific encounter rate and/or resource overlap are likely to be higher. This may have led to the local displacement of *N. swarthi*. However, *N. swarthi* still appear able to occupy some suboptimal habitat in the presence of *R. rattus*. Within the Arid Zone at La Bomba, *N. swarthi* occurs in areas inland from the high density cactus core or probable "source habitat". However, its densities in these suboptimal habitats are notably lower (Fig. 3) and as mentioned, reproduction may cease under certain conditions suggesting that such low quality peripheral areas might act as "sink habitat" (Pulliam 1988; Pulliam and Danielson 1991; D.B. Harris, unpublished data).

In conclusion, there is no obvious spatial segregation and *N. swarthi* activity did not vary with *R. rattus* density. However, the falsification of our initial hypotheses through this preliminary exploration of pattern does not eliminate the premise of competitive coexistence in this system. Temporal variation in resource availability with intra- and inter-annual climatic fluctuation may provide the axis of environmental heterogeneity necessary for species coexistence (Kotler and Brown 1988). It has been demonstrated that food-limited *R. rattus* populations can undergo extreme fluctuations in density in Galápagos thorn scrub (Clark 1980). This almost certainly leads to occasional local extinction during dry periods in the Galápagos arid zone (Clark 1980). Importantly, this seems particularly feasible on the exceptionally arid, rain-shadowed north coast of Santiago (D.B. Harris, unpublished data). This periodic respite from interference by the larger *R. rattus* may be sufficient to allow coexistence of the two species without the need for *N. swarthi* to adjust its space use, habitat preferences and activity patterns. The other vital part of any mechanism of coexistence is a trade-off between the abilities of the competitors to utilise different parts of the axis (Kotler and Brown 1988). In this case the trade-off may be based on interference competition, resulting in behavioural dominance by the larger, aggressive *R. rattus*, perhaps with priority access to the most preferred resources during the wet, resource rich season while the native *N. swarthi* may be the superior, or exclusive, exploiter of the locally abundant endemic cactus, as suggested by the high *N. swarthi* to *R. rattus* ratio on the coastal trap grids (Fig. 3). The fruits of the *Opuntia* cactus are plentiful in the wet season and the succulent cladodes are available year round. Superior or exclusive exploitation of cactus may explain why *N. swarthi* is able to maintain stable population levels throughout the dry season when availability of alternative resources is low (D.B. Harris, unpublished data). Alternatively this trade-off may be described by resource partitioning as a consequence of exploitation competition. Further research is needed to define the resource axis of environmental heterogeneity and to distinguish between the alternative mechanisms of interference and exploitation.

Hypotheses for future testing

We hypothesise that the coexistence of *N. swarthi* and *R. rattus* is facilitated by temporal variation in resource availability (e.g. Ben-Natan et al. 2004) coupled with a difference in resource use which may have evolved to reduce competition and/or may be dictated by morphological or physiological feeding constraints (e.g. Jenkins and Ascanio 1993; Begon et al. 1996). As the presence or absence, microhabitat selection and abundance patterns of *N. swarthi* are all closely correlated with *Opuntia* cactus density, we speculate that cactus might be a crucial resource refuge for *N. swarthi*. Indeed, if *N. swarthi* were the superior exploiter or had exclusive access to *Opuntia* resources, then coexistence may be possible despite the likely costs of behavioural sub-ordinance to aggressive interference (Keddy 2001; D.B. Harris, unpublished data). This hypothesis should direct future research towards a study of interspecific diet relations across seasons, with particular emphasis on the role of the cactus as a resource refuge. Interestingly, preliminary captive observations show that individual *R. rattus* either will not, or are unable to, consume cactus fruits even when the fruits are opened and pulp exposed. Furthermore, while *N. swarthi* regularly climb and forage in the cactus canopy, we have no evidence for ascent of cacti by *R. rattus* (D.B. Harris and S.D. Gregory, personal observation).

It is important to note that implicit within our coexistence hypothesis is the assumption that the two species compete. The historical pattern of Galápagos rodent extinctions certainly suggests that *R. rattus* is reducing the survival of *N. swarthi* in its last apparent stronghold. However, there is no unequivocal, scientific evidence to support our postulation. We therefore recommend the use of a replicated "press experiment" (sensu Bender et al. 1984). This would involve repression of *R. rattus* density in experimental plots. The demographic response of individual *N. swarthi* to *R. rattus* density repression should then be monitored with a focus on vital rates such as survival and fecundity (Krebs 1995; Begon et al. 1996; Eccard and Ylonen 2003). Any impact of *R. rattus* on *N. swarthi* should then be compared in low versus high density cactus areas to test for habitat-dependent competition which may provide further support for the proposed mechanism of competition. We predict that competition will be more severe in low density cactus habitat.

In the meantime, a thorough search of high density cactus patches on other islands may reveal further extant populations of "extinct" Galápagos rodents.

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