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Prickly coexistence or blunt competition? *Opuntia* refugia in an invaded rodent community

Stephen David Gregory · David W. Macdonald

Abstract Endemic *Nesoryzomys swarthi* and invasive *Rattus rattus* exist in unlikely sympatry in Galápagos as female *N. swarthi* suffer from competition with *R. rattus*. This study evaluates the role of feeding habits in facilitating their co-occurrence. Spool-and-line tracking of 85 *N. swarthi* and 33 *R. rattus* was used to quantify their selected diets, foods of which were used in captive trials of 46 *N. swarthi* and 34 *R. rattus* to quantify their preferred diets. Selected diets were compared between species and seasons using niche measures, and contrasted to preferred diets to qualify inferences about competition. Diet overlap was highest in the wet season when food—particularly fruit—abundance was highest and *R. rattus* diet breadth was broadest. Preferred and selected diets were marginally correlated for *R. rattus* but uncorrelated for *N. swarthi*, suggesting that *R. rattus* interfere with *N. swarthi* foraging. Diet overlap was highest between female *N. swarthi* and *R. rattus*, perhaps due to female breeding requirements. Male *N. swarthi* avoided *R. rattus*-preferred foods, possibly to avoid aggressive encounters with *R. rattus*. During the dry season, when foods declined and the *R. rattus* population crashed, diet overlap was lowest as *R. rattus* diet narrowed in the absence of fruits. Female, and particularly male, *N. swarthi* diet broadened, with emphasis on acquiring *Opuntia* foods but *N. swarthi*-preferred and selected diets were uncorrelated, suggesting that their foraging was inhibited by *R. rattus*. In conclusion, the narrower diet breadth of *R. rattus* in contrast to *N. swarthi* suggests that this species may be less adapted to food acquisition at this site, particularly when fruits are absent. The year-round presence of *R. rattus*, however, appears to inhibit *N. swarthi* foraging for its preferred diet, and they instead specialise on *Opuntia* foods, which were uneaten by *R. rattus* and may provide *N. swarthi* with a localised competition refuge from encounters with *R. rattus*.

Keywords Competition refuge · Diet partitioning · Invasive species · *Nesoryzomys swarthi* · *Rattus rattus*

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S. D. Gregory · D. W. Macdonald
Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK

Present Address:
S. D. Gregory (✉)
Ecologie, Systématique et Evolution, Université Paris-Sud XI, Bâtiment 362, 91405 Orsay Cedex, France
e-mail: stephen.gregory@u-psud.fr

Introduction

Empirical investigations of species coexistence can, and frequently are, presented in a common trade-off-based conceptual framework called niche theory (e.g. Bryce et al. 2002). According to this framework, the niche of each species is quantified as a hypervolume, with axes corresponding to measures of their requirements (Hutchinson 1957) and contrasted using measures of niche overlap (Colwell and Futuyma 1971; Schoener 1974; Hurlbert 1978; Petriatis 1979). To coexist, the theory states that one or more species must accept a trade-off on at least one axis of requirement, thereby permitting the species to share limited resources (Gause 1934). Over time, the continued acceptance of this trade-off may lead to the niche being partitioned, thus promoting long-term coexistence (Vandameer 1972).

Naturally occurring rodent communities provide extensive empirical support for niche partitioning, with communities shown to segregate space (e.g. Morris 1996), time (e.g. Kronfeld-Schor and Dayan 2003) and diets (e.g. Driessen 1999). If, however, ecologically similar species are brought together unnaturally, as occurs in a biological invasion, the lack of co-evolutionary time and subsequent niche partitioning should intensify the struggle for coexistence (MacArthur and Levins 1967). This prediction is supported by several recent mammalian extinctions that have been attributed, at least in part, to the effects of an alien species (for a review, see MacPhee and Flemming 2001). Most of these mammalian extinctions have occurred in the Galápagos Islands, where an extensive range of anecdotal evidence has led many authors to speculate that the extinction of 9 of 12 Galápagos rice rat species was a result of competitive exclusion by the recently introduced alien species *Rattus rattus* (Clark 1984; but see Dexter et al. 2004 for an alternative hypothesis). In 1997, however, an expedition to the North coast arid zone of Santiago rediscovered a small population of one of these previously presumed extinct species, *Nesoryzomys swarthi*, in sympatry with *R. rattus* (Dowler et al. 2000). This rediscovery presents a rare opportunity to study the mechanism(s) underpinning species coexistence in a recently invaded rodent community.

Several lines of evidence place the rediscovery of *N. swarthi* alongside *R. rattus* at odds with the prevailing competitive exclusion hypothesis of Galápagos rodent extinctions. Recent work suggests that they are sympatric throughout the range of *N. swarthi*, and that within this range they share a preference for the same microhabitat and are active throughout the night (Harris et al. 2006). Taken together (but conceding that nothing is known about *N. swarthi* interactions with sympatric house mice, *Mus musculus*, or their predators the barn owl, *Tyto alba punctatissima*, or short-eared owl, *Asio flammeus galapagoensis*) these findings suggest that the two species have substantial niche overlap in space and time, a necessary condition for competition (Gause 1934). Indeed, an experimental impact assessment of *R. rattus* on *N. swarthi* has revealed evidence that smaller female *N. swarthi* were more likely than males to be displaced in aggressive encounters with the behaviourally dominant *R. rattus*, resulting in a net negative impact of *R. rattus* on *N. swarthi* (Harris and Macdonald 2007a). Nevertheless, these rodent species have been sympatric for an unusually long period (up to 400 years: Patton et al. 1975) when compared, for example, with the reported displacement of *N. indefessus* by *R. rattus* from the neighbouring island of Santa Cruz over a period of just 4 years (Rambech 1971, as cited in Clark 1984), and the reason(s) for this remain unclear (Harris et al. 2006; Harris and Macdonald 2007a).

Recent theoretical developments in species coexistence suggest that rodent species might coexist through their different capacities to survive in spatially (e.g. Amarasekare 2003) or environmentally variable environments (e.g. Chesson and Warner 1981) and that these capacities may differ between seasons (e.g. Rosenzweig and Abramsky 1997) and sexes (e.g. Monamy and Fox 1999). In the Galápagos, arid zone *R. rattus* populations crash during periods of drought when foods are limited (Clark 1980), while *N. swarthi* maintains a year-round stable population (Harris and Macdonald 2007b). This imbalance could create a state of constant competitive disequilibrium that seasonally alleviates the impact of *R. rattus* on *N. swarthi* (Chesson and Warner 1981; Rosenzweig and Abramsky 1997). Perhaps this difference in the species' responses to the decline in foods could be a consequence of their diet selection. For example, the increasing cost incurred when foraging for a progressively diminishing preferred food may ultimately result in reduced fitness of the consumer (Armstrong and McGehee 1980). Conversely, a consumer might switch its preferences to exploit an abundant food, thereby maintaining its fitness (Kotler and Brown 1988).

Nothing is known of the dietary habits of *N. swarthi* nor of *R. rattus* at this locality and so the overarching aim of this investigation was to evaluate the role of diet partitioning in facilitating their co-occurrence at La Bomba. In common with the few reported investigations of coexistence in invaded communities (e.g. Bryce et al. 2002), dietary habits were analysed using niche measures, and the feasibility of diet partitioning was appraised according to predictions of trade-off-based models. Based on our knowledge of the population dynamics of *N. swarthi* and *R. rattus* at La Bomba, and the nature and mechanism of their competitive interactions, predictions from a combination of several models were expected to characterise the niche dynamics of this system. We hypothesised that (1) each species' diet breadth would be broad when foods were abundant (Schoener 1982), (2) *R. rattus* diet breadth would remain broad during food shortage because it is behaviourally dominant to *N. swarthi* (Case and Gilpin 1974), and (3) the seasonal crash in the *R. rattus* population would allow *N. swarthi* to maintain a broad diet during periods of food shortage (Abrams 1986). In terms of diet overlap, these predictions would equate to similar levels of overlap throughout the wet and dry seasons at La Bomba.

To test these predictions while stemming sources of error inherent in these types of analysis, a novel mix of methods was employed to measure the selected and preferred diets of each species. Spool and line tracking was used to identify, without bias, those plants visited by foraging individuals of each species (Colwell and Futuyma 1971; Holt 1987) and quantify their selected diets under field conditions of sympatry. Captive diet selection trials

were used to quantify the preferred diet of each species when offered selected foods in the absence of their competitor, which were then used to qualify statements regarding the highly contested relationship between niche overlap and competition (e.g. Abrams 1980; Lawlor 1980). In addition to the main aim of this investigation, the results reported here also represent the first description of *N. swarthi* feeding habits and a detailed description of arid zone *R. rattus* feeding habits in the Galápagos.

Methods

Study site and seasonality

This study was carried out during 2004 at a site known locally as La Bomba, situated on the central north coast of Santiago in the Galápagos archipelago. The prevailing trade winds that bring rain to the Galápagos approach from the south-east so that Santa Cruz and the highlands of Santiago cast a combined rainshadow over La Bomba. This results in an arid habitat characterised by the cactus *Opuntia galapageia* var. *galapageia* (Og), trees [*Bursera graveolens* (Bg), *Cordia lutea* (Cl) and *Croton scouleri* (Cs), plus an additional tree], shrubs [*Clerodendrum molle* var. *molle* (Cm), *Castela galapageia* (Cg), *Lantana peduncularis* (Lp), *Scutia spicata* var. *pauciflora* (Ss), and *Vallesia glabra* (Vg), plus another four shrub species], and 21 vine and herbaceous plants excluding grasses.

Galápagos is subject to two distinct seasons. The first, known as the hot wet season (hereafter "wet") spans January to May and sees the arrival of the rains (average rain >50–70 mm/month) and daily temperatures ranging from 26 to 30°C. The second, a "dry" season known as the garua season, spans June to December and gets its name from the local word for the perpetual mist engulfing the highlands throughout this season. Coastal regions are very dry during the garua season (average rain <10 mm/month) with daily temperatures ranging from 20 to 24°C (data courtesy of the Charles Darwin Research Station). Approximately once every 3–7 years this dichotomous pattern is broken with the arrival of El Niño (Webster and Palmer 1997), resulting in prolonged and frequently intensified hot-wet season conditions that promote growth and reproduction of terrestrial organisms (Snell and Rea 1999). This study was carried out over both seasons in a non-El Niño year, and analyses were carried out separately for each season using R (R Development Core Team 2008) unless otherwise specified.

Detection of potential food plants

No previous studies have reported the feeding habits of *N. swarthi*, and no studies have been undertaken on arid zone *R. rattus* at La Bomba so it was first necessary to identify plant foods. Spool-and-line tracking was used to determine those plants selectively visited by each rodent species in the field. Briefly, spool-and-line is a tracking technique whereby a cotton bobbin encased within a protective cover is affixed to an animal and the free end is tied to a stationary object before the animal is released to undertake its normal activity. As the animal moves the line plays out from the centre of the bobbin and catches on vegetation/terrain as it passes. Under optimal conditions, like those at La Bomba where the characteristically broken "aa" lava readily caches spool line (Key and Woods 1996), the resulting line can be followed and the animal's movements recorded at a very fine scale (for further discussion of this method, see Harris et al. 2006; Boonstra and Craine 1986). Although plants may have been visited for reasons other than foraging, the likelihood of the tracked individuals being hungry was maximised by capturing them from first emergence (1700 hours) in Tomahawk Live traps (Model 201, Tomahawk Live Trap, Tomahawk, WI) baited with peanut-scented rag and spooling them approximately 4 h later. Weight and sex were recorded for all captures and each was given an individual mark so that it was not mistakenly spooled more than once in each season. Before release at its point of capture, each individual was fitted with a No.7 cotton bobbin (Danfield, Leigh, UK) adapted to weigh less than 5% of its body weight.

Analysis of the spool-line (=Chosen) was carried out the following morning. Lines were usually longer than 70 m and the first 10 m of the line was considered to constitute a flight response and was not analysed. Thereafter, the presence of any plant part [defined as leaf (L), fruit (F), flower (R), seed (S) or cactus pad (P)] was recorded above and within a 10 cm band either side of the line for each 1 m segment of alternate 5 m sections (i.e. 1, 2,…, 5, 11, 12,…, 15, etc.). In order to provide a measure of the plant parts available to each individual, a line transect of the same length radiating in a random direction from the start point of the Chosen line was analysed in the same way (=Random).

Firstly, to determine if the spooled animals were selectively visiting particular plant species, data recorded for each plant part (i.e. L, F, etc.) were pooled by plant species for each Chosen and Random line. The resulting measures of plant visitation and availability were then ordinated using detrended correspondence analysis (DCA; Hill and Gauch 1980), whereby the plant species was used as the measure of "species" and the line type represented "site". While using DCA to ordinate the Random data alone would reveal any pattern underlying the plant community, incorporating the Chosen data, which is heavily biassed towards plants visited by the

foraging animals, would reveal any selectivity gradient (Bryce et al. 2002). DCA was chosen over other existing multivariate methods of ordination because the underlying iterative algorithm—reciprocal averaging—results in scores that incorporate both a measure of the samples containing the species and a measure of the species in the sample (Hill 1973), so better accounting for highly selective individual animals (Bolnick et al. 2003). DCA results in orthogonal and normally distributed sample scores for the first extracted axis that were used to compare Chosen and Random lines on the first extracted axis using a two-way univariate ANOVA with the animal ID as a blocking factor. The second DCA axis was not interpreted as DCA has well-known distortions for higher axes (Hill and Gauch 1980).

Following the use of DCA to determine if animals were being selective, another reciprocal averaging analysis, two-way indicator species analysis (TWINSPAN), was used to classify decisively each plant species into either a Selected or Avoided group. This method was employed to overcome the human subjectivity otherwise inherent in determining the importance of each plant species (Colwell and Futuyma 1971). To promote decisive classification based on a selectivity criterion, both the Chosen and Random data were input into the analyses and the cut-off points were set from 1. Both DCA and TWINSPAN were undertaken using the Community Analysis Package v.3.0 (Henderson and Seaby 1999).

Palatability of plant parts and preferred diet

Plant parts from the selected plants were offered to wild-caught animals held in captivity to determine which were used as foods, and to assess their relative preference in the species' diets. The plant parts offered were from plants selected by either or both species to overcome any bias in plant visitation caused by interspecific competition (Pimm et al. 1985). Animals used in the trials were captured and processed following the same protocol used for those animals tracked with spool-and-line.

Trials were designed so that animals selected foods under a perceived threat of predation. Animals were trialled individually at their point of capture in plastic crates (57 × 36.5 × 30.5 cm) fitted with wire mesh lids so as not to preclude the animals' awareness of aerial predators. A refuge was provided at one end of the crate to which animals could retreat. The predation threat associated with each food under natural conditions was not known; to account for this uncertainty the foods were provided ad libitum in separate Petri dishes at different distances from the refuge and their locations were randomised before each trial. Free water is extremely scarce at La Bomba and therefore was not provided. All of the plant parts were

harvested from the locality within 1 h prior to commencement of the trial, and care was always taken to select only mature fruits and seeds as described in a plant guide (McMullen 1999). Trials were undertaken shortly after emergence and terminated after 1 h as at least one species of rodent has been shown consistently to consume a larger range of foods early in the evening than during other periods of the night (Plesner-Jensen 1993). At the end of the trial, the food remains were collected and weighed, accounting for inedible parts.

Selected and preferred diet measures and comparisons

Niche measures were chosen to quantify each species' selected diet (from the spool-and-line tracking) and preferred diet (from the food preference trials). The mean of all individual's proportional utilisation of each food was taken to represent the species' selected and preferred diets. Overlap measures were calculated using the FT index proposed by Smith and Zaret (1982):

$$FT = \sum \sqrt{p_{1i} \times p_{2i}}$$

where p_{1i} and p_{2i} represent the proportions of the ith food visited/eaten by species 1 and 2, respectively. The value of FT varies between 0 and 1, representing no overlap and complete overlap, respectively. Smith and Zaret (1982) demonstrated that the FT was among the least biased measures of overlap, and that it was unaffected by unequal sample sizes. Food availability was not included in overlap calculations because individuals of both species were tracked throughout the same habitat and within a short time-frame such that differences in individual resource availabilities would be similar for both species and would not affect measures of niche overlap (Lawlor 1980). Since this treatment resulted in single measures that precluded statistical testing (Smith 1982), randomisation tests were used to compare "groups" of animals (i.e. species within seasons, sexes within species, etc.) to strengthen qualitative inferences. Randomisation distributions of 1,000 FT values were constructed by bootstrapping the original data for the groups under scrutiny, calculating FT for the bootstrap samples, and repeating 1,000 times (Mueller and Altenberg 1985). This method captured the variation in the raw data and allowed the calculation of 95% confidence intervals as the 2.5% and 97.5% values of the sorted FT randomisation distribution. To determine if two FT values differed, the differences between all the unsorted values of the two FT randomisation distributions were used to construct a randomisation distribution of 1,000 difference values from which the 95% confidence range of the true difference was drawn. If the 95% confidence range of the difference did not overlap 0 then the distributions were considered to be substantially dissimilar.

Measures of selected and preferred diet breadth were calculated using Hurlbert's niche breadth measure (Hurlbert 1978):

$$B = 1 \bigg/ \sum (p_i^2 / q_i)$$

where p_i and q_i represent the proportions of the ith food visited/eaten and available, respectively. B was standardised to vary between 0 and 1, representing exclusive utilisation of one food and equal utilisation of all the foods, respectively (B'; Hurlbert 1978). Food availability, considered important in delineating breadth measures (Hurlbert 1978), was set to be equal in measures of preferred diet breadth (equal to $1/i$), but for the selected diet breadth, availability was calculated as the mean proportional occurrence of each food type on the Random lines. In this way, the difference in food availability in the field and captive conditions was accounted for in diet breadth measures. Niche breadth measures are biased, and choice of a measure is dependent on whether common or rare resources are important. Unlike other measures, Hurlbert's B' does not underestimate the importance of rare foods that might be critical during periods of food scarcity when competitive interactions should be strongest (Krebs 1999). The bootstrap approximated 95% confidence range was calculated as for FT as a measure of variation in B' and to assess the differences in B' between groups.

To support inferences of interspecific competition, foods were ranked based on their mean proportional utilisation after accounting for their availability, and compared between selected and preferred diets using Kendall's tau-b test of concordance. High correlation between a species' selected and preferred diets indicated that it was obtaining its preferred diet when in sympatry. Comparisons were made between *N. swarthi* and *R. rattus*, between both sexes of *N. swarthi* and between each sex of *N. swarthi* and *R. rattus*. Separate sex comparisons were not drawn for *R. rattus* due to small sample sizes for the separate sexes.

Invertebrates

The main drawback of using spool-and-line tracking to quantify selected diet is its inability to detect motile invertebrates. To overcome this deficiency, invertebrate consumption by each species was quantitatively compared by way of faecal analysis. Faecal pellets were collected from traps occupied by different individuals and were stored in 70% ethanol until they were transported to the laboratory for analysis. A sample of two pellets for each animal were soaked in soapy water and individually teased apart in a Petri dish under a binocular microscope ($\times 40$ magnification) (Luo et al. 1994). The area of the ocular view containing chitinous insect remains was estimated to

the nearest 10% with the aid of a graticule and repeated for five independent views. An average % cover was derived for each animal, which were then grouped by species and sex and compared within and between seasons in ANOVA.

Results

Food identification

Over 30 m of Chosen spool-line data were collected for each of 44 *N. swarthi* (23♀/21♂) and 15 *R. rattus* (8/7) in the wet season and 41 *N. swarthi* (21/20) and 18 *R. rattus* (13/5) in the dry season along with the corresponding Random line data (S1). These data were ordinated together using DCA to reveal any underlying selectivity. The first two extracted axes explained 30.4 and 45.0% of the variation in the *N. swarthi* spooling data, and 54.5 and 86.1% of the variation in the *R. rattus* spooling data in the wet and dry seasons, respectively. DCA biplots constructed for each species in each season (Fig. 1) revealed a general trend for Random samples to cluster around the centre and left side of DCA 1, and the Chosen samples to fall to the right. It was hypothesised in the Methods that such a spread would emerge if DCA weighted the Random lines by gradients underlying the plant community but the Chosen lines by a selectivity gradient caused by animal selectivity. Indeed, the emergence of this spread in all the samples (but to a lesser extent in *N. swarthi* selection in the wet season) suggests that the method extracted a DCA axis that could represent a selectivity gradient increasing in strength from the left side of the axis to the right. To test if DCA 1 could be considered a measure of selectivity, Chosen and Random sample scores along DCA 1 were compared for each species by two-way univariate ANOVA with individual ID as a blocking factor (Table 1). Both *N. swarthi* and *R. rattus* Chosen sample scores were significantly higher than their corresponding Random scores in both seasons, and individual selectivity was significant for *N. swarthi* in both seasons and *R. rattus* in the wet season only. The variation in the selectivity of individual *R. rattus* foraging in the dry season was not significant, suggesting that all of these animals visited similar plants regardless of the location in which they were spooled.

No discernible clustering of plant species is perceptible in Fig. 1; however, a comparison of the location of individual plant species along DCA 1 between seasons shows a high degree of consistency for each species. TWINSPAN was used to classify the plant species after one division (i.e. into one of two groups). The group with the positive TWINSPAN indicator species was the Selected group. In each biplot, the ellipse encapsulates the Selected plants (Fig. 1) and it can be seen that the plant species in the
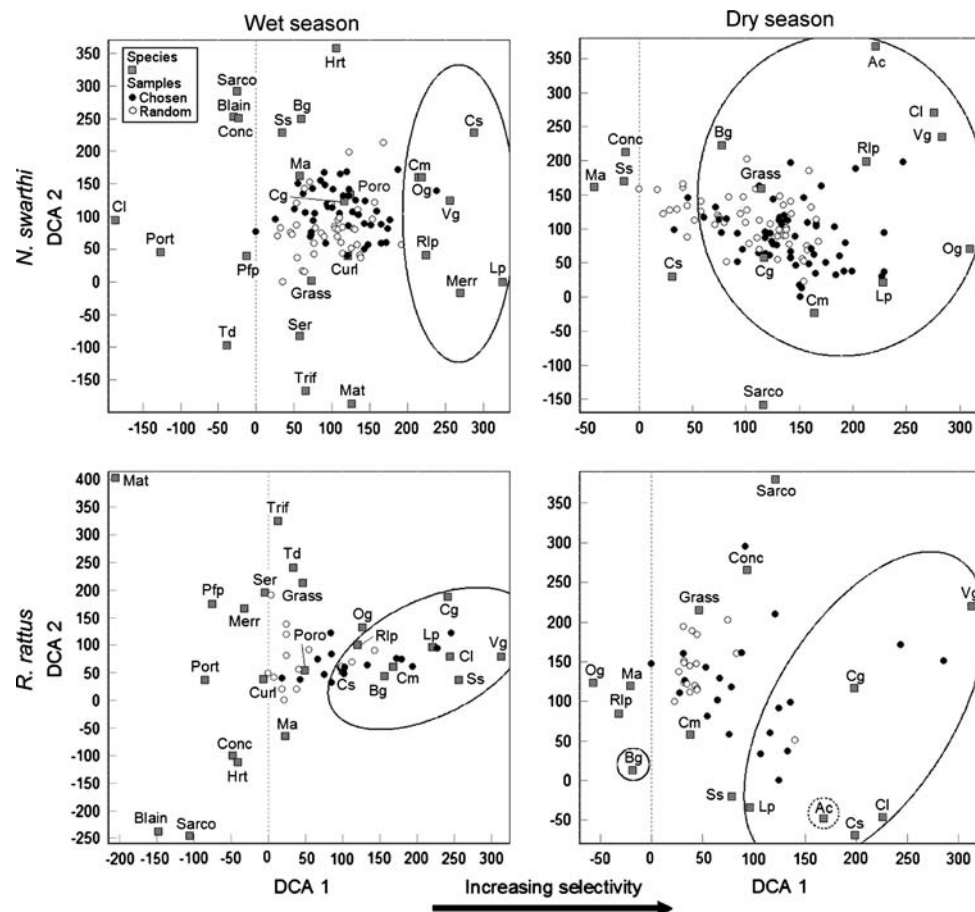
Fig. 1 Detrended correspondence analysis (DCA) joint plots of *Nesoryzomys swarthi* and *Rattus rattus* selectivity in the wet and dry seasons, respectively. Axis 1 corresponds to a selectivity gradient increasing from left to right (see text). *Ellipses* encapsulate the plant species classified as Selected by TWINSPAN analysis. A *broken line ellipse* encapsulates Ac because it was not classified as Selected by TWINSPAN. Plant abbreviations: *Bg Bursera graveolens*, *Cl Cordia lutea*, *Cs Croton scouleri*, *Ac Acacia rorudiana*, *Curl Desmodium procumbens*, *Ma Mentzelia aspera*, *Pfp Boerhaavia caribaea*, *Conc Tetramerium nervosum*, *Port Portulaca oleracea*, *Blain Blainvillea dichotoma*, *Td Tephrosia decumbens*, *Mat Tiquilia nesiotica*, *Poro Porophyllum ruderale*, *Merr Merremia aegyptica*, *Cm Clerodendrum molle*, *Lp Lantana peduncularis*, *Vg Vallesia glabra*, *Ss Scutia spicata*, *Cg Castela galapageia*, *Sarco Sarcostemma angustissimum*, *Og Opuntia galapageia*, *Hrt Ipomea triloba*, *Ser*, *Trif*, *Grass*, *Rlp* Unidentified

Selected groups consistently fall on the right side of Axis 1 [*B. graveolens* (Bg) and *Acacia insulae* (Ac) give exception to this rule for *R. rattus* in the dry season].

Twenty-three *N. swarthi* and 17 *R. rattus* were offered plant parts from Selected plants in both the wet and dry seasons. No individual ate herbaceous plant parts nor flowers or leaves from woody plants, and consequently these were excluded from further analysis. The remaining plant parts were eaten by both species in both seasons with the exception of *O. galapageia* fruit, which was not eaten by *R. rattus* in either season.

Seasonal food availability

Foods selected by both species were all highly seasonal, with the exception of *O. galapageia* pads, *V. glabra* fruits and *C. molle* seeds, which changed little in their availability between the wet and dry seasons (Fig. 2). Fruits of *B. graveolens* and *S. spicata* were absent at La Bomba during the dry season and *O. galapageia* fruits were effectively absent in the wet season.

Overlap in *N. swarthi* and *R. rattus* diets

When sympatric with *R. rattus* in the wet season, *N. swarthi*'s selected diet consisted primarily of *O. galapageia* fruits and pads (Fig. 3a), and this specialisation was embodied in a moderately narrow measure of niche breadth (Table 2). Similarly, *R. rattus*' selected diet breadth was also narrow, although it ate primarily *V. glabra* and *C. lutea* fruit (Fig. 3a). Both species ate comparable amounts of *B. graveolens* and *S. spicata* fruits in this season, resulting in similar diet breadths (difference = 0.14; 95% confidence range = −0.25, 0.48) and high selected diet

Table 1 Partial ANOVA tables for comparison of chosen and random line sample scores on Axis 1 of detrended correspondence analysis (DCA) ordinations in each season

Effect	n	df	Mean squares	F	P
Nesoryzomys swarthi					
Wet					
Individual	44	43	2,598.548	2.551	0.001
Line		1	5,648.011	5.546	0.023
Error		43	1,018.476		
Dry					
Individual	41	40	3,085.353	3.850	<0.001
Line		1	36,162.000	45.125	<0.001
Error		40	801.375		
Rattus rattus					
Wet					
Individual	15	14	14.591	2.647	0.040
Line		1	149.553	27.134	<0.001
Error		14	5.512		
Dry					
Individual	18	17	5.624	1.103	0.421
Line		1	32.836	6.438	0.021
Error		17	5.100		
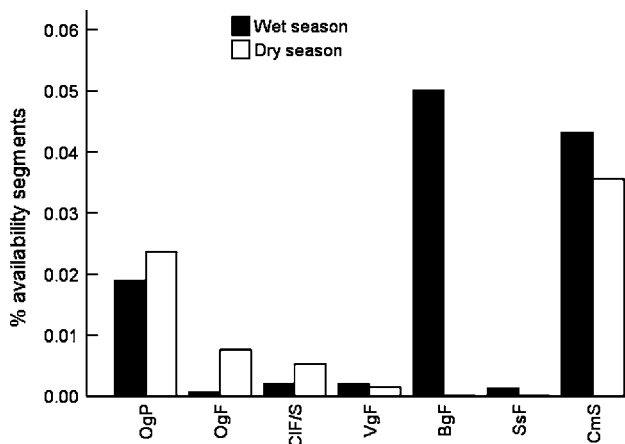
Fig. 2 Food availability (as the percentage of segments in which each food was present on *Random lines*) in both seasons. Plant part abbreviations: *OgP Opuntia galapageia* pad, *OgF O. galapageia* fruit, *ClF Cordia lutea* fruit, *ClS C. lutea* seed, *VgF Vallesia galabra* fruit, *BgF Bursera graveolens* fruit, *SsF Scutia spicata* fruit, *CmS Clerodendrum molle* seed

overlap (Table 3). The breadth of *N. swarthi* selected diet was similar to its preferred diet (−0.21; −0.47, 0.12); however, the rank order of foods in each diet were not correlated (Kendall's tau-b; $W = 0.138$, $P = 0.702$) as illustrated by the low rank of *B. graveolens* fruit in its selected diet compared to its preferred diet and *O. galapageia* fruit that were selected but not preferred (Fig. 3b).

In contrast, *R. rattus*' selected and preferred diet breadths were also similar (−0.19; −0.36, 0.14) but the food ranks in each diet were marginally correlated ($W = 0.690$, $P = 0.056$; Fig. 3b).

As in the wet season, the selected diets in the dry season consisted primarily of *O. galapageia* foods for *N. swarthi* and *V. glabra* fruits and *C. lutea* seeds for *R. rattus* (Fig. 3c). The breadth of *N. swarthi* selected diet was narrower in the wet season compared to this season (−0.40; −0.67, −0.06), and was broader than that of *R. rattus* in this season (0.62; 0.33, 0.78). The selected diet of *R. rattus*, on the other hand, remained similarly narrow between seasons (Table 2). Despite the broadening of *N. swarthi* diet breadth in this season, selected diet overlap was similar to that observed in the wet season (Table 3). Foods were ranked differently in *N. swarthi* selected and preferred diets ($W = 0.000$, $P = 1.000$) as is evident from its use of *C. lutea* and *C. molle* seeds (Fig. 3d), and its selected diet breadth was broader than its preferred diet breadth (0.13; −0.03, 0.32; Table 2). In contrast, *R. rattus*' diet breadth was similar for its selected and preferred diets (−0.07; −0.23, 0.18), and again food ranks were marginally correlated between them ($W = 0.738$, $P = 0.077$; Fig. 3d).

Overlap in separate sex *N. swarthi* and *R. rattus* diets

In the wet season, male *N. swarthi* were highly specialised and their selected diet consisted principally of *O. galapageia* fruits, *O. galapageia* pads and *S. spicata* fruits (Fig. 4a). Female *N. swarthi*'s selected diet was less specialised than that of males, though not substantially (−0.17; −0.66, 0.26; Table 2), and incorporated *C. lutea* and *V. glabra* fruits (Fig. 4a). Although intersexual overlap in selected diet was high in this season, differences in their diet breadths manifested as an important difference in their diet overlap with *R. rattus*, which was higher for females than for males (−0.19; −0.38, 0.04; Table 3). Male *N. swarthi* selected diet breadth was marginally narrower than that of its preferred diet (−0.35; −0.57, 0.04) because it additionally selected *C. lutea* and *V. glabra* fruits in small amounts as part of its preferred diet (Fig. 4b). In contrast, the measure of female *N. swarthi* preferred diet breadth was not different to that of its selected diet (−0.12; −0.47, 0.41; Table 2), and all foods were present in both diet measures (Fig. 4b). Nevertheless, food ranks were uncorrelated for both sex's selected and preferred diets (male: $W = −0.276$, $P = 0.444$; female: $W = −0.138$, $P = 0.702$). Fruit of *B. graveolens* was the preferred food of both male and female *N. swarthi*; however, it was not ranked highly in either sex's selected diet in this season. Both *B. graveolens* and *C. lutea* fruit constituted larger proportions of female *N. swarthi* preferred diet than that of male *N. swarthi* (Fig. 4b).

Fig. 3 Comparison of *N. swarthi* and *R. rattus* selected and preferred diets in the wet season (**a**, **b**) and the dry (**c**, **d**). Hurlbert's selection B' calculated as p/q, where p is the mean proportion of food in the diet and q is the mean proportion that food is of all the available foods. Plant part abbreviations as in Fig. 2
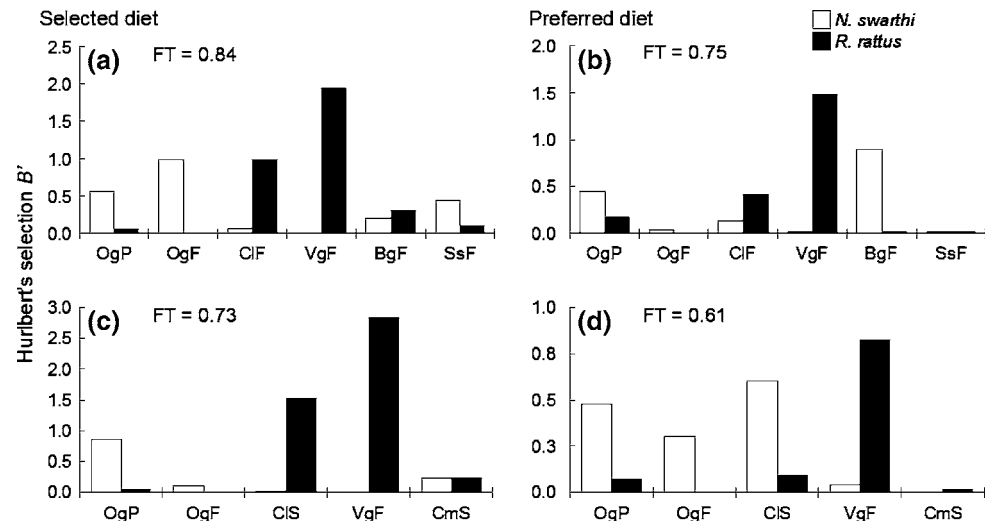
Table 2 Selected and preferred diet breadth measures for each species and each sex of *N. swarthi* in both seasons calculated using Hurlbert's B' (1978); 95% confidence range given in brackets

Species	Wet season		Dry season	
	Selected diet	Preferred diet	Selected diet	Preferred diet
N. swarthi	0.43 (0.18–0.72)	0.62 (0.47–0.72)	0.83 (0.69–0.93)	0.70 (0.54–0.78)
Male	0.29 (0.09–0.66)	0.62 (0.45–0.72)	0.82 (0.63–0.94)	0.71 (0.49–0.80)
Female	0.46 (0.13–0.86)	0.57 (0.35–0.73)	0.84 (0.62–0.93)	0.61 (0.36–0.69)
R. rattus	0.29 (0.14–0.57)	0.48 (0.34–0.56)	0.22 (0.10–0.42)	0.29 (0.22–0.39)

Table 3 Interspecific diet overlap measures for *N. swarthi* and separates sexes of *N. swarthi* with *R. rattus* in both seasons calculated using Smith and Zaret's FT (1982); 95% confidence range given in brackets

Species	Wet season		Dry season	
	Selected diet	Preferred diet	Selected diet	Preferred diet
N. swarthi:*R. rattus*	0.84 (0.67–0.92)	0.75 (0.60–0.82)	0.73 (0.49–0.84)	0.61 (0.37–0.74)
Male:*R. rattus*	0.69 (0.48–0.80)	0.73 (0.54–0.82)	0.74 (0.48–0.84)	0.62 (0.29–0.78)
Female:*R. rattus*	0.87 (0.66–0.94)	0.77 (0.57–0.83)	0.71 (0.46–0.81)	0.56 (0.30–0.69)
Male:female	0.88 (0.71–0.94)	0.97 (0.79–0.99)	0.99 (0.93–1.00)	0.97 (0.78–0.99)

Male *N. swarthi*'s selected diet was substantially narrower in the wet season compared to the dry season (−0.53; −0.78, −0.14) and was very similar to that of females in this season (−0.02; −0.25, 0.22; Table 2). Although female diet breadth also broadened over the same period, there was a greater degree of overlap in the range of female *N. swarthi* diet breadths between the seasons compared to males. The change in male *N. swarthi*, and to a lesser extent female, diet breadth resulted in a very high measure of intersexual overlap in selected diet, which was substantially lower in the wet season compared to this season (−0.12; −0.27, −0.02; Table 3). No such difference was observed for intersexual overlap between the seasons in preferred diets (−0.01; −0.16, 0.13). Each sex of *N. swarthi* ate mostly *O. galapageia* pads when in sympatry with *R. rattus* in the dry season (Fig. 4c), and less *C. lutea* seed and *V. glabra* fruit than would be expected from their ranks in their preferred diets (male: $W = -0.200$, $P = 0.624$; female $W = 0.00$, $P = 1.000$; Fig. 4c, d). In contrast to the wet season, male (0.11; −0.10, 0.36) and particularly female (0.23; 0.02, 0.50) selected diets were broader than their preferred diets, as male *N. swarthi* specialised on *C. lutea* seeds and female *N. swarthi* consumed more *O. galapageia* pads in their preferred diets (Fig. 4d).

Invertebrates

Faeces of *R. rattus* contained more chitinous material than that of *N. swarthi* in the wet season but not in the dry (species × season interaction: $F = 14.989$, $P < 0.001$; Fig. 5). There was no difference in the amount of chitinous material in faeces between the sexes ($F = 0.895$, $P = 0.346$).

Fig. 4 Comparison of male and female *N. swarthi* selected and preferred diets to those of *R. rattus* in the wet season (**a**, **b**) and the dry (**c**, **d**). Hurlbert's selection B' calculated as p/q, where p is the mean proportion of food in the diet and q is the mean proportion that food is of all the available foods. Plant part abbreviations as in Fig. 2
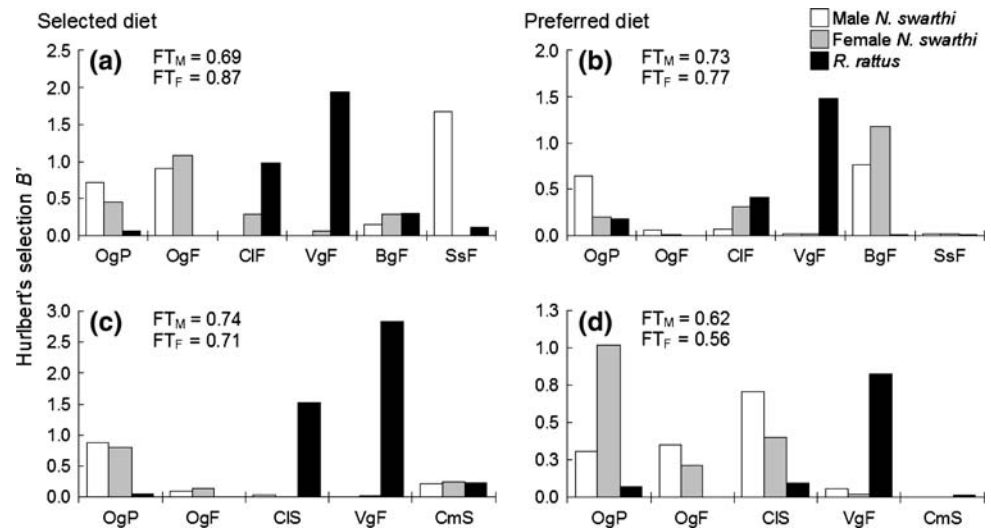

Discussion

Interspecific overlap in *N. swarthi* and *R. rattus* selected diets was not substantially different between the wet and dry seasons despite, in contrast to hypothesis (1), *N. swarthi* exhibiting a narrow selected diet breadth in the wet season that broadened in the dry season. Although the measures of diet overlap were high, suggestive of interspecific competition (Schoener 1982), closer inspection of the foods constituting the species' selected diets revealed that *R. rattus* tended to select fruits year-round while

Fig. 5 Mean percentage of insect matter in the faeces of each species in each season. *Bars* 1 SE

N. swarthi selected *Opuntia* foods. This would suggest that the two species have distinct preferences for particular foods but overlap in less preferred foods (MacArthur and Levins 1967). Measures of concordance between *N. swarthi* selected and preferred food ranks were, however, uncorrelated in both seasons, suggesting that they were not selecting foods according to their preferred rank in the field. This was in contrast to *R. rattus*, whose selected and preferred food ranks were marginally correlated in both seasons. These findings suggest that *R. rattus* and *N. swarthi* may have shared preferences, and that the latter is inhibited from obtaining its preferred foods when sympatric with *R. rattus*. One explanation for this scenario might be that *R. rattus* inhibit *N. swarthi* from selecting its preferred foods, perhaps through interspecific interference competition, for which *N. swarthi* compensate by using a narrower range of alternative foods. Such dynamics are predicted by the centrifugal community organisation model of habitat selection, which postulates that species coexistence can occur if the behaviourally subordinate species can survive better in a secondary habitat than the behaviourally dominant species (Rosenzweig and Abramsky 1997). In this case, *N. swarthi* may use *O. galapageia* fruits that *R. rattus* either do not, or cannot, use. An alternative explanation for this pattern might be that *N. swarthi* have different predators, or different susceptibility to the same predators through, for example, differences in body size (Dickman et al. 1991), that may have prevented *N. swarthi*, but not *R. rattus*, accessing its preferred foods in the field.

Also in contrast to hypothesis (1), *R. rattus* exhibited a narrow selected diet breadth in the wet season when foods were most abundant. In accordance with hypothesis (2), however, *R. rattus*' selected diet breadth remained similar as foods declined in the dry season. A simple explanation
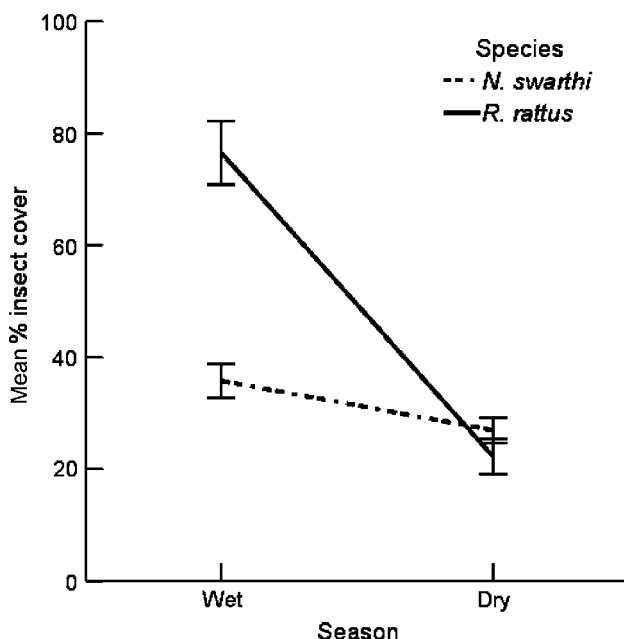
for this might be that, thanks to its behavioural dominance, *R. rattus* was able to select its preferred foods throughout the year (Case and Gilpin 1974). A subtlety different explanation might be that *R. rattus* selected all the foods that it could palate in both the wet and dry seasons, and that the dry season decline in these palatable foods drives the seasonal crash in the local *R. rattus* population (Clark 1980). Assuming the latter explanation, *N. swarthi* selected diet breadth dynamics conformed to hypothesis (3), suggesting that, as the competitive pressure exerted by *R. rattus* declined, *N. swarthi* were able to select a wider range of foods during the dry season. Such broad measures of diet breadth represent more general feeding across the available foods, a behaviour that has been interpreted as an adaptation to environmentally uncertain environments whereby the species maintains the dietary plasticity necessary to exploit seasonally abundant foods (Rotenberry and Wiens 1980). In contrast, the consistently narrow diet breadth of *R. rattus* suggests that it may not be well adapted to food acquisition at this site.

When considered at the species level, one may perceive dietary plasticity as an attribute of all individuals in the population. If, however, one inspects population variation by classes of individuals, for example sex, it may be possible to attribute some of the variation to differences between these classes. It has been shown that interspecific competition between *N. swarthi* and *R. rattus* is sex-specific (Harris and Macdonald 2007a), and the separate analyses for male and female *N. swarthi* presented here suggest that the probability of interspecific encounter may vary by sex. When sympatric with *R. rattus*, overlap in male and female selected diets was lowest in the wet season, which appeared to be due to the highly specialised *O. galapageia* diet of male *N. swarthi* compared to females. Again, the simplest explanation would be that male and female *N. swarthi* had distinct dietary preferences during this season but, when contrasted with their preferred diets, male *N. swarthi* selected diet was seen to omit *C. lutea* and *V. glabra* foods, which were the preferred foods of *R. rattus*. This observation seems to suggest that male *N. swarthi* in sympatry with *R. rattus* avoid *C. lutea* and *V. glabra* fruits to avoid interspecific encounter. By this logic, smaller female *N. swarthi*, which may be breeding in this season, and thus compelled by dietary requirements to seek *C. lutea* and *V. glabra* fruits, might be more prone to interspecific interference competition with *R. rattus* such that it might amount to competitive displacement (Eccard and Ylönen 2002). Although this speculation might support the recent finding of sex-specific interspecific competition in this community (Harris and Macdonald 2007a), the possibility that this pattern was produced by intraspecific interactions cannot be disregarded. It has been hypothesised, for example, that the coexistence of *Psuedomys higginsi* and *R. lutreolus* in Australia is facilitated by intersexual differences in habitat selection whereby female *R. lutreolus* oust males into non-preferred habitat during the non-breeding season (Monamy 1997; Monamy and Fox 1999).

Similar selected and preferred diet breadths of male and female *N. swarthi* in the dry season suggests an absence of such an intersexual discrepancy in this season. Given that their diet breadths broaden from the wet season to the dry, it could be construed that the dry season crash in the *R. rattus* population might alleviate interspecific competition to the extent that male *N. swarthi* are able to acquire their preferred diet in this season. Inspection of the concordance between selected and preferred diets, however, again reveals that the composition of both male and female selected diets differ from their preferred diets, suggesting that they may forage strategically to minimise the frequency of aggressive encounters with *R. rattus* in the dry season. This may be because foods that are available at this time are fewer and more ephemeral (Price 1984) and are prone to heightened aggressive defence by the last remaining *R. rattus* (Schoener 1983). Indeed, Harris et al. (2006) found that *N. swarthi* activity was marginally extended in an area of high *R. rattus* density compared to an area of low *R. rattus* density, and hypothesised that this reflected increased foraging activity to obtain sufficient nutrition when frequently displaced from shared food by sympatric *R. rattus*.

In summary, the niche dynamics described here best conform to the centrifugal community organisation model whereby *N. swarthi* utilise *Opuntia* foods when *R. rattus* is abundant, and expand their diet to include more of their preferred foods as *R. rattus* numbers seasonally decline. Moreover, these dynamics appear to be driven largely by male *N. swarthi* diet selection rather than that of females. If the assumptions underlying the methods were upheld (e.g. that tracked individuals were selecting plants for food rather than protection, Selected and Preferred diet comparisons were valid, etc.), it would seem that *O. galapageia* may be instrumental to this observed co-occurrence at La Bomba in two respects. Firstly, it provides male and, to a lesser extent, female *N. swarthi* with an almost exclusive secondary food source to utilise in the presence of *R. rattus*. By utilising this non-preferred food source male and, in the dry season, female *N. swarthi* may be able to reduce their frequency of interspecific encounters with *R. rattus* (e.g. Terman 1974). If this is the case then it would lend support to the hypothesis proposed by Harris et al. (2006) that *O. galapageia* may facilitate coexistence by providing *N. swarthi* with a competition refuge (sensu Durant 1998) from interference competition with *R. rattus*. A replicated and randomised experimental manipulation of *Opuntia*

foods in areas of *N. swarthi* and *R. rattus* sympatry would be required to confirm or refute this hypothesis.

Secondly, *O. galapageia* may provide *N. swarthi* with a vital resource throughout the year, and particularly in the dry season when alternative foods disappear. Furthermore, it is interesting to speculate that the avoidance or inability of *R. rattus* to use this food source may catalyse its seasonal population crash at La Bomba. Closer scrutiny of *R. rattus* selected diet reveals that it comprised predominantly fruits in both seasons, as supported by its diet preferences and previous work on *R. rattus* diet in the Galápagos (Clark 1982). Both the diversity of fruits and their abundance are dramatically depleted with the transition from the wet season to the dry (Fig. 2; Clark 1980). In addition, insect abundance is purportedly lower in the dry season (Peck 2001) such that they are probably taken opportunistically in similar amounts by both species (Fig. 5). Rather than switching to alternative, more abundant foods, for example *Opuntia* foods, strong positive concordance between its selected and preferred diets in both seasons suggest that *R. rattus* was acquiring its preferred foods in the field, and the observed narrowing of its preferred diet in the dry season suggests that fewer foods were found to be palatable in this season. It follows that, as the cost of foraging for these diminishing foods increases, the consumer population incurs reduced fitness (Armstrong and McGehee 1980) and, possibly in conjunction with the reduced availability of free water, may cause the crash of *R. rattus* populations in the arid zone during the dry season (Clark 1980).

While these findings offer hope for the persistence of *N. swarthi* at its final stronghold of La Bomba, where *O. galapageia* densities are at their highest (Harris et al. 2006), it should be noted that *O. galapageia* populations are themselves in danger. Climate change models predict more frequent and intense El Niño phenomena (Webster and Palmer 1997), and such conditions have already been documented to have devastating effects on the survival and recruitment of Galápagos *Opuntia* (Hamann 2004). This risk of cactus mortality emphasises the need for further research into habitat-dependent competition and coexistence between *R. rattus* and *N. swarthi*.

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