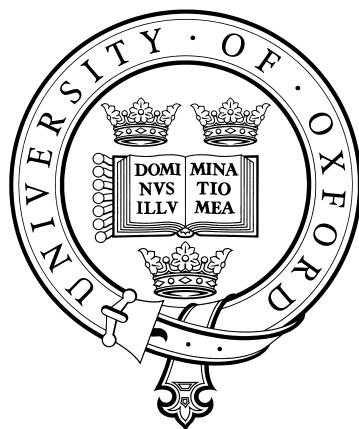


INTERSPECIFIC OVERLAP IN RESOURCE AND
SPACE USE OF THE ENDEMIC SANTIAGO RICE
RAT AND THE INVASIVE BLACK RAT ON
SANTIAGO, GALÁPAGOS



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ABSTRACT

The recent rediscovery of the Santiago Galápagos Rice rat, *Nesoryzomys swarthi*, in sympatry with the invasive Black Rat, *Rattus rattus*, unveiled a rare opportunity to investigate the co-existence between an endemic and invasive small mammal with a view to providing important ecological information for theory and conservation. Of the few studies undertaken on this system it is known that dominant *Rattus* lower the survival of female *Nesoryzomys*, they overlap in space and are not thought to partition time. The broad aim of this work was to investigate the role of food acquisition in facilitating this coexistence. Here follow the major findings:

1. In the wet season captive male *Nesoryzomys* diet was different to that selected when sympatric with *Rattus*. It was concluded that male *Nesoryzomys* were selecting cactus when sympatric with *Rattus* to reduce the frequency of aggressive encounters at shared food patches.
2. In contrast, captive female *Nesoryzomys* selected a similar diet to that when sympatric with *Rattus* and, perhaps driven by their breeding dietary requirements, were hypothesised to encounter *Rattus* at food patches more frequently than males.
3. Foods declined in the dry season along with *Rattus*, but when captive both *Nesoryzomys* sexes selected a different diet to when sympatric with *Rattus* suggesting that scarce and ephemeral foods were monopolised by the last remaining *Rattus*.
4. Cactus foods became a large constituent of *Nesoryzomys* diet in the dry season perhaps to avoid aggressive encounters with *Rattus* but perhaps also to obtain essential nutrients and water. In contrast, *Rattus* rarely ate cactus pads and chose never to consume cactus fruits.
5. The discrepancy in *Nesoryzomys* male and female food acquisition was reflected in their use of space. The spatial activity of males in the wet season was lower in areas of high *Rattus* activity compared with females. Also at this time, males were more likely than females to use areas with cactus fruits.
6. In the dry season both sexes used areas with cactus fruits and not areas of high *Rattus* activity.
7. In immature cactus habitat without large cacti and cactus fruit, male *Nesoryzomys* spatial activity was positively correlated, and female's negatively correlated, with *Rattus* activity in both seasons. This sex disparity was perhaps due to the higher probability that smaller female *Nesoryzomys* would retreat from encounters with *Rattus* than males.
8. The seasonal change in *Nesoryzomys* body mass did not vary in mature (with cactus fruit) versus immature (without cactus fruit) habitat suggesting that the fruits mediate interference competition rather than exploitation competition.
9. *Nesoryzomys* were found to practise coprophagy, particularly at times of plentiful cactus fruit when other foods were scarce. It was hypothesised that this was an adaptive behaviour to optimise energetic gain from cactus fruits. *Rattus* were not coprophagic.

In conclusion, these findings help to further describe the mechanism that underlies the survival impact of *Rattus* on *Nesoryzomys* and suggest that endemic cactus are crucial to *Nesoryzomys* persistence in sympatry with *Rattus*.

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DEDICATION

To my dear grandmother, Margaret Leaney (Bunny), who sadly passed away
during the completion of this thesis

Margaret Leaney
1911-2002

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CHAPTER 1

GENERAL INTRODUCTION

1.1 BIOLOGICAL INVASIONS

“At James Island there is a rat [that] belongs to the old-world division of the family, and as this island has been frequented by ships for the last hundred and fifty years, I can hardly doubt that this rat is merely a variety”

Darwin (1913)

Through transboundary activities, such as commerce and recreation, humans have a history of inadvertently or deliberately introducing species to habitats beyond their native ranges (Mooney, 2005). Generalising from surveys undertaken in Britain, Williamson and colleagues (1986) proposed that only 10% of these species introductions would successfully establish in their newfound habitat, upon accomplishing which they become known as *introduced species* (IUCN Invasive Species Specialist Group [ISSG]). Williamson and colleagues (1986) further postulated that of the 10% of species that become introduced species, another 10% would spread and become ecological or economic pests, whereby they become known as *invasive species* (ISSG). This sequence of events (from introduction to establishment and spread) is regarded by invasion biologists as the process by which a species becomes *invasive*, and is called a *biological invasion* (Williamson, 1999).

Elton (1958) was among the first to note the ‘convolution of the World’s fauna and flora’ and to express concern for its ecological consequences for biological diversity. Now, almost half a century on, invasive species are considered to be the single greatest threat to insular biodiversity (Chapin *et al.*, 2000) and the second greatest threat to biodiversity worldwide (Vitousek *et al.*, 1997). In essence, the threat posed by invasive species pertains to their potential to cause genetic loss by displacing local populations or even entire species; however, in reality reports linking invasive species (cause) to species extinctions (effect) have been mostly anecdotal leading some authors to suggest that invasive species pose a negligible threat to biodiversity (Simberloff, 1981) and even locally enrich it (Sax *et al.*, 2002). Indeed, in a meta-analysis of the 2003 IUCN Red List of Threatened Species, Gurevitch and Padilla (2004) found few species extinctions for which invasive species were

explicitly implicated and consequently concluded that they were not important in species extinctions. Like Gurevitch and Padilla (2004), other proponents of this view have used meta-analysis techniques or literature reviews to reach similar general conclusions across a broad range of taxa (e.g. Ebenhard 1988). By conducting detailed analyses on individual taxa however, opponents of this view have reported contrary findings and testify that invasive species are the leading cause of bird extinctions, and the second leading cause of extinctions in fishes and mammals (Clavero & García-Berthou 2005; and references therein).

The literature debate on the threat of invasive species to global biodiversity is set to continue into the near-future because, unfortunately, it is based on contradiction. In actual fact, the reason that the debate exists at all is that the impacts of invasive species have not been adequately documented. The 90% of - apparently benign - introduced species that do not successfully establish viable populations (Williamson *et al.*, 1986) are those cultivated species that fuel countries economies and adorn their recreational park-lands and for which no ecological or economic impact assessments have been attempted. This paradox is one of many that have been highlighted in the discipline of invasion biology. Pimentel and colleagues (2000) have discussed the costs involved in controlling the arrival and spread of invasive species and contrasted it with the economic value of non-native species used in agriculture. Perhaps the most noteworthy paradox concerns the very notion of a biological invasion. Brown and Sax (2004) stress that although biological invasions are considered “unnatural”, species invasions have, and indeed still do, occur naturally in the form of range expansion and colonisation events (see also Brown & Sax 2004 and Cassey *et al.* 2005 for current debate).

Recognising clear parallels between the processes that underlie biological invasions and community assembly, Brown and Sax (2004) looked beyond the existing and projected problems posed by invasive species [themselves subject to extensive research and review since Elton (1958): see Mooney (2005)] and called for a “more balanced approach in the study of invasive species, with increased emphasis on the search for insights into

basic research questions". They were not the first authors to appreciate this resourceful perspective. Macdonald and Thom (2001) discussed the role of biological invasions as unintended "natural" experiments and Shea and Chesson (2002) explicitly proposed the use of existing community ecology theory as a framework for studying biological invasions. These recommendations have led to a preponderance of studies aimed at establishing general rules of community "invasibility" (e.g. Davies *et al.* 2005) and isolating specific traits common to successful invaders (e.g. Sakai *et al.* 2001), but few studies have employed the community ecology framework to investigate cases of competition between invasive and native species, especially among animals (Davies, 2003).

In a recent book on competition, Keddy (2001) defined it as "the negative effect that one species has upon another by consuming, or controlling access to, a resource that is limited in availability". This definition of interspecific competition supposes (but does not explicitly state) that the limited resource is shared by and essential to both competing species. Support for the existence of competition has been found in almost all functional guilds (see Keddy 2001 for a review) and has received extensive empirical support in naturally occurring small mammal communities (e.g. Abramsky *et al.* 2005). Yet, very few studies have specifically investigated the role of interspecific competition in structuring invaded communities and this is probably an artefact of the minor role that intraguild interactions are thought to have in species extinctions (Davies, 2003). Nevertheless, competition with invasive species has caused dramatic declines in native populations of such diverse taxa as ants (Porter & Savignano, 1990), geckos (Petren & Case, 1996), and many marine species (Coles *et al.*, 1999) and furthermore, has been implicated in the extinction of many mammalian species, particularly on islands (see MacPhee & Flemming 2001 for a review). Among these latter cases were several species of rodent from the Galápagos Islands that are reported as having succumbed to extinction through competition with the aggressively invasive Black rat, *Rattus rattus* (Clark, 1984; Key & Muñoz Heredia, 1994).

1.2 THE GALÁPAGOS RICE RATS

Whether they arrived to the Galápagos indirectly via now-submerged islands (Christie *et al.*, 1992) or directly from the continent aboard vegetation rafts (Thornton, 1971), three small mammal species successfully colonised the Galápagos and diverged to form an impressive array of 12 species of endemic rodents (Clark, 1984). One of these successful colonisers arrived 3-3.25 million years ago and diversified into the 8 unique rodent species now grouped together in the genus *Nesoryzomys*, or true Galápagos Rice rats (Patton & Hafner, 1983). Of the other two genera; *Megaoryzomys* arrived before the *Nesoryzomys* ancestor and diverged into two rodent species, and *Oryzomys*, which were introduced in relatively recent times (<1000 years) by aboriginal South Americans, also diverged into two species (Clark, 1984) although the integrity of the Galápagos *Oryzomys* taxonomic classification has been questioned by Patton and Hafner (1983) and the species are listed as sub-species in the recent Wilson and Reeder (2005).

The ecology and behaviour of the Galápagos Rice rats remain largely undescribed (Key & Muñoz Heredia, 1994) and this is because three quarters of them (9 of 12) were considered extinct by 1934 (Clark 1984; Table 1.1). The little knowledge that does exist is based on fossil analysis, occasional observations and scant historic records accrued since Darwin's visit in 1835 (Waterhouse, 1839; Eshelman, 1978; Hutterer & Hirsch, 1979; Clark, 1980a; Steadman, 1985; Steadman *et al.*, 1991). By 1995, only two species, *N. narboroughi* and *O. bauri*, were known to be extant and another, *N. fernandinae*, was unclassified because it had only been described from a skull retrieved from an owl pellet (Hutterer & Hirsch, 1979). In 1997, however, an expedition led by Robert Dowler discovered the first live specimens of *N. fernandinae* on Fernandina but also, and perhaps more importantly, rediscovered a population of the previously presumed extinct Santiago Rice rat, *N. swarthi*, in a secluded region on the north central coast of Santiago (Dowler & Carroll, 1996; Dowler *et al.*, 2000). While these findings raised hope for the survival of the Galápagos Rice rats, it also raised the extinction stakes, especially since *N. swarthi*

was found to have a restricted distribution in which it is found in sympatry with rodent invaders *Rattus* and the House mouse, *Mus musculus*.

1.3 INVADERS OF THE GALÁPAGOS

Rattus and *Mus*, along with other small mammals, pose arguably the biggest threat to native biodiversity of all known invasive species, particularly on islands (Courchamp *et al.*, 2003). Along with the Brown rat, *Rattus norvegicus*, *Rattus* and *Mus* have evolved to advantage for the activities of *Homo sapiens* to such an extent that they are often grouped together and uniquely labelled as *commensal* species (Lever, 1985). By living in sympatry with humans these commensal species have developed a high degree of ecological plasticity including tolerance of extreme temperatures and diverse dietary habits, and moreover, they have adopted classic *r*—selected life histories (Meehan, 1984; Lund, 1994). These traits afford them an important advantage when cast ashore in inhospitable environments such as the Galápagos Islands and increase their propensity to predate on or compete with native species (Sakai *et al.*, 2001).

Almost inevitably, these commensal invaders reached the Galápagos Islands by hitch-hiking aboard whaling vessels and pirate ships that visited the archipelago for two centuries following its accidental discovery in 1535 (Steadman & Zousmer, 1988). Indeed, phylogenetic work has revealed that *Rattus* first arrived to the Galápagos during the late 16th century to James Bay on Santiago (Patton *et al.*, 1975). By the time Darwin stepped onto Santiago in 1835, *Rattus* was abundant both there and on many of the other islands including San Cristóbal where Darwin was the first and last person known to see the San Cristóbal Galápagos Rice rat, *O. galapagoensis* (Waterhouse, 1839; Heller, 1904). *Rattus* was introduced to the Galápagos on two further occasions, the last being to a World War II air base located on Baltra, an island separated from Santa Cruz by a very narrow body of water (Patton *et al.*, 1975). An early resident of Santa Cruz described an abundance of ‘native rats’ — later to be identified as *N. indefessus* and *N. darwini* — that within

Table 1.1: Current status of each Galápagos rodent species (modified from Clark 1984).

Species	Island	Collected	Current status	<i>Rattus?</i>
<i>Nesoryzomys swarthi</i> ¹	Santiago	First: 1906 (Orr, 1938)	Abundant in range	Yes
<i>Oryzomys bauri</i> ²	Santa Fé	First: 1891 (Allen, 1892)	Abundant island-wide	No
<i>Nesoryzomys narboroughi</i> ¹	Fernandina	First: 1899 (Heller, 1904)	Abundant island-wide	No
<i>Nesoryzomys fernandinae</i>	Fernandina	First: 1995 (Dowler <i>et al.</i> , 2000)	Abundant island-wide	No
<i>Oryzomys galapagoensis</i> ²	San Cristóbal	First and last: 1835 (Waterhouse, 1839)	Extinct	Yes
<i>Nesoryzomys indefessus</i>	Baltra	First: 1898-9 (Heller, 1904)	Extinct	Yes
	Santa Cruz	First: 1906 (Orr, 1938) Last: 1930 (Chapin, 1935)	Extinct	Yes
<i>Nesoryzomys darwini</i>	Santa Cruz	(Orr, 1938) Last: 1930 (Chapin, 1935)	Extinct	Yes
<i>Nesoryzomys</i> sp. (x2)	Isabela	Known from subfossils (Steadman, 1981)	Extinct	Yes
<i>Nesoryzomys</i> sp.	Rabida	Known from subfossils (Dexter <i>et al.</i> , 2004)	Extinct	Yes
<i>Megaoryzomys curioi</i>	Santa Cruz	Known from subfossils (Niethammer, 1964)	Extinct	Yes
<i>Megaoryzomys</i> sp.	Isabela	Known from subfossils (Steadman & Ray, 1982)	Extinct	Yes

^{1,2} These pairs of species are considered as one species by Patton and Hafner (1983) and ² also by Wilson and Reeder (2005)

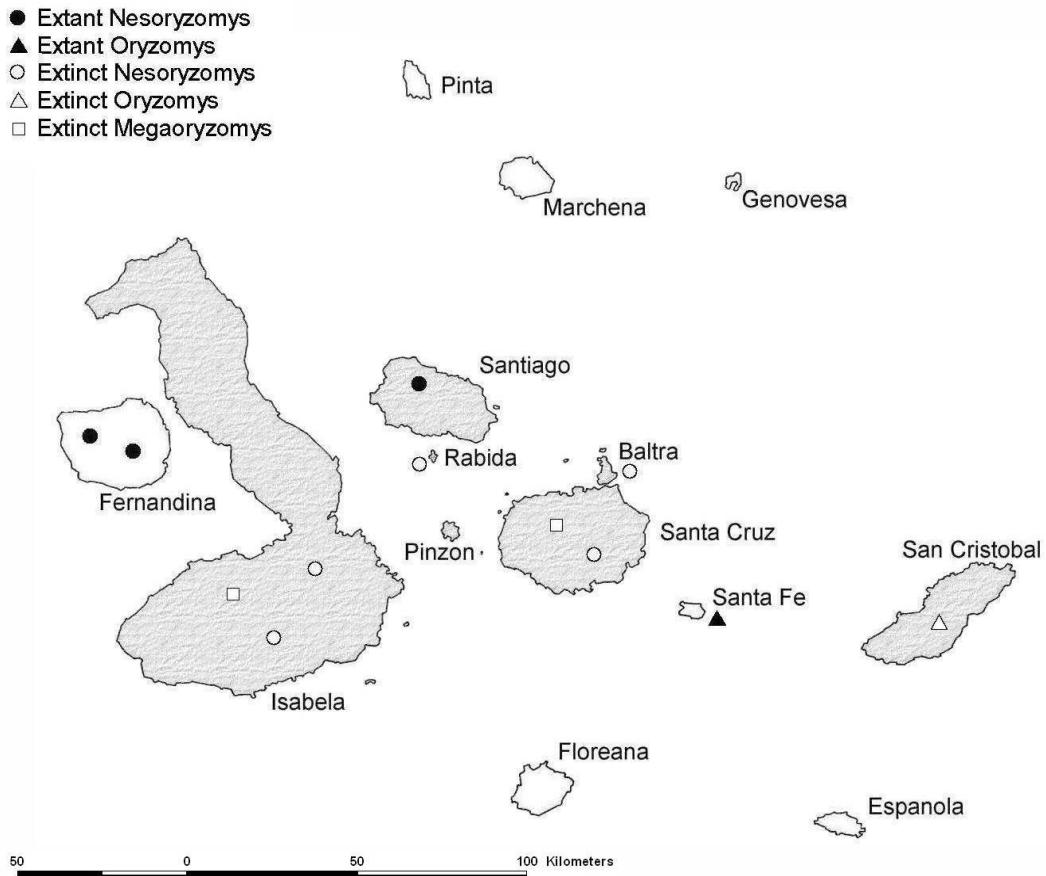


Figure 1.1: Current status of Galápagos endemic rodents. Shaded islands host *Rattus*.

4 years had been replaced by *Rattus* (Rambech [1934] in Clark 1984). This pattern of expatriation is thought to have been repeated multiple times until by 1997 the endemic and introduced rodents were exclusively allopatric in their distributions (Figure 1.1). On the basis of this anecdotal evidence, authors and scientists postulated that Galápagos Rice rats could not live in sympatry with *Rattus* and consequently implicated it in the catastrophic decline of the Galápagos Rice rats (Brossel, 1963; Steadman *et al.*, 1991; Key & Muñoz Heredia, 1994).

Findings from a recent series of studies by Harris and Macdonald (in press) and Harris and colleagues (2006; Appendix A) have provided important support to the prevailing hypothesis of interspecific competition between *Nesoryzomys* and *Rattus*. In a replicated species removal experiment, Harris and Macdonald (in press) were able to isolate a neg-

ative effect of *Rattus* on female, but not male, *Nesoryzomys* survival. Furthermore, from captive interspecific encounters they demonstrated that *Rattus* was behaviourally dominant to both sexes of *Nesoryzomys* but importantly, that female *Nesoryzomys* were more likely to be displaced than male *Nesoryzomys*. Taken together these findings were interpreted as evidence for sex-mediated interspecific interference competition by *Rattus* on *Nesoryzomys* (Harris & Macdonald, in press). Harris and colleagues (2006; Appendix A) surveyed the entire north coast of Santiago, including the historical *Nesoryzomys* range, for the presence of *Nesoryzomys* populations. They found that *Nesoryzomys* was absent from its type locality, where several specimens were last collected in 1906 (Orr, 1938), but that *Rattus* was omnipresent. Furthermore, they discovered that *Nesoryzomys* was sympatric with *Rattus* in its entire range and that they both shared a preference for the same microhabitat components. One intriguing finding was that *Nesoryzomys*, but not *Rattus*, showed a strong positive distribution and density relationship with the island's endemic cactus, *Opuntia galapageia*, implying that it may play a role in mitigating the interspecific competition of *Rattus* on *Nesoryzomys* (Harris *et al.* 2006; Appendix A).

1.4 LOCATION AND CLIMATE OF THE GALÁPAGOS

The Galápagos archipelago consists of 13 large ($>10\text{ kms}$) volcanic islands and many smaller islands, islets and rocks located on the Nazca plate at the intercept with the Cocos and Pacific tectonic plates (Jackson, 1993). As an oceanic archipelago it has always existed in isolation never less than 950kms west of continental Ecuador (Figure 1.2). Its annual climate is uncharacteristically dry for its tropical location and yet it is highly variable between years (Colinvaux, 1984). Two discernable seasons are recognised that are directly attributable to changes in the Pacific current system. Between January and June warm water arrives at the archipelago from the Panama Basin which causes higher air temperatures and cloud formation. At this time the climate in the Galápagos is hot with frequent heavy rainfall averaging 50-70mm/month and daily temperatures

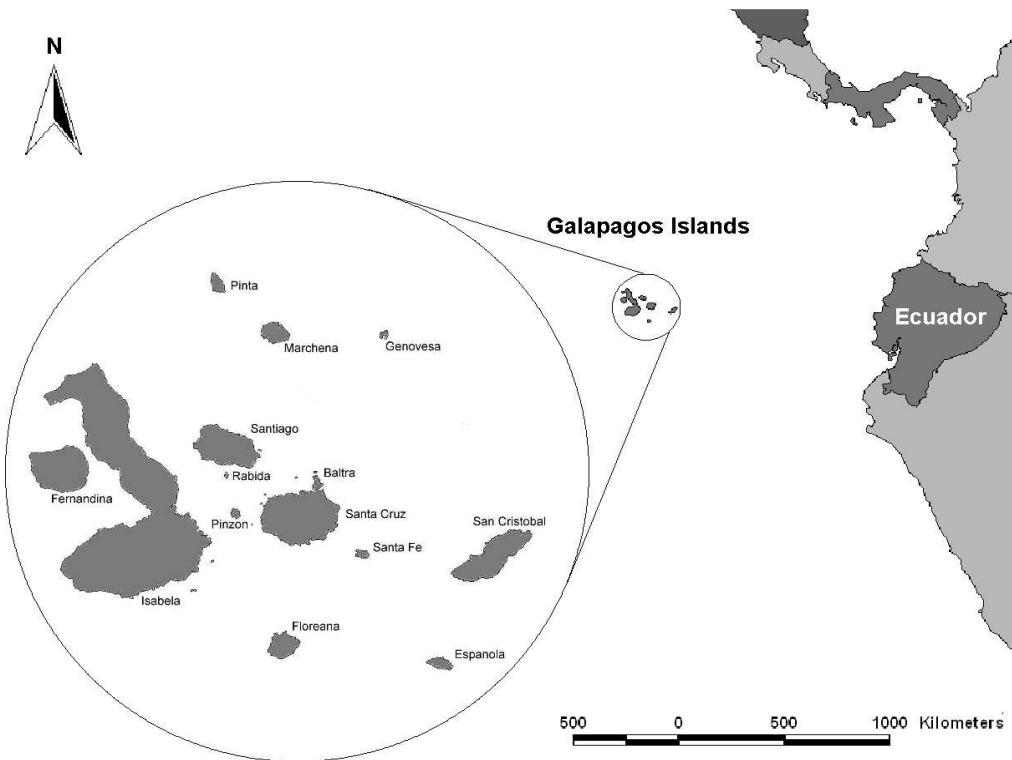


Figure 1.2: Location of the Galápagos Islands with reference to continental Ecuador.

ranging from 26-30°C, and is so-called the hot-wet season. By the end of June and until December, the Peruvian Humboldt current swathes the archipelago in cool waters that bring down air temperatures creating an inversion layer at 300 to 600m asl. All evaporating moisture is captured in the inversion layer and delivered to the highland areas in the form of a mist locally known as *garua*, from which this season takes its name. During this season the rainfall averages <10mm/month and frequently fails in leeward coastal regions, and daily temperatures range from 20-24°C (CDRS rainfall data 2005).

Approximately once every 3-7 years this dichotomous pattern is broken when the Humboldt Current is suppressed by large-scale waves brought east from the warmer regions of the Pacific (Webster & Palmer, 1997). This phenomenon, named by the Peruvians as ‘El Niño’, results in prolonged and frequently intensified hot-wet season conditions that promote growth and reproduction of terrestrial organisms (Snell & Rea, 1999). El Niño events are followed by their antithesis; a prolonged dry period called La Niña. Although

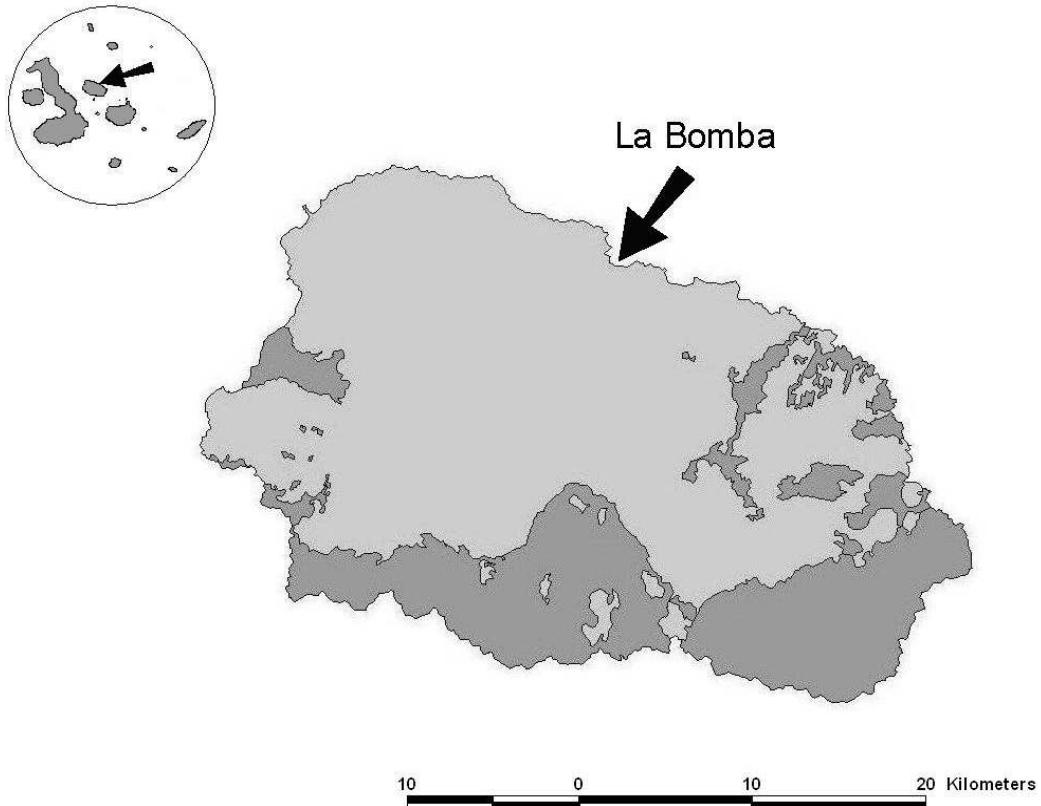


Figure 1.3: Map of Santiago showing the location of La Bomba. Light areas are vegetated and darker areas are lava flows.

only occasional, these extreme distortions of the normal climate impose strong selective pressure on species that reside in the Galápagos (Wiens, 1977).

1.5 STUDY SITE

At 585km² Santiago is the fourth largest island and, second to Fernandina, it is the largest uninhabited island in the archipelago. At its highest point Santiago reaches 905m asl and ranks as the third highest island in the group. It shares a common habitat zonation with the other five largest and highest islands in the group that has been described in detail by Wiggins and Porter (1971). This study was carried out at a site locally known as La Bomba that is situated in the Arid Zone on the central north coast of Santiago (Figure 1.3). The habitat is characterised by the cactus *Opuntia* var. *galapageia*, trees; *Bursera*

graveolens, *Cordia lutea* and *Croton scouleri*, shrubs; *Clerodendrum molle* var. *molle*, *Castela galapageia*, *Lantana peduncularis*, *Scutia spicata* var. *pauciflora*, and *Vallesia glabra* and is host to an additional 1 tree and 4 shrub species, and 21 vine and herbaceous plants excluding grasses. The terrain at La Bomba is composed of ‘aa’ lava, a lava type that is characteristically serrated and broken.

1.6 STUDY SPECIES

1.6.1 SANTIAGO RICE RAT, *NESORYZOMYS SWARTHI*

General information

It is believed that the ancestor of *Nesoryzomys*, probably a species of *Sigmodontomys* or *Melanomys* (Weksler, 2003), arrived to the Galápagos between 3–3.25 million years ago (Patton & Hafner, 1983) from the South American continent. The type specimen was collected by J. S. Hunter of the 1906 California Academy of Science expedition from the vicinity of Sullivan Bay. It was first described over 30 years later and named in memory of ornithologist and member of the 1932 Templeton Crocker expedition Harry Schelwaldt Swarth (1878–1935) (Orr, 1938). No specimens were collected between its discovery and description and so Orr (1938) suggested that it had probably been driven to extinction by introduced rodents (*Rattus* and *Mus*). Nevertheless, suspicion of *Nesoryzomys* survival was aroused with the recovery of a ‘fresh skull’ from James Bay in 1965 (Peterson, 1966), but later dampened following a series of unsuccessful survey efforts conducted by the Clarks during the 1970s (D. A. Clark pers comm.). It wasn’t until 1997 that an expedition led by Dowler caught any live specimens since their discovery. On this occasion they were captured at La Bomba alongside *Rattus* (Dowler *et al.*, 2000). This uncertain sympatry with *Rattus* together with its limited range and isolation render *Nesoryzomys* vulnerable to extinction and it is now regarded the most threatened land mammal in the Galápagos. It has been listed as “vulnerable” in the IUCN Red List (IUCN, 2004).

Autecology

Adult *Nesoryzomys* are sexually dimorphic and males (\bar{x} 114.83g) are larger than females (\bar{x} 91.08g). They are omnivorous (Chapter 2) and nocturnal (Harris *et al.* 2006; Appendix A). Relative to other Cricetine rodents, *Oryzomys* and *Nesoryzomys* appear to have adopted a desert rodent strategy of high survival/low reproduction (Harris & Macdonald, 2007): individual longevity exceeds 2 years and reproductive activity is seasonal and follows the arrival of the hot season rains (December) with an estimated mean litter size of 3.09. Together with *Oryzomys* of Santa Fe (Clark, 1980a) there is evidence to suggest that *Nesoryzomys* is food and/or water limited (Harris & Macdonald, 2007).

Distribution

Nesoryzomys is limited to a 13km stretch of the north central coast of Santiago (Harris *et al.* 2006; Appendix A) but according to historical accounts *Nesoryzomys* was found beyond this at Sullivan Bay on the north east coast of Santiago (Orr, 1938). Evidence accrued from habitat investigations at several scales suggest that *Nesoryzomys* distribution is closely linked to the distribution of the large endemic cactus, *Opuntia* (Harris *et al.* 2006; Appendix A); *Nesoryzomys* presence across Santiago is positively correlated to the distribution of *Opuntia*, it actively selects microhabitat dominated by *Opuntia* and finally, *Nesoryzomys* abundance is highest at La Bomba (N. Dexter pers com.) where *Opuntia* density is at its highest.

1.6.2 BLACK RAT, *RATTUS RATTUS* L.

General information

Rattus is native to India although it is now found worldwide, except in Polar Regions (Innes, 2005). Through predation, competition and disease, *Rattus* poses a serious threat to native fauna and flora, particularly insular species (Atkinson, 2001), and may compete with native rodent species (Alvarez & Gonzalez, 1991; Goodyear, 1992; Stephenson, 1993;

Stephenson *et al.*, 1994; Goodman, 1995; Pergams *et al.*, 2000; Russell & Clout, 2004) notably in the Galápagos (Brosset, 1963; Clark, 1984; Key & Muñoz Heredia, 1994; Dowler *et al.*, 2000; Harris & Macdonald, in press). Genetic analyses place the first introduction of *Rattus* to the Galápagos in the late 1600's to at James Bay, Santiago (Patton *et al.*, 1975). At the last recording, it had spread to and successfully colonised 33 islands in the archipelago (CDRS, unpublished data).

Autecology

Adult *Rattus* males (\bar{x} 171.78g) are heavier than females (\bar{x} 133.24g) but not larger in body or tail length (Harris & Macdonald, 2007). Like *Nesoryzomys*, they are omnivorous and nocturnal (Clark, 1980b, 1981, 1982). Although capable of continuous breeding in various environments (Ewer, 1971), it is a seasonal breeder in Galápagos and like *Nesoryzomys* its breeding is confined to the wet season (Harris & Macdonald, 2007). As with *Nesoryzomys*, this again suggests that their populations are limited by food and/or water (Clark, 1980b). *Rattus* is not well adapted to the Galápagos arid zone where during dry seasons and prolonged dry periods its population tends to crash, almost to the point of local extinction (Clark, 1978; Harris & Macdonald, 2007). *Rattus* is behaviourally dominant to *Nesoryzomys* and has been shown to have a negative impact on its survival at La Bomba (Harris & Macdonald, in press).

Distribution

As mentioned above, *Rattus* has colonised 33 islands and rocks in the Galápagos (CDRS, unpublished data). Within this distribution it has successfully colonised every terrestrial habitat in the Galápagos (Clark, 1978). Where it occurs in sympatry with *Nesoryzomys* on Santiago the two species share a preference for microhabitat dominated by *Opuntia* and there is no evidence to suggest that the two species are temporally or spatially segregated (Harris *et al.* 2006; Appendix A).

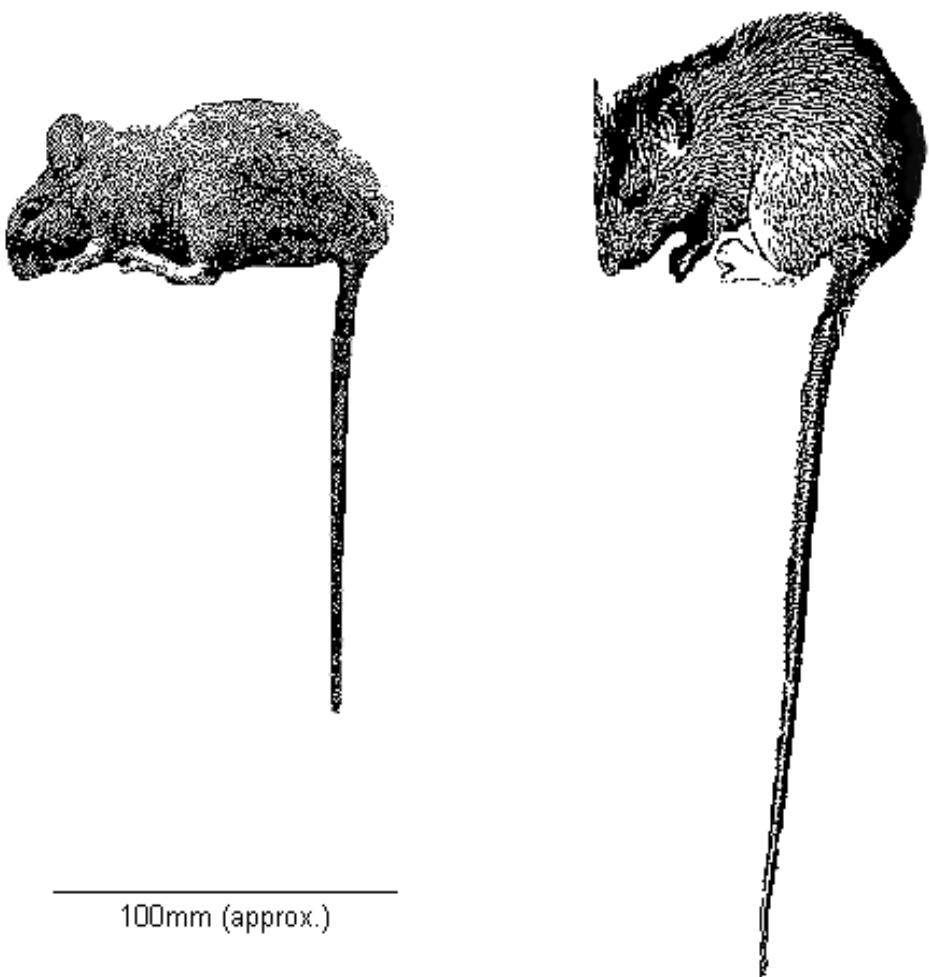


Figure 1.4: Sketch to show the relative size of *Nesoryzomys* (left) and *Rattus* (right) with particular emphasis on the tail, a key identification feature.

1.7 OBJECTIVES

This thesis is structured sequentially according to the order in which the investigations were carried out:

In Chapter 2, I report results from intensive spool-and-line tracking and semi-natural resource selection trials carried out for both species in each season. These techniques were deployed to answer the questions: Do *Nesoryzomys* and *Rattus* use plant species in proportion to their occurrence? And why might they use some plant species disproportionately? To what extent do the diets overlap when the species are allopatric compared to when they are sympatric? And are there differences in male and female *Nesoryzomys* dietary overlap with *Rattus*? I used the spool-and-line data to identify those plants that each species visits more than random and then offered the resources available on those plants to individuals in captive semi-natural resource selection trials to determine which were important dietary resources. From these trials I was able to determine the preferred diet of each species and compare this to their foraging pattern under conditions of sympatry. Quantitative comparisons were made within a community ecology framework, specifically niche theory.

In Chapter 3, I sought to test the increased encounter hypothesis emerging from Chapter 2. I report the presence and relative strength of the relationship between *Nesoryzomys* and *Rattus* activity in contrasting mature and immature *Opuntia* habitats during cactus fruiting and non-fruiting seasons. Does *Nesoryzomys* avoid *Rattus*? And is this relationship seasonal? How is this relationship affected by the presence of *Opuntia*? Or by *Opuntia* fruits? Is there any difference between the relationships of male and female *Nesoryzomys* with *Rattus* or *Opuntia*? The relationships pertaining to these questions were examined simultaneously using a multivariate approach adapted to account for possible effects of autocorrelation.

In Chapter 4, I attempt to consolidate a hypothesis that emerges from both the previous Chapters; that *Opuntia* fruits play an important role in the observed species

coexistence at La Bomba. I report the findings from a simple investigation of coprophagy using faecal analysis. Do *Rattus* perform coprophagy? How does the incidence of coprophagy vary across seasons and with availability of different resources? These questions are answered using conventional statistical procedures and the results are discussed with reference to other selected rodent species.

CHAPTER 2

PRICKLY COEXISTENCE OR BLUNT COMPETITION? THE IMPORTANCE OF *OPUNTIA* IN AN INVADED RODENT COMMUNITY

2.1 ABSTRACT

Endemic *Nesoryzomys swarthi* and invasive *Rattus rattus* are found in unlikely sympatry in an invaded small mammal community in the Galápagos. Previous studies show that they compete, but that spatial segregation plays no role in the localized coexistence. This study tested the hypothesis that coexistence is facilitated by different feeding habits. Spool-and-line tracking 85 *Nesoryzomys* and 33 *Rattus* identified plant parts as potential foods. Preferences for these foods were assessed for each species in individual cafeteria-style trials of 46 *Nesoryzomys* and 34 *Rattus* and compared to their sympatric diets, estimated from the spool-and-line tracking data, using measures of niche breadth and overlap. Diet overlap in sympatry was highest in the wet season when food - particularly fruit - abundance was high and *Rattus* diet breadth was broad. Sympatric diet and captive food preferences were strongly positively correlated for *Rattus* but weakly correlated for *Nesoryzomys*, suggesting that interspecific interference may limit *Nesoryzomys* foraging behavior. Diet overlap was highest between sympatric female *Nesoryzomys* and *Rattus* suggesting that females were compelled to forage for foods preferred by *Rattus*. Male *Nesoryzomys* shared food preferences with female counterparts but evaded interspecific interference by avoiding foods preferred by *Rattus*. During the dry season, when foods were scarce, diet overlap in sympatry was low as *Rattus* diet narrowed in the absence of fruits. In contrast, *Nesoryzomys*, specifically male *Nesoryzomys*, diet broadened with emphasis placed on acquiring *Opuntia* foods. Nevertheless, *Nesoryzomys* food preferences were again weakly correlated with their diet in sympatry. There was no difference between *Nesoryzomys* sexes in their food preferences or their diet overlap with *Rattus* in this season. In conclusion, the narrower diet breadth of *Rattus* in contrast to *Nesoryzomys* suggests that it may be less adapted to food acquisition at this site, particularly when fruits are absent. Nonetheless, year-round presence of *Rattus* inhibits *Nesoryzomys* foraging for its preferred diet, which instead specializes on *Opuntia* foods that were uneaten by *Rattus* and provide *Nesoryzomys* with a localized resource refuge.

2.2 INTRODUCTION

Theoretical explanations for the mechanisms of coexistence in ecological communities have received empirical support from competitively structured rodent communities with regard to segregation of temporal activity (e.g. Kronfeld-Schor & Dayan 2003), spatial activity (e.g. Morris 1996) and resource utilization (e.g. Driessen 1999). Furthermore, recent theoretical developments suggest that rodent species might coexist through their different capacity to survive in spatially (e.g. Amarasekare 2003) or environmentally variable environments (e.g. Chesson & Warner 1981). None of these mechanisms is exclusive, and a consensus is developing that coexistence might be achieved through the interactions of several of them. For example, North American desert rodent communities are reported to coexist through the combined actions of food partitioning, spatial and temporal food renewal and differences in foraging strategies (Brown, 1989).

Although community ecology theory has generally been derived from, and applied to, naturally occurring communities, it is an appropriate framework through which to study biologically invaded communities. Indeed, some community ecologists have deliberately introduced species into a system in which they are otherwise naturally absent, in order to observe the response(s) of the resident community member(s) to the invader (e.g. Crowell & Pimm 1976). Such investigations represent a clear parallel to the type of impact assessments that invasion biologists are encouraged to conduct to assess the impact of an invasive species on ecologically similar and biologically important species (Macdonald & Thom, 2001; Shea & Chesson, 2002). Nevertheless, examples of the use of community ecology theory in this context are few, perhaps reflecting the rapid extinction of native species that lack pre-adapted strategies to cope with an invading species (Ebenhard, 1988). Reports of such extinctions among mammalian guilds are largely confined to insular ecosystems, and include several rodent species, lagomorphs and a bat (see MacPhee & Flemming 2001 for a review). In the few reported investigations of competition between native and invasive mammals, community ecology theory, and specifically

niche theory, has often served as the analytical backbone to investigations. For example, Bryce and colleagues (2002) used niche theory to assess habitat overlap between the invasive Grey squirrel, *Sciurus carolinensis*, and the native Red squirrel, *Sciurus vulgaris*, in Craigvinean Forest in Scotland.

Convinced by an extensive range of anecdotal evidence (for a summary see Clark 1984), many authors suggested that the extinction of 9 of 12 Galápagos Rice Rat species was a result of competitive exclusion by a recent invasive species to the Galápagos, *Rattus rattus* (Clark 1984; but see Dexter *et al.* 2004 for an alternative hypothesis). However, in 1996 an expedition to the arid zone on the North Coast of Isla Santiago rediscovered a small population of one of these previously presumed extinct species, *Nesoryzomys swarthi*, in sympatry with *Rattus* (Dowler *et al.*, 2000). Although this rediscovery appears to be at odds with the prevailing competitive exclusion explanation for the extinction of Galápagos rodents, a recent study by Harris and Macdonald (in press) found experimental evidence for a negative survival impact of *Rattus* on female *Nesoryzomys*, and a second recent study has provided the first evidence of a contraction in *Nesoryzomys* distribution (Harris *et al.* 2006; Appendix A).

Despite the demonstrated interspecific competition between *Nesoryzomys* and *Rattus*, they have been sympatric for an unusually long period (up to 400 years: Patton 1975) when compared, for example, with the reported displacement of *N. indefessus* by *Rattus* from the neighboring island of Santa Cruz within 4 years (Rambech [1934] in Clark 1984). Furthermore, both species have been shown to share a preference for the same microhabitat and to be active throughout the night (Harris *et al.* 2006; Appendix A). Together these findings suggest that the two species are in a state of competitive coexistence at their site of sympatry but that spatial and temporal segregation play little or no role in facilitating it. Instead it has been hypothesized that the observed periodic crashing of arid zone *Rattus* populations during periods of drought alleviate their competitive effect on the *Nesoryzomys* population (Clark, 1980b), which may create a state of constant disequilibrium that promotes local coexistence (Chesson & Warner, 1981).

Indeed, Clark (1980b) suggests that arid zone *Rattus* populations are food limited, and it is the decline in foodstuffs associated with seasonal drought that causes this observed crash. He also suggests that at least one allopatric Rice rat species, *Oryzomys bauri*, is food limited but can maintain a year-round stable population (Clark, 1980a). Perhaps this difference in the species' responses to the decline in foodstuffs could be a consequence of their food 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 & McGehee, 1980). Conversely, a consumer might switch its preferences to exploit an abundant food thereby maintaining its fitness (Kotler & Brown, 1988), and perhaps the sex-specific competitive effect of *Rattus* is a manifestation of intersexual differences in food selection by *Nesoryzomys* (Gales, 1982; Kincaid & Cameron, 1985).

In this study, a combination of spool-and-line tracking and semi-natural diet trials was used first to identify, and then to quantify, each species' diet in allopatry, which was then compared to their diet in sympatry, as estimated from the spool-and-line tracking (Clode & Macdonald, 1995; Macdonald & Thom, 2001). The consumption of one food may influence the choice of another (Manly *et al.*, 1993), resulting in non-independent observations that preclude statistical analysis using conventional methods; to circumvent this, niche measures were employed to draw comparisons and significance testing was assessed by permutation procedures (Mueller & Altenberg, 1985). Although the concept of a quantifiable niche proposed by Hutchinson (1957) attracted widespread debate over what aspect of a niche should be measured (e.g. Holt 1987), and how it should be measured (e.g. Hurlbert 1978), the response to such criticism has resulted in an extensive literature dedicated to defining and quantifying the niche which has ultimately served to strengthen the Hutchinsonian concept (Leibold, 1995). Nevertheless, uncertainty still surrounds the relationship between measures of niche overlap and interspecific competition (e.g. Abrams 1980), and so food preferences for each species (allopatric diet) were also quantified using niche measures to support inferences about interspecific competition pertaining to overlap

in sympatric diet. Since two distinct seasons occur at the study site, and correspond to Schoener's (1982) 'fat' and 'lean' times, the investigation was conducted separately with the foods available at the locality in each season. In addition, the results reported here also represent the first description of *Nesoryzomys* feeding habits and a detailed description of arid zone *Rattus* feeding habits in the Galápagos.

2.3 METHODS

2.3.1 STUDY SITE AND SEASONALITY

This study was carried out at a site known locally as La Bomba, situated on the central north coast of Santiago in the Galápagos archipelago, during 2004. The prevailing trade winds that bring rain to the Galápagos approach from the southeast so that Santa Cruz and the highlands of Santiago cast a combined rainshadow over La Bomba. This results in an arid habitat characterized by the cactus *Opuntia galapageia* var. *galapageia* (Og), trees; *Bursera graveolens* (Bg), *Cordia lutea* (Cl) and *Croton scouleri* (Cs), shrubs; *Clerodendrum molle* var. *molle* (Cm), *Castela galapageia* (Cg), *Lantana peduncularis* (Lp), *Scutia spicata* var. *pauciflora* (Ss), and *Vallesia glabra* (Vg) with an additional tree, four shrub species, and 21 vine and herbaceous plants excluding grasses (given in Appendix B). The terrain at La Bomba is 'aa' lava that is characteristically serrated and broken and readily snags spool line (Key & Woods, 1996).

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 >50-70mm/month) and daily temperatures ranging from 26-30°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 <10mm/month) with daily temperatures ranging from 20-24°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 & Palmer, 1997), resulting in prolonged and frequently intensified hot-wet season conditions that promote growth and reproduction of terrestrial organisms (Snell & Rea, 1999). This study was carried out over both seasons and analyses were carried out separately for each season.

All experimental protocols complied with the current laws of the country in which they were performed (Ecuador) and the guidance of the UK Animals (Scientific Procedures) Act 1986. All statistical analyses were carried out using SPSS (v14.0) unless otherwise specified.

2.3.2 DETECTION OF FREQUENTLY VISITED PLANTS

No previous studies have reported the feeding habits of *Nesoryzomys* or arid zone *Rattus* at La Bomba and so it was necessary first 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 (usually for small mammals it is affixed between the shoulder blades) 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 lines plays out from the centre of the bobbin and catches on vegetation/terrain as it passes. Under optimal conditions, like those at La Bomba, the resulting line can be followed and the animals movements recorded at a very fine scale. Interested readers are directed towards Harris et al. (2006; Appendix A) and Boonstra and Craine (1994) for further discussions of this method. Although visited plants may have been visited for reasons other than foraging, the likelihood of the tracked individuals being hungry was maximized by capturing them at first emergence in Tomahawk Live traps (Model #201, 40.6 x 12.7 x 12.7cm, Tomahawk Live Trap Co. PO Box 323, Tomahawk, WI 54487) baited with peanut scented rag. Weight, sex and reproductive condition 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 spool (Danfield Ltd, Leigh, England) (see Harris *et al.* 2006; Appendix A for a discussion of this method) adapted to weigh less than 5% of their body weight.

Analysis of the spool line (=Chosen) was carried out the following morning. Lines were usually longer than 70m and the first 10m of the line was considered to constitute a flight response and was not analyzed. Thereafter the presence of any plant part (defined here as leaf (L), fruit (F), flower (R), seed (S) and cactus pad (P)) was recorded above and within a 10cm band either side of the line for each 1m segment of alternate 5m sections. 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 analyzed in the same way (=Random).

Firstly, to determine if the spooled animals were selective in their use of the environment, the data for each plant part were pooled by plant species for both Chosen and Random lines separately before ordination of the Chosen and Random line data together using detrended correspondence analysis (DCA) (Hill & Gauch, 1980). While using DCA to ordinate the Random data alone would reveal any pattern underlying the plant community, incorporating the Chosen data, which is heavily biased towards plants visited by the foraging animals, would reveal any selectivity (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 the measure of the samples containing the species and the 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 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.

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 & 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 & Seaby, 1999).

2.3.3 PALATABILITY OF PLANT PARTS AND FOOD PREFERENCES

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 importance 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 trialed individually at their point of capture in plastic crates (57 x 36.5 x 30.5cm) fitted with wire mesh lids that did not preclude the animals' awareness to 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 and so to account for this uncertainty the foods were provided *ad lib* in separate Petri dishes at different distances from the refuge and before each trial their locations were randomized. Free water was extremely scarce at La Bomba and therefore was not provided. All of the plant parts were harvested from the locality within 1hr 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 immediately after capture (Butler *et al.*, 2006) and terminated after 1hr 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 after accounting for inedible parts.

2.3.4 SYMPATRIC AND ALLOPATRIC DIET OVERLAP

Niche measures were chosen to quantify each species' sympatric and allopatric diet in order to overcome the non-independence of observations on feeding animals (Hurlbert, 1984). Individual measures of sympatric diet were quantified from the spool-and-line tracking (only foods present on either the Chosen and/or Random line were counted for each individual) and measures of allopatric diet from the food preference trials. The mean of the individual proportional utilization was taken to represent the species' diet selection. Overlap measures were calculated using the FT index proposed by Smith and Zaret (1982):

$$FT = \sum \sqrt{p_{1i} \cdot p_{2i}} \quad (2.1)$$

where p_{1i} and p_{2i} represent the proportions of the i th 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 their inclusion produces measures that reflect consumer-resource interactions rather than consumer-consumer interactions (Lawlor, 1980). Since sample sizes were not considered sufficiently large for accurate statistical inference (Smith, 1982), a randomization distribution was constructed from 1000 overlap measures created from bootstrapped resamples of the original data (Mueller & Altenberg, 1985). This randomization distribution was used to calculate 95%

confidence intervals and to assess hypotheses statistically by calculating the proportion of the randomization distribution that exceeded the actual overlap value under scrutiny. Measures of sympatric and allopatric diet breadth were calculated using Hurlbert's niche breadth measure (Hurlbert, 1978):

$$B = \frac{1}{\sum (p_i^2/q_i)} \quad (2.2)$$

where p_i and q_i represent the proportions of the i th food visited/eaten and available respectively. B was standardized to vary between 0 and 1 representing exclusive utilization of one food and equal utilization 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 allopatric diet breadth (equal to $1/i$), but for measures of sympatric diet breadth, availability was calculated as the mean proportional occurrence of each food type on the random lines. Measures of niche breadth that consider availability are biased and choice of a measure is dependent on whether common or rare resources are important: Hurlbert's B' does not underestimate the importance of rare foods that might be very important during periods of food scarcity when competitive interactions should be strongest (Krebs, 1999). Both confidence intervals and the seasonal difference in B' were determined using the approaches adopted for statistical testing of overlap hypotheses.

To support inferences of interspecific competition, foods were ranked based on their mean proportional utilization after accounting for their availability, and compared between sympatric and allopatric diets using Kendall's Tau b test of concordance. High correlation between a species sympatric and allopatric diets indicated that it was obtaining its preferred diet when in sympatry. Comparisons were made between *Nesoryzomys* and *Rattus*, between both sexes of *Nesoryzomys* and between each sex of *Nesoryzomys*

and *Rattus*. Separate sex comparisons were not drawn for *Rattus* due to small sample sizes for the sexes separately.

2.3.5 INVERTEBRATES

The main drawback of using spool-and-line tracking to quantify sympatric 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 (x40 magnification) (Luo *et al.*, 1994). The area of the ocular view containing chitinous insect remains was estimated to the nearest 10 percent with the aid of a graticule and repeated for 5 independent views. An average percent cover was derived for each animal, which were then grouped by species and sex and compared within and between seasons in ANOVA.

2.4 RESULTS

2.4.1 FOOD IDENTIFICATION

Over 30m of Chosen spool line data were collected for each of 41 *Nesoryzomys* and 18 *Rattus* in the dry season and 44 *Nesoryzomys* and 15 *Rattus* in the wet season along with the corresponding random line data (Table 2.1). These data suggest that some plant species occur in Chosen lines more frequently than Random lines, for example *Opuntia* occurred in a mean of $2.7 \pm 3.0\text{SD}$ sections of *Nesoryzomys* Chosen lines in the dry season compared to $0.7 \pm 1.2\text{SD}$ sections of the corresponding Random lines. These data were ordinated together using DCA to reveal such selectivity. The first two extracted

axes explained 45.0 and 30.4% of the variation in the *Nesoryzomys* spooling data and 86.1 and 54.5% of the variation in the *Rattus* spooling data in the dry and wet seasons respectively. DCA joint plots constructed for each species in each season (Figures 2.1 and 2.2) reveal a distinct disparity in the positions of the Chosen and Random sample points; in each case the Random samples cluster around the centre and left side of Axis 1 while the Chosen samples consistently fall to the right. This observed spread suggests that Axis 1 best represents a selectivity gradient increasing in strength from the left side of the axis to the right. To test if the spread of Chosen and Random samples were statistically different their corresponding sample scores were compared for each species by two-way univariate ANOVA (Table 2.2). Both *Nesoryzomys* and *Rattus* Chosen sample scores were significantly higher than their corresponding Random scores in both seasons and individual selectivity was important for *Nesoryzomys* in both seasons and *Rattus* in the wet season only. The variation in the selectivity of individual *Rattus* foraging in the dry season was not important, that is to say that these animals all visited similar plants regardless of the location in which they were spooled. Axis 2 was not interpreted as DCA has well-known distortions for higher axes (Hill & Gauch, 1980).

Table 2.1: Mean (\pm SD) number of 1m line sections containing each plant for Chosen lines (Line = 1) and Random lines (Line = 2) for both *Nesoryzomys* (Sp = N) and *Rattus* (Sp = R) in both the Dry and Wet seasons. Absent plants are indicated by a dash (—) and plants rarely recorded (and therefore not included in the analysis) are noted by trace (t). Plant abbreviations are *Acacia rorundiana* (Ac), *Blainvillea dichotoma* (Blain), *Boerhavia caribaea* (Pfp), *Bursera graveolens* (Bg), *Castela galapageia* (Cg), *Clerodendrum molle* (Cm), *Cordia lutea* (Cl), *Croton scouleri* (Cs), *Desmodium procumbens* (Curl), *Ipomea tribola* (Hrt), *Lantana peduncularis* (Lp), *Mentzelia aspera* (Ma), *Merremia aegyptica* (Merr), *Opuntia galapageia* (Og), *Porophyllum ruderale* (Poro), *Portulaca oleracea* (Port), *Sarcostemma angustissimum* (Sarco), *Scutia spicata* (Ss), *Tephrosia decumbens* (Td), *Tetramerium nervosum* (Conc), *Tiquila nesiotica* (Mat), *Vallesia galabra* (Vg), unspecific grasses (Grass), and unidentified plants (Rlp, Ser, Trif).

Season	Sp	N	Line	Ac	Blain	Pfp	Bg	Cg	Cm	Cl	Cs	Curl	Hrt	Lp	Ma
Dry															
	N	41	1	0.2±0.8	—	t	0.1±0.4	3.5±2.7	6.3±5.0	0.5±1.3	0.1±0.4	—	—	1.2±1.6	2.4±2.9
		41	2	0.2±0.8	—	t	0.1±0.3	1.8±2.0	4.2±3.4	0.5±1.1	0.1±0.4	—	—	0.9±1.2	5.0±5.3
	R	18	1	0.1±0.3	—	t	0.1±0.2	2.2±2.3	5.6±5.0	3.4±4.1	0.2±0.6	—	—	0.6±1.6	2.6±3.2
		18	2	0.0±0.0	—	t	0.0±0.0	1.5±1.4	4.3±3.3	0.4±0.8	0.0±0.0	—	—	0.5±0.8	4.3±3.2
Wet															
	N	44	1	—	0.3±0.8	3.0±2.5	3.7±5.0	1.7±2.1	8.8±6.2	0.7±2.1	0.6±1.2	8.5±4.7	0.4±1.1	2.8±3.5	8.1±5.4
		44	2	—	0.2±0.4	4.8±4.1	3.1±3.4	1.1±1.6	6.0±3.5	0.2±0.7	0.3±1.0	11.8±5.7	0.5±0.8	2.2±4.0	8.5±5.0
	R	15	1	—	0.3±0.9	1.5±1.6	7.4±4.7	2.4±2.9	9.3±4.8	2.2±2.9	1.0±1.2	6.4±5.1	0.0±0.0	1.4±2.3	5.4±4.2
		15	2	—	0.6±1.2	4.1±3.7	4.8±4.2	1.3±1.8	6.1±5.0	0.2±0.6	0.8±1.1	11.4±6.1	0.4±0.6	0.9±1.0	6.9±5.7
	Merr	Og	Poro	Port	Sarco	Ss	Td	Conc	Mat	Vg	Grass	Rlp	Ser	Trif	
Dry															
	t	2.7±3.0	—	—	0.4±1.1	0.2±1.0	t	1.1±1.6	t	0.5±1.2	5.2±3.9	0.4±0.7	—	—	
	t	0.7±1.2	—	—	0.5±1.3	0.3±0.9	t	1.2±1.7	t	0.1±0.4	8.0±4.1	0.5±0.8	—	—	
	t	0.3±0.7	—	—	0.4±1.2	0.2±0.4	t	1.2±1.3	t	2.0±5.6	4.5±5.0	0.3±0.6	—	—	
	t	0.5±0.8	—	—	0.0±0.0	0.0±0.0	t	1.0±1.7	t	0.3±0.9	7.8±5.0	0.6±1.2	—	—	
Wet															
	0.6±1.1	1.9±2.4	0.3±0.8	1.0±1.4	0.3±0.9	0.2±0.6	0.6±1.0	2.4±2.6	0.1±0.5	0.2±0.6	3.5±2.6	0.7±1.2	2.2±2.0	0.4±0.7	
	0.6±1.4	0.6±0.8	0.4±0.5	1.8±2.7	0.3±0.9	0.1±0.3	1.1±1.9	1.8±2.7	0.2±0.6	0.2±0.7	5.9±3.4	0.6±1.3	4.4±4.1	0.7±1.4	
	0.2±0.6	0.4±0.5	0.2±0.6	1.1±1.8	0.1±0.5	0.8±1.5	0.3±0.7	1.6±2.2	0.0±0.0	4.5±6.6	3.0±2.2	0.5±0.9	1.1±1.0	0.3±1.0	
	0.5±0.8	0.6±0.7	0.3±0.6	2.4±2.3	0.7±1.3	0.1±0.5	1.2±1.2	1.7±2.7	0.3±0.8	0.5±1.0	5.6±4.5	0.8±0.9	3.1±3.0	0.7±1.6	

Table 2.2: Partial ANOVA tables for comparison of Chosen and Random line sample scores on Axis 1 of DCA ordinations in each season.

		Effect	N	d.f.	Mean squares	F	p
<i>Nesoryzomys</i>	Dry	Individual	41	40	3085.35	3.85	< 0.01
		Line		1	36162.00	45.12	< 0.01
		Error		40	801.38		
	Wet	Individual	44	43	2598.55	2.55	< 0.01
		Line		1	5648.01	5.55	0.02
		Error		43	1018.48		
<i>Rattus</i>	Dry	Individual	18	17	5.62	1.10	0.42
		Line		1	32.84	6.44	0.02
		Error		17	5.10		
	Wet	Individual	15	14	14.59	2.65	0.04
		Line		1	149.55	27.13	< 0.01
		Error		14	5.51		

Figures 2.1 and 2.2 show no discernable clustering of plant species however a comparison of the location of individual plant species along Axis 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 plot the ellipse encapsulates the Selected plants (Figures 2.1 and 2.2) and it can be seen that the plant species in the Selected groups consistently fall on the right side of Axis 1 (*B. graveolens* (Bg) and *Acacia insulae* (Ac) give exception to this rule for *Rattus* in the dry season).

Twenty three *Nesoryzomys* and 17 *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 *Opuntia* fruit that was not eaten by *Rattus* in either season.

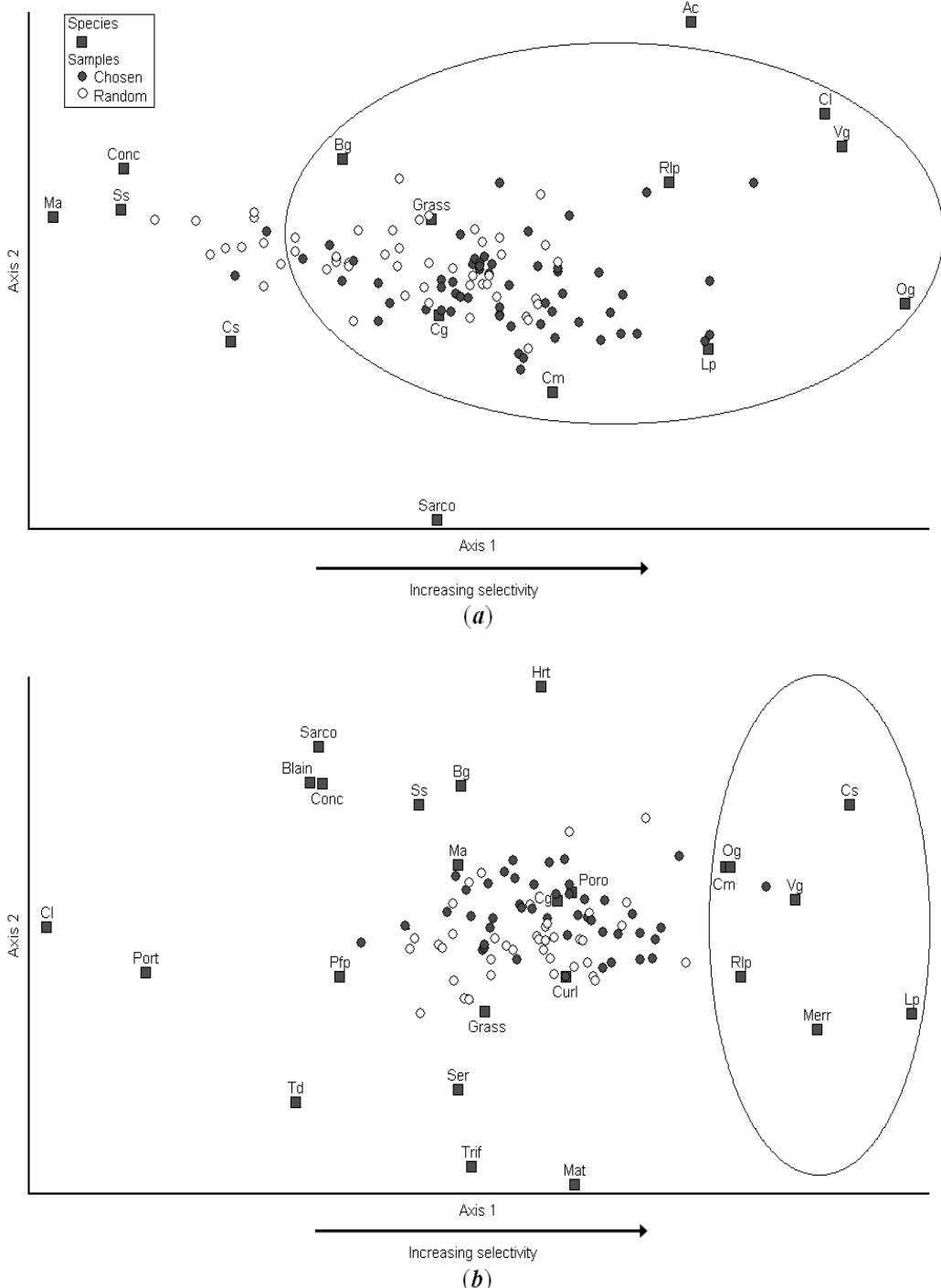


Figure 2.1: DCA joint plots of *Nesoryzomys* selectivity in the dry (a) and wet (b) seasons. Axis 1 corresponds to a selectivity gradient increasing from left to right. Ellipses encapsulate the plant species classified as *Selected* by TWINSPAN analysis. Plant abbreviations are *Acacia rorundiana* (Ac), *Blainvillea dichotoma* (Blain), *Boerhavia caribaea* (Pfp), *Bursera graveolens* (Bg), *Castela galapageia* (Cg), *Clerodendrum molle* (Cm), *Cordia lutea* (Cl), *Croton scouleri* (Cs), *Desmodium procumbens* (Curl), *Ipomea tribola* (Hrt), *Lantana peduncularis* (Lp), *Mentzelia aspera* (Ma), *Merremia aegyptica* (Merr), *Opuntia galapageia* (Og), *Porophyllum ruderale* (Poro), *Portulaca oleracea* (Port), *Sarcostemma angustissimum* (Sarco), *Scutia spicata* (Ss), *Tephrosia decumbens* (Td), *Tetramerium nervosum* (Conc), *Tiquila nesiotica* (Mat), *Vallesia galabra* (Vg), unidentified plants (Grass, Rlp, Ser, Trif).

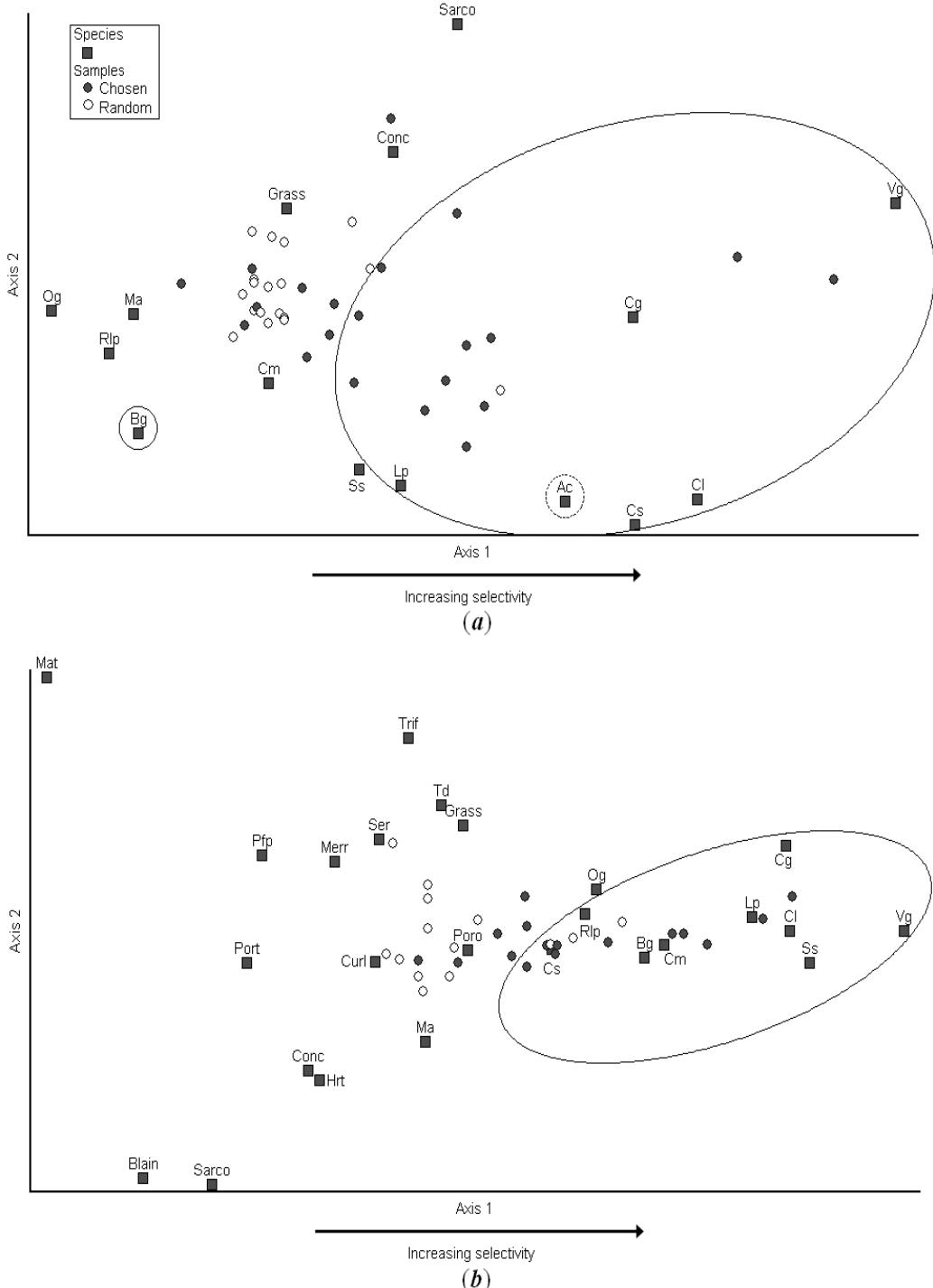


Figure 2.2: DCA joint plots of *Rattus* selectivity in the dry (a) and wet (b) seasons. Axis 1 corresponds to a selectivity gradient increasing from left to right. Ellipses encapsulate the plant species classified as *Selected* by TWINSPAN analysis. Broken line ellipses encapsulate plant species that belong outside the *Selected* group. Plant abbreviations are *Acacia rorundiana* (Ac), *Blainvillea dichotoma* (Blain), *Boerhavia caribaea* (Pfp), *Bursera graveolens* (Bg), *Castela galapageia* (Cg), *Clerodendrum molle* (Cm), *Cordia lutea* (Cl), *Croton scouleri* (Cs), *Desmodium procumbens* (Curl), *Ipomea tribola* (Hrt), *Lantana peduncularis* (Lp), *Mentzelia aspera* (Ma), *Merremia aegyptica* (Merr), *Opuntia galapageia* (Og), *Porophyllum ruderale* (Poro), *Portulaca oleracea* (Port), *Sarcostemma angustissimum* (Sarco), *Scutia spicata* (Ss), *Tephrosia decumbens* (Td), *Tetramerium nervosum* (Conc), *Tiquila nesiotica* (Mat), *Vallesia galabrah* (Vg), unidentified plants (Grass, Rlp, Ser, Trif).

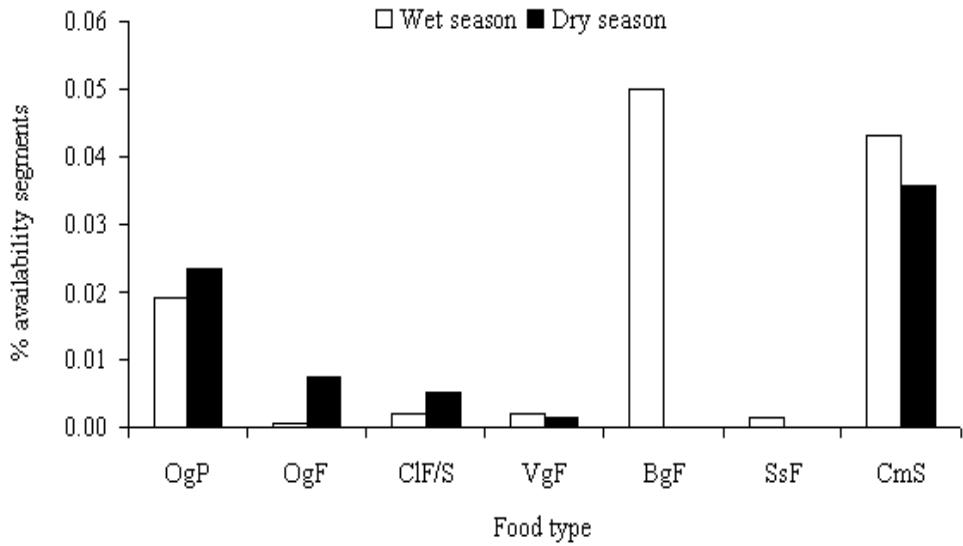


Figure 2.3: Food availability (as a % of availability segments) in both seasons. Plant part abbreviations are: *Opuntia galapageia* pad (OgP), fruit (OgF), *Cordia lutea* fruit (ClF), seed (ClS), *Vallesia glabra* fruit (VgF), *Bursera graveolens* fruit (BgF), *Scuita spicata* fruit (SsF), and *Clerodendrum molle* seed (CmS).

2.4.2 SEASONAL FOOD AVAILABILITY

Foods selected by both species were all highly seasonal with the exception of *Opuntia* pads that changed little in their availability between the wet and dry seasons (Figure 2.3). *B. graveolens* and *S. spicata* fruits were absent at La Bomba during the dry season and *Opuntia* fruits were effectively absent in the wet season.

2.4.3 OVERLAP IN *NESORYZOMYS* AND *RATTUS* DIETS

In the wet season *Nesoryzomys* sympatric diet primarily consisted of *Opuntia* fruits and pads (Figure 2.4a) and this specialization was embodied in a moderately narrow measure of niche breadth. *Rattus* was more specialized than *Nesoryzomys*, although not significantly ($P = 0.099$, Table 2.3), and primarily ate *V. glabra* and *C. lutea* fruit (Figure 2.4a). Nevertheless, both species ate comparable amounts of *B. graveolens* and *S. spicata* fruits resulting in high diet overlap when sympatric in this season (Table 2.4). *Nesoryzomys* diet breadth in allopatry was similar to that when sympatric with *Rattus* ($P = 0.087$)

Table 2.3: Sympatric and allopatric diet breadth measures for each species and each sex of *Nesoryzomys* in both seasons calculated using Hurlbert's B' (1978). 95% confidence range given in brackets.

Species	Dry season		Wet season	
	Sympatry	Allopatry	Sympatry	Allopatry
<i>Nesoryzomys</i>	0.83 (0.69-0.93)	0.70 (0.54-0.78)	0.43 (0.18-0.72)	0.62 (0.47-0.72)
Male	0.82 (0.63-0.94)	0.71 (0.49-0.80)	0.29 (0.09-0.66)	0.62 (0.45-0.72)
Female	0.84 (0.62-0.93)	0.61 (0.36-0.69)	0.46 (0.13-0.86)	0.57 (0.35-0.73)
<i>Rattus</i>	0.22 (0.10-0.42)	0.29 (0.22-0.39)	0.29 (0.14-0.57)	0.48 (0.34-0.56)

however the rank orders of foods in each diet were not correlated (Kendall's tau-b, $t = 0.138$, $P = 0.702$) as illustrated by the low rank of *B. graveolens* fruit in the sympatric diet compared to the allopatric diet (Figure 2.4b). In contrast, the food ranks in *Rattus* allopatric and sympatric diets were strongly correlated ($t = 0.690$, $P = 0.056$, Figure 2.4b) and its allopatric and sympatric diets were also similar ($P = 0.062$).

As in the wet season, the sympatric diets in the dry season primarily consisted of *Opuntia* foods for *Nesoryzomys* and *V. glabra* fruits and *C. lutea* seeds for *Rattus* (Figure 2.4c). *Nesoryzomys* sympatric diet breadth was broader in this season than in the wet season ($P = 0.003$) reflecting a more generalized feeding strategy, while *Rattus* was similarly specialized in both seasons ($P = 0.176$, Table 2.3). Despite the generalized feeding of *Nesoryzomys*, interspecific overlap in sympatric diets was less in this season than in the wet season ($P = 0.024$) as *Nesoryzomys* incorporated less *C. lutea* seeds and shared fewer foods with *Rattus* than in the wet season. Foods were ranked differently in *Nesoryzomys* sympatric and allopatric diets ($t = 0.00$, $P = 1.000$) as is evident from *C. lutea* and *C. molle* seeds (Figure 2.4d), and its allopatric diet breadth was significantly narrower than its sympatric diet breadth ($P < 0.001$, Table 2.3). In contrast, *Rattus'* diet breadth was similar for its allopatric and sympatric diets ($P = 0.190$) and again food ranks were strongly correlated between them ($t = 0.738$, $P = 0.077$, Figure 2.4d). Despite the broadening of *Nesoryzomys* allopatric diet in this season ($P = 0.047$), interspecific diet overlap was lower than in the wet season ($P = 0.019$) as a consequence of *Rattus* further specializing upon *V. glabra* fruit ($P < 0.001$).

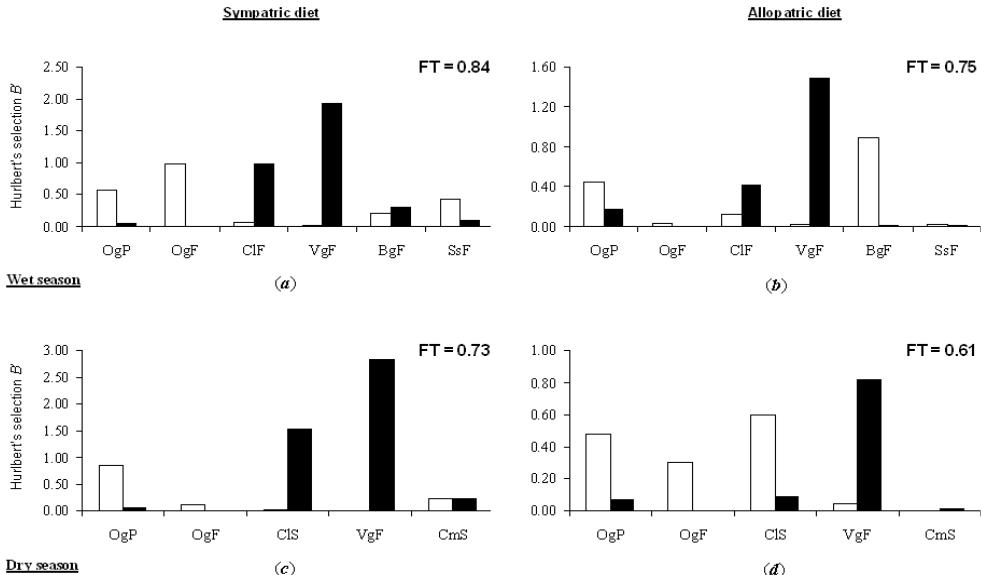


Figure 2.4: Comparison of *Nesoryzomys* (white bars) and *Rattus* (black bars) diet selection (Hurlbert's selection B' calculated as p_i^2/q_i , where p is the mean proportion of food i in the diet and q is the mean proportion that food i is of all the available foods) in the wet season (a and b) and the dry (c and d). Plant part abbreviations are: *Opuntia galapageia* pad (OgP), fruit (OgF), *Cordia lutea* fruit (CIS), seed (ClS), *Vallesia glabra* fruit (VgF), *Bursera graveolens* fruit (BgF), *Scuita spicata* fruit (SsF), and *Clerodendrum molle* seed (CmS).

2.4.4 OVERLAP IN SEPARATE SEX *NESORYZOMYS* AND *RATTUS* DIETS

In the wet season male *Nesoryzomys* were very specialized and their sympatric diet principally consisted of *Opuntia* fruits, *Opuntia* pads and *S. spicata* fruits (Figure 2.5a). Female *Nesoryzomys* were similarly specialized to male *Nesoryzomys* ($P = 0.139$, Table 2.3) but, also incorporated *C. lutea* and *V. glabra* fruits but not *S. spicata* fruits in their sympatric diet (Figure 2.5c). Although intersexual sympatric diet overlap was high in this season, differences in their diet breadths manifested in significantly different overlap with *Rattus* that was higher for females than for males ($P < 0.001$, Table 2.4). Male *Nesoryzomys* allopatric diet breadth was significantly broader than that of its sympatric diet ($P = 0.045$) because it selected both *C. lutea* and *V. glabra* fruits, but also *Opuntia* and *S. spicata* fruits, in small amounts as part of its allopatric diet (Figure 2.5b). In contrast, the measure of female *Nesoryzomys* allopatric diet breadth was not different to that of its sympatric diet ($P = 0.271$, Table 2.3) and all foods were present in both

Table 2.4: Interspecific diet overlap measures for *Nesoryzomys* and separates sexes of *Nesoryzomys* with *Rattus* in both seasons calculated using Smith and Zaret's FT (1982). 95% confidence range given in brackets.

Species	Dry season		Wet season	
	Sympatry	Allopatry	Sympatry	Allopatry
<i>Nesoryzomys</i> : <i>Rattus</i>	0.73 (0.49-0.84)	0.61 (0.37-0.74)	0.84 (0.67-0.92)	0.75 (0.60-0.82)
Male: <i>Rattus</i>	0.74 (0.48-0.84)	0.62 (0.29-0.78)	0.69 (0.48-0.80)	0.73 (0.54-0.82)
Female: <i>Rattus</i>	0.71 (0.46-0.81)	0.56 (0.30-0.69)	0.87 (0.66-0.94)	0.77 (0.57-0.83)
Male:Female	0.99 (0.93-1.00)	0.97 (0.78-0.99)	0.88 (0.71-0.94)	0.97 (0.79-0.99)

diet measures (Figure 2.5d). Nevertheless, food ranks were not correlated for either sex's sympatric and allopatric diets, indeed they were weakly negatively correlated for both sexes (male: $t = -2.76$, $P = 0.444$, female: $t = -0.138$, $P = 0.702$). *B. graveolens* fruits were the preferred food in allopatric male and female *Nesoryzomys* diets however it was not ranked highly in either sex's sympatric diet in this season. Both *B. graveolens* and *C. lutea* fruit constituted larger proportions of female *Nesoryzomys* allopatric diet than for male *Nesoryzomys* (Figure 2.5b and 2.5d), nevertheless there was high intersexual overlap as a consequence of similar diet breadths in allopatry ($P = 0.155$), and there was no difference in their dietary overlap with *Rattus* ($P = 0.172$, Table 2.4).

In contrast to overlap in wet season sympatric diets, there was no difference between male and female *Nesoryzomys* overlap with *Rattus* in the dry season ($P = 0.201$), and this was as a consequence of a substantial broadening of the male *Nesoryzomys* diet breadth ($P = 0.002$) such that it was not different from that of female *Nesoryzomys* ($P = 0.347$) that also significantly broadened ($P = 0.038$, Table 2.3). This concurrent broadening of diets was epitomized in a very high measure of intersexual overlap in sympatric diet that was significantly higher than the same measure in the wet season ($P < 0.001$, Table 2.4).

Each sex of *Nesoryzomys* ate mostly *Opuntia* pads when in sympatry with *Rattus* (Figure 2.5e and g) but less *C. lutea* seeds and *V. glabra* fruits than would be expected from their ranks in allopatry diets (male: $t = -0.200$, $P = 0.624$, female $t = 0.00$, $P = 1.000$, Figure 2.5f and h). Comparison of male and female allopatric diets breadth revealed no difference in this season ($P = 0.233$) and they were similar to those for the wet season

(male: $P = 0.054$, female: $P = 0.180$). However in contrast to the wet season, both male and female allopatric diets were narrower than those when sympatric with *Rattus* (male: $P = 0.003$, female: $P < 0.001$) as male *Nesoryzomys* specialized on *C. lutea* seeds and female *Nesoryzomys* consumed more *Opuntia* pads (Figure 2.5f and h). Nevertheless, these intersexual differences in allopatric diet were not apparent in interspecific overlap with *Rattus* that was similar for both sexes in this season ($P = 0.149$) but the female specialization on *Opuntia* pads did manifest in lower interspecific overlap with *Rattus* compared the wet season ($P < 0.001$).

2.4.5 INVERTEBRATES

Rattus faeces contained more chitinous material than did those of *Nesoryzomys* ($F_{1,144} = 12.68$, $P < 0.001$), although there was no difference between sexes ($F_{1,144} = 0.89$, $P = 0.346$), and faeces of both species contained more chitinous material in the wet season ($F_{1,144} = 23.51$, $P < 0.001$). The species x season interaction was significant ($F_{1,144} = 14.99$, $P < 0.001$), which demonstrated that *Rattus* faeces contained more chitinous material than *Nesoryzomys* in the wet season but not in the dry (Figure 2.6).

2.5 DISCUSSION

Interspecific overlap in sympatric *Nesoryzomys* and *Rattus* diets was higher in the wet season than in the dry. This was attributable to the narrower sympatric diet of *Rattus* in the dry season compared to the wet, rather than a narrowing of sympatric *Nesoryzomys* diet that, on the contrary, actually increased in breadth over the same period. According to predictions of seasonal changes in niche breadth both species should specialize in their use of diminishing shared foods to minimize the costs of resource competition (Schoener, 1982). If resource competition is highly asymmetrical then only the less efficient competitor need narrow the composition of its diet, while the more efficient competitor may

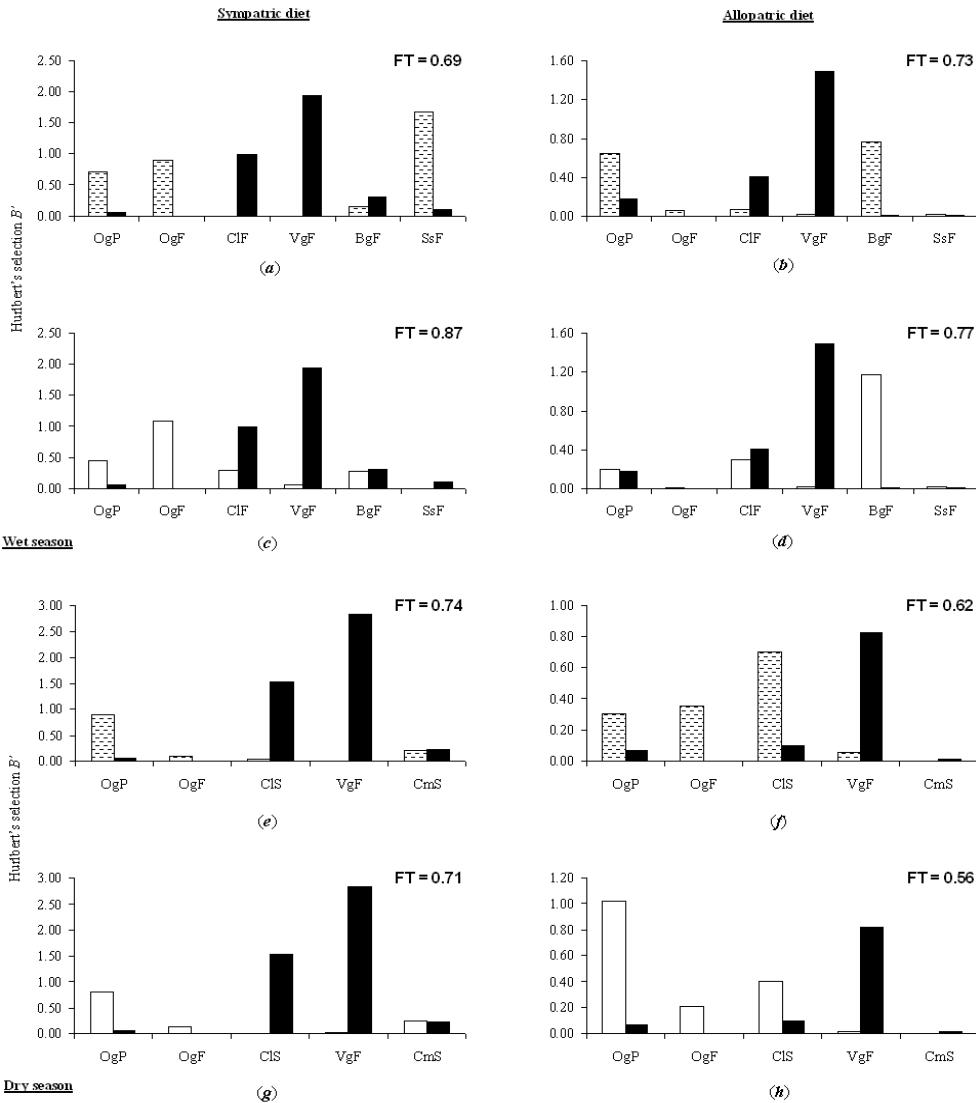


Figure 2.5: Separate comparisons of male (thatched bars) and female *Nesoryzomys* (white bars) diet selection (Hurlbert's selection B' calculated as p_i^2/q_i , where p is the mean proportion of food i in the diet and q is the mean proportion that food i is of all the available foods) to *Rattus* (black bars) in the wet season (male: a and b, female: e and f) and the dry (male: c and d, female g and h). Plant part abbreviations are: *Opuntia galapageia* pad (OgP), fruit (OgF), *Cordia lutea* fruit (ClF), seed (ClS), *Vallesia galabra* fruit (VgF), *Bursera graveolens* fruit (BgF), *Scuita spicata* fruit (SsF), and *Clerodendrum molle* seed (CmS).

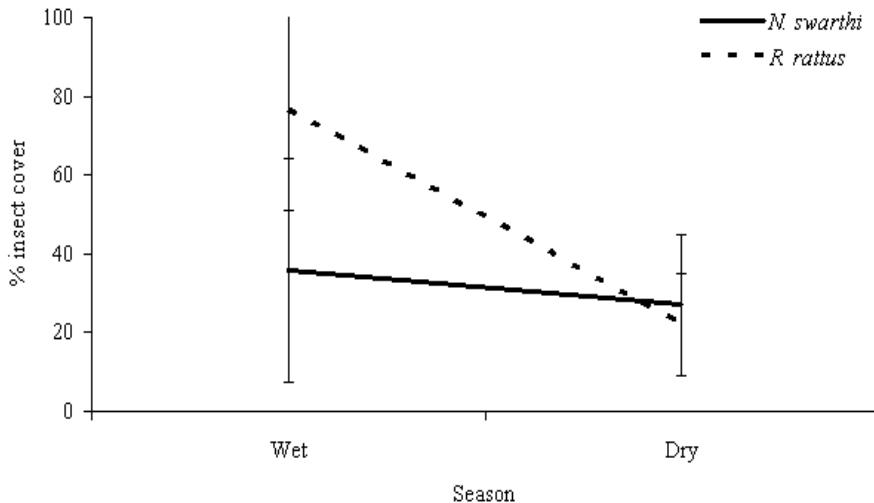


Figure 2.6: Mean proportion of insect matter in the faeces of each species in each season. Bars represent standard error (SE).

actually broaden its use of the available foods. It would seem then that *Nesoryzomys* is the more efficient resource competitor in this invaded community. However, closer scrutiny of *Rattus* sympatric diet reveals that it comprised predominantly fruits in both seasons, as supported by the allopatric diet and previous work on *Rattus* diet in the Galápagos (Clark, 1982). Since the prevalence of fruiting plants and abundance of fruits quickly diminishes with progression from the wet season to the dry, in adhering to a frugivorous diet *Rattus* diet breadth would also be expected to narrow. Indeed, the strong correlations between its diets when in allopatry and in sympathy in both seasons demonstrate that it was acquiring its preferred foods in the field and the observed narrowing of its allopatric diet in the dry season suggests that fewer foods were found to be palatable in this season. So although it seems that *Rattus* niche measures conform to predicted seasonal dynamics (Schoener, 1982), these findings suggest that the observed narrowing of diet from a ‘fat’ to a ‘lean’ time is an obligatory response to a diminishing food supply rather than an adaptive behaviour to minimize resource competition with *Nesoryzomys*. It follows that as the cost of foraging for these diminishing foods increases the consumer population incurs reduced fitness (Armstrong & McGehee, 1980) and, possibly in conjunction with the reduced availability of free water, may cause the crash of *Rattus* populations in the

arid zone during the dry season (Harris & Macdonald, in press).

In contrast to the narrowing of *Rattus* sympatric diet in the dry season, that of *Nesoryzomys* broadens and is broader than *Rattus* in both seasons. Broad measures of niche 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 & Wiens, 1980). With the population crash of *Rattus*, it would also seem that *Nesoryzomys* is not required to specialise its diet in sympathy during the dry season but can consume a broader diet to minimize the costs of foraging for diminishing foods. However, closer inspection of the foods selected by *Nesoryzomys* in sympathy reveals distinct disparities with the foods selected in the diet selection trials. In captivity, *Nesoryzomys* preferred *B. graveolens* fruits and *C. lutea* seeds in the wet and dry seasons respectively but, spool-and-line tracking results suggest that these constituted negligible quantities in their seasonal diets when sympatric with *Rattus*. Furthermore, these foods were an important feature of *Rattus* diets in sympathy and allopatry. In contrast, *Opuntia* foods constituted a disproportionately large amount of *Nesoryzomys* diet in sympathy when compared to its rank importance in their allopatric diet. These results can scarcely be explained by the methods employed to measure the species diets in sympathy but seem to be readily explained by the presence of interspecific interference competition at shared food patches where the larger competitor (*Rattus*) gains priority access to foods and aggressively displaces the smaller competitor (*Nesoryzomys*) (e.g. Abramsky *et al.* 2005). If this were the case, by switching to *Opuntia* foods that are effectively unused by *Rattus*, *Nesoryzomys* may be adopting a foraging strategy to minimize the frequency of aggressive encounter. Previous research suggests that stressful interspecific encounters involving a dominant and subordinate animal can reduce the survival of the subordinate (Eccard & Ylönen, 2002; Harris & Macdonald, in press).

Separate analysis for male and female *Nesoryzomys* revealed that this apparent interspecific interference competition could be sex-specific. When sympatric with *Rattus*,

overlap in male and female diet was very high in the dry season but significantly lower in the wet season, which was due to the highly specialized diet of male *Nesoryzomys* in this season. This finding could be explained by the different dietary preferences - or even requirements - of male and female *Nesoryzomys* for *C. lutea* and *V. glabra* foods however, *C. lutea* and *V. glabra* were both consumed by males in allopatry, albeit in small amounts. Instead, this observation seems to suggest that male *Nesoryzomys* in sympatry with *Rattus* avoid *C. lutea* and *V. glabra* fruits in the wet season to avoid encounters with *Rattus*. Although the relation of niche overlap measures to interspecific competition is disputed (e.g. Abrams 1980), female diet overlap with sympatric *Rattus* was significantly higher than that for males. In contrast, overlap in male and female allopatric diet was very high and their degree of dietary overlap with *Rattus* was not different. Perhaps by avoiding *Rattus* male *Nesoryzomys* avoid repeated aggressive encounters that amount to competitive displacement, unlike females that being smaller, might have higher energetic requirements, or being mothers in this season, might have special nutrient requirements, are compelled to seek *C. lutea* and *V. glabra* fruit and are frequently displaced (Eccard & Ylönen, 2002). This differential displacement would support Harris and Macdonald's finding of sex-specific interspecific competition which demonstrated that smaller female *Nesoryzomys* survival increases when *Rattus* is removed (Harris & Macdonald, in press).

While female *Nesoryzomys* have higher overlap in sympatric diet with *Rattus* in the wet (breeding) season, a prerequisite for resource competition for food is that the shared foods are in limited supply so that their consumption by one competitor is to the detriment of the other (Keddy, 2001). Although seasonal food availability was measured in this study, it is not known whether the observed levels of availability would be limiting to the rodent community. Nevertheless, both the number of foods and their abundance in the wet season considerably exceed those in the dry season (Clark, 1980b). In addition, insect abundance is purportedly higher in the wet season (Peck, 2001), which *Rattus* are shown to exploit to a greater degree than *Nesoryzomys*. For these reasons, although female survival may be reduced through a high rate of aggressive encounters at shared food

patches, resource competition is probably absent in the wet season. Indeed, the similar measures of female (but not male) *Nesoryzomys* allopatric and sympatric diet breadths in this season suggest that although their diet composition may differ when sympatric with *Rattus*, they still acquire access to these essential foods some of the time. However, this inference doesn't apply to the dry season when food abundance is at its lowest, many insects have perished (Peck, 2001) and breeding has ceased. In this season both the composition and breadth of male and female *Nesoryzomys* sympatric diets are different to their allopatric diets suggesting that they forage strategically to minimize the frequency of aggressive encounters with *Rattus*. Thus, although the crash of the *Rattus* population should alleviate the effects of interference and resource competition in the dry season, it seems that because the foods that are available at this time are fewer and more ephemeral (Price, 1984) they are prone to heightened aggressive defense by the last remaining *Rattus* (Schoener, 1983). Indeed, Harris et al. (2006; Appendix A) found that *Nesoryzomys* activity was marginally extended in areas of high *Rattus* density compared to areas of low *Rattus* density, and suggested that this might reflect increased foraging activity to obtain sufficient nutrition when frequently displaced from shared food by sympatric *Rattus*.

Instead it seems that *Opuntia* may be instrumental to the observed coexistence at La Bomba. In seasonal diet selection trials *Nesoryzomys* ate both *Opuntia* pads and fruits in appreciable amounts whereas *Rattus* ate only small quantities of pad and no *Opuntia* fruit. This dichotomy was more pronounced in measures of their sympatric diets in which *Nesoryzomys* heavily utilized *Opuntia* foods and *Rattus* very rarely. Further support for *Rattus* indifference to *Opuntia* fruit was provided by a parallel investigation. Forty individuals of varying sex, age and size were held captive for up to 8hrs in rodent-proof enclosures and offered *Opuntia* fruit as food. Despite being caught shortly after emergence (permitting the animals a short period of foraging), none of these individuals consumed the offering during their captivity. To determine if these observations were due to lack of hunger or unfamiliar surroundings, all animals were provided with a post-experiment peanut butter bait ball which all of the animals consumed (Appendix C). Together these

findings suggest that the recent invader, *Rattus*, despite being an obligatory specialist upon fleshy fruits, has not become adapted to utilize the relatively abundant *Opuntia* foods. So, by selecting *Opuntia* foods, male *Nesoryzomys* in the wet season and both sexes of *Nesoryzomys* in the dry season should be able to reduce the frequency of aggressive encounters with *Rattus* by avoiding areas occupied by the aggressive invader (e.g. Terman 1974) while capitalizing on almost exclusive access to this nutritional, water rich resource. This lends support to the hypothesis proposed by Harris et al. (2006; Appendix A) that *Opuntia* may facilitate this coexistence by providing *Nesoryzomys* with a competition refuge from interference competition with *Rattus* (Durant, 1998). While this hypothesis offers hope for the persistence of *Nesoryzomys* at the final stronghold of La Bomba here *Opuntia* densities are at their highest (Harris et al. 2006; Appendix A), it should be noted that *Opuntia* populations are themselves in danger. Climate change models predict more frequent and intense El Niño phenomena (Webster & Palmer, 1997) and such conditions have already been documented to have devastating effects on survival and recruitment of *Opuntia* species (Hamann, 2004). This risk of cactus mortality emphasizes the need for further research into habitat-dependent competition and coexistence between *Rattus* and *Nesoryzomys*.

In this study community ecology theory, specifically niche theory (Chesson, 1991), was used to quantify and compare the diets of an endemic and invasive rodent species in sympatry in the Galápagos arid zone. Despite the apparent similarities between processes structuring natural communities and the processes underlying an early biological invasion (Shea & Chesson, 2002), few cases exist in the literature that exploit niche theory to study the impact of on IAS on the invaded community. This study demonstrates the suitability of community ecology theory to studies of invaded communities.



A spool that sheared off from a Santiago Rice rat foraging in a cactus canopy.

CHAPTER 3

SPATIAL EVIDENCE FOR COMPETITION

BETWEEN NATIVE AND INVASIVE RATS, AND IT'S

RELATION TO *OPUNTIA* CACTI

3.1 ABSTRACT

A recently rediscovered invaded small mammal community in the Galápagos has been shown to be structured by interspecific interference competition. The negative competitive effect of dominant *Rattus rattus* is sex-specific, causing reduced survival in the female endemic rats, *Nesoryzomys swarthi*, but not males. In addition to the higher displacement susceptibility of smaller females, sex-differences in their breeding dietary requirements may compel female *Nesoryzomys* to share certain foods with *Rattus* while male *Nesoryzomys* are able to switch to an endemic cactus competition refuge. In this way, cactus foods are presumed to facilitate the regional coexistence of the endemic and invasive rodent. The purpose of this study was to investigate the relative influence of *Rattus* and the distribution of cactus foods on the space use of *Nesoryzomys* to clarify the role of cactus in facilitating coexistence under different seasonal food availabilities. Spatially-explicit models, presented in a path analysis framework, were constructed to compare simultaneously the influence of these variables in contrasting cactus habitats and seasons. According to the predicted patterns the models generated strong support for the existence of sex-specific interspecific interference competition. Female *Nesoryzomys* was less negatively influenced by *Rattus* space use than males when breeding in habitat with all cactus foods and male space use was more influenced by the distribution of cactus foods than females. There was no difference in *Nesoryzomys* seasonal weight change in habitat with and without important cactus resources and so cactus foods were thought to provide male *Nesoryzomys* with a competition refuge from interference with *Rattus*. In contrast, male and female *Nesoryzomys* were equally negatively influenced by *Rattus* space use in the non-breeding season and male space use was positively influenced by *Rattus* space use in the absence of important cactus foods. Finally, cactus foods had a stronger influence on *Nesoryzomys* space use than did *Rattus* space use when non-cactus foods were in short supply and *Rattus* populations were critically low. During this time cactus foods may provide *Nesoryzomys* with important nutrition and water.

3.2 INTRODUCTION

If communities are structured by interspecific interference competition, their member species must exhibit some spatial or temporal segregation to avoid competitive exclusion (Morris *et al.*, 2000). It has been suggested that the cost of temporal segregation is high compared to spatial segregation, therefore rendering it rare in natural communities (Schoener 1974; but see Kronfeld-Schor & Dayan 2003). Spatial segregation, on the other hand, should be more common and is frequently manifested as habitat segregation (e.g. Morris 2003). In its most conspicuous form, spatial segregation is observed as the dominant species effectively excluding the subordinate from shared habitat at all times (e.g. Heske *et al.* 1984) but in its subtler form this exclusion may only occur when both species are present at the same time. For example, the behaviourally dominant Egyptian Sand gerbil, *Gerbillus pyramidum*, displaces the Allenby's gerbil, *G. andersoni allenbyi*, from rich food patches so that when artificial food patches were added to shared habitat *G. pyramidum* displaced *G. a. allenbyi* to its non-preferred habitat (Ziv *et al.*, 1993; Ziv & Kotler, 2003). A hypothetical model based on such behavioural interactions was proposed by Terman (1974). He designed controlled laboratory trials to determine if the Frequency of Interspecific Contact (FIC) under varying conditions could explain the coexistence of the dominant Cotton rat, *Sigmodon hispidus*, and subordinate Prairie vole, *Microtus ochrogaster*. He found *S. hispidus* to exclude *M. ochrogaster* from shared space in the absence and in low density cover, but not in high density cover, which was taken to constitute a competition *refuge* (Terman, 1974). The FIC model has widespread application as exemplified by an example emerging from the study of a guild of large carnivores of the Serengeti. Durant (1998) revealed that male cheetahs avoided areas of high prey and corresponding high competitor densities but that breeding females did not. She hypothesised that male cheetahs were selectively using these areas as *competition refuges* but that females could not due to their breeding requirements (Durant, 1998).

Twelve rodent species have been recorded from the Galápagos Islands since Darwin's

visit of 1835 (Clark, 1984) however in 1994, Key and Muñoz Heredia (1994) reported that two thirds of these species had become extinct through competitive exclusion with the introduced rodent, *Rattus rattus*. Two years later in 1996, one of these species that was presumed extinct, *Nesoryzomys swarthi*, was re-discovered in sympatry with *Rattus* on Isla Santiago (Dowler & Carroll, 1996; Dowler *et al.*, 2000). Although this re-discovery appeared to be at odds with the report of Key and Muñoz Heredia (1994), a recent study by Harris and Macdonald (in press) found experimental evidence for a negative survival impact of *Rattus* on female *Nesoryzomys*. Furthermore, they established that *Rattus* displaced *Nesoryzomys* through aggressive contact at artificial shared food patches and that this aggressive displacement was more likely to affect smaller female *Nesoryzomys* that retreated from encounters more frequently than males. This interspecific interference competition could have led to the displacement of *Nesoryzomys* from the site where it was first collected over 100 years ago and where *Rattus* still abound (Harris *et al.* 2006; Appendix A; Orr 1938). Nevertheless, in spite of the threats to it, genetic dating of the introduction of *Rattus* to Santiago suggests that *Nesoryzomys* has survived alongside *Rattus* for an unusually long period (up to 400 years: Patton 1975) when compared to the displacement of *N. indefessus* from Santa Cruz by *Rattus* within 4 years [Rambech, 1971 in Clark 1984]

Harris and Macdonald's findings constitute evidence that, where they are sympatric, *Nesoryzomys* and *Rattus* are in a state of competitive coexistence. Further work has also revealed that temporal segregation should play little or no role in facilitating this coexistence (Harris *et al.* 2006; Appendix A). It has been found however, that *Nesoryzomys* distribution and abundance are highly positively correlated with the presence and density of the endemic cacti, *Opuntia galapageia* (Harris *et al.* 2006; Appendix A). In a study of *Nesoryzomys* and *Rattus* diets evidence was found to suggest that male and female *Nesoryzomys* selected a non-preferred diet in the presence of *Rattus* throughout the year and avoided foods that were mutually preferred by *Rattus* (Chapter 2). Female *Nesoryzomys* gave exception to this rule in the breeding season when they acquired their preferred

diet and were found to share mutually preferred foods with *Rattus*. As a substitute to preferred foods both male and female *Nesoryzomys* consumed predominantly cactus foods, including fallen pads and fruits, particularly during the period when non-cactus foods became scarce. In contrast to *Nesoryzomys*, *Rattus* was indifferent to cactus foods and used only cactus pads rarely (Chapter 2). Consequently, when non-cactus foods became very rare, *Rattus* underwent a seasonal population decline to near-extinction (Clark, 1980b; Harris & Macdonald, 2007). Taking these findings together, in Chapter 2 it was suggested that cactus foods were important for *Nesoryzomys* insofar as they provided it with a competition refuge from interference with *Rattus* (with the exception of breeding females) as well as the nutrition, and perhaps water, necessary to endure the period of non-cactus food scarcity (Chapter 2).

In this study, a series of models was constructed to inspect simultaneously the effects of *Rattus* space use and the distribution of cactus foods on both male and female *Nesoryzomys* space use. The aim was to investigate the hypothesis put forward in Chapter 2 that *Nesoryzomys* and *Rattus* should show spatial segregation and that the degree of segregation would differ between the sexes and in habitat with and without a competition refuge. In addition, these models were also designed to illustrate the influence of each cactus variable separately so that their relative importance on *Nesoryzomys* space use could be assessed within and between habitats. A similar modelling approach to the one adopted here was used by Palomares (1998) to model the space use of Iberian lynx in relation to the relative abundance of both rabbits and mongooses, and shrub cover in Doñana National Park, however the models presented here differ in their statistical control of spatial autocorrelation (Legendre & Legendre, 1998).

3.2.1 VARIABLES AND PREDICTED RELATIONSHIPS

Based on the few existing investigations of this recently rediscovered rodent community, the effects of several factors were predicted to influence *Nesoryzomys* space use (Figure

3.1). Space use was measured as the number of individuals live-trapped in predefined sampling units over time to quantify the intensity with which they used spatially distinct areas (a measure hereafter referred to as *activity*: see Methods). Harris and Macdonald (in press) experimentally demonstrated that *Rattus* are behaviourally dominant to *Nesoryzomys* and compete with them when sympatric. In addition, in Chapter 2 it was found that *Nesoryzomys* avoided foods preferred by *Rattus* and it was hypothesised that this would be evident as spatial avoidance. Based on these findings it is hypothesised that areas of high male and female *Nesoryzomys* activity will be negatively correlated with areas of high *Rattus* activity (Figure 3.1 “Rr”). When surveying for *Nesoryzomys* presence on Santiago, Harris and colleagues (Harris *et al.* 2006; Appendix A) found that *Nesoryzomys* presence was highly correlated with the presence of cacti. Furthermore, they demonstrated that *Nesoryzomys* density was strongly positively correlated with cactus density and that, at a finer scale, *Nesoryzomys* selected microhabitat characterised by cactus. To determine if *Nesoryzomys* activity was influenced by large cacti, its activity was measured in habitat with large cacti (*mature cactus habitat*) and without large cacti (*immature cactus habitat*). High *Nesoryzomys* activity and areas with high densities of large cacti were expected to be positively correlated (Figure 3.1 “OG”). Large cacti have the capacity to bear fruit (Racine & Downhouser, 1974) and although they may do this year-round, there is a distinct cactus fruiting season from January - February. In the investigation of *Nesoryzomys* and *Rattus* diets at La Bomba presented in Chapter 2 it was found that cactus fruit were important in *Nesoryzomys* diet, but not that of *Rattus*. To determine how *Nesoryzomys* activity was influenced by cactus fruits, it was measured in the season of few cactus fruits (*non-fruiting season*) and in the season of many cactus fruits (*fruiting season*). *Nesoryzomys* activity was expected to be highest in areas with many cactus fruits during times of plentiful fruit (Figure 3.1 “Fr”). The investigation in Chapter 2 also found cactus pads to be important in *Nesoryzomys* diet and observed bark-stripping in small cacti throughout La Bomba (pers obs.; Baxter & Hansson 2001). Consequently, small cacti and pad fall were also expected to influence

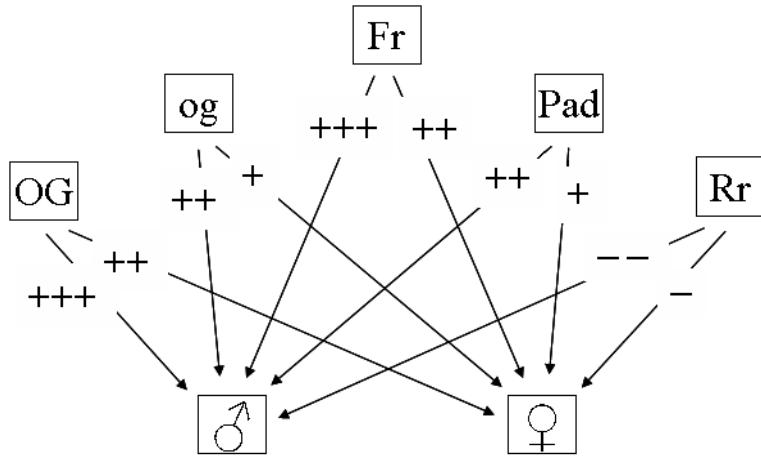


Figure 3.1: Hypothesised relationships of *Rattus* (Rr), large cactus (OG), cactus fruits (Fr), small cactus (og), and fallen pads (Pad) on male (σ°) and female (φ) *Nesoryzomys* activity. Signs indicate the expected nature and strength of relationships.

positively *Nesoryzomys* activity (Figure 3.1 “og” and “Pad” respectively), but to a lesser extent than large cacti that were considered to produce more cactus foods (Racine & Downhouser, 1974). Although, each variable was expected to influence the activity of *Nesoryzomys*, they were also expected to affect each differently. In Chapter 2 it was found that male, but not female, *Nesoryzomys* more readily switched from their preferred diet to a predominantly cactus diet when sympatric with *Rattus*, presumably to avoid aggressive encounters. Based on this finding, differences were expected between the influence of *Rattus* and cactus variables on male and female *Nesoryzomys* activity (Figure 3.1 “ σ° ” and “ φ ” respectively).

3.3 METHODS

3.3.1 SITE SELECTION AND SAMPLING DESIGN

This study was carried out at a site known locally as La Bomba, situated on the central north coast of Santiago in the Galápagos archipelago, during 2004. The prevailing trade winds that bring rain to the Galápagos approach from the southeast so that Santa Cruz and the highlands of Santiago cast a combined rainshadow over La Bomba (Hicks

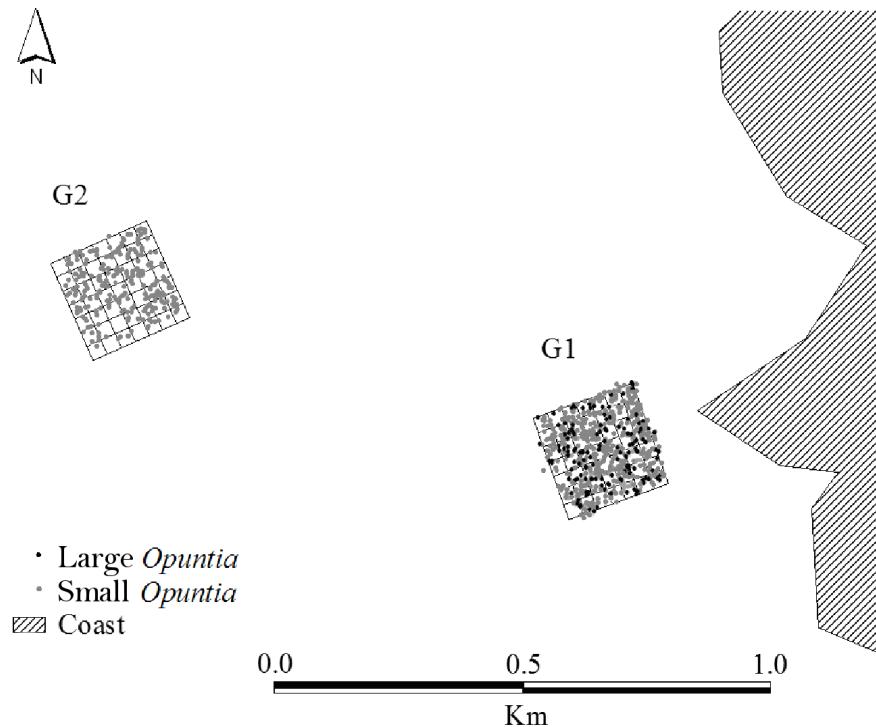


Figure 3.2: Location of grids in mature (G1) and immature (G2) cactus habitat in relation to the coast at La Bomba.

& Mauchamp, 1996). This results in an arid habitat characterised by the cactus *Opuntia galapageia*, trees; *Bursera graveolens*, *Cordia lutea* and *Croton scouleri*, and shrubs; *Clerodendrum molle* var. *molle*, *Castela galapageia*, *Lantana peduncularis*, *Scutia spicata* var. *pauciflora*, and *Vallesia glabra*.

Galápagos is subject to two distinct seasons; the wet season and the dry (garua) season. The wet season sees the arrival of the rains that initiate plant and insect reproduction providing plentiful non-cactus food for *Nesoryzomys* and *Rattus* (Chapter 2). Little to no precipitation falls in arid habitat during the dry season and consequently many insects perish, plants descend into dormancy and non-cactus food for the rodent species is comparatively rare (Chapter 2). Unlike most other plant species in the arid habitat, cacti produce fruit year-round however the main fruiting event occurs during the dry season. The methods outlined below were carried out in the cactus non-fruiting (wet) season when non-cactus foods are abundant and again in the fruiting (dry) season when non-cactus foods are scarce.

Sites for two 4.41ha (210 x 210m) trapping grids were selected within the known bounds of *Nesoryzomys* range: one in mature cactus habitat (G1) and one in immature cactus habitat (G2) (Figure 3.2). In each area a 7 x 7 grid was marked out with divisions 30m apart using a handheld GPS (Garmin GPS 12CXL, Garmin International Inc.). This design effectively subdivided each grid into 49 sampling units for each of which measures of all variables given in Table 3.1 were recorded. These sampling units are hereafter referred to as *grid cells* (Palomares *et al.*, 1998; Wiegand *et al.*, 1999).

3.3.2 MEASURING THE VARIABLES

Species' activity was assessed in each grid cell by live-trapping. Two Tomahawk traps (Model #201, 40.6 x 12.7 x 12.7cm, Tomahawk Live Trap Co., PO Box 323, Tomahawk, Wisconsin, USA) were placed at the centre of all grid cells and an additional Sherman trap (Model #LFATDG, 22.9 x 8.9 x 7.6cm, H. B. Sherman Traps Inc., Tallahassee, Florida, USA) was placed in each grid cell on G1 to prevent trap saturation (Gurnell & Flowerdew, 1990). Animals were trapped for 5 nights in each season. Traps were baited with a mixture of peanut butter and rolled oats and were set after dusk and checked at dawn. The first time each animal was captured its species, sex, weight, reproductive condition, and point of capture were recorded and it was marked with an individual passive integrated transponder (type FDX-B, Francis Scientific Instrument, Cambridge, UK). For each recapture thereafter the unique identification number and trap location were recorded. *Nesoryzomys* exhibited so called 'trap-happy' behaviour such that the probability of catching all resident animals was expected to be high. To diminish bias from trap-happiness, *Nesoryzomys* activity was measured as the number of individual animals captured in each grid cell over each 5-day trapping period. For consistency, *Rattus* grid cell activity was measured in the same way. These trapping protocols complied with the current laws of the country in which they were performed (Ecuador) and the guidance of the UK Animals (Scientific Procedures) Act 1986.

Table 3.1: Measured variables. All variables were measured for each of 49 30x30m grid cells in mature and immature cactus habitat.

Variable name	Description	Units
Species' activity	Number of individuals trapped per trapping session	Counts
Large cacti	Number of large cacti (canopy pads ≥ 50)	Counts
Fruit	Estimated number of fruits in canopy	Counts ≈ 10
Small cacti	Number of small cacti (canopy pads < 50)	Counts
Fallen pads	Number of fresh fallen cladodes	Counts

Cactus variables were measured in each grid cell by way of survey. In each grid cell the numbers of large and small cacti, fruits in the canopy and fallen pads were counted. Cactus size was classified as large or small based on the number of pads composing the plant canopy after Racine and Downhouser (1974) (Table 3.1). Fruit were counted in the cactus canopy and not on the ground beneath the canopy because cactus surveys were conducted before trapping to minimise disturbance to resident animals. In this way, fruit in the cactus canopy was used as a surrogate measure of fruit on the ground that were considered to be available to *Nesoryzomys*. When counting fallen cactus pads, care was taken to record fresh pads only. This criterion was assessed by piercing the pad skin to reveal a small section of the fleshy interior. Only those with moist interiors were recorded. All cactus variables were recorded on G1 but the absence of large fruit-bearing cacti from G2 meant that only a subset of these variables (all but large cactus and fruit counts) could be measured there.

3.3.3 STATISTICAL ANALYSIS

The aim of this study was to measure the influence of each of the variables in Table 3.1 on male and female *Nesoryzomys* activity. To reduce the inevitable complexity of the models, it was decided to present them in a path analysis framework. The hypothesised relationships were graphically displayed as a path diagram and, in adhering to conventional annotations, a straight single-headed arrow represents a hypothesised direct

relationship between two variables, a curved double-headed arrow represents a correlation between variables and the path coefficients are given as standardised regression coefficients. Finally, the unexplained residual error in each model is denoted as U and their path coefficients are set to 1 in order to identify the models and to set the scale of measurement (Mitchell, 2001). The path analysis was carried out in AMOS 6.0 (Arbuckle, 2005) but due to statistical non-independence of the input data (discussed below) the significance testing was carried out using permutations in FSTAT 2.9.3 (Goudet, 1995), which reports more precise probability values than the permutation procedures built into AMOS 6.0.

Data collected in each habitat could not be combined into a single model for each season because, based on direct count estimates of *Nesoryzomys* abundance, there were more *Nesoryzomys* on G1 in both seasons than on G2 (G-test with Williams' correction; non-fruiting season $G_{adj} = 21.98$, d.f. = 1, $p < 0.01$, fruiting season $G_{adj} = 22.22$, d.f. = 1, $p < 0.01$, Figure 3.3). If analysed together, this discrepancy would have wrongly suggested that *Nesoryzomys* avoid areas with small cacti. Furthermore, sites selected for the grids were deliberately chosen for their contrasting cactus composition. From grid cell cactus counts (large and small), the cactus density was calculated as 0.018 cacti/m² on G1 and 0.006 cacti/m² on G2. These densities were compared statistically by bootstrapping the grid cell data for G1 to create a randomisation distribution of 1000 cactus density measures against which the observed G2 measure was compared. This procedure revealed that cactus density was significantly higher on G1 than on G2 ($P < 0.001$, Figure 3.2). The difference in *Nesoryzomys* and cactus densities between G1 and G2 therefore rendered a unified model inappropriate. Nevertheless, the *Nesoryzomys* to cactus ratio was similar on both grids in the non-fruiting (G1 = 0.091, G2 = 0.096) and fruiting seasons (G1 = 0.080, G2 = 0.060), and so meaningful comparisons could be drawn between separate models constructed for each habitat in each season.

Conventional path analysis requires, among other assumptions, that observations are independent. The sampling design adopted in this study, whereby data are recorded from

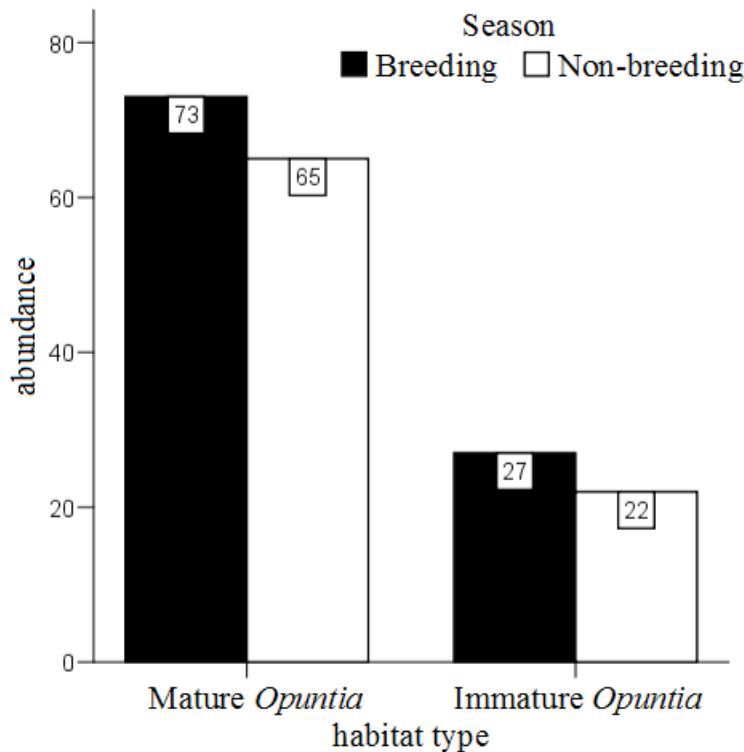


Figure 3.3: *Nesoryzomys* abundance in mature and immature cactus habitat in each season.

adjoining grid cells, was expected to violate the assumption of independent observations. To overcome this, variables were first adjusted to account for their spatial autocorrelation using Mantel tests. A Mantel test is a simple linear regression technique that proceeds from dissimilarity matrices and can be used to investigate and control for spatially dependent observations by inclusion of a matrix of pairwise distances between samples. The residuals from a Mantel test are space-adjusted although they are also non-independent and so it is recommended that the statistical significance of the Mantel correlation (r) is assessed using permutation procedures (Manly, 1993). The regression model and type of permutation procedure used here were those proposed by Manly (1993) and were executed in the program FSTAT.

Measures of *Nesoryzomys* and *Rattus* activity and cactus variables were converted to matrices of pairwise grid cell differences using PopTools 2.6.7 (Hood, 2005) and a matrix of spatial dissimilarity between grid cells (hereafter *Geog matrix*) was constructed using cell coordinates according to the equation:

$$D(i, j) = 1 / (\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}) \quad (3.1)$$

where $D(i, j)$ is the reciprocal of Euclidean distance between grid cells i and j , and x and y are coordinates for grid cells i and j (Fortin & Gurevitch, 2000). All variables were regressed with the Geog matrix in Mantel tests using FSTAT and the residuals were used in the path analysis carried out in AMOS. Significance was tested using 10,000 permutations in FSTAT unless otherwise stated. The α level for significance was Bonferroni adjusted to account for multiple testing as stated along with the results (Sokal & Rohlf, 2005). To determine if the variables influenced male and female *Nesoryzomys* differently, a male-female activity interaction matrix (Dow & Cheverud, 1985) was constructed and conditioned for space using FSTAT as outlined above. The same analyses were repeated with these male-female residuals in place of the separate sexes of *Nesoryzomys*. Significance testing of the interactions with the cactus variables was also adjusted for multiple testing using Bonferroni adjustment where α on $G1 = 0.05/5 = 0.010$ and $G2 = 0.05/3 = 0.017$.

Finally, previous work on *Nesoryzomys* and *Rattus* suggests that, although interspecific interactions might occur at non-cactus food patches, resource competition between the two species should be weak (Chapter 2). To assess if large cacti or cactus fruit were important in providing *Nesoryzomys* with an alternative food to interspecific resource competition the mean seasonal changes in body mass of adult male and female *Nesoryzomys* (male $\geq 80g$, female $\geq 70g$: Harris & Macdonald 2007) were compared between G1 and G2 while holding for initial body mass in ANCOVA (García Berthou, 2001). Juveniles were excluded from the analysis because their weights were expected to change over time due to normal growth. If resource competition was strong then the mean seasonal change in body mass of *Nesoryzomys* would be impoverished on G2 without large cacti and cactus fruits compared to G1.

3.4 RESULTS

3.4.1 *RATTUS* AND *NESORYZOMYS* ACTIVITY

Both male and female *Nesoryzomys* activity were negatively correlated to *Rattus* activity in both seasons and in both habitats (Table 3.2, Figure 3.4) suggesting a degree of spatial avoidance. There were, however, two notable exceptions. First, the negative relationship between female *Nesoryzomys* activity and *Rattus* activity on G1 was not statistically significant in the non-fruiting season and the male-female interaction was significant (Mantel correlation, $r = -0.186$, $P < 0.001$), which together suggest that male *Nesoryzomys* avoid *Rattus* to a greater degree than female *Nesoryzomys* in this season. Second, male *Nesoryzomys* activity was positively correlated to *Rattus* activity in both seasons on G2 and the male-female interactions were both significant (non-fruiting $r = 0.251$, $P < 0.001$, fruiting $r = 0.128$, $P < 0.001$), which suggests that female *Nesoryzomys* avoid *Rattus* to a greater degree than males in habitat without mature cacti.

3.4.2 CACTUS RESOURCES AND *NESORYZOMYS* ACTIVITY

On G1, both male and female *Nesoryzomys* activity was high in areas with a high large cactus density in the non-fruiting season and male activity was higher than that of females in areas of high small cactus density (although the interaction was not statistically significant after Bonferroni adjustment; $r = 0.068$, $P = 0.019$). Furthermore, male activity was higher than females' in areas with abundant cactus fruit in the non-fruiting ($r = 0.096$, $P < 0.001$) and fruiting season ($r = 0.199$, $P < 0.001$). In the fruiting season, male activity was higher than females' in areas with a high large cactus density ($r = 0.102$, $P < 0.001$) and lower than females' in areas with a high small cactus density ($r = -0.078$, $P = 0.007$) and abundant fallen pads ($r = -0.098$, $P = 0.001$, Table 3.2, Figure 3.4).

On G2, male *Nesoryzomys* activity was higher than that of females in areas of high small cactus density in the non-fruiting season ($r = 0.314$, $P < 0.001$) but lower than

Table 3.2: Mantel correlations (r) and standardised regression coefficients (β) with their standard error (SE) for predicted relationships between male (σ^{\prime}) and female (φ) *Nesoryzomys* activity and *Rattus* activity (Rr), and large cactus (OG), small cactus (og), cactus fruit (Fr) and pad (Pad) distributions in mature (G1) and immature (G2) cactus habitat in the non-fruited and fruiting seasons.

Season	Sex	Parameter	G1			Parameter	G2		
			r	β	SE		r	β	SE
Non-fruiting	σ'	Rr	-0.273	-0.246	0.028	Rr	0.142	0.121	0.028
		OG	0.073	0.065	0.031	OG	—	—	—
		og	-0.125	-0.058	0.027	og	0.273	0.274	0.025
		Fr	-0.033	-0.127	0.028	Fr	—	—	—
		Pad	0.111	0.119	0.024	Pad	0.027	-0.043	0.021
	φ	R^2 0.097			R^2 0.091				
		Rr	-0.094	0.011	0.026	Rr	-0.216	-0.205	0.027
		OG	0.024	0.102	0.030	OG	—	—	—
		og	-0.281	-0.306	0.028	og	-0.166	0.174	0.025
		Fr	-0.196	-0.291	0.030	Fr	—	—	—
		Pad	0.046	0.170	0.030	Pad	0.054	0.101	0.022
		R^2 0.152			R^2 0.079				
Fruiting	σ'	Rr	-0.122	-0.146	0.027	Rr	0.083	0.098	0.021
		OG	0.132	-0.063	0.040	OG	—	—	—
		og	-0.075	-0.068	0.025	og	-0.372	-0.377	0.023
		Fr	0.285	0.333	0.033	Fr	—	—	—
		Pad	0.004	0.013	0.026	Pad	-0.001	0.027	0.027
	φ	R^2 0.109			R^2 0.148				
		Rr	-0.183	-0.195	0.028	Rr	-0.090	-0.088	0.020
		OG	0.051	-0.150	0.036	OG	—	—	—
		og	0.013	0.001	0.036	og	-0.289	-0.274	0.024
		Fr	0.150	0.247	0.032	Fr	—	—	—
		Pad	0.208	0.229	0.024	Pad	-0.213	-0.200	0.021
		R^2 0.113			R^2 0.130				

Note: Bold G1 β coefficients are significant at Bonferroni adjusted $\alpha = 0.05/15 = 0.003$ and bold G2 β coefficients are significant at Bonferroni adjusted $\alpha = 0.05/6 = 0.0083$. Model parameters for which the male-female interaction is significant are indicated in bold. SE was assessed from 1000 bootstrap resamples of the data in AMOS 6.0 (Arbuckle, 2005).

females' in the fruiting season ($r = -0.133$, $P < 0.001$). Male *Nesoryzomys* activity was also higher than that of females in areas with abundant fallen pads in the fruiting season ($r = 0.135$, $P < 0.001$).

3.4.3 CACTUS RESOURCES AND *RATTUS* ACTIVITY

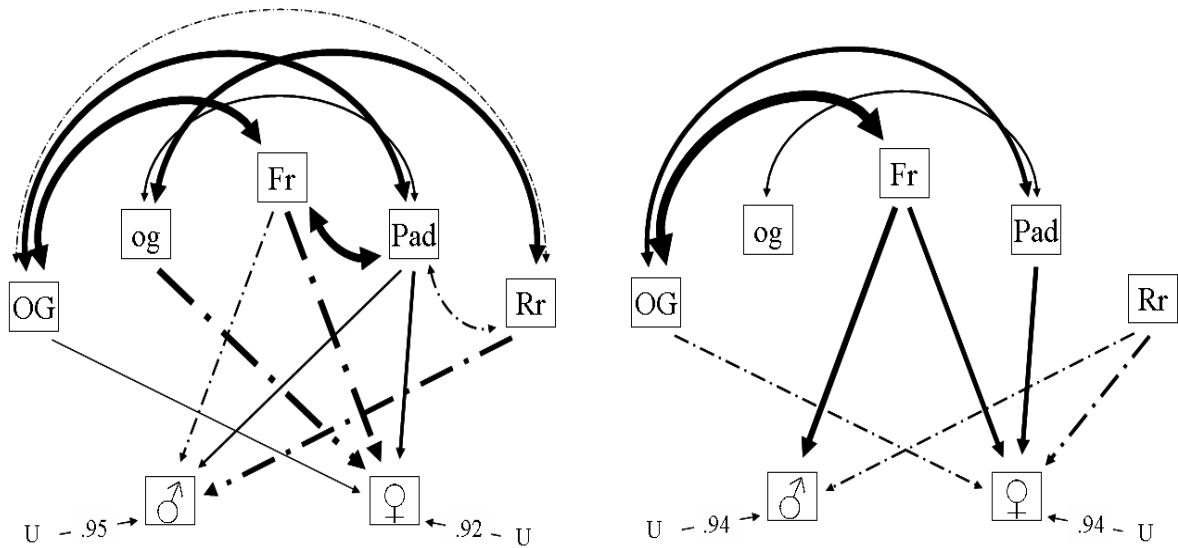
Rattus activity was significantly negatively correlated with large cactus density and positively correlated to small cactus density in the non-fruiting season on G1. Furthermore, it was negatively correlated with fruits and fallen pads in this habitat at this time, although these relationships might be explained in part by the negative correlation between *Rattus* activity and large cactus density, as indicated by the strong positive correlations between these variables (Table 3.3). *Rattus* activity in G2 was highest in areas with a high density of small cacti, as on G1. In the fruiting season, *Rattus* activity was uncorrelated to any variables recorded on either grid (Table 3.3, Figure 3.4).

3.4.4 OVERALL MODEL FIT

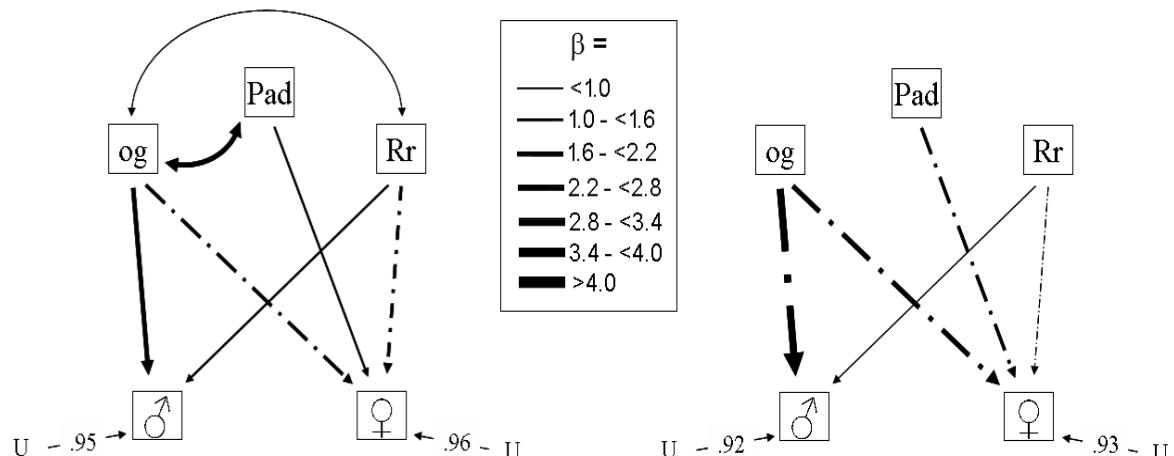
As the space-adjusted residuals used in these analyses were non-independent, conventional measures of overall model fit were expected to give spurious results and were not calculated. Nevertheless, R^2 values were calculated from multiple matrix regressions in FSTAT and are presented in Table 3.2. The combined effects of *Rattus* activity and cactus resources explained little of the total variation in male and female *Nesoryzomys* activity in either habitat in either season.

3.4.5 SEASONAL CHANGE IN *NESORYZOMYS* CONDITION

There was no significant effect of grid (ANCOVA, $F_{1,35} = 1.061$, $P = 0.310$), sex ($F_{1,35} = 1.029$, $P = 0.317$) or the grid and sex combination ($F_{1,35} = 2.238$, $P = 0.144$) on the seasonal change of adult male or female *Nesoryzomys* body mass when controlling for



G1



G2

Breeding

Non-breeding

Figure 3.4: Solved path diagrams for mature (G1) and immature (G2) cactus habitat in the fruiting and non-fruiting seasons. Solid lines are positive and dashed lines are negative path coefficients. Single-headed straight arrows represent direct relationships, double-headed curved arrows represent correlations and U denotes the unexplained residual error calculated as $(1 - R^2)^{0.5}$. Variable abbreviations are: *Rattus* activity (Rr), large cactus (OG), cactus fruit (Fr), small cactus (og) and fallen pads (Pad) on male (σ) and female (φ) *Nesoryzomys* activity.

Table 3.3: Mantel correlations (r) between *Rattus* activity (Rr), and large cactus (OG), small cactus (og), cactus fruit (Fr) and pad (Pad) distributions in mature (G1) and immature (G2) cactus habitat in the non-fruiting (below diagonal) and fruiting seasons (above diagonal).

	G1					G2	
Rr	OG	Fr	Pad	Rr	og	Pad	
Rr	-0.007	0.037	0.079	-0.037		0.034	-0.040
OG	-0.086		0.063	0.587	0.240	—	—
og	0.341	0.074		0.004	0.132	0.080	0.060
Fr	-0.094	0.374	0.029		0.032	—	—
Pad	-0.117	0.321	0.129	0.397		0.023	0.244

Note: Bold G1 correlations are significant at Bonferroni adjusted $\alpha 0.05/10 = 0.005$ and bold G2 correlations are significant at Bonferroni adjusted $\alpha 0.05/3 = 0.017$.

animals initial weights (Figure 3.5).

3.5 DISCUSSION

Modelling the relationships between male and female *Nesoryzomys* and *Rattus* activity has further supported the hypothesis that interspecific interference competition plays a role in organising the rodent community at La Bomba. Moreover, inclusion of cactus foods in the models has revealed support for the suggestion that cacti play a role in mitigating the effect of this interference competition.

3.5.1 FREQUENCY OF INTERSPECIFIC CONTACT AND CACTUS

Both a species press experiment (Harris & Macdonald, in press) supported by a study of *Nesoryzomys* and *Rattus* diets (Chapter 2) led to the conclusion that interference competition, manifest through aggressive encounters, is the mechanism underlying the observed competition between *Nesoryzomys* and *Rattus* at La Bomba. These findings suggested that behaviourally subordinate *Nesoryzomys* would seek to minimise the frequency of interspecific contact with the dominant *Rattus* (Chapter 2). This fundamental hypothesis formed the basis of the Frequency of Interspecific Contact (FIC) model proposed by

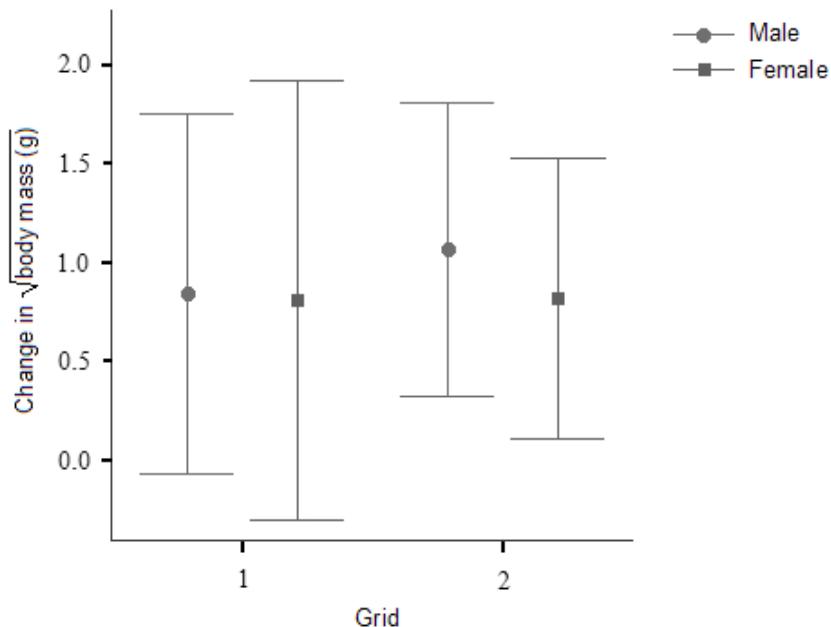


Figure 3.5: Seasonal change in adult male and female *Nesoryzomys* body mass in mature (G1) and immature (G2) cactus habitat.

Terman (1974). He found that the FIC between subordinate *Microtus ochrogaster* and dominant *Sigmodon hispidus* was high in sparse habitat leading to the eventual competitive exclusion of *M. ochrogaster*. This result, however, was altered by the addition of dense patches of cover that functioned as competition refugia for *M. ochrogaster* and facilitated its coexistence with *S. hispidus*. Terman carried out these experiments in a laboratory setting but proposed that this finding could explain *M. ochrogaster* and *S. hispidus* coexistence where they were naturally sympatric. He also hypothesised that his model could be extended to explain coexistence in other communities structured by interference competition.

Recent work has hypothesised that the endemic cactus, *Opuntia galapageia*, provides *Nesoryzomys* with a competition refuge from interference competition with *Rattus* (Chapter 2). It was hypothesised that where cactus were present *Nesoryzomys* had the option to avoid aggressive encounters with *Rattus* over shared food patches by utilising more

cactus foods. The aim of this study was to verify whether that finding would manifest in *Nesoryzomys* spatial avoidance of *Rattus* and whether this could be explained by their use of areas with a high density of the cactus competition refuge. Based on Terman's FIC model, the results presented here lend strong support to the hypothesis that large cacti and cactus fruits are important competition refugia for *Nesoryzomys* however there are some limitations that are discussed.

3.5.2 MATURE CACTUS HABITAT

In the mature cactus habitat where large cactus and cactus fruits were present male *Nesoryzomys* activity was negatively correlated with that of *Rattus* in both seasons, indicating that their FIC was low. Although, both male and female relationships with fruit in the non-fruiting season were negative, the male relationship was less negative than that of females suggesting that, in this season, males encounter areas of cactus fruit more frequently than females. These results suggest that the presence of large cactus and/or cactus fruits in mature cactus habitat may provide male *Nesoryzomys* access to a competition refuge in the wet season thus allowing them to avoid encounters with *Rattus*. Moreover, these models suggest that the competition refuge does not have to be strongly selected but rather it must be present so that *Nesoryzomys* can utilise it as an alternative to certain foods that are preferred by *Rattus* in order to reduce their FIC. In contrast, a lack of evidence for a negative correlation between *Rattus* and female *Nesoryzomys* activity in the non-fruiting season in mature cactus habitat suggests that they do not/cannot avoid *Rattus* during this period. In previous work it was suggested that this might be explained by the sex-difference in male and female dietary requirements during breeding whereby the requirements of breeding females might compel them to share foods with *Rattus*. Perhaps the cost of a high FIC and potential competitive displacement are negligible compared to the benefits reaped from successful reproduction (Chapter 2), or perhaps once in breeding condition, females have no option but to forage

for non-cactus foods in the immediate vicinity of their nests. A similar conclusion was reached from an investigation of space use by members of a large African carnivore guild. Within this guild, cheetah were subordinate to lion and hyena and generally minimised their activity in areas of high prey, and correspondingly high competition, densities. This spatial avoidance was, however, found to be stronger for male than for female cheetah. It was concluded that female cheetah were forced by their breeding requirements to remain active in areas with a high density of prey (Durant, 1998). The hypothesis that the high FIC between *Rattus* and female *Nesoryzomys* in the breeding (non-fruiting) season is a consequence of breeding requirements is further supported by their low FIC in the non-breeding (fruiting) season when breeding has ceased and female activity is negatively correlated to that of *Rattus*. By the fruiting season when non-cactus foods were more limited and the FIC with *Rattus* should have been higher both males and females became strongly positively associated with cactus fruit and their relationships with *Rattus* were negative, although it should be acknowledged that the low numbers of *Rattus* in this season degraded the linear relationship between this variable and others that is required for the Mantel correlation (Appendix F). The seasonal decline in *Rattus* numbers however meant that the FIC was low and that interference competition was negligible. Thus by switching to cactus fruits, rather than avoiding *Rattus*, *Nesoryzomys* were selecting for cactus fruits for their nutritional, and perhaps water, content.

3.5.3 IMMATURE CACTUS HABITAT

In contrast, in the immature cactus habitat where large cactus and cactus fruits were completely absent male *Nesoryzomys* activity was positively correlated with that of *Rattus* in both seasons. This indicates that male *Nesoryzomys* and *Rattus* FIC should be high and therefore that immature cacti do not provide male *Nesoryzomys* with a competition refuge. Under high FIC and in habitat where a competition refuge is not available, male *Nesoryzomys* might be expected to avoid *Rattus*, as embodied by a strong negative

relationship in these models. Harris and Macdonald (*unpublished manuscript*), however, have shown that male *Nesoryzomys* are less likely to retreat from aggressive encounters with *Rattus* than female *Nesoryzomys*, and so may be better able to co-occupy space with *Rattus* when shared food is scarce. Alternatively, Harris and colleagues (2006; Appendix A) found that both *Nesoryzomys* and *Rattus* were active throughout the night but that *Nesoryzomys* were active for longer in areas with a high *Rattus* density. They concluded that *Nesoryzomys* was obliged to increase their foraging effort to fulfil their dietary needs possibly as a consequence of being displaced from shared food patches by *Rattus*. This explanation suggests that male *Nesoryzomys* may use areas of high *Rattus* activity but outside of *Rattus* peak activity periods (e.g. Ziv *et al.* 1993). Again in contrast to males, female *Nesoryzomys* in immature cactus habitat have a negative relationship with *Rattus* in both seasons. This relationship is more likely to be explained by the higher probability that smaller female *Nesoryzomys* are aggressively displaced from areas with *Rattus* (Harris and Macdonald, *unpublished manuscript*) than their use of small cacti as a competition refuge because if small cacti were a viable competition refuge then males too would be expected to use them to ameliorate their FIC with *Rattus*, which they do not. Furthermore, females, at least during dry years, have been shown not to breed in the breeding season in immature cactus habitat (Harris and Macdonald, *unpublished manuscript*) and so they would not have the drive to utilise foods preferred by *Rattus* and hence would be less likely to use areas occupied by *Rattus*. With minor exceptions cactus foods had a negative influence on *Nesoryzomys* activity throughout the year in this habitat suggesting that these foods do not suffice as competition refugia in either season.

3.5.4 POPULATION DYNAMICS AND THE FIC

An alternative explanation for the importance of large cacti and cactus fruits to *Nesoryzomys* is that they provide it with an alternative food to mitigate the negative effect

of interspecific resource competition with *Rattus* (e.g. Kalcounis-Rüppell & Millar 2002). If this were the case however, then individual *Nesoryzomys* in immature cactus habitat would lose more weight as non-cactus foods seasonally declined than those in mature cactus habitat because they do not have access to cactus fruit to buffer their reduced food intake from *Rattus* dominated foods (e.g. Boonstra 1994). There was, however, no difference in the mean seasonal weight change between mature and immature cactus habitat, supporting previous work that ruled out resource competition and citing interference competition as the important structuring force in this community (Chapter 2, Harris and Macdonald, *in press* Harris & Macdonald *in press*). In other words, *Nesoryzomys* were able to obtain sufficient nutrition to maintain a similar body condition in habitat with and without large cacti and cactus fruits across this period suggesting that the main benefit of large cacti and cactus fruits was as an occasional alternative food that *Nesoryzomys*, particularly male *Nesoryzomys*, could seek to avoid aggressive encounters with *Rattus*. While this test confirms that resource competition should not be occurring in either habitat it does not prove that large cacti and cactus fruits do provide *Nesoryzomys* with a competition refuge to reduce FIC and maintain survival; this is simply inferred. To provide such evidence the researcher would have to measure habitat-dependent survival which was not recorded here. When the FIC and thus interference competition is substantially lessened by the decline in *Rattus* numbers by the end of the fruiting season however, large cacti and cactus fruits are less important as a competition refuge and become more important for their provision of nutrition, and perhaps water (Chavez-Ramirez *et al.*, 1997), that is scarce in this season. Indeed, this might explain the strong selection for cactus fruits in the mature cactus habitat.

Although large cacti and cactus fruits are not essential as foods in the presence of *Rattus*, their high density in mature cactus habitat might, however, explain the differences in *Nesoryzomys* abundance between the immature and mature cactus habitats. The FIC experienced in obtaining non-cactus foods in this season when *Rattus* are abundant should be higher in immature cactus habitat where competition refugia are absent and

Nesoryzomys should have a higher chance of encountering *Rattus* over shared foods. In this way the density of competition refugia will mediate the FIC which in turn will limit the number of subordinate animals that can coexist with a dominant (Terman, 1974). This hypothesis might explain why *Nesoryzomys* can attain highest densities in areas with high large cactus and cactus fruit densities (e.g. G1) compared to areas with a low density of small cacti (e.g. G2, Figure 3.3).

3.5.5 CONCLUSIONS

In summary, the models presented here suggest that cactus foods, and particularly cactus fruits, provide male *Nesoryzomys* with a competition refuge from interspecific encounters with *Rattus* in mature cactus habitat in the non-fruiting season. In contrast, in habitat where cactus food availability is low male *Nesoryzomys* and *Rattus* activity is highly correlated with possible temporal partitioning. Cactus fruits do not benefit female *Nesoryzomys* in mature cactus habitat during the breeding season when their activity is uncorrelated with that of *Rattus*, perhaps because they both forage for mutually preferred foods that female, but not male *Nesoryzomys*, require for successful breeding. This is in contrast to habitat where breeding is absent and female *Nesoryzomys* and *Rattus* activity are negatively correlated year-round. Cactus fruits are less important as a competition refuge when *Rattus* numbers are low in the fruiting season however they are more important to *Nesoryzomys* when non-cactus foods are scarce when they provide them with nutrition, and perhaps water, until the flourishing of plant and insect foods in the wet season.

3.5.6 CACTUS FOODS AND *RATTUS* ACTIVITY

No relationships were hypothesised between cactus foods and *Rattus* activity in either habitat in either season however the models developed here do suggest that some inter-

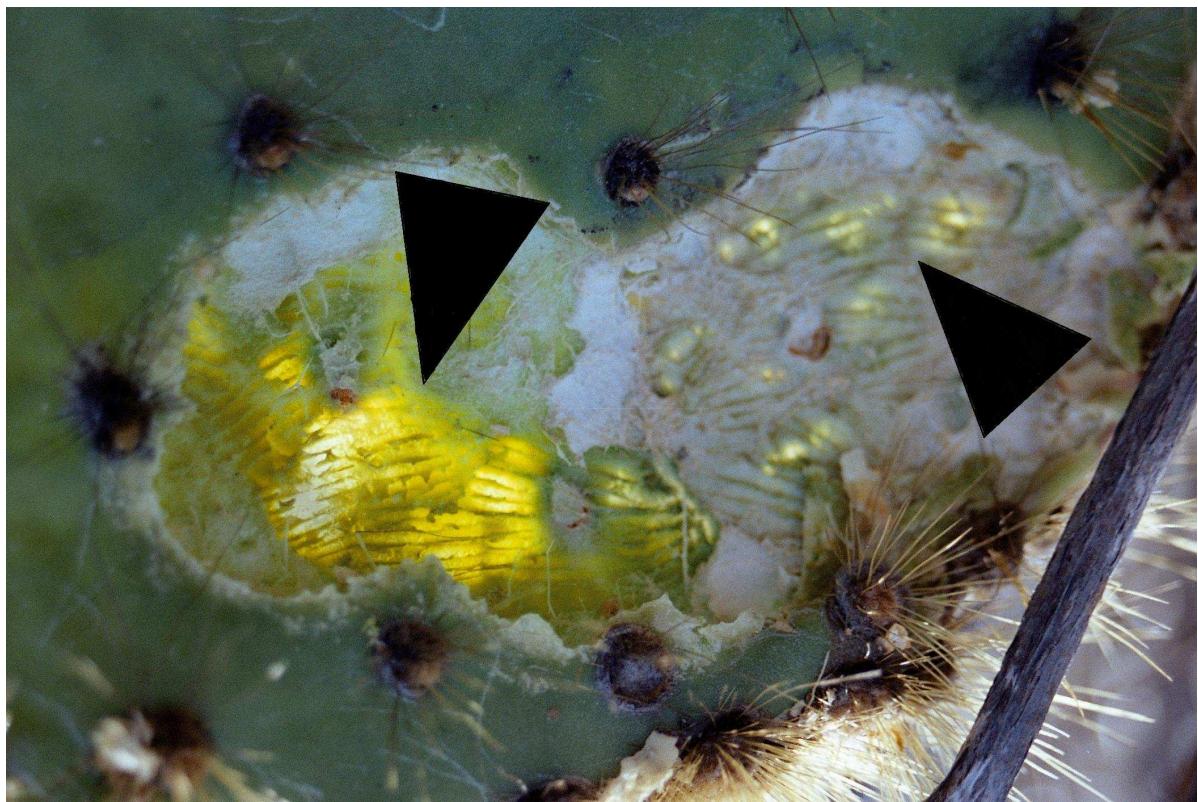
esting relationships may exist. Although from dietary preference trials it was found that cactus foods were not important in the diet of *Rattus* (Chapter 2), there was a strong positive correlation between *Rattus* activity and areas of high small cactus density in both cactus habitats in the non-fruiting season. A similar relationship was found for male *Nesoryzomys* and it was hypothesised that they might use these plants for food. *Rattus* are also known to consume the fleshy interior of cactus pads (Chapter 2) and therefore there seems no reason why the same hypothesis for male *Nesoryzomys* cannot be drawn for *Rattus*. Regarding areas of many large cacti, *Rattus* activity was lowest in these areas. This suggests that these areas are avoided by *Rattus*, a finding that is inexplicable given the current understanding of this system.

Rattus activity was uncorrelated to any cactus foods in either habitat in the fruiting season. Before discussing the biological significance of these findings, it is important to acknowledge that these results could be a consequence of the poor linear relationships between these variables (Appendix F). Presuming that the observed relationships are sufficient to detect important correlations between the variables, it seems that *Rattus* do not use cactus foods in this season. This is in contrast to *Nesoryzomys* that become more correlated to cactus foods in this season and do not undergo a localised population crash similar to that of the *Rattus* population.

3.5.7 OVERALL MODEL FIT

Although these models reveal some strong relationships between the selected variables, the amount of variation explained by the chosen variables was small in both habitat models. One explanation offered for this is the degraded linear relationships between *Rattus* and all other model variables in the fruiting season (Appendix F). The Mantel regression assumes approximately linear relationships between variables (Legendre, 2000), and so the *Rattus* results for this season should be interpreted with caution. On a more general note, despite its strengths, path analysis has many shortcomings but among the most

serious is the assumption, rarely fulfilled, that the majority of important variables are included in the specified model (e.g. Mitchell-Olds & Shaw 1987). Model parameters should be selected on the basis of previous knowledge of the system under study (Petratit *et al.*, 1996). In this instance, few studies have been undertaken on this recently rediscovered and remote system and consequently the models presented here include only those factors that have been hypothesised to influence *Nesoryzomys* activity and fitness (see 3.2 Introduction). Continuing research suggests that many other foods may be important to both *Nesoryzomys* and *Rattus*. Rainfall promotes plant and animal growth at La Bomba and may also provide ephemeral water sources (Snell & Rea, 1999). A second introduced rodent species at La Bomba, *Mus musculus*, may also be an important competitor and inclusion of its activity might account for some of the unexplained variation in the models (Moro & Bradshaw, 2002; Harris & Macdonald, in press). Indeed, inclusion of any one of these variables could, and probably would, change the strength of the observed relationships, but may also alter the directions of the relationships. Nevertheless, the strong relationships of *Nesoryzomys* with *Rattus* and *Opuntia* cactus as revealed here confirm that these variables should be central to any further studies proposed for this invaded system and indeed to any conservation plans conceived to protect *Nesoryzomys*. Finally, although the statistical approach adopted here allowed each grid cell to be treated as an independent replicate for sampling requirements, the study was only carried out in two areas. To extrapolate from such results may give spurious conclusions, however, given the highly restricted range of *Nesoryzomys*, to extrapolate from these findings might also prove to be a meaningless exercise.



A cactus pad showing feeding signs by a Santiago Rice rat (indicated by arrows).

CHAPTER 4

BEHAVIOURAL ADAPTATIONS OF THE SANTIAGO RICE RAT FOR EXPLOITING ENDEMIC *OPUNTIA* CACTUS FRUIT

4.1 ABSTRACT

Endemic Santiago Rice Rat, *Nesoryzomys swarthi*, survives in sympatry with the recently invasive Black Rat, *Rattus rattus*, in the arid zone of Santiago in the Galápagos. In this zone non-cactus food supply, driven by the seasonal conditions, varies between extremes of high and low availability. During periods of low non-cactus food availability *Nesoryzomys* are supposed to acquire a relatively poor quality diet and this is compounded by their displacement from preferred food patches by sympatric *Rattus*. In response *Nesoryzomys* has been found to consume a non-preferred and presumably poor quality cactus diet. Here it was found that *Nesoryzomys* practise coprophagy and that the incidence of coprophagy was highest in habitat with and at a time when cactus fruit abundance was highest. This time also corresponded to a period when non-cactus foods were scarce and monopolised by *Rattus*. Closer inspection revealed that faeces collected from coprophagic animals consistently contained cactus seed cases. From these findings it is hypothesised that during periods of scarce non-cactus foods *Nesoryzomys* consumes a poor quality diet of predominantly cactus fruits but optimises its nutritional gain from these fruits by reingesting the cactus seeds along with some faecal material. The reasons that *Nesoryzomys* might practise coprophagy are discussed.

4.2 INTRODUCTION

Extreme environmental events can have major effects upon primary production and consequently upon food availability to consumers (e.g. Noy-Meir 1973; Holmgren *et al.* 2001). These “bottom up” effects are frequently most pronounced in low productivity habitats such as deserts (e.g. Jaksic 2001; Gutierrez & Meserve 2003) where periods of severe food scarcity may have a strong influence on terrestrial small mammal population dynamics (e.g. Meserve *et al.* 1995; Yunger *et al.* 2002). The selective pressure of these events upon population variation in food utilisation traits may, through the bottleneck effect,

often lead to the evolution of behavioural adaptations (Wiens, 1977). If these events are infrequent then typical characters that may be enhanced include high fecundity and behavioural traits (Wiens, 1977).

Studies of resource competition frequently investigate the role of food partitioning in facilitating species coexistence (e.g. Schoener 1974), however, few studies consider how the species utilise the limiting foods. Studies of seed-caching, for example have shown that this food utilisation behaviour can have important implications for desert Heteromyid coexistence (Price & Joyner, 1997; Price *et al.*, 2000; Price & Mittler, 2003). Behaviours such as seed caching can be classed as what Grime (1977) termed a ‘stress tolerance’ and Southwood (1977) termed an ‘adversity tolerance’ strategy. These strategies include an array of behaviours evolved to maximise the conservation of foods. Another example of a stress tolerance behaviour is the reingestion of nutrient rich faeces, commonly referred to as coprophagy (Hirakawa, 2001).

Kenagy and Hoyt (1980) scrutinized small mammal species with a range of feeding strategies for evidence of coprophagy and found that although the behaviour was widespread, it was only frequently performed in herbivorous species. Controlled diet manipulations have demonstrated that in many species coprophagy is driven by diet quality as individuals kept on a poor diet would more frequently reingest their faeces (Cranford & Johnson, 1989). This behaviour has been well studied in lagomorphs, in which it is facilitated by morphological adaptations such as an enlarged caecum, and caviomorphs, which lack any such morphological adaptations. Like caviomorphs, most other rodent species do not have the advanced morphological adaptations evolved in lagomorphs for coprophagy. Instead, rodents usually carefully examine faeces before choosing to reingest or discard it (Hirakawa, 2001). Those faeces that are reingested have been shown in many species to be high in proteins and water (Kenagy & Hoyt, 1980; Hirakawa, 2001).

The endangered Santiago Rice rat, *Nesoryzomys swarthi*, was recently rediscovered on Santiago in sympatry with the recently introduced aggressive black rat, *Rattus rattus*. Through a detailed study of their diets it has been shown that during the wet season

when food is abundant the coexistence of *Nesoryzomys* with the behaviourally dominant *Rattus* is facilitated by exclusive access to *Opuntia* cactus foods that provide the subordinate *Nesoryzomys* with a competition refuge from interspecific interference competition. When foods become scarce however, and interference competition should be at its strongest, the *Rattus* population, through food or water deprivation, dies off to levels of near-extinction allowing *Nesoryzomys* a period of respite from interference competition with *Rattus*. However, despite this crash in density of *Rattus*, according to captive preference trials which revealed that *Nesoryzomys* prefer non-cactus foods; it seems that *Nesoryzomys* are still unable to acquire their preferred foods while in sympatry with *Rattus*. It was concluded from these findings that the few remaining *Rattus* were aggressively defending the few ephemeral non-cactus foods available in the cactus fruiting season so that *Nesoryzomys* were forced to switch from their preferred diet to a non-preferred diet of predominantly cactus foods (Chapter 2).

Being a non-preferred diet, the predominantly cactus diet of *Nesoryzomys* during the period of food shortage is also presumed to be a poor quality diet. The aims of this investigation were to determine if *Nesoryzomys* on a presumed poor diet of cactus fruits would tend to practise coprophagy. For comparison, the incidence of coprophagy in *Rattus* was also recorded. It was hypothesised that coprophagy would be common in *Nesoryzomys* during the cactus fruiting period when preferred non-cactus foods were rare and when it relies on abundant cactus fruits for nutrition, and would be unrelated to cactus fruit abundance in *Rattus*. To investigate these hypotheses, the incidence of coprophagic behaviour was measured for each species in habitat with and without cactus fruit and contrasted for times of high and low cactus fruit abundance.

4.3 METHODS

4.3.1 STUDY SITE AND TRAPPING PROTOCOL

This study was carried out at a site known locally as La Bomba, situated on the central north coast of Santiago in the Galápagos archipelago, during 2004-5. The prevailing trade winds that bring rain to the Galápagos approach from the southeast so that Santa Cruz and the highlands of Santiago cast a combined rainshadow over La Bomba. This results in an arid habitat characterized by trees; *Bursera graveolens*, and *Cordia lutea*, and shrubs; *Clerodendrum molle*, *Castela galapageia* and *Lantana peduncularis* and the endemic cactus, *Opuntia galapageia* var. *galapageia*. In Chapter 3 it was reported that cacti exhibit a discrete density gradient at La Bomba wherein the highest cactus density is at the coast. Furthermore, it was reported that large cactus plants, that are capable of producing fruit (Racine & Downhouser, 1974), are almost absent from habitat approximately 1 km inland from the coast. This study was conducted over two periods of different cactus fruit abundance namely; the *fruiting* and *non-fruiting* seasons.

Six additional 7x7 trapping grids, with stations 30m apart, were marked out in habitat at the outer extremes of the declining cactus gradient so that, including grids 3 (=G1) and 8 (=G2) trapped during 2004 to measure species spatial activity, there were four grids located in habitat with large cactus plants (hereafter referred to as *mature cactus habitat*; grids 2, 13, 3 and 4) and four located in habitat without large cactus plants (hereafter referred to as *immature cactus habitat*; grids 5, 6, 7, and 8, Figure 4.1).

On each of these grids 20 trap stations were randomly selected and the distance (m) was measured to the nearest tree, bush and cactus and its nearest neighbour, according to the method outlined by Greenwood (1996). These measures were used to compare the densities of each type of plant (hereafter referred to as *plant*) between the coastal and inland grids using t-tests. At each trap station, two Tomahawk live traps (Model #201, 40.6 x 12.7 x 12.7cm, Tomahawk Live Trap Co., PO Box 323, Tomahawk, Wisconsin, USA) were erected to capture each species. Each night a different selection of these traps

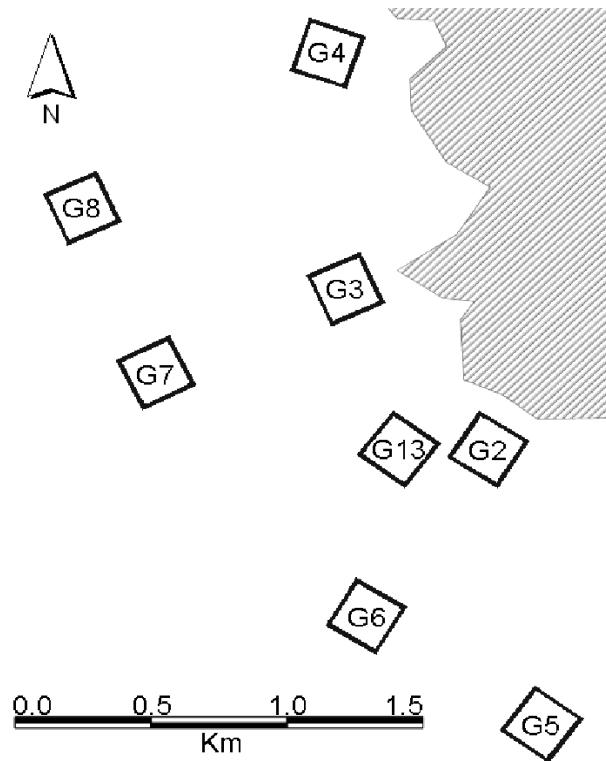


Figure 4.1: Grid locations in relation to the coast (thatched area) at La Bomba. G3 and G8 were trapped during 2004 as part of the spatial activity investigation and all other grids were trapped for faeces collection during 2004-5.

was set after dusk and checked before dawn permitting animals a period of normal foraging before and after capture. Traps were baited with peanut-scented rag to ensure that subsequent behaviours were not affected by the earlier consumption of high energy bait. All experimental protocols complied with the current laws of the country in which they were performed (Ecuador) and the guidance of the UK Animals (Scientific Procedures) Act 1986.

4.3.2 FAECAL SAMPLING AND COPROPHAGY

To contrast *Nesoryzomys* coprophagic behaviour in areas with and without cactus fruit, faecal samples were collected from individuals captured in both habitats and in both seasons. To facilitate collection of uncontaminated faecal matter, the rear end of each

Tomahawk trap was elevated \approx 10mm upon stones beneath which a concave 130 x130mm square of 1.5x1.5mm metal mesh was placed with edges flush to the bottom of the trap. This design allowed for the collection of faecal material that dropped through the bottom of the rear end of the trap without risk of it being trampled underfoot. The rear end of each trap was covered with a piece of tarpaulin under which animals preferred to reside thereby maximising the amount of faecal material collected.

Traps were checked before dawn and biometric measurements were recorded for each captured individual as outlined above. Faecal material was transferred to sample tubes that were filled with 70% alcohol and sealed before transportation to the laboratory. In the laboratory, the content of each tube was poured into a Petri dish and the pellets examined for evidence of consumption. Coprophagy was recorded as having occurred if the faecal matter was broken into many small pieces (pieces $<25\%$ of a whole pellet) and only if these small pieces constituted $\geq 50\%$ of the faecal material collected. This criterion was based upon observations of captive animals that had occasionally been observed to perform coprophagy, leaving such small pieces as the remainder of the consumed pellets. The faecal material was then lightly crushed and screened for the presence of cactus seed cases under a x40 binocular light microscope (Luo *et al.*, 1994). The number of animals exhibiting coprophagy was recorded in mature and immature cactus habitat in each season and the effects of cactus habitat type and season and the habitat*season interaction on the numbers of coprophagic and non-coprophagic animals was investigated using hierarchical log linear analysis. Log linear analysis was also used to determine if the number of faecal collections containing cactus seeds was different between the mature and immature cactus habitats. These statistical analyses were carried out using SPSS (v14.0).

4.4 RESULTS

4.4.1 HABITAT COMPARISONS

Comparison of cactus density in both habitats confirmed that density is higher in mature cactus habitat ($= 0.011/m^2$, SD = 0.001) compared to immature cactus habitat (cactus = $0.002/m^2$, SD = 0.000, $t_6 = 7.979$, P <0.001). Tree density was similar in both mature ($= 0.007/m^2$, SE = 0.001) and immature cactus habitats ($= 0.008/m^2$, SE = 0.001, $t_6 = -0.335$, P = 0.749) however bush density was higher in mature ($= 0.049/m^2$, SE = 0.003) compared to immature cactus habitat ($= 0.031/m^2$, SD = 0.005, $t_6 = 2.988$, P = 0.024).

4.4.2 COPROPHAGY

Individual *Rattus* exhibited no coprophagic behaviour on coastal (n = 8) or inland habitats (n = 16) and so no further analysis was conducted for *Rattus*. In contrast, the overall proportion of *Nesoryzomys* individuals demonstrating coprophagic behaviour was 79 and 28% on coastal and inland habitats respectively.

Closer inspection of the numbers of coprophagic and non-coprophagic *Nesoryzomys* revealed a significant habitat*season*coprophagy interaction ($G = 23.886$, d.f. = 1, P <0.001, Figure 4.2) suggesting that the number of coprophagic *Nesoryzomys* individuals in each habitat was affected differently by season (Table 4.1). Separate examination of the main effect of habitat and season revealed that there were more coprophagic *Nesoryzomys* than expected in mature cactus habitat ($G = 14.788$, d.f. = 1, P <0.001) and fewer coprophagic *Nesoryzomys* than expected in immature cactus habitat ($G = 9.241$, d.f. = 1, P = 0.002) in both seasons combined while there were more coprophagic *Nesoryzomys* than expected in the fruiting season when non-cactus foods were scarce ($G = 67.013$, d.f. = 1, P <0.001) but not in the non-fruiting season when non-cactus foods were abundant ($G = 1.852$, d.f. = 1, P = 0.174).

Table 4.1: Observed numbers of coprophagric and non-coprophagric *Nesoryzomys* in mature and immature cactus habitat in both the non-fruited and fruiting seasons.

Season	Cactus habitat		Coprophagric	Non-coprophagric	Total
Non-fruited	Mature	Observed	15	11	26
		Expected	12	14	
	Immature	Observed	18	26	44
		Expected	21	23	
		Total	33	37	70
Fruited	Mature	Observed	56	4	60
		Expected	39	21	
	Immature	Observed	3	27	30
		Expected	20	10	
		Total	59	31	90

No *Nesoryzomys* faecal pellets that exhibited signs of consumption contained cactus seed cases in the non-fruited season in either habitat. In the fruiting season, 95 and 13% of *Nesoryzomys* faecal pellets exhibiting signs of consumption contained cactus seed cases in the mature and immature cactus habitat respectively, and statistical comparison revealed the incidence was different between habitats ($G = 65.074$, d.f. = 1, $P < 0.001$). As expected, no *Rattus* faecal pellets contained any traces of cactus seeds.

4.5 DISCUSSION

The results presented here provide compelling evidence that *Nesoryzomys* practice a type of coprophagy at La Bomba and that *Rattus* do not. Moreover, the results indicate that *Nesoryzomys* reingest their faeces with an express intent. Wild-caught *Nesoryzomys* exhibited a high incidence of coprophagric behaviour and this result was somewhat surprising because *Nesoryzomys* is omnivorous and coprophagy is thought to be uncommon in granivorous and omnivorous rodent species (Kenagy & Hoyt 1980; Table 4.2). Rather, however, than being practised universally across distinct cactus habitats and over the entire year, further analysis of the distribution and incidence of coprophagric individuals has revealed that *Nesoryzomys* most frequently practice coprophagy in areas and at

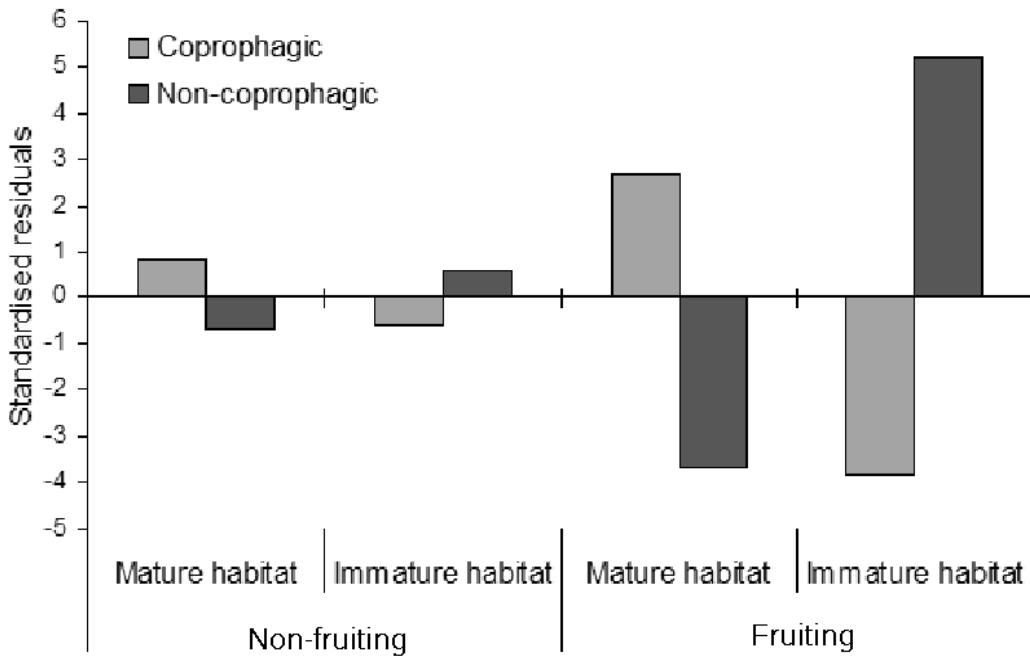


Figure 4.2: Plot of standardised observed-expected residuals for counts of coprophagic and non-coprophagic *Nesoryzomys* in mature and immature cactus habitat in each season.

times when there are large numbers of cactus fruit. This finding suggests that faecal reingestion is associated with the consumption of cactus fruits. As might be expected *Nesoryzomys* appear to consume this food most frequently in the cactus fruiting season when it is most abundant and non-cactus foods are comparatively scarce (Chapter 2). Given this knowledge it could be construed that *Nesoryzomys* consume cactus fruits and then reingest their faeces after the fruits/seeds have passed through the digestive system. This hypothesis receives support from the second finding reported here. Faeces of coprophagic animals in the mature cactus habitat in the fruiting season where cactus fruits were abundant were significantly more likely to contain cactus seeds than faeces from coprophagic animals in the immature cactus habitat where cactus fruits were absent. Although comparison of the habitats revealed that the bush density was higher in mature than immature cactus habitat this was not expected to confound the results as there was a difference in the incidence of coprophagy within habitats between seasons when no changes in bush density would be expected to occur.

Table 4.2: Reingestion activities of 13 rodent species observed by Kenagy and Hoyt (1980).

Family	Species	Mode of feeding	Reingestion
Heteromyidae	<i>Perognathus formosus</i>	Granivorous	Rare
	<i>P. longimembris</i>	Granivorous	Rare
	<i>Dipodomys microps</i>	Herbivorous	Frequent
	<i>D. merriami</i>	Granivorous	Rare
Geomyidae	<i>Thomomys bottae</i>	Herbivorous	Rare
Muridae	<i>Peromyscus maniculatus</i>	Omnivorous	Rare
	<i>P. crinitus</i>	Omnivorous	Rare
	<i>Neotoma lepida</i>	Omnivorous	Rare
	<i>Microtus californicus</i>	Herbivorous	Frequent
Aplodontidae	<i>Aplodontia rufo</i>	Herbivorous	Rare
Sciuridae	<i>Spermophilus saturatus</i>	Herbivorous	Rare
	<i>Ammospermophilus leucurus</i>	Omnivorous	Not observed
	<i>Eutamias minimus</i>	Omnivorous	Not observed

Faeces collected from wild-caught *Rattus*, on the other hand, did not exhibit any signs of consumption (indeed regular recovery of complete faecal pellets suggested that the method of faeces collection was effective) nor contained any cactus seed cases in either habitat or in either season [despite the occurrence of coprophagy in the closely related *R. norvegicus* (Hirakawa, 2001)]. It is possible however that *Rattus* reingested faeces whole although this is uncommon in rodent species (G. Kenagy, pers com.). Instead, together with knowledge of *Rattus* diet at La Bomba, these finding suggest that by not eating cactus foods (Appendix C) there appears either no requirement or advantage for *Rattus* to practice coprophagy. By contrast to *Nesoryzomys* though, *Rattus* undergo a significant population reduction with the decline in non-cactus foods. This suggests that there may in fact be an advantage to practising coprophagy, which *Rattus* does not reap and that may result in it suffering nutritional deprivation.

While collectively the results construct a convincing case for *Nesoryzomys* reingesting their faeces with the specific intention of consuming cactus seed contents, there might be other viable explanations that could explain the results observed here. For example, perhaps *Nesoryzomys* consume whole cactus seeds but the seed cases are broken down at some stage during the digestive process and the faeces itself are reingested to im-

prove water retention (Tracey & Walsberg, 2002). Nevertheless, the number of feasible alternative explanations appear few. What is certainly a more contentious issue is for what reason *Nesoryzomys* should practice coprophagy at all. There are many competing theories that may explain why small mammal species reingest faeces (Hirakawa, 2001) and some of these might explain why there was some coprophagy in areas without cactus fruit and during the cactus non-fruiting season. During these times cactus seed cases were effectively absent from faecal material suggesting that the animals were reingesting faeces without regard for its cactus seed content. Cranford and Johnson (1989) suggest that coprophagy in rodents is a mechanism by which animals can gain additional nutrition from a poor quality diet while Tracey and Walsberg (2002) cite coprophagy as a behavioural adaptation to maximise water retention. Under both of these hypotheses, *Nesoryzomys* should have been acquiring a nutritionally or water poor diet throughout the year, even when alternative foods were abundant. Indeed it was found that *Rattus* reduced *Nesoryzomys* access to almost all available foods other than cactus fruits (and pads) throughout the year. However, cactus foods are known to be high in their water content (e.g. Schmidt-Nielson 1964) so a suboptimal, high cactus diet should not be water deficient which does not support a greater need for coprophagy to increase water retention. Alternatively, the poor diet hypothesis remains plausible. As mentioned, the diet *Nesoryzomys* selected when sympatric with *Rattus* was different to its preferred diet (Chapter 2). If this non-preferred diet is nutritionally inferior to its preferred diet then nutritional supplementation appears to be a fitting reason to explain coprophagy in *Nesoryzomys*. Aside from the reasons why *Nesoryzomys* might practise coprophagy, it may also play an interesting role in the coexistence of *Nesoryzomys* and *Rattus* at La Bomba. By the end of the fruiting season when *Rattus* numbers are at their lowest, the additional nutrition gained from reingested faeces or cactus seeds may be sufficient for *Nesoryzomys* to avoid foods preferred by *Rattus* thereby lessening their likelihood of encounter and perhaps avoiding interspecific competition of any form. These thoughts can be likened to the use of coprophagy by lagomorphs and rodents to minimise their exposure to aerial

predators (Hirakawa, 2001; Price & Mittler, 2003).

4.6 CONCLUSIONS

The findings of this study lend further support to the growing literature that cactus foods are important to *Nesoryzomys* survival. Here it is postulated that faeces reingestion, but more commonly reingestion of faeces containing cactus seeds, by *Nesoryzomys* is an important behaviour expressed with the specific intent to maximise their nutritional gain from cactus foods. This behaviour might have the effect of mitigating interspecific competition with *Rattus*. Indeed, it may be this very behaviour that permits *Nesoryzomys* to survive at La Bomba when *Rattus* populations undergo periodic crashes. It seems that the 3.3 millions years that *Nesoryzomys* have inhabited Santiago (Patton *et al.*, 1975) have allowed it sufficient time to evolve coprophagy or tolerance to cactus seed toxins (Kenward & Holm, 1993) that afford it an adaptive advantage over *Rattus* that has not evolved these adaptations in the comparatively short period since its arrival to Santiago (up to 400 years; Patton *et al.* 1975). What is more certain is that if *Opuntia* resources are pivotal in the survival of *Nesoryzomys* in the presence of *Rattus*, then the outlook for *Nesoryzomys* is alarming. As climate warms, El Niño phenomena are predicted to become more intense and more frequent (Webster & Palmer, 1997) and this is expected to have a catastrophic effect on *Opuntia* survival and recruitment (Hamann, 2004). If these predictions materialise and the value of the cactus refuge is diminished then it seems likely that the future of *Nesoryzomys* will converge with the history of the 7 other Galápagos Rice rat species that succumbed to the competitive effect of *Rattus* (Key & Muñoz Heredia, 1994).



Cactus fruits showing feeding signs of the Santiago Rice rat. From left to right: whole cactus fruit, two fruits showing fresh feeding signs, two consumed fruits showing progressive dessication.

CHAPTER 5

GENERAL DISCUSSION

Two key topics arise from the investigations presented here. Both Chapters 2 and 3 report a sex-specific difference in interspecific interactions between *Nesoryzomys* and *Rattus* where female *Nesoryzomys* are found to have higher dietary and spatial overlap with *Rattus* when breeding during the food-rich wet season. Common to the results in Chapters 2 and 3 and the topic of Chapter 4 is the strong relationship between *Nesoryzomys* and the endemic cactus, *Opuntia galapageia*, which both provides male *Nesoryzomys* with a competition refuge from interspecific competition with *Rattus* and provisions both sexes of *Nesoryzomys*, but not *Rattus*, with important nutrition and water during the food-poor dry season.

When considered along with previous work undertaken on this invaded rodent community at La Bomba, these findings support and build on the existing knowledge and theories about the mechanisms facilitating this unlikely coexistence and outline important considerations for the future conservation of *Nesoryzomys*.

5.1 NESORYZOMYS AND RATTUS

Interference competition has been implicated as a structuring force in rodent communities inhabiting a range of biomes around the World (e.g. the Negev Desert, Israel: Ziv & Kotler 2003; Kotler *et al.* 2005; Wasserberg *et al.* 2006; the Sonoran Desert, USA: Brown *et al.* 1979; the Chihuahuan Desert, USA: Brown & Munger 1985; Brown 1989; Brown & Heske 1990; Northern Hemisphere boreal forests, Finland: Grant 1972; Eccard *et al.* 2002; Eccard & Ylönen 2002; the Appalachian Mountains deciduous forests: Wolff *et al.* 1983; and Colorado Grassland Biome, USA: Stapp 1997). In each community the evidence in support of interspecific competition has been derived from a range of laboratory and field techniques including staged encounters (e.g. Bleich & Price 1995; Courtalon *et al.* 2003), trapping and tracking (e.g. Maitz & Dickman 2001; Ziv *et al.* 1993) and species manipulations (e.g. Kincaid & Cameron 1982; Stapp 1997; Eccard & Ylönen 2002). All of these techniques have recently been used to detect and investigate the mechanisms of

interspecific competition in structuring the rodent community in Galápagos.

Results from a replicated press experiment (*sensu* Bender *et al.* 1984) showed that when *Rattus* populations were depressed, female *Nesoryzomys* survival was higher on treatment grids compared to controls (Harris and Macdonald, *unpublished manuscript*). Begon and colleagues (1996) stated that interspecific competition should cause a reduction in fecundity, survivorship or growth in one species through resource exploitation or interference with another. According to Begon and colleagues' statement the findings of Harris and Macdonald constitute evidence for interspecific competition, where *Rattus* negatively affects the survival of female *Nesoryzomys* (Harris and Macdonald, *unpublished manuscript*). Continuing their investigation, Harris and Macdonald demonstrated that *Rattus* was behaviourally dominant to *Nesoryzomys*, but that retreat frequency was size dependent so that the smaller female *Nesoryzomys* were more likely than males to retreat from interspecific encounters in staged interspecific trials with *Rattus* (Harris and Macdonald, *unpublished manuscript*).

In Chapter 2, the observed interspecific competition between *Nesoryzomys* and *Rattus* was investigated with a mechanistic approach (*sensu* Tilman 1982, 1987) through a study of diets (as advocated by Price 1984). Findings in the wet season revealed that diet overlap was highest between female *Nesoryzomys* and *Rattus* when foods were relatively abundant and both species were breeding (Harris and Macdonald, *unpublished manuscript*). A similar sex-difference was noted by Tew and colleagues (2000) when studying microhabitat selection in Wood mice, *Apodemus sylvaticus*. They explained that female *A. sylvaticus* selected a different microhabitat to males because the food plants of their chosen microhabitat were required for successful breeding (Tew & Macdonald, 1994). Kincaid and Cameron (1985) also reached a similar conclusion about sex-differences in habitat selection by the Cotton rat, *Sigmodon hispidus* and in follow-up studies they, with other authors, were able to confirm that breeding female *S. hispidus* do indeed have special dietary requirements (Randolph *et al.*, 1995; Hellgren & Lochmiller, 1997; Cameron & Randolph, 1997). The preferred diet of female *Nesoryzomys* in allopa-

try was found to be similar to their diet selected when sympatric with *Rattus*, suggesting that they were meeting their dietary requirements in the field and there was not likely to be competition for foods. In contrast, the diet of male *Nesoryzomys* was different under allopatric and sympatric conditions suggesting that it was not acquiring its preferred diet when sympatric with *Rattus* in this season. Instead the results showed that it selected a predominantly cactus diet in the field. This finding exposed a sex-difference in male and female diet acquisition when sympatric with *Rattus* during the breeding season whereby females had a significant dietary overlap with *Rattus* and males did not. If we presume that interspecific dietary overlap increases the likelihood of encounters with *Rattus* then this result might contribute to the disparity in male and female survival as observed by Harris and Macdonald (*unpublished manuscript*), i.e. smaller females are not only more likely to be displaced but are also subject to a higher frequency of encounters with *Rattus*.

In Chapter 3, the spatial activity of male and female *Nesoryzomys* was modelled in relation to that of *Rattus*. Interspecific competition driven by interference should always result in some spatial or temporal segregation of the competitor's activity (Morris *et al.*, 2000; Morris, 2003) and so male *Nesoryzomys* activity was expected to be low in areas of high *Rattus* activity relative to the activity of female *Nesoryzomys*, which were expected to forage in areas alongside *Rattus*, particularly during the breeding season when non-cactus foods and *Rattus* are abundant. The modelling confirmed this hypothesis and demonstrated that male *Nesoryzomys* activity was significantly lower, both absolutely and relative to female activity, in areas of high *Rattus* activity. This suggests that, to male *Nesoryzomys*, the benefits of avoiding mutually preferred foods exceed the costs of a higher frequency of interspecific contact. Examples of interspecific avoidance between small mammal competitors are numerous in the literature. Perhaps the most thorough investigation of this phenomenon in small mammals comes from investigations of gerbilline rodents of the Negev Desert. Over a decade of research in this system has demonstrated that the Egyptian Sand gerbil, *Gerbillus pyramidum*, is behaviourally dominant to Allenby's gerbil, *G. andersoni allenbyi*, frequently displacing it from rich food patches. This

finding has frequently been shown to manifest in spatial segregation of these species where *G. a. allenbyi* is frequently displaced to non-preferred habitat (e.g. Ziv *et al.* 1993; Ziv & Kotler 2003), although a difference in foraging strategies is also perceived to be highly important in the facilitation of coexistence (see Brown 1989; Brown *et al.* 1994).

The difference in the sexes' relationships with *Rattus* was hypothesised to be the outcome of their different dietary requirements in the breeding season. This hypothesis is - at least anecdotally - supported by the contrasting findings in the non-breeding (dry) season when there was no difference in male and female *Nesoryzomys* diet overlap with *Rattus* in sympatry or allopatry (Chapter 2) and male and female diet overlap was near-complete both in the presence and absence of *Rattus*. Nevertheless, the diet in sympatry with *Rattus* differed from that in allopatry for both sexes suggesting that neither sex was acquiring its preferred foods, perhaps due to interference by *Rattus*. This finding was somewhat surprising because *Rattus* undergo a seasonal population decline in the dry season (Harris and Macdonald, *unpublished manuscript*), unlike *Nesoryzomys* that remain relatively stable (Harris and Macdonald, *unpublished manuscript*), such that the per capita effect of *Rattus* interference on *Nesoryzomys* should be substantially less (Chesson & Warner, 1981). However, if, as hypothesised by Clark (1980b), the *Rattus* decline is due to the diminishing fruits and seeds in this season, then it seems likely that *Rattus* should invest more effort in defending these ephemeral foods from *Nesoryzomys* (Slobodkin *et al.*, 1967). The modelling results from Chapter 3 supported these findings by demonstrating that both sexes of *Nesoryzomys* equally avoided areas of high *Rattus* activity in the dry season.

In conclusion, the results from two quite different studies, a dietary study presented in Chapter 2 and a spatial modelling exercise presented in Chapter 3, describe precisely the same seasonal relationships between male and female *Nesoryzomys* and *Rattus*. These results provide strong support for year-round segregation of spatial activity between the species in response to interspecific interference by *Rattus* on *Nesoryzomys*. Female *Nesoryzomys* provide the only exception to this rule during the breeding season when its

dietary requirements oblige it to share foods, and therefore space, with *Rattus*.

5.2 NESORYZOMYS AND CACTI

Behavioural dominance ensures priority access to shared resources (e.g. food or habitat) (Keddy, 2001) and under strong asymmetric competition it can lead to the partitioning of resources through either behavioural avoidance (Schoener, 1974) or character displacement (Connell, 1980) that both ultimately serve to promote species coexistence, or it can lead to competitive exclusion (Gause, 1934). Since its inception, however, contemporary competition theory has conceded that a subordinate species can coexist with a dominant species on a shared resource if the subordinate species has a competitive advantage in, or can gain exclusive access to, an alternative resource (e.g. food or habitat) within the area of sympatry (MacArthur, 1958; Hutchinson, 1959). Terman (1974) demonstrated this in a laboratory setting for the naturally sympatric Prairie vole, *Microtus ochrogaster*, and the Cotton rat, *Sigmodon hispidus*. He was able to show that the dominant *S. hispidus* would exclude the subordinate *M. ochrogaster* when there was little cover and the frequency of interspecific contact was high. He was also able to show, however, that by adding patches of dense cover the two species could coexist.

The results of the diet studies presented in Chapter 2 showed that pads and fruits of the endemic cactus, *Opuntia*, were eaten by *Nesoryzomys* but rarely by *Rattus*, particularly cactus fruits that were apparently unpalatable to *Rattus*. Equivalent consumer-resource relationships involving cacti have been recorded for a range of wildlife from large ungulates (e.g. deer, Janzen 1986) to rodents (e.g. Schmidt-Nielson 1964). For example, many researchers have found that Woodrats, *Neotoma* spp., regularly consume *Opuntia* cacti for food (see Brown *et al.* 1972 and references therein). A similar finding emerged from a small mammal study by Reichman (1975) in Arizona. He studied diet overlap in several rodent species in habitat similar to that of La Bomba (Figure 5.1) and found that although all species ate some *Opuntia* foods *Perognathus baileyi* strongly preferred

these foods and coexisted with the other rodents by specialising upon them. Previous to the work presented here, *Nesoryzomys* dietary habits were completely undescribed and so records of *Nesoryzomys* consuming *Opuntia* should not have been documented. In an impact assessment of large ungulate herbivory on cacti at La Bomba, however, Hicks and Mauchamp (1996) noted an abundance of cacti showing signs of consumption that they attributed to goats and burros. The presence of spines on *Opuntia* pads is known to be an effective deterrent to ungulate herbivory as demonstrated by their preference for plant parts with experimentally removed spines (Chavez-Ramirez *et al.*, 1997). According to these findings, Hicks and Mauchamp's conclusion seems erroneous and a convincing alternative explanation is that the damage is a consequence of *Nesoryzomys* ascending and consuming intact cactus pads (pers obs.), particularly during the dry season. It seems then, that Hicks and Mauchamp's alleged goat damage could constitute the first (but unrecognised) evidence of *Nesoryzomys* feeding on *Opuntia*. In contrast to the eager cactus consumption noted in *Nesoryzomys*, cactus pads appeared to be unattractive or unimportant to *Rattus* and they did not eat cactus fruits in either season. Although not confirmed in *O. galapageia* var. *galapageia*, many other cacti of the genus *Opuntia* have been shown to have calcium oxalate crystals in their succulent fleshy interior (Theimer & Bateman, 1992). Furthermore, depending on the level of these oxalates, they can be effective deterrents against herbivory by peccaries (Theimer & Bateman, 1992). Perhaps a high level of oxalates in *O. galapageia* is a sufficient deterrent to *Rattus*.

Closer examination of cactus in the diet of *Nesoryzomys* in Chapter 2 revealed that it was not a highly preferred food when measured in allopatry but that it was a highly utilised food when *Nesoryzomys* was sympatric with *Rattus*. Taking each season separately revealed that cactus foods were important in male *Nesoryzomys* diet in the wet season but not females that were compelled by breeding requirements to forage for foods shared with *Rattus*. Food availability in the wet season, however, was substantially higher than food availability in the dry season and as such it was not deemed limiting. This precluded resource competition as the type of competition occurring between *Nesoryzomys*



Figure 5.1: *Opuntia* habitat in Arizona (top) and La Bomba (bottom) where species of rodents are known to specialise on cactus pads and fruits. Arizona pictures from Reichman (1975).

and *Rattus* in the wet season but invited the possibility that cactus foods, particularly cactus fruits, were important to *Nesoryzomys* as a competition refuge from interspecific aggressive encounters with *Rattus*. When foraging in an area with cactus fruits or pads, male *Nesoryzomys* could choose to eat these foods and in doing so could reduce the costs of aggressive encounters. This hypothesis was tested in Chapter 3 using spatially-explicit models of *Nesoryzomys* activity and the distributions of cactus foods which demonstrated that areas of cactus foods, particularly fruits, were used by male *Nesoryzomys* more than females in the wet season. A similar finding emerged from an investigation of space use by members of a large African carnivore guild. Within this guild, cheetah were subordinate to lion and hyena. Male cheetah were found to minimise their activity in areas of high shared prey and high competitor densities to a greater degree than females that were forced by their breeding requirements to remain active in areas with a high density of prey (Durant, 1998).

As non-cactus resources decline in the dry season *Rattus* populations are reported to crash to levels of near-extinction (Clark, 1980b) whereas *Nesoryzomys* populations have the capacity to remain relatively stable (Harris and Macdonald, *unpublished manuscript*). The crash of *Rattus* populations is postulated to reduce the per capita Frequency of Interspecific Contact (FIC) effect of *Rattus* on *Nesoryzomys* to negligible levels. By deduction then, the observed switch of *Nesoryzomys* to cactus resources, but particularly cactus fruits, reported in Chapter 2 and Chapter 3 in this season suggests that cactus foods provide *Nesoryzomys* with nutrients, or perhaps more importantly water, to sustain it when alternative foods are scarce. Similarly, *Neotoma* spp. are believed to meet their daily water requirements by consuming cactus pads (Schmidt-Nielson, 1964). This requirement is postulated to underlie the very strong positive linear relationship between *Neotoma* and *Opuntia* density observed for several species of *Neotoma* (see Brown *et al.* 1972 and references therein). Cactus consumption by peccaries during the dry season in Texas is also purported to be a mechanism to obtain water (Zervanus & Day, 1977). Whether *Nesoryzomys* consumes cactus foods for nutrition or for water awaits further

investigation. What is known is that *Rattus*, which also have daily water requirements (Meehan, 1984), do not readily consume cactus pads or the abundant cactus fruits in the dry season and undergo a dramatic population crash during the dry season in *Opuntia* habitat (Clark 1980b; Harris and Macdonald, *unpublished manuscript*).

The results from the cactus fruit palatability trials reported in Appendix C provide unequivocal evidence of consumption by *Nesoryzomys* but not by *Rattus* that either does not or cannot consume them. Cases such as this, where one species has exclusive access to an alternative food, are rarely reported in the literature, especially among small mammal species. Nevertheless, some interesting cases in the literature have reported similar findings. To explain the coexistence of three *Neotoma* species, Dial (1988) quantified their diets and concluded that each species specialised on different foods, and importantly, that one species, *N. albigena*, was the only species to eat ‘appreciable amounts’ of the succulent plant, *Yucca baileyi*. Similarly, the Brush mouse, *Peromyscus boylii*, is able to coexist with the California mouse, *P. californicus*, because *P. boylii* diet is predominantly made up of acorns that are relatively unused by *P. californicus* (Kalcounis-Rüppell & Millar, 2002). Interestingly, another example arises from the shared use of acorns: the invasive grey squirrel, *Sciurus carolinensis*, has been shown to have almost exclusive access to acorns in Britain (Moller, 1983) giving it a competitive advantage over the red squirrel, *S. vulgaris*, which it is thought to exclude (Gurnell *et al.*, 2004; Wauters *et al.*, 2002b,a). Given that the last two examples both involve acorns, one might ask whether these acorn-specialist species share some common capability that neither share with their congeners. Kenward and Holm (1993) took a similar approach to that reported in Appendix C to address this question. They fed captive *S. carolinensis* and *S. vulgaris* on a mixed diet containing acorns and noted that *S. carolinensis* ate the acorns and *S. vulgaris* did not. Moreover, when fed on an acorn only diet *S. vulgaris* lost weight and after longer periods most died. Kenward and Holm measured the undigested and unabsorbed nutrients in the faeces of dying *S. vulgaris* and concluded that high levels of phytotoxins in acorns inhibited effective nutrient absorption which ultimately caused their death (Kenward & Holm, 1993).

Whether a similar mechanism promotes resource partitioning in the *Peromyscus* species remains to be tested.

If specialisation on acorns requires physiological or behavioural adaptation to cope with their phytotoxicity, perhaps cactus foods, particularly fruits, have similar phytotoxins that *Nesoryzomys* has evolved to tolerate and that *Rattus* has not. In Chapter 4 it was reported that *Nesoryzomys* performs faeces reingestion, also known as coprophagy and that *Rattus* does not. Although this behaviour was practised in both seasons, the highest incidence of coprophagy occurred in the cactus fruiting (dry) season in mature cactus habitat when non-cactus foods were scarce and monopolised by *Rattus*. This high incidence of coprophagic behaviour corresponded to the time and habitat in which there was the highest abundance of cactus fruits suggesting that coprophagy was linked with cactus fruit consumption. This supposition was supported by the finding that faeces subject to coprophagy consistently contained cactus seed cases. From these findings, it was concluded that *Nesoryzomys* eats cactus fruits and then optimises its nutritional return on these fruits by way of reingesting the seeds. While this case was convincing, it was beyond the scope of this work to investigate the precise details of *why* and *how* *Nesoryzomys* practises coprophagy. Perhaps it represents an adaptive behaviour to overcome the cost of eating phytotoxins in cactus fruits. Under laboratory conditions, Sorensen and colleagues (2005b) showed how a specialist herbivorous Woodrat, *N. stephensi*, fed on a diet of juniper berries high in phytotoxins, absorbed fewer toxins than a congeneric generalist Woodrat, *N. albigenula*, suggesting that it had evolved a physiological adaptation to overcome the high levels of phytotoxins. Moreover, they recorded that *N. stephensi* also consumed a larger quantity of the juniper diet and in doing so maximised its energy intake relative to the noxious cost (Sorensen *et al.*, 2005a). It could also, however, be a mechanism to conserve nutrients or water when feeding upon a poor diet. Again under laboratory conditions, rodents were fed on high and low quality diets but some were fitted with collars to prevent coprophagy. From these tests it was found that coprophagy was an important behaviour practised to supplement poor diets (Kenagy, 1973; Kenagy & Hoyt,

1980; Kenagy *et al.*, 1999; Tracey & Walsberg, 2002). The answers to these questions demand further research. What is clear however is that *Nesoryzomys* are highly dependent on cactus fruits during the dry season when levels of alternative foods are critically low, while *Rattus* that do not consume this seasonally abundant food suffer serious population declines in this season (Clark 1980b; Harris and Macdonald, *unpublished manuscript*).

In conclusion, cactus foods and particularly cactus fruits appear to fulfil two very important but quite distinct roles in facilitating the coexistence of *Nesoryzomys* and *Rattus* at La Bomba. During periods of plentiful non-cactus fruits when *Rattus* is abundant and the potential for interference competition is high, cactus fruits provide male *Nesoryzomys* with an important competition refuge from *Rattus*, without which its survival would likely be reduced. When non-cactus foods are scarce and *Rattus* are few, however, the cactus foods that are effectively unused by *Rattus* provide *Nesoryzomys* with important nutrition and water to sustain them until non-cactus foods are renewed in the wet season. Why *Rattus* do not use cactus foods cannot be explained by the work carried out here. The literature, however, suggests that *Opuntia* cacti possess phytotoxins that are an effective deterrent to many herbivores and usually require physiological or behavioural adaptations to tolerate. During the dry season when it is expected to consume many cactus fruits, *Nesoryzomys* also reingests *Opuntia* seeds from its faeces, a behavioural adaptation that may permit *Nesoryzomys* to tolerate *Opuntia* phytotoxins. No such behaviour was recorded for *Rattus* suggesting that 3-400 years on Santiago may not have been sufficient time for the evolution of such adaptations.

5.3 A HOLISTIC EXPLANATION

The conclusions about the competitive coexistence of *Nesoryzomys* and *Rattus* imply that both species are competing over shared foods, however, the conclusions about *Nesoryzomys* and cactus imply that by using cactus *Nesoryzomys* can avoid sharing foods with *Rattus*, with the important exception of female *Nesoryzomys* during the breeding season.

Taken together, these conclusions suggest a rather more complicated explanation. The effect of interference competition for shared food patches in the wet season when foods are abundant (relative to the dry season) is weak (e.g. Christopher & Barrett 2006). This is illustrated by the ability of smaller, disproportionately subordinate female *Nesoryzomys* to acquire their preferred diet when sympatric with *Rattus* in the wet season (Chapter 2). Perhaps foods are not limiting to the rodent populations in this season when numbers are lower due to the dry season declines (Wiens 1977; Harris and Macdonald, *unpublished manuscript*). This is not, however, to say that interspecific competition is absent in the wet season: although female *Nesoryzomys* acquire their preferred diet, they may be frequently displaced from food patches when attempting to do so and this might cause them to shift territories (Eccard & Ylönen 2002; Harris and Macdonald, *unpublished manuscript*). Furthermore, this is less likely in male *Nesoryzomys* that appear to select a predominantly cactus diet to avoid *Rattus* and are less easily displaced when they do encounter *Rattus* (Harris and Macdonald, *unpublished manuscript*). As food availability declines with progression into the dry season foods become more limiting and therefore interference competition over food patches is likely to be stronger. It seems though, that the seasonal crash in *Rattus* populations (Clark 1980b; Harris and Macdonald, *unpublished manuscript*) lower the per capita effect of interference competition on *Nesoryzomys* to the extent that the effect is negligible. In addition, *Nesoryzomys* are able to switch diet in this season to use cactus foods, and particularly fruits that are not available to *Rattus*, and thereby avoid aggressive encounters with *Rattus* at food patches. Apart from serving to further mitigate the effect of interspecific competition, by switching to cactus foods in this season *Nesoryzomys* maintain a relatively stable population density (Harris and Macdonald, *unpublished manuscript*) and become the dominant exploitation competitor of all the available foods at La Bomba. This in turn, may allow them to exploit foods beneath the critical level necessary for *Rattus* to survive thereby assisting the *Rattus* population decline to near-extinction by the end of the dry season (Aunapuu & Oksanen, 2003).

5.4 FURTHER INSIGHTS FROM THE LITERATURE

While the holistic explanation outlined above presents a feasible, even likely, explanation for the coexistence of *Nesoryzomys* and *Rattus* at La Bomba, there are many other studies in the literature that should be briefly recognised as suggesting exclusive alternative explanations or contributory factors in the observed coexistence.

1. It is possible that if species possess different foraging strategies, behavioural dominance conveys only a weak competitive advantage to the dominant species. For example, Ziv and Kotler (2003) found that *G. a. allenbyi* depleted artificial seed patches to a lower level in the presence of the behaviourally dominant *G. pyramidatum*, than in its absence. Perhaps *Nesoryzomys* is a more efficient exploiter of food patches, a so called “crumb-picker”, whereas *Rattus* forages less efficiently but over a larger number of patches, a so called “cream-skimmer” (*sensu* Kotler & Brown 1988).
2. If a habitat is a mosaic of patches within a ‘superpatch’, then coexistence can be attained even if there is no difference in the behaviourally dominant or subordinate competitors dispersal abilities (Atkinson & Shorrocks, 1981, 1984). This was empirically confirmed in the field (Inouye, 1999).
3. Differences in the competitor’s fecundity or longevity can facilitate coexistence, as demonstrated between parasitoid wasps (Bonsall *et al.*, 2004). *Rattus* at La Bomba, and throughout the Galápagos, show a distinct *r* strategy compared to the high longevity and low fecundity strategy of *Nesoryzomys* (Harris and Macdonald, *unpublished manuscript*).
4. Fluctuating environmental heterogeneity can create spatial and temporal niche opportunities that can facilitate the coexistence of competitors (Chesson & Warner, 1981). This has received empirical support from Wolff (1996) among others.

5.5 WHAT DOES THE FUTURE HOLD FOR *NESORYZOMYS*?

According to the proposed holistic explanation, under the prevailing conditions *Rattus* poses no *immediate* threat to *Nesoryzomys* survival. According to Harris and Macdonald (*unpublished manuscript*), however, the outlook for longer term survival (≥ 100 years) of *Nesoryzomys* is bleak. They say that *Nesoryzomys* security hinges on several independent but intertwined factors of local to global scale.

5.5.1 *RATTUS*

At a local scale, the presence of *Rattus* has a negative survival impact on *Nesoryzomys* (Harris and Macdonald, *unpublished manuscript*) but all the available evidence suggests that this survival impact is relatively weak. It should be acknowledged, however, that the work presented here and the work of Harris and Macdonald was generally carried out during a prolonged period of drought. If the same investigations were carried out under wetter conditions, which are characterised by high food availability, the findings may have painted a different picture. Indeed, the results of a recent food addition experiment show that *Rattus* respond numerically and physiologically to increased food availability and in doing so exert a negative survival impact on female *Nesoryzomys*. Furthermore, although *Nesoryzomys* gained weight in treatment grids the extra food did not enhance *Nesoryzomys* reproductive activity (Harris and Macdonald, *unpublished manuscript*). These findings emphasise the need to repeat these experiments under wet conditions, or at the very least, regularly monitor *Nesoryzomys* individual and population responses to the presence of *Rattus* under wet conditions.

5.5.2 *MUS*

Mus musculus is also present on Santiago and could have an important effect on *Nesoryzomys* survival. According to general relationships between body size and dominance

(Maynard-Smith & Brown, 1986), *Mus* is expected to be behaviourally subordinate to *Nesoryzomys*, nevertheless this factor may be insignificant given its other life history traits (Meehan, 1984). *Mus* is a classic *r* strategist whereby its response to favourable conditions is to maximise its mean growth rate (*r*). This life history strategy response was observed during a food addition experiment at La Bomba when *Mus* response increased dramatically on areas where the food was evenly distributed (Harris and Macdonald, *unpublished manuscript*). It follows that, although behaviourally subordinate to *Nesoryzomys*, *Mus*, by weight of numbers, could affect *Nesoryzomys* food acquisition by rapidly depleting food patches, although it should be observed that *Mus* is frequently considered an invertebrate specialist (e.g. Moro & Bradshaw 2002) and did not eat cactus fruit in palatability trials [pers. obs., although the sample size was small (n=3)].

5.5.3 CLIMATE CHANGE AND EL NIÑO

As emphasised by the food addition experiment carried out at La Bomba, both *Rattus* and *Mus* readily and rapidly responded to artificial increases in food availability, whereas *Nesoryzomys* did not (Harris and Macdonald, *unpublished manuscript*). It follows that the per capita effect of introduced rodents on *Nesoryzomys* would be much higher under prolonged periods of wet conditions and abundant foods, as characterised by the conditions of El Niño (Snell & Rea, 1999). Climate change forecasts predict an increased frequency of strong intensity El Niño events across the globe (Webster & Palmer, 1997) and by inference this would likely have important, but currently unpredictable, repercussions for *Nesoryzomys* at La Bomba (but see Harris and Macdonald, *unpublished manuscript*).

A more certain outcome of increasing strong El Niño events, is a detrimental impact to *Opuntia* populations across the Galápagos archipelago including La Bomba. Hamann (2004) has documented the short- and long-term impacts of past El Niño events on *Opuntia* survival and recruitment and has shown that the effects are severe and long-lived. According to the conclusions discussed here, a loss of cacti at La Bomba would

have a negative effect on *Nesoryzomys* survival, not least coupled with the increased availability of alternative foods accompanying the El Niño.

The consequences of periodic extreme climate conditions will be hard to quantify because reliable results are replicated results and most of these extreme events, including El Niño, are by nature long-term phenomena.

5.6 CONCLUSIONS

The future for *Nesoryzomys* appears bleak. Climate change, driven by global warming, seems likely to cause an increased frequency of El Niño events and since they appear to drive the major threats to *Nesoryzomys* survival perhaps the future of *Nesoryzomys* is in the hands of us all. In the meantime, however, steps can be taken to maximise the chance that *Nesoryzomys* will exist indefinitely including controlling or eradicating the invasive rodent species, *Rattus* and *Mus*, and preventing their reinvasion, but a discussion of their feasibility is beyond the scope of this thesis (interested readers are directed the thesis of D. B. Harris (2006)). However, one proposed plan to aid *Nesoryzomys* survival does not escape brief mention; the plan to translocate small populations of *Nesoryzomys* to islets around Santiago. While this measure might be necessary when considering a total eradication of *Rattus* and *Mus* from Santiago, the findings of this work (and countless others) emphasise the importance of considering species ecological requirements (e.g. Gerber *et al.* 2003). Although from the work presented in this thesis it could be argued that cacti are only important to *Nesoryzomys* in the presence of *Rattus* (or *Mus*?), there is no reason to believe that *Nesoryzomys* survival does not hinge on cacti in the absence of *Rattus*.

5.7 A COMMENT ON INVASION ECOLOGY

“...human-assisted invasions are effectively breaking down biogeographical barriers, and the resulting global mixing renders idle one of the most prolific means of generating biodiversity: isolation. If we cannot stop this McDonaldization of the biosphere, we stand to lose a substantial part of global biodiversity and may well find that we need variety not just as the spice of life — but for life itself.”

Lövei 1997

A recent vogue in the literature on invasive species and invasion biology is to question the concern of Invasion biologists for the spread and proliferation of invasive species (see Sax *et al.* 2005). While many of the paradoxes outlined in this flood of literature are watertight, it is the similarities underpinning these paradoxes that Invasion biologists capitalise on when faced with impact assessments. For example, many authors have lengthily pointed out that a biological invasion can be used as an opportunity to study the processes that underlie some rudimentary theories of community ecology (Sax & Brown, 2000) and yet these sorts of ecological studies have long been recognised as precursors to any control and eradication plan (Martin *et al.*, 2000; Kiesecker *et al.*, 2001). Rather than concentrating effort on reviewing such paradoxes, let us combine efforts towards tackling the problem of invasive species before it becomes too late. Let it not be forgotten that the rate of species introductions has reached ‘unnatural’ levels, for example, the complete insect fauna of the Hawaiian Islands arose from one successful colonisation every 50,000 - 100,000 years compared to the current rate of 15-20 insect species establishing each year (Beardsley, 1979 in Vitousek *et al.* 1997), nor that globally invasive species are causing substantial biodiversity loss at an ever increasing rate (e.g. Chapin *et al.* 2000). In view of these rate increases, prevention, control and eradication of invasive species should always remain the ultimate goals. After all, with an ever-increasing human population and associated border breaching, global change and land use intensification, the number of opportunities to study biological invasions at various stages of ‘succession’ is set to increase exponentially too...

Table 5.1: *Opuntia* species and characteristics from the Galápagos islands where endemic rodent species are known to have existed. † adapted from Wiggins and Porter (1971).

Island	<i>Opuntia</i> species	Tree	Volume (mm ³)			Endemic rodent species	Extant	<i>Rattus</i>
			Fruit †	Seed †	Total seed			
Santiago	<i>O. galapageia galapageia</i>	Y	5575	10	600	<i>N. swarthi</i>	Y	Y
Isabela	<i>O. echios inermis</i>	Y	36086	3.5	1050	<i>N.</i> } spp.*	N	Y
	<i>O. insularis</i>	N	36316	6	1200			
Fernandina	<i>O. insularis</i>	N	36316	6	1200	<i>N. narboroughi</i> <i>N. fernandinae</i>	Y	N
Santa Cruz	<i>O. e. gigantea</i>	Y	55983	3.5	1400	<i>N. darwini</i>	N	Y
	<i>O. e. echios</i>	N	35386	14	2800	<i>N. indefessus</i>		
San Cristobal	<i>O. megasperma orientalis</i>	Y	187526	133	6650	<i>O. galapagoensis</i>	N	Y
Santa Fé	<i>O. e. barringtonensis</i>	Y	138795	19	6688	<i>O. bauri</i>	Y	N

* Currently undescribed (see Steadman 1982)

5.8 FUTURE WORK

The following list outlines the areas of further work that have arisen from completing this thesis.

Search for other Galápagos Rice rat species

Nesoryzomys was only rediscovered after 4+ failed relocation attempts over 90+ years. The islands of the Galápagos are remote and inhospitable but nevertheless, a thorough search of them for other populations of ‘extinct’ Galápagos Rice rats should be a priority. Robert Dowler with the help of Felipe Cruz and Project Isabela continue to pursue this very deserving aim. Based on the findings presented here, arid habitats with or without invasive rats appear to be a good starting point. Furthermore, the presence of cactus and their productivity (fruit and seed volume) might also be considered an important search criterion (Table 5.1).

Experimental investigation of short-term El Niño effects

Santiago would be an excellent setting for an experimental investigation of the short-term effects of El Niño rains on the coexistence of the Santiago invaded rodent community. This project would summon knowledge of community ecology theory, invasion ecology, climate change and modelling and would output findings with theoretical appeal and worldwide application, not least in Galápagos which is predicted to see a rise in the frequency and intensity of El Niño events.

APPENDICES

APPENDIX A: HARRIS, GREGORY AND MACDONALD, 2006

DISCLAIMER: The following study was not wholly the work of the author of this thesis but the author substantially contributed to it. It is included here for ease of reference.

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COMMUNITY ECOLOGY

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. swarthy* activity patterns (spatial and temporal), and microhabitat partitioning. We found that *N. swarthy* 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. swarthy* did not vary with local density of *R. rattus*. However, pre-dawn and post-dusk *N. swarthy* 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. swarthy* 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 Demaraia 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).

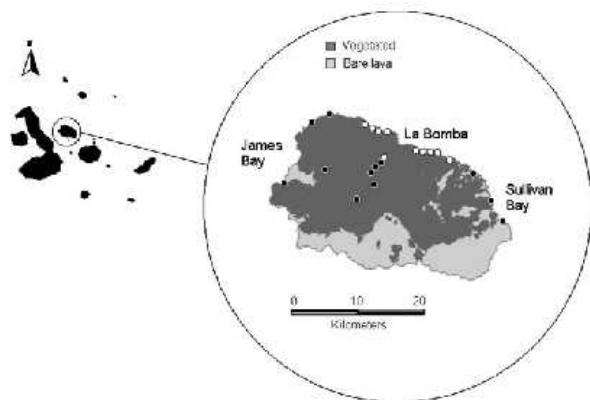
An unexpected opportunity to explore such a system has arisen between endemic rodents and introduced black rats in the Galápagos Islands following the rediscovery, in 1997, of a population of the endangered rice rat *Nesoryzomys swarthi* on the north-central coast of Santiago Island (Dowler et al. 2000). 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 (Brossel 1963; Niethammer 1964; Clark 1984). How-

ever, 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. swarthy* 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 km² 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 $23.95^{\circ}\text{C} \pm 0.14$ 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 Litoral (Coastal) Zone, Arid Zone, Transition Zone, Scalesia Zone, Zanthoxylum Zone, Miconia Zone and Fern-Sedge (Pampa) Zone (McMullen 1999). The Santiago rice rat (*N. swarthy*) 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. swarthy* have focused on southern and highland regions (Clark 1984; Dowler et al. 2000; CDRS, unpublished data) but have failed to find any *N. swarthy* 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. swarthy* (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. swarthy*, baited hair tubes were used to survey for the presence or absence of *N. swarthy* 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. swarthy* was maximised by surveying in August (2004), a predictably dry time of year (Snell and Rea 1999) when *N. swarthy* 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. swarthy*. 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 ($0^{\circ}11'10''S$, $90^{\circ}41'59''W$). 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; $406.4 \times 127 \times 127$ 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. swarthy* 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. swarthy* 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 \times width \times 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. swarthy* (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. swarthy* were tracked on the low density *R. rattus* grid and 12 *N. swarthy* 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 indicated 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. swarthy* only", "*R. rattus* only", "both species" or "neither species" over the 10 days. Fisher's 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. swarthy* 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. swarthy* 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). Micro-habitat 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. swarthy* 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. swarthy* (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. swarthy* 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. swarthy* 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. swarthy*-occupied sites (nine of nine) contained mature cacti and cactus density was estimable at five of these sites [mean cactus density: $0.00239/m^2 \pm 0.000622$ (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. swarthy* was positively correlated with cactus density ($r(6)=0.962, P=0.001$) 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. swarthy* 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. swarthy*. However, it was clear that the ratio of *N. swarthy* 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. swarthy*) and low (8 *R. rattus*:79 *N. swarthy*) black rat density areas confirming that the comparison of *N. swarthy* 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. swarthy* 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

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

<i>R. rattus</i> density	<i>N. swarthy</i> sex	<i>N</i>	% 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
		31	100	1.97	1.97	223
		48	100	1.55	1.55	218
High	Male	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
		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
		41	95	0.19	0.31	90
Low	Female	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		

N No. of fixes

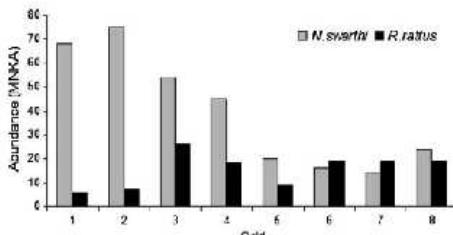


Fig. 3 Abundance (MNKA) of *N. swarthy* and *R. rattus* from live-trapping on four coastal (1–4) and four inland (5–8) grids at the start of the 2003 wet season (December 2002–January 2003)

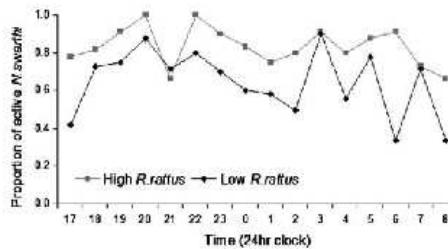


Fig. 4 The proportion of active individuals (*N. swarthy*) at hourly intervals (1700–0800)

active animals on high *R. ratus* 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. swarthy* 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. ratus* 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. ratus* is a subset (Fig. 5). This is probably due to the smaller sample of spooled *R. ratus*. 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).

Spatial distribution

The distribution of species between trap types (*R. ratus* only, *N. swarthy* only, *R. ratus* and *N. swarthy* 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. swarthy* is now restricted to a 14 km strip on the north-central coast of Santiago. There was no evidence

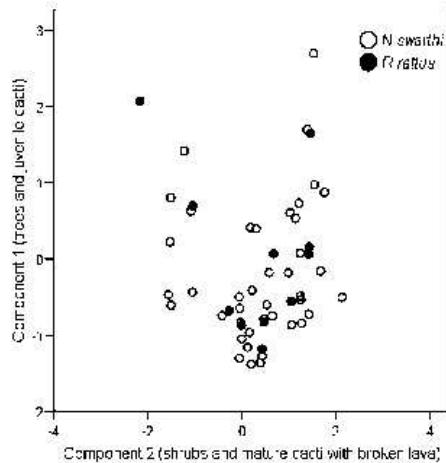


Fig. 5 Microhabitat use. Ordination plot of chosen spool route microhabitat data for the first two microhabitat components for *N. swarthy* (open symbols) and *R. ratus* (closed symbols)

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

Plant species/lava type	Component		
	1	2	3
<i>Bursera graveolens</i>	0.671	-0.178	-0.075
<i>Croton scouleri</i>	0.721	0.159	0.303
<i>Opuntia galapageia (juvenile)</i>	0.595	-0.001	-0.531
<i>Opuntia galapageia (adult)</i>	0.381	0.543	-0.355
<i>Clerodendrum molle</i>	-0.046	0.483	0.545
<i>Castela galapageia</i>	0.470	-0.429	0.518
<i>Lantana peduncularis</i>	0.264	0.485	0.208
<i>Scutia spicata</i>	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*)

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

	<i>N. swarthy</i> +	<i>N. swarthy</i> -	<i>P</i>
2002, coast (grid 2)			
<i>R. rattus</i> +	6	1	
<i>R. rattus</i> -	38	4	0.554
2002, coast (grid 4)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	27	8	
<i>R. rattus</i> -	9	5	0.476
2003, coast (grid 1)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	9	1	
<i>R. rattus</i> -	38	1	0.370
2003, coast (grid 2)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	5	1	
<i>R. rattus</i> -	42	1	0.232
2003, coast (grid 3)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	27	1	
<i>R. rattus</i> -	21	0	1.000
2003, coast (grid 4)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	34	0	
<i>R. rattus</i> -	15	0	Test invalid ^a
2003, inland (grid 5)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	13	6	
<i>R. rattus</i> -	20	10	1.000
2003, inland (grid 6)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	14	14	
<i>R. rattus</i> -	12	9	0.774
2003, inland (grid 7)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	9	20	
<i>R. rattus</i> -	7	13	1.000
2003, inland (grid 8)			
<i>N. swarthy</i> +			
<i>R. rattus</i> +	17	7	
<i>R. rattus</i> -	20	5	0.520

^a Grid 4, 2003 analysis was invalid as all traps were occupied by *N. swarthy*

of *N. swarthy* 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. swarthy* range contraction since *R. rattus* introduction, substantiating the need to analyse the *N. swarthy*-*R. rattus* relationship at the last apparent stronghold.

Given that *R. rattus* is larger, more aggressive and behaviourally dominant to *N. swarthy* (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. swarthy* 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. swarthy* in the high density *R. rattus* area compared to the low density *R. rattus* area.

Nevertheless, radio-tracking of *N. swarthy* 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. swarthy* 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. swarthy* 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. swarthy* 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. swarthy* 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. swarthy* and *R. rattus* have been sympatric up to 400 years (Patton et al. 1975; Morris 1983). By comparison, *R. rattus* and *N. indefexsus* 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. swarthy* 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. swarthy*. 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. swarthy* was correlated with cactus density and the proportion of mature cacti. This may reflect a positive relationship between consumer (*N. swarthy*) and preferred resources in this chosen habitat (Rosenzweig 1991). The importance of *Opuntia* cactus to *N. swarthy* is further supported by a lack of *N. swarthy* 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. swarthy*-*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. swarthy* 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. swarthy*. However, *N. swarthy* still appears able to occupy some suboptimal habitat in the presence of *R. rattus*. Within the Arid Zone at La Bomba, *N. swarthy* 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. swarthy* 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. swarthy* 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. swarthy* may be the superior, or exclusive, exploiter of the locally abundant endemic cactus, as suggested by the high *N. swarthy* 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. swarthy* 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. swarthy* 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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APPENDIX B: LA BOMBA PLANT SPECIES

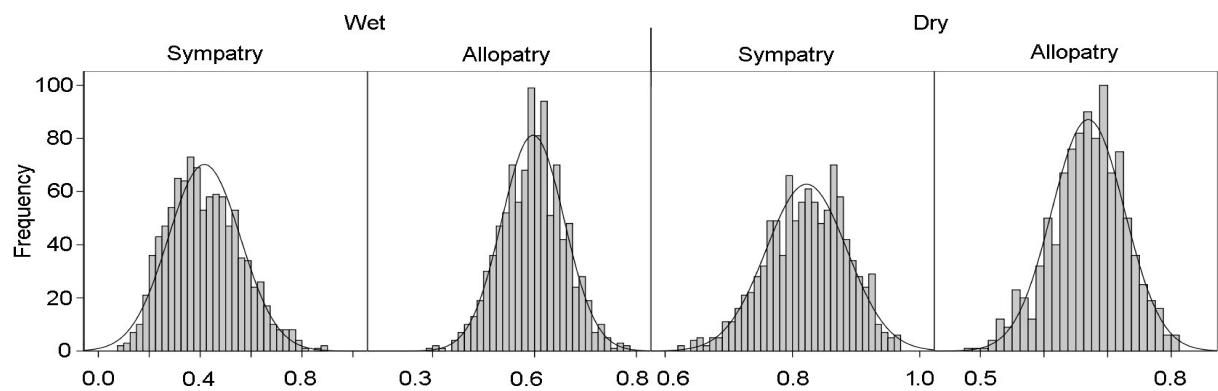
Table B: List of plant species (in alphabetical order) visited by spooled animals at La Bomba and their corresponding abbreviations used in the text

Species name	Abbreviation
<i>Acacia rorudiana</i>	Ac
<i>Boerhaavia caribaea</i>	Pfp
<i>Blainvillea dichotoma</i>	Blain
<i>Bursera graveolens</i>	Bg
<i>Castela galapageia</i>	Cg
<i>Cordia lutea</i>	Cl
<i>Clerodendrum molle</i> var. <i>molle</i>	Cm
<i>Croton scouleri</i>	Cs
<i>Desmodium procumbens</i>	Curl
<i>Evolvulus convolvuloides</i>	Evol
<i>unspecific grasses</i>	Grs
<i>Ipomea triloba</i>	Hrt
<i>Lantana peduncularis</i>	Lp
<i>Mentzelia aspera</i>	Ma
<i>Merremia aegyptica</i>	Merr
<i>Opuntia galapageia</i> var. <i>galapageia</i>	Og
<i>Porophyllum ruderale</i>	Poro
<i>Portulaca oleracea</i>	Port
<i>RLP</i>	RLP
<i>Sarcostemma angustissimum</i>	Sarco
<i>Scutia spicata</i> var. <i>pauciflora</i>	Ss
<i>Ser</i>	Ser
<i>Tephrosia decumbens</i>	Td
<i>Tetramerium nervosum</i>	Conc
<i>Tiquilia nesiotica</i>	Mat
<i>Trif</i>	Trif
<i>Vallesia glabra</i> var. <i>galbra</i>	Vg

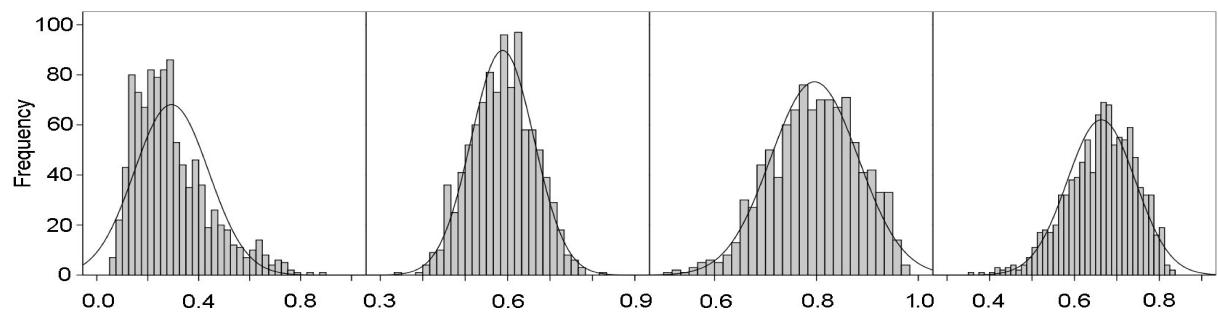
APPENDIX C: CACTUS FRUIT PALATABILITY TRIALS

To test whether either species could consume cactus fruit, individuals of both species were captured for use in captive palatability trials. Each night traps were set with a peanut scented rag and checked one hour after being set. Captured individuals were identified to species and examined for their sex, weight and reproductive condition. Each occupied trap was subsequently transferred to a plastic rodent-proof enclosure (57 x 36.5 x 30.5cm). Captive animals were offered cactus fruit as food and trialled for up to 8 hrs. Only mature fruit were used in the trials and care was taken to ensure that cactus fruit were of similar size and weight. After the period of captivity, each animal was presented with a ball of peanut butter and rolled oats before it was released at its point of capture. The enclosures were then inspected for cactus fruit remains. A total of 13 *Nesoryzomys* and 40 *Rattus* were trialled in cactus fruit palatability trials. In contrast to *Nesoryzomys* individuals that invariably ate the pulp and seeds, no *Rattus* individual ate any part of the cactus fruits offered. Furthermore, all *Rattus* (and *Nesoryzomys*) ate the post-trial bait mixture before their release, indicating a willingness to feed under the trial conditions.

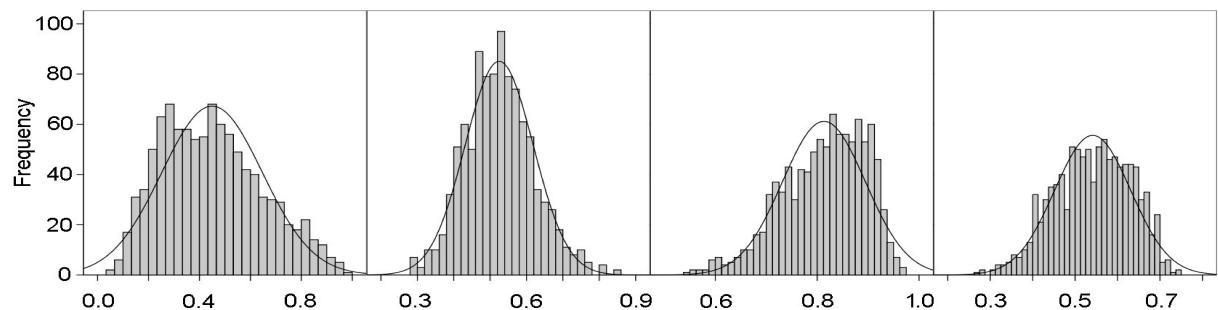
APPENDIX D: RANDOMISATION DISTRIBUTIONS



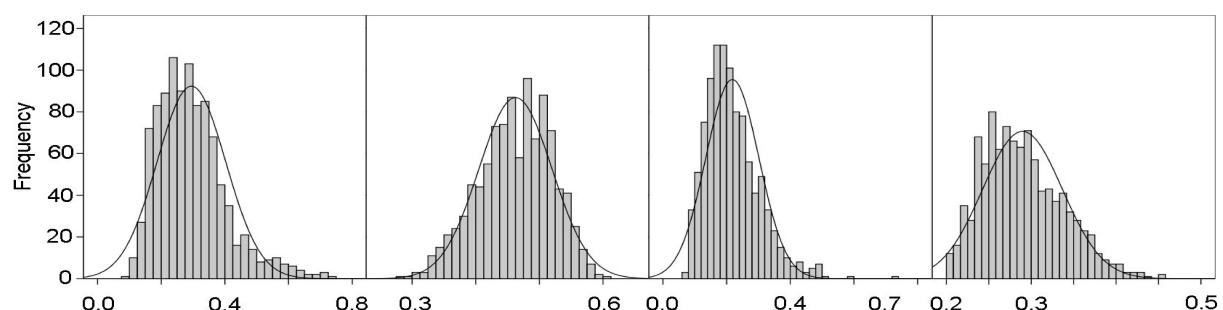
All *Nesoryzomys*



Male *Nesoryzomys*



Female *Nesoryzomys*



All *Rattus*

APPENDIX E: GARMIN GPS 12CXL ERROR ESTIMATION

Two handheld Garmin 12CXL GPS devices were used during the fieldwork undertaken for this work. Although most GPS waypoints that were marked were recorded for their relative positions, a short exercise was conducted to estimate the error of the devices.

METHOD

At hourly intervals for nine consecutive hours, GPS1 and GPS2 were taken to the exact same position and given 5 minutes to detect satellites before a waypoint was marked using each device. This procedure was replicated on a second day. The waypoints were plotted in ESRI ArcMap and the distance from mean centre waypoint to all other waypoints was calculated in Ranges 7. The estimated device error was taken to be the mean of the waypoint distances from the mean centre waypoint, itself averaged over both days. For GPS1 the error was an average of 1.5m and for GPS2 the error was an average of 2.46m.

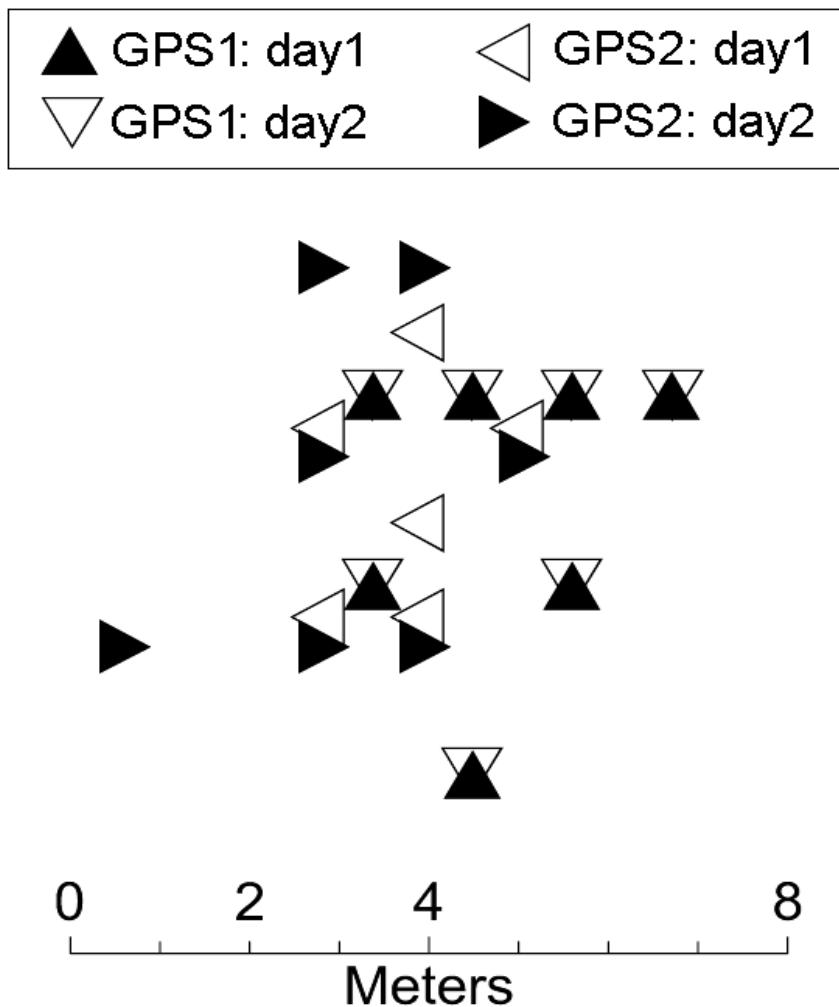
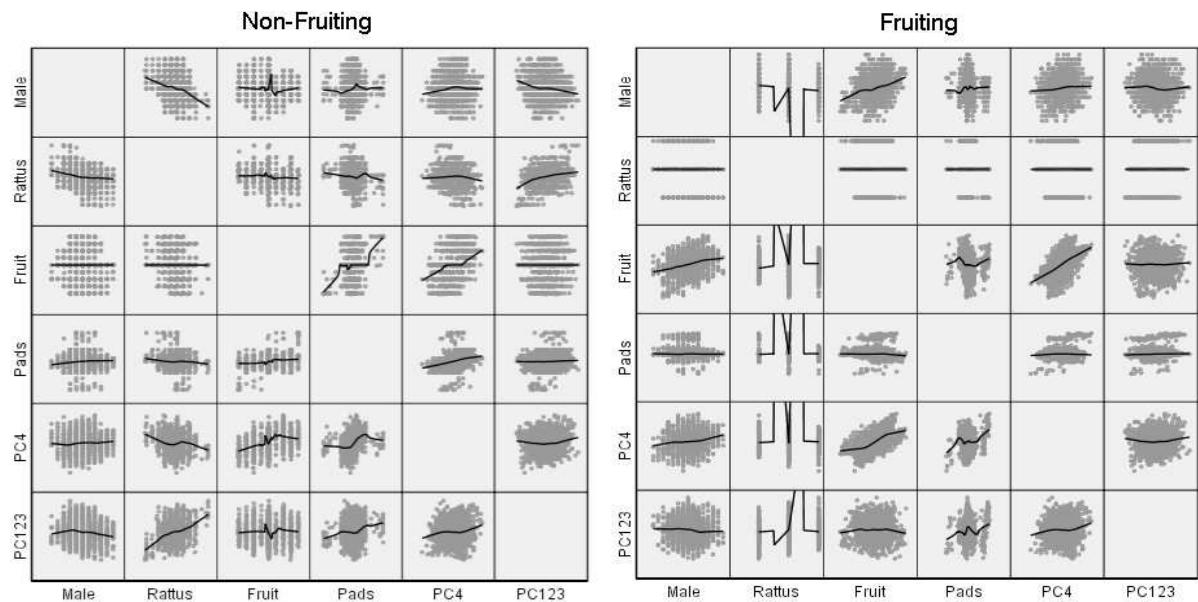


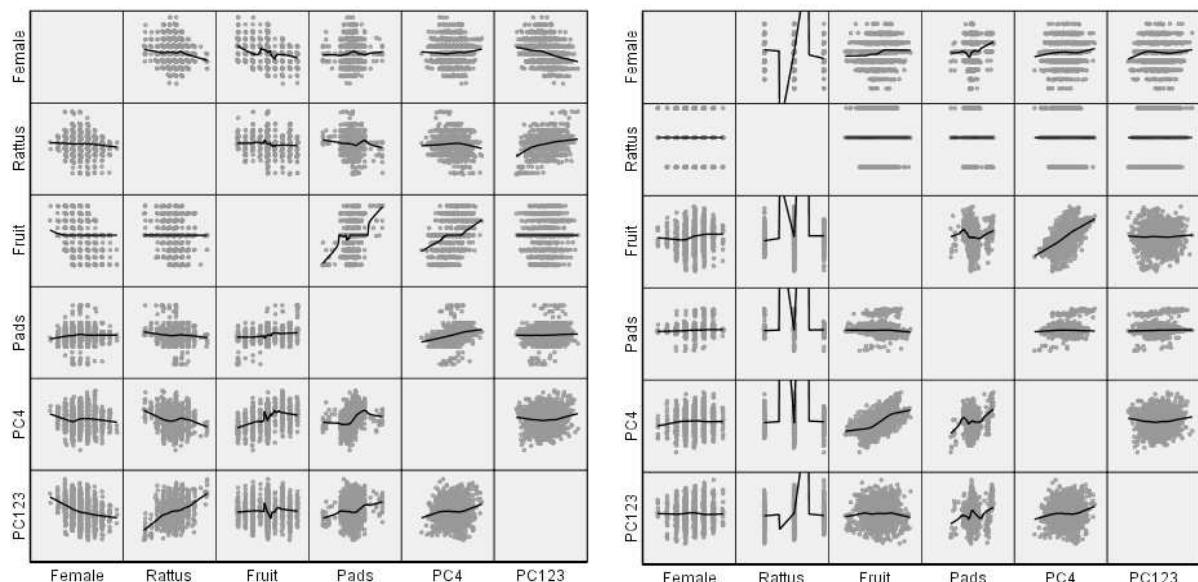
Table E: Distances from mean centre waypoint (MCW) to all locations and overall mean distance for each GPS device over two days. All distance (dist) are measured in metres (m) and are approximate

GPS	Day	Area (Ha)	MCW	Location of waypoint									Mean dist	Overall mean
				1	2	3	4	5	6	7	8	9		
1	1	0.001	44	04	23	25	43	44	45	46	45	44	1.50	1.50
		actual dist		4.00	2.24	2.24	1.00	0.00	1.00	2.00	1.00	0.00		
1	2	0.001	44	04	23	25	43	44	45	46	45	44	1.50	1.50
		actual dist		4.00	2.24	2.24	1.00	0.00	1.00	2.00	1.00	0.00		
2	1	0.001	22	20	23	42	44	62	63	23	62	22	2.33	2.33
		actual dist		2.00	1.00	2.00	2.83	4.00	4.12	1.00	4.00	0.00		
2	2	0.001	42	13	14	24	33	35	44	13	44	44	2.46	2.46
		actual dist		3.16	3.61	2.83	1.41	3.16	2.00	3.16	2.00	2.00		

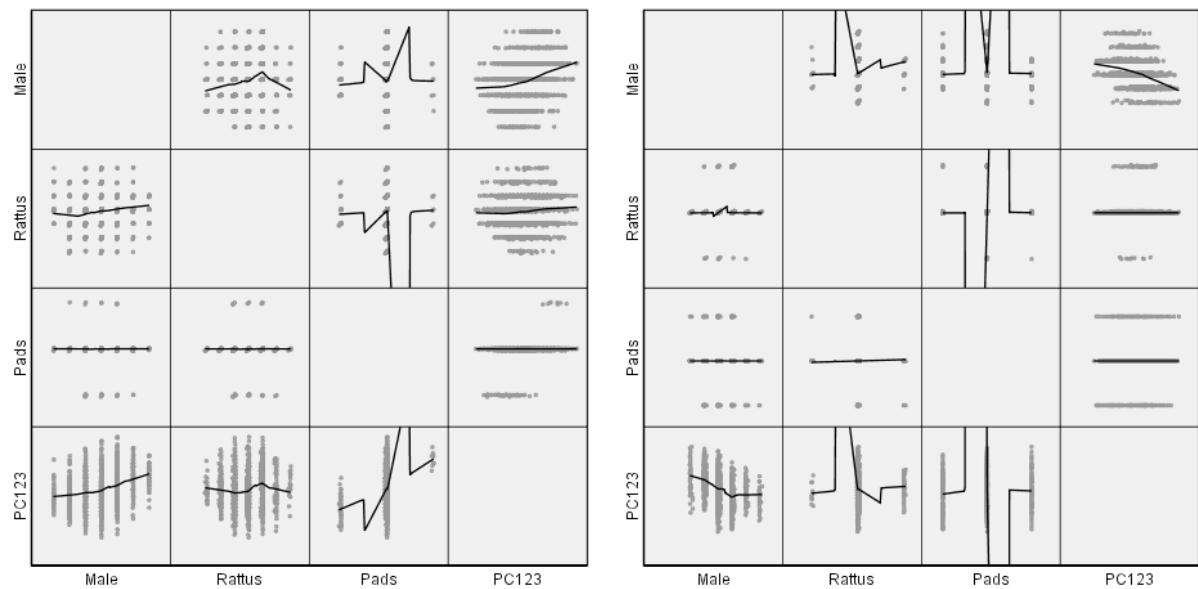
APPENDIX F: VARIABLE MATRIX SCATTERPLOTS



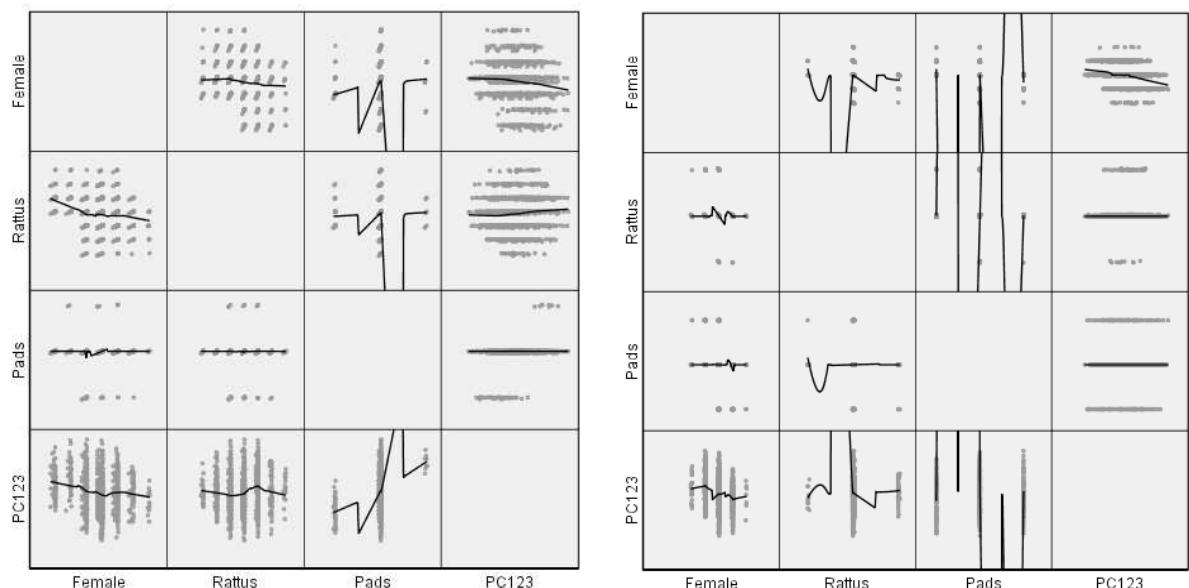
Male *Nesoryzomys*



Female *Nesoryzomys*



Male *Nesoryzomys*

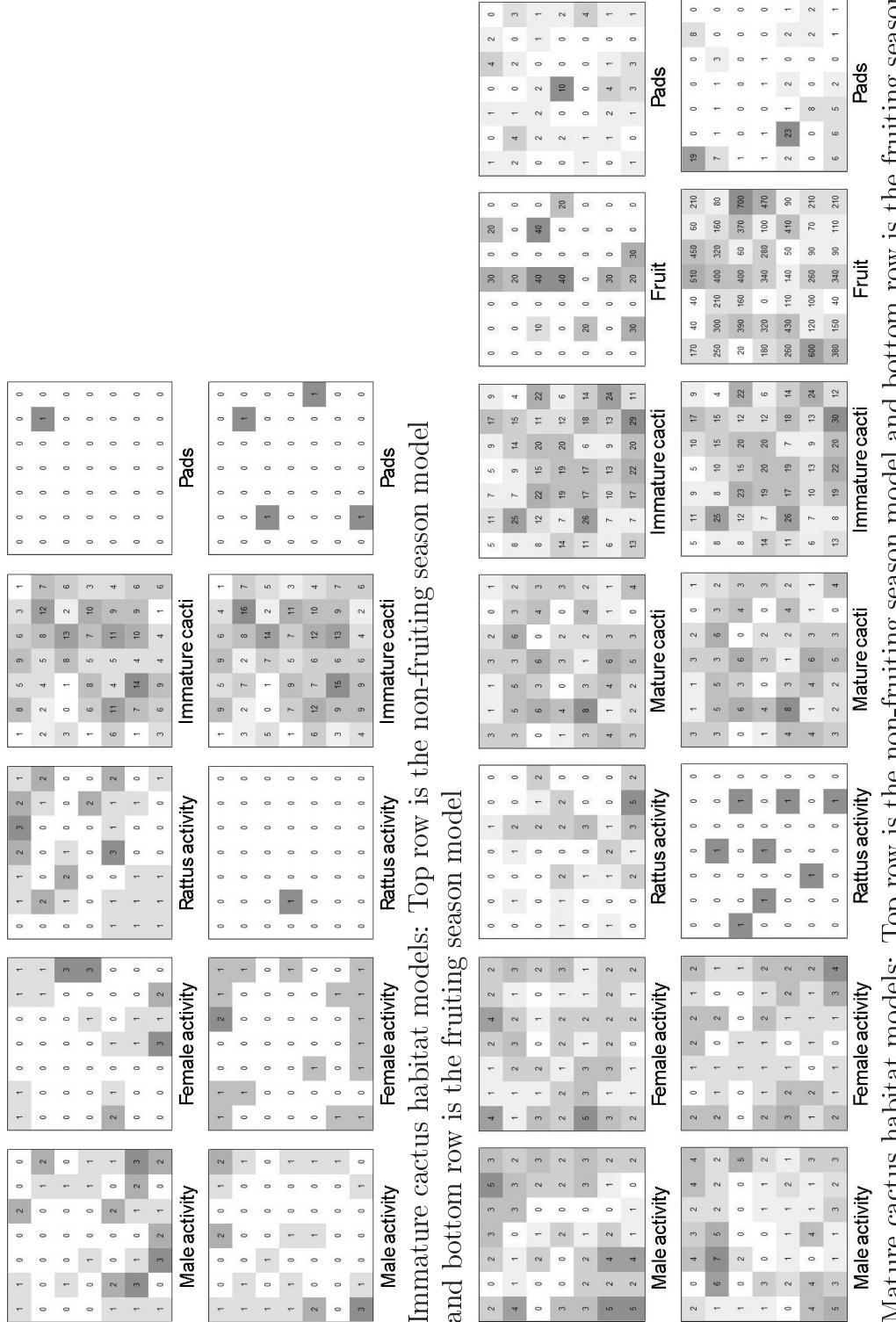


Female *Nesoryzomys*

Matrix scatter plots for each sex of *Nesoryzomys* with *Rattus* and each cactus variable in Mature (upper four plots) and Immature (lower four plots) cactus habitat in the Non-Fruiting and Fruiting seasons. Fit line is the Loess line using 50% of the data points and a probability function kernel (Epanechnikov).

APPENDIX G: MODEL DIAGRAMS

Variables presented in pictorial form where the darker the grid cell shading the higher the relative value of the variable. Grid cell values are given. Note the small values for *Rattus* in the fruiting season in both habitats and small values for pads in both seasons in the Immature cactus habitat.



Mature cactus habitat models: Top row is the non-fruiting season model and bottom row is the fruiting season model

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