

# The island syndrome and population dynamics of introduced rats

James C. Russell · David Ringler ·  
Aurélien Trombini · Matthieu Le Corre

Received: 20 October 2010 / Accepted: 13 May 2011 / Published online: 5 June 2011  
© Springer-Verlag 2011

**Abstract** The island syndrome predicts directional changes in the morphology and demography of insular vertebrates, due to changes in trophic complexity and migration rates caused by island size and isolation. However, the high rate of human-mediated species introductions to some islands also increases trophic complexity, and this will reduce the perceived insularity on any such island. We test four hypotheses on the role of increased trophic complexity on the island syndrome, using introduced black rats (*Rattus rattus*) on two isolated coral atolls in the Mozambique Channel. Europa Island has remained relatively pristine and insular, with few species introductions, whereas Juan de Nova Island has had many species introductions, including predators and competitors of rats, anthropogenically increasing its trophic complexity. In the most insular environments, the island syndrome is expected to generate increases in body size and densities of rodents but decreases in the rates of reproduction and population cycling. Morphology and reproduction were compared using linear regression and canonical discriminant analysis, while density and population cycling were compared using spatially explicit capture–recapture analysis. Results were compared to other insular black rat populations in the

Mozambique Channel and were consistent with predictions from the island syndrome. The manifestation of an island syndrome in rodents depends upon the trophic composition of a community, and may not relate to island size alone when many species additions, such as invasions, have occurred. The differing patterns of rodent population dynamics on each island provide information for future rodent eradication operations.

**Keywords** Body-size · Demography · Density · *Rattus rattus* · Spatially explicit capture–recapture

## Introduction

Changes in the ecological and evolutionary processes within insular populations following colonisation are collectively referred to as the island syndrome (Adler and Levins 1994; Blondel 2000). The island syndrome is driven by differences in island size and isolation, relative to other islands or continental mainlands, which occur through island size determining the level of habitat and trophic complexity, while isolation controls the rate of migration to and from islands. Changes that take place as part of the syndrome occur in morphology, demography and behaviour (Blondel 2000). Changes in body size and morphological traits, the ‘island rule’, have received particular attention (e.g. Pergams and Ashley 2001; Palkovacs 2003; Millien and Damuth 2004; Lomolino 2005; Meiri et al. 2008), and for mammals can depend on whether the species is a carnivore (Meiri et al. 2005) or herbivore (Raia and Meiri 2006), and how it interacts with its predators, prey or competitors.

Understanding what drives the island syndrome allows the impacts of future community and environmental

---

Communicated by Jörg Ganzhorn.

---

J. C. Russell · D. Ringler · A. Trombini · M. Le Corre  
ECOMAR, Université de la Réunion,  
15 avenue René Cassin, 97715 Saint Denis, France

*Present Address:*

J. C. Russell (✉)  
School of Biological Sciences, Department of Statistics,  
University of Auckland,  
Private Bag 92019, Auckland, New Zealand  
e-mail: j.russell@auckland.ac.nz

changes on islands to be more robustly predicted. This especially has application in the face of adaptation to widespread human-driven global change (Vitousek et al. 1997; Gillespie et al. 2008), and particularly the increase in species richness on islands due to biological invasions (Sax et al. 2002). The net increase in species richness that occurs on islands as a result of species introductions can be expected to increase the number of trophic interactions on an island (Zavaleta et al. 2000; Tylianakis et al. 2008). Ultimately, this might mean that, even when an island is completely isolated, insularity is not solely defined by area but also depends upon the species richness and identity of constituent community members, both native and introduced.

Rodent populations have been a valuable model for generating and testing theories of population dynamics (Krebs 1999; Hanski et al. 2001), but most studies come from continental systems (e.g. Singleton et al. 1999; but see Foster 1964; Gliwicz 1980) in temperate environments (Krebs 1999). For rodents, the island syndrome predicts that traits such as body size and density are expected to increase, whereas rates of reproduction and population cycling are expected to decrease (Adler and Levins 1994). Introduced rats (*Rattus rattus*, *R. norvegicus* and *R. exulans*) are distributed on over 80% of the world's archipelagos (Atkinson 1985) and have made important contributions to testing ecological hypotheses (Tamarin and Malecha 1971; Clark 1980; Cheylan et al. 1998; Harris and Macdonald 2007). Hypotheses from the island syndrome could be widely tested using introduced rats. Introduced rats are able to be compared, as a natural experiment, on a great variety of island areas, habitats, climates and trophic regimes, all factors known to affect their distributions and population dynamics (Russell and Clout 2004). Rat introductions have been relatively recent (usually within the past few centuries) and so comparisons can be made knowing that adaptations have occurred within ecological time-scales. Additionally, the genus *Rattus* is morphologically conservative (Rowe et al. 2011), and so differences in body morphology and condition are likely to reflect ecological adaptations to local environments. Studies of the ecological and evolutionary processes in introduced rat populations can also provide important data for conservation management, where factors such as predator size affect impacts on the recipient community (Jones et al. 2008) or where control programmes favour targeting rats during non-breeding periods at lowest densities (Innes et al. 2001).

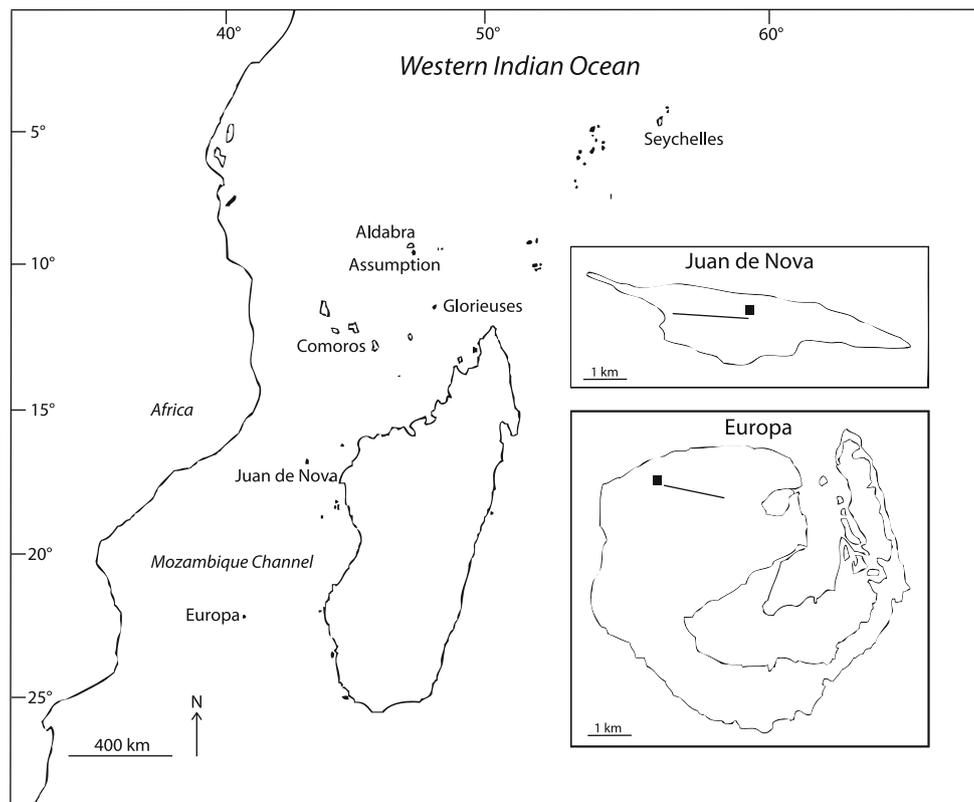
We consider two coral atolls in the Mozambique Channel which, despite their biogeographic similarities, are notable for their differing rodent population dynamics. Given both islands are fully isolated, we explore the effect of increased trophic complexity on the island syndrome, as

a result of a high rate of species introductions to one atoll. We compare Europa Island, which has remained relatively natural, with Juan de Nova Island, which has had its trophic complexity anthropogenically increased by the introduction of novel species including mammals, land birds and plants. For introduced mammals, any distance effect is factored out due to complete oceanic isolation, such that non-volant mammals cannot naturally disperse (Russell et al. 2004), while the sizes of both islands lie within a similar order of magnitude. We expect rats on the pristine island (Europa) to behave more like an insular population, and on the island with anthropogenically increased species richness (Juan de Nova) more like a continental population, regardless of original island size. We test four hypotheses of the island syndrome which we expect to differ predictably between the two islands; (1) morphology, (2) reproduction, (3) density and (4) cycling. The island syndrome predicts that on more trophically complex islands the number of inter- and intra-trophic interactions (e.g. predation and competition) will be greater. These interactions are expected to generate feedbacks limiting body-size and density in small rodent populations, while elongating breeding seasons and de-stabilising (fluctuating) population cycles (see Adler and Levins 1994). Following the island syndrome, we therefore expect rat morphology (1) and density (3) to be greater on Europa, whereas we expect reproduction (2) and population cycling (4) to be greater on Juan de Nova.

## Materials and methods

### Sites

Europa (2,223 ha; 22°21'S, 40°21'E) and Juan de Nova (561 ha; 17°03'S, 42°45'E) are two low-lying (<10 m elevation) coralline atolls in the Mozambique Channel (Fig. 1). Both islands are French overseas territories, part of the Îles Éparses ('scattered islands') managed by the Terres Australes et Antractiques Françaises (TAAF). The islands are subject to a productive cyclonic season in the Austral summer [November–April, mean 6-monthly cumulative rainfall 480.9 mm (2000–2008)] and a dry season in the Austral winter [May–October, mean 6-monthly cumulative rainfall 72.1 mm (2000–2008)]. Temperature is relatively constant [monthly mean 26.6°C, range 22.2–29.5 (2000–2008)], and monthly rainfall and temperature are strongly correlated between the islands ( $r = 0.88$  and  $0.95$ , respectively). On Europa, black rats are the only introduced mammalian predator, although they co-exist with goats (*Capra hircus*) and a small population (approx. 30 pairs) of barn owls (*Tyto alba*), all present since at least 1860. On Juan de Nova, cats (*Felis catus*),



**Fig. 1** Western Indian Ocean Islands with Juan de Nova and Europa inset. Buildings and airstrips are indicated

black rats and mice (*Mus musculus*) have all been present since at least the middle of the twentieth century. Both islands are classified as uninhabited, but since 1973, French military patrols (15 people) have been regularly stationed on each.

On Europa, the north-western area of the island about the airstrip is dominated by 850 ha of 5-m-high canopy dry indigenous forest composed of *Euphorbia stenoclada* and *Ficus marmorata*. At the northern point within this area is a small 96-ha historical sisal plantation (*Agave sisalina* and *Furcraea foetida*). The remainder of the island is 0.5-m-high plains of herbaceous *Sclerodactylon macrostachyum*, which periodically floods following tropical cyclones. Goats heavily browse the lower 2-m strata of forest. The large lagoon supports an additional 836 ha of various mangrove species and a 2.65-ha islet at the northern entrance, both habitats visited by rats. Settlement attempts in both 1860 and 1910 were not successful. Overall, the vegetation of the island remains native and less than 10% of the plant species are introduced (Le Corre and Jouventin 1997).

On Juan de Nova, the centre of the island consists of 15-m-high canopy forest composed of introduced *Casuarina equisetifolia*, as a result of historical guano mining and forest clearance. The eastern and western points are dominated by 0.5-m-high herbaceous *Sclerodactylon*

*macrostachyum* and 1.50-m-high *Tournefortia argentea*. Cats are present across the island at a density of approximately  $10 \text{ ha}^{-1}$  and mice are widespread and abundant. Many other species of land birds, invertebrates and plants have been introduced during the course of twentieth century inhabitation. Overall, the vegetation of the island has been almost completely modified by human activities and less than 20% of the plant species are native (V. Boulet, personal communication).

#### Sampling

On both islands, rats were kill-trapped during single sessions in the Austral summer (January–February) and winter (August–September) of 2007, and live-trapped during single sessions in two different habitats in the Austral summer (February–March) and winter (July–August) of 2008. Kill and live-trapping occurred in neighbouring, but not identical, locations. Live-trapping was undertaken in forest and grassland habitats with 49 cage traps (BTS–Mécanique; Manu, France) on a  $7 \times 7$  grid at 10-m spacing. Traps were baited and opened in the evening and checked every morning for 10 consecutive days. Each rat live-captured was sexed, weighed, ear-tagged and released. The ear-tag number and the position in the grid were recorded for each recapture event. After 10 days, all rats caught were

euthanized for subsequent laboratory dissection. Mice were also live-trapped on Juan de Nova by the same protocol.

### Morphology, reproduction and diet

Sex, body mass and four morphological traits (body, tail, foot and ear length), were recorded for all rats in both 2007 and 2008. Rats were dissected, and for males, epididym length and testis length and body mass were recorded. For females, the number of embryos and the presence of any uterine scars were recorded. Reproductive analysis was used to determine the mean body mass for classifying adults by sexual maturity. Island-specific sigmoidal cumulative sexual maturity curves (the proportion of sexually reproductive individuals by body mass) were constructed for both males and females with 95% confidence intervals. For males, the presence of enlarged testes ( $\geq 12$  mm), and for females, the presence of embryos or uterine scars were both clear indications of sexual maturity.

Linear regression of the four morphological traits on body mass was used to examine variation in body conditions (body mass was  $\log_{10}$ -transformed for normality). Any influence of island, year, season or sex on the four correlated rat morphological traits was assessed simultaneously with canonical discriminant analysis (CDA) and multivariate analysis of variance (MANOVA) for both the full and individual explanatory variable models (Krzyszowski 2000). Only adults were analysed to prevent biases induced from different age structures among groups. Data were standardised prior to analysis by subtracting means and dividing by standard deviations. Multivariate normality and homogeneity of group variances were visually assessed from marginal distributions and a reduced space plot of a principal components analysis (PCA). The Pillai–Bartlett test statistic was used to assess significance of our explanatory variables. Variation in sex-ratios and age structure (adult-juvenile ratios) among populations was tested for with two-tailed binomial tests. Morphological data were compared to other studies on islands in the Mozambique Channel: Glorieuse, Mayotte, Seychelles and Madagascar.

Diet was assessed using stomach content analysis of a subset of animals. We compared the frequency of occurrence of six different stomach items in rats: vegetation, insects, avian (feathers and eggshell), mammalian (hair), human refuse, and parasites. Differences among groups were tested for with analysis of variance (ANOVA).

### Density and cycling

Density ( $D$ ) was estimated using maximum-likelihood spatially explicit capture–recapture (ML SECR) implemented in program DENSITY (Borchers and Efford 2008) for

rats in 2008. Standard mark–recapture analysis estimates population size ( $N$ ) from a grid but density estimates are confounded by the inability to estimate the true area trapped. Distance sampling estimates the probability of detection of an individual as a function of distance from its range centre. By combining these two methods within a conditional maximum likelihood framework, the number of range centres of rats on and about the trapping grid can be estimated, and hence an estimate of density. We assume a Poisson distribution of range centres (i.e. random) with a hazard curve detection function parameterised by  $g_0$  (the probability of detection when trap and range centre coincide),  $\sigma$  (the spatial scale of the detection function) and  $b$  (the shape parameter). Removals in the population (i.e. accidental deaths during trapping) are assigned known capture histories of 0 with probability equals 1 following death. We implement a likelihood conditional on  $N$  in order to account for individual removals (i.e. accidental death during sampling). Although our live-traps usually only caught one individual, no likelihood solution is currently available for single-catch devices, but the multi-catch likelihood performs equivalently without bias, even in the presence of significant trap saturation (Borchers and Efford 2008). The ‘capture function’, which in many ways is related to an animal’s actual home-range (Borchers and Efford 2008), is estimated using a half-normal detection function and calculating the 95% circular probability density area of capture as

$$A = \pi(1.96\sigma)^2$$

When comparing density estimates, we use a conservative test where means which lie outside confidence intervals are considered statistically significant differences (Goldstein and Healy 1995).

## Results

We trapped and analysed 430 rats from both islands over 2 years (2007–2008). On Europa, rats were conspicuous at all except the hottest time of the day. In contrast, on Juan de Nova, rats were rarely observed, putatively a behavioural adaptation to cat presence.

### Hypothesis 1 (morphology) and 2 (reproduction)

Rats on both islands were in excellent body condition, with few ecto-parasites and no mange. Morphological traits explained only 58% of the variation in  $\log_{10}$  (body mass) (Table 1; adjusted  $r^2 = 0.58$ , all  $p < 0.05$ ). Morphological data appeared distributed multivariate normal with homogeneity of group variances. Island, year, season and sex were all significant explanatory variables in the full

**Table 1** Body mass, body and tail length measurements (mean and range) of adult black rats (*Rattus rattus*) (foot and ear length not presented)

Island	Year	Season	Sex	<i>n</i>	Body mass (g)	Range	Head and body length (mm)	Range	Tail length (mm)	Range
Europa	2007	Summer	M	8	159	129–225	177	165–205	236	210–255
			F	11	171	129–209	186	185–205	237	190–260
		Winter	M	31	172	127–238	193	163–228	212	190–235
			F	26	164	125–229	189	150–218	243	191–243
	2008	Summer	M	15	175	139–220	201	173–240	210	185–235
			F	12	157	129–198	201	182–215	213	202–230
		Winter	M	23	160	123–247	197	172–240	210	175–232
			F	11	153	126–179	200	177–225	217	183–235
Juan de Nova	2007	Summer	M	16	133	103–156	165	148–189	207	165–235
			F	12	119	95–155	153	135–170	215	200–240
		Winter	M	7	107	90–140	169	151–185	197	180–205
			F	4	104	93–113	166	149–185	187	166–210
	2008	Summer	M	32	113	88–175	176	155–202	199	180–220
			F	17	111	90–153	174	145–195	202	179–235
		Winter	M	13	116	91–140	187	175–198	201	185–215
			F	19	102	89–129	180	170–205	199	187–218

MANOVA model ( $p < 0.01$ ); however, in single explanatory variable models, sex was no longer a significant predictor of differences in morphology ( $p > 0.05$ ). In both the MANOVA and CDA, the greatest morphological difference among groups was attributable to island identity, as expected given only adults were analysed and adulthood was conditional on body mass. The first two CDA axes explained 90% of the variation in morphological traits. Axis one was negatively correlated with body, ear and foot length ( $r = -0.73, -0.57, -0.88$ ), while axis two was negatively correlated with tail length ( $r = -0.98$ ).

For all rats (including juveniles), there was no significant departure from a 1:1 sex ratio for any group comparisons (Table 2; all  $p > 0.05$ ). The proportion of adults in the population fluctuated non-significantly around an average of 0.6 on Juan de Nova (Table 2; all  $p > 0.05$ ), but on Europa was not constant around an average (Table 2; 2007 summer and winter  $p < 0.05$ ) fluctuating from 0.43 in summer to 0.73 in winter. Pregnancy was rarely recorded

(<10% of adult females) although placental scars were common in adult females (65% on Europa and 57% on Juan de Nova).

Size at sexual maturity differed significantly between islands. Sexual maturity in 80% of males was achieved on Europa at 122.1 g (95%CI 114.2, 128.8,  $n = 119$ ), while on Juan de Nova at 88.1 g (95%CI 80.9, 94.2,  $n = 103$ ). Sexual maturity of females occurred at approximately the same body mass as for males, although results are left-censored as the recorded indicator of sexual maturity (reproduction) may not occur immediately following maturity.

We analysed 220 stomachs from both islands, sampling both sexes and seasons, and calculated frequency of occurrence of food items (Table 3). On both islands, rat diet similarly consisted almost exclusively of vegetation and invertebrates. On Juan de Nova, no evidence of rats preying on mice was found from diet analysis. When considered alone, birds and their eggs were a significantly

**Table 2** Proportions of male and adult black rats

Island	Year	Season	<i>n</i>	Proportion male	Proportion adults
Europa	2007	Summer	47	0.45	0.40
		Winter	73	0.47	0.78
	2008	Summer	60	0.62	0.45
		Winter	50	0.54	0.68
Juan de Nova	2007	Summer	41	0.49	0.68
		Winter	18	0.50	0.61
	2008	Summer	82	0.57	0.60
		Winter	62	0.45	0.52

**Table 3** Frequency of occurrence of food items in black rat stomachs 2007–2008 (years and sexes pooled)

Island	Season	<i>n</i>	Vegetation (%)	Invertebrate (%)	Avian (%)	Mammalian (%)	Refuse (%)	Parasites (%)
Europa	Summer	43	97.7	97.7	0.0	0.0	9.3	48.8
	Winter	63	98.4	84.1	3.2	0.0	4.8	60.3
Juan de Nova	Summer	89	89.9	82.0	16.9	0.0	16.8	68.6
	Winter	25	100.0	72.0	0.0	0.0	12.0	60.0

**Table 4** Density estimates (per hectare) of black rats with 95% confidence intervals

Island	Habitat	Summer 2008		Winter 2008	
		Mean	95% CI	Mean	95% CI
Europa	Forest	65	49.7, 83.5	36	25.0, 49.4
	Grassland	15 <sup>a</sup>	– <sup>b</sup>	8	2.7, 18.4
Juan de Nova	Forest	26	16.5, 39.5	13	6.5, 22.7
	Grassland	20	9.8, 37.3	3	1.1, 7.3

<sup>a</sup> Estimate based on one capture session assuming fixed  $g_0$  and  $\sigma$  from winter 2008 (tropical cyclone ‘Jokwe’ locally eradicated rats)

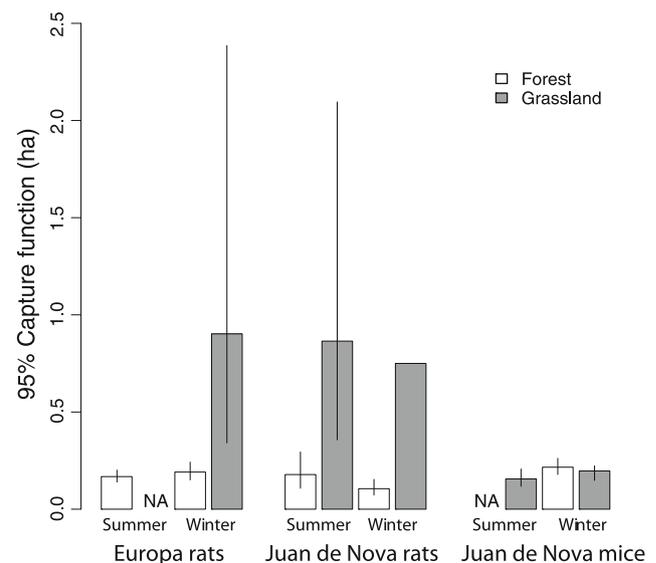
<sup>b</sup> Inestimable parameter

increased component of rat diet on Juan de Nova in summer ( $F_{1,3} = 49.23$ ,  $p < 0.01$ ), coinciding with the massive seasonal influx of sooty terns (*Onychoprion fuscatus*). However, this effect is swamped by no significant differences in the overall diet of rats with respect to sex, season or island when considering all food items simultaneously (all  $p > 0.05$ ). Endo-parasites were recorded in two-thirds of rat stomachs overall, with no significant differences between sex, season or island.

#### Hypothesis 3 (density) and 4 (cycling)

Estimated rat densities varied from 3 to 65 rats per hectare (Table 4). Rat density was significantly higher on Europa than Juan de Nova in forest habitat in both seasons, but relatively similar in grassland habitats. On both islands density increased significantly at least twofold from winter (dry season) to summer (wet season). Rat 95% capture functions were around 0.25 ha in forest and 1 ha in grassland, independent of season (Fig. 2). Density was not correlated with capture probability  $g_0$  ( $r = 0.42$ ,  $t_5 = 1.03$ ,  $p = 0.35$ ). Coefficients of variation varied greatly for our density estimates, and only fell under a generally acceptable threshold of 20% once rodent densities were above  $25 \text{ ha}^{-1}$ . Standard errors of density estimates were generally consistent and less than 10.

Although density increased on both islands in summer, on Europa, this was primarily due to an increase in the proportion of juveniles from seasonal summer breeding recruitment (Table 2). The absolute number of adults on Europa remained constant throughout the year. In contrast, on Juan de Nova, the proportion of adults was constant

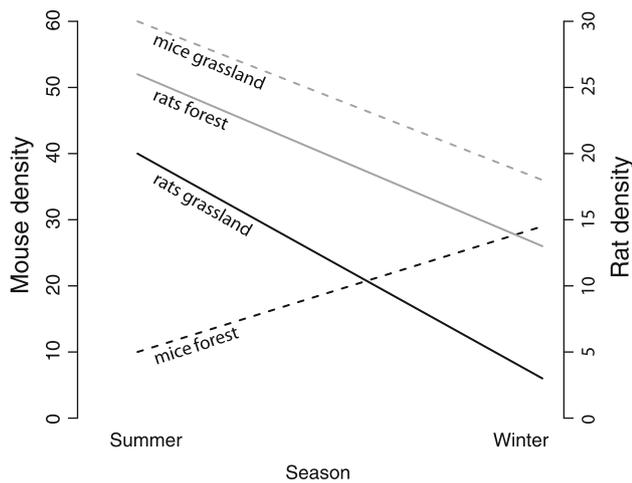


**Fig. 2** Rat (*Rattus rattus*) and mouse (*Mus musculus*) 95% probability capture functions with 95% confidence intervals (except Juan de Nova grassland rats in winter)

throughout the year (Table 2), suggesting an elongated breeding season and constant mortality across both adults and juveniles.

#### Mice

On Juan de Nova, mouse densities (mean  $\pm$  SE) behaved in a complex fashion (Fig. 3). In summer, mice were most abundant in grassland ( $60 \pm 10.9 \text{ ha}^{-1}$ ) compared to forest where densities were very low and inestimable ( $<10 \text{ ha}^{-1}$ ). In winter, mice density decreased in grassland habitats



**Fig. 3** Rat and mouse densities on Juan de Nova 2008 (generated from data in Table 4 and mouse densities, not presented)

( $36 \pm 6.1 \text{ ha}^{-1}$ ). However, conversely, density increased in forest habitats ( $29 \pm 5.1 \text{ ha}^{-1}$ ). Mouse 95% capture functions remained around 0.25 ha regardless of season or habitat (Fig. 2).

**Discussion**

Island syndrome

On Europa, black rats were larger, reproduced seasonally, at a higher density in forest habitat, and relatively stable number of adults across seasons in the population, but with cyclic density due to summer juvenile recruitment. They effectively behaved as a population with high insularity, following predictions from the island syndrome. On Juan

de Nova, black rats were smaller, reproduced throughout the year, at a lower density in forest habitat, and both juvenile and adult population size fluctuated seasonally. They effectively behaved more like a continental population, co-existing with predators and competitors, when compared with Europa. These differences occurred despite Europa being the larger island of the two. These results emphasise the dynamic inter-play between morphology, body condition, age-structure, density and reproduction on population demography. When any of these is considered in isolation, interpretation of population dynamics may be confounded.

Different founder population origins may also explain observed differences between islands (e.g. Patton et al. 1975); however, the genus *Rattus* is highly morphologically conservative despite genetic differentiation (Rowe et al. 2011).

Significant haplotype diversity exists in black rat populations of the Western Indian Ocean region, both within and among islands (Tollenaere et al. 2010), and analysis of black rats in the Îles Éparses (Europa, Juan de Nova and Glorieuse) shows they group within the Western Indian Ocean region black rats (Russell et al. 2011). These minor haplotype variations are unlikely to have generated island-specific founder effects, and black rats from different islands can share a common haplotype (e.g. Juan de Nova and Glorieuse) yet demonstrate island-specific adaptations (Table 5).

Body-size

The effect of insularity and latitude on body-size, the ‘island rule’, has received much attention, and changes in body-size of rodents have been variously attributed to

**Table 5** Black rat morphological data from other studies in the Mozambique Channel region

Island	Area (ha)	Year	n/sex	Body mass (g)	Head and body length (mm)	Cats	Mice	Source
Glorieuse	462	2008	11/M 19/F	123.0 123.0	177.0 172.0	✓	×	Bonnaud, unpublished
Mayotte	37,400	2007	43/M 57/F	142.0 130.0	184.0 176.0	✓	✓	Desvars et al., unpublished
Seychelles <sup>a</sup>	2–286	1999–2000	199/M 171/F	NA NA	167.2 158.0	✓	×	Hill et al. (2003, Table 3)
Madagascar (Andringitra Nature Reserve)	31,160	1993	9/M + 1/F	105.7	167.0	✓	✓	Goodman and Carleton 1996: Table 2
Madagascar (Ranomafana National Park)	41,600	2000	9/M	119.0	170.9	✓	✓	Miljutin and Lehtonen (2008, Appendix Table 1)

<sup>a</sup> Seychelle Islands: Curieuse (mice present), Denis (mice present), Félicité, Grand Soeur, Marianne, North, Thérèse

extrinsic (latitude, Yom-Tov et al. 1999; climate, Millien and Damuth 2004) and intrinsic (resource availability, Banks and Dickman 2000; predation, Norrdahl et al. 2004) factors, or trade-offs, among them (Palkovacs 2003). Because our islands shared similar climates and lie within the same biogeographic region, we do not believe extrinsic factors are likely explanations for differences in body condition. On Juan de Nova, intrinsic factors such as predation by cats, and to a lesser extent resource competition with mice, are likely to have created selective pressure limiting the body-size of rats. Predators can affect body-size not only directly through predation but also indirectly through altering the age-ratio of individuals in a population (Norrdahl et al. 2004; Bonnaud et al. 2008). In the absence of either predation or competition, rats are much larger on Europa. On neighbouring Mozambique Channel islands where black rats coexist with cats, and sometimes mice, body mass and length were similar to Juan de Nova as would be expected (Table 5). This decreasing body-size trend with trophic complexity appears globally consistent where black rats are also larger on islands where they lack predators and competitors in the western Mediterranean (Ventura and López-Fuster 2000; Michaux et al. 2002) and New Zealand (Harper et al. 2005; Harper 2006). These trophic interactions are important for determining the direction of body size change in insular mammals (Raia and Meiri 2006), but can depend on whether the species is carnivorous or herbivorous. We found omnivorous rats, which often function as a mesopredator (Russell et al. 2009), were intermediate to carnivores and herbivores, with body size being regulated by both resource base as well as interactions with competitors and predators.

#### Community regulation

On both islands, rat population dynamics were primarily driven by bottom-up processes associated with seasonal rainfall, but on Juan de Nova, top-down processes also played a subsidiary role. Bottom-up processes particularly affected body condition, juvenile recruitment, density in grassland habitat and population cycling. Summer precipitation increases vegetation and has flow-on effects to invertebrates and rodents, as found in other dry systems (Clark 1980; Brown and Ernest 2002; Stapp and Polis 2003). In the nearby Seychelles, introduced rats also undergo seasonal cycles in the absence of both native and introduced predators (Hill et al. 2003). Introduced rats are able to persist throughout prolonged dry periods (Barker and Adolph 1953), but rainfall-associated seasonal cycles in density and reproduction of black rats have been found on other tropical islands such as Hawaii (Tamarin and Malecha 1971) and the Galapagos (Clark 1980). Seabirds also play an important resource input role on islands

(Sánchez-Piñero and Polis 2000), but on Europa and Juan de Nova, they did not play a major direct role as prey items for rats.

Top-down processes associated with trophic complexity from strongly interacting predators and competitors (introduced cats and mice) particularly affected body size, maximum density in forest habitat, and mortality. Rats respond most rapidly to bottom-up processes (Krebs 1999; Harris and Macdonald 2007), but the presence of strongly interacting predators and competitors may dampen any bottom-up driven release (Ruscoe et al. 2006). However, on neighbouring Madagascar, the presence of competitively inferior species, such as endemic rodents, appears to have little impact on black rats (Ganzhorn 2003), as is also the case in the Galapagos (Harris and Macdonald 2007). On Juan de Nova, bottom-up-driven rat population increases, particularly in forest habitat, were dampened by top-down controls and did not reach the same densities as on Europa. Similar top-down dampening of bottom-up-driven rodent increases by strongly interacting introduced predators has been observed in New Zealand (Ruscoe et al. 2006). Cats on Juan de Nova consume more rats in winter when breeding sooty terns are absent, but also when rat density is otherwise lower due to seasonal effects (30% frequency of occurrence in winter compared to 20% in summer; Peck et al. 2008). This predation likely explains the elevated winter mortality, lower densities and elongated breeding season observed on Juan de Nova, but this level of top-down control was not able to prevent the substantial bottom-up-driven increase of rats in summer (at least a twofold increase in density on both islands). Continental cycles of small rodents can be driven by bottom-up resource inputs in dry environments (e.g. Brown and Ernest 2002) or top-down predation in high latitude environments (e.g. Hanski et al. 2001), although for the latter, these cycles are strongest when the predator is a co-evolved specialist (Hansson 1987). For generalist predators such as cats, population oscillations in prey are expected to be dampened, but we found the magnitudes of population oscillation were similar for both our populations.

#### Complex responses

On Juan de Nova, mice also apparently responded to bottom-up processes, but this was mediated by interactions with high-density rat competitors (Russell and Clout 2004; Caut et al. 2007; Harris and Macdonald 2007). As expected in grassland, where rat densities are overall lower, mouse density also increased in summer. However, in forest, mouse density conversely decreased in summer. Asymmetrical interspecific competition in summer with the higher density of rats in the forest could explain this, possibly forcing the inferior competitor to emigrate as

others have observed (Banks and Dickman 2000). In winter, when rat densities were lower, mice were only limited by resource availability. Which of these controls dominates appears to be determined by a threshold density of rats (on Juan de Nova, around 20 ha<sup>-1</sup>). The average range length of mice was also surprisingly high and similar to that of rats.

### Conservation implications

On Juan de Nova, rats fulfil a mesopredator role where they are an important food source of cats (the superpredator), especially over winter when the cats primary prey (sooty terns) are absent, but themselves appear to have very little impact on breeding sooty terns, as others have found elsewhere (Rodríguez et al. 2006; Hughes et al. 2008). These bottom-up-driven system dynamics conform to ‘hyperpredation’ and ‘competitor release effect’ identified by others on oceanic islands (Courchamp et al. 2000; Caut et al. 2007). Top-down-controlled ‘mesopredator release’ of rats on Juan de Nova, especially during the current cat eradication campaign (Peck et al. 2008), is unlikely to occur or impact seabirds (Russell et al. 2009).

The results of our study provide important guidance for rodent eradication planners, particularly on tropical islands where data are lacking on introduced rat population dynamics (Howald et al. 2007). On both islands, rat density displayed some level of seasonality, suggesting winter is the optimal time to target rats for eradication, when they are at their lowest densities. The eradication of introduced rodents should be seen as a medium-term priority for the ongoing conservation and restoration of these islands (Russell and Le Corre 2009), particularly on Europa, where the larger body size of rats mean they can threaten a greater variety of seabird prey species (Jones et al. 2008).

From the fundamental species–area relationship, Europa should have a greater number of species in its community. However, due to introductions of strongly interacting species with novel functional identities (e.g. mammalian predators; Blackburn et al. 2005), the number of strong trophic interactions is greater for introduced rats on Juan de Nova. We have shown that the presence of strongly interacting predators and competitors on Juan de Nova reduces perceived insularity, and that the island syndrome is likely to govern introduced rat population dynamics. Therefore, even when an island is completely isolated, its perceived insularity is not solely defined by area but also depends upon the species richness and identity of constituent community members. In essence, insularity remains in the eye of the beholding species.

**Acknowledgments** This research is part of the ALIENS programme funded by ANR biodiversity (ANR-05-BDIV-003-03) and MEDAD

programme “Ecosystèmes Tropicaux”. We thank the Préfet des Terres Australes et Antractiques Françaises (TAAF) for authorisation to work in the Iles Eparses, and the Forces Armées de la Zone Sud de l’Océan Indien (FAZSOI) for transport and occasional other logistical support. Thanks to the fieldworkers who trapped rats on all the islands, particularly Fabien Jan on Europa and Thibault Sauvaget on Juan de Nova. Data for Mayotte were kindly provided by Amélie Desvars, Michel Pascal and Gwenael Vourch (INRA–Institut National de la Recherche Agronomique). Thanks to Murray Efford for discussion on implementing ML SECR methods, Brian McArdle for discussion on multivariate methods and Lise Ruffino, Grant Harper, Elaine Murphy, Jörg Ganzhorn and two anonymous referees for comments on the manuscript.

### References

- Adler GH, Levins R (1994) The island syndrome in rodent populations. *Q Rev Biol* 69:473–489
- Atkinson IAE (1985) The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In: Moors PJ (ed) Conservation of island birds. International Council for Bird Preservation Technical Publication No. 3, Cambridge, pp 35–81
- Banks PB, Dickman CR (2000) Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. *Can J Zool* 78:1775–1783
- Barker JP, Adolph EF (1953) Survival of rats without water and given sea water. *Am J Physiol* 173:495–502
- Blackburn TM, Petchey OL, Cassey P, Gaston KJ (2005) Functional diversity of mammalian predators and extinction in island birds. *Ecology* 86:2916–2923
- Blondel J (2000) Evolution and ecology of birds on islands: trends and prospects. *Vie et Milieu* 50:205–220
- Bonnaud E, Vidal E, Zarzoso-Lacoste D, Torre F (2008) Measuring rodent incisors from scats can increase accuracy of predator diet studies. An illustration based on island cats and rats. *C R Biol* 331:686–691
- Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385
- Brown JH, Ernest SKM (2002) Rain and rodents: complex dynamics of desert consumers. *Bioscience* 52:979–987
- Caut S, Casanovas JG, Virgos E, Lozano J, Witmer GW, Courchamp F (2007) Rats dying for mice: modelling the competitor release effect. *Austral Ecol* 32:858–868
- Cheylan G, Granjon L, Britton-Davidian J (1998) Distribution of genetic diversity within and between Western Mediterranean island populations of the black rat *Rattus rattus* (L. 1758). *Biol J Linn Soc* 63:393–408
- Clark DB (1980) Population ecology of *Rattus rattus* across a desert-montane forest gradient in the Galápagos Islands. *Ecology* 61:1422–1433
- Courchamp F, Langlais M, Sugihara G (2000) Rabbits killing birds: modelling the hyperpredation process. *J Anim Ecol* 69:154–164
- Foster JB (1964) Evolution of mammals on islands. *Nature* 202:234–235
- Ganzhorn JU (2003) Effects of introduced *Rattus rattus* on endemic small mammals in dry deciduous forest fragments of western Madagascar. *Anim Conserv* 6:147–157
- Gillespie RG, Claridge EM, Roderick GK (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Mol Ecol* 17:45–57
- Gliwicz J (1980) Island populations of rodents: their organisation and functioning. *Biol Rev* 55:109–138

- Goldstein H, Healy MJR (1995) The graphical presentation of a collection of means. *J R Stat Soc A* 18:175–177
- Goodman SM, Carleton MD (1996) The rodents of the Reserve Naturelle Integrale d'Andringitra, Madagascar. *Fieldiana: Zoology (New Series)* 85:257–283
- Hanski I, Henttonen H, Korpimäki E, Oksanen L, Turchin P (2001) Small rodent dynamics and predation. *Ecology* 82:1505–1520
- Hansson L (1987) An interpretation of rodent dynamics as due to trophic interactions. *Oikos* 50:308–318
- Harper GA (2006) Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators. *NZ J Ecol* 30:321–333
- Harper GA, Dickinson KJM, Seddon PJ (2005) Habitat selection by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. *NZ J Ecol* 29:251–260
- Harris DB, Macdonald DW (2007) Interference competition between introduced black rats and endemic Galápagos rice rats. *Ecology* 88:2330–2344
- Hill MJ, Vel T, Shah NJ (2003) The morphology, distribution and conservation implications of introduced rats, *Rattus* spp. in the granitic Seychelles. *Afr J Ecol* 41:179–186
- Howald G, Donlan CJ, Galván JP, Russell JC, Parkes J, Samaniego A, Wang Y, Veitch CR, Genovesi P, Pascal M, Saunders A, Tershy B (2007) Invasive rodent eradication on islands. *Conserv Biol* 21:1258–1268
- Hughes BJ, Martin GR, Reynolds SJ (2008) Cats and seabirds: effects of feral Domestic Cat *Felis tigris* eradication on the population of Sooty Terns *Onychoprion fuscatus* on Ascension Island, South Atlantic. *Ibis* 150:122–131
- Innes JG, King CM, Flux M, Kimberley MO (2001) Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983–1987. *NZ J Zool* 27:57–78
- Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. *Conserv Biol* 22:16–26
- Krebs CJ (1999) Current paradigms of rodent population dynamics—what are we missing? In: Singleton GR, Hinds LA, Leirs H, Zhang Z (eds) *Ecologically-based rodent management*. ACIAR Monograph No. 59, Canberra, pp 33–48
- Krzyszowski WJ (2000) Principles of multivariate analysis: a user's perspective. Oxford University Press, New York
- Le Corre M, Jouventin P (1997) Ecological significance and conservation priorities of Europa Island (western Indian Ocean), with special reference to seabirds. *Rev Ecol* 52:205–220
- Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. *J Biogeogr* 32:1683–1699
- Meiri S, Dayan T, Simberloff D (2005) Area, isolation and body size evolution in insular carnivores. *Ecol Lett* 8:1211–1217
- Meiri S, Cooper N, Purvis A (2008) The island rule: made to be broken? *Proc R Soc Lond B* 275:141–148
- Michaux JR, De Bellocq JG, Sarà M, Morand S (2002) Body size increase in insular rodent populations: a role for predators? *Glob Ecol Biogeogr* 11:427–436
- Miljutin A, Lehtonen JT (2008) Probability of competition between introduced and native rodents in Madagascar: an estimation based on morphological traits. *Est J Ecol* 57:133–152
- Millien V, Damuth J (2004) Climate change and size evolution in an island rodent species: new perspectives on the island rule. *Evolution* 58:1353–1360
- Norrdahl K, Heinilä H, Klemola T, Korpimäki E (2004) Predator-induced changes in population structure and individual quality of *Microtus* voles: a large-scale field experiment. *Oikos* 105:312–324
- Palkovacs EP (2003) Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103:37–44
- Patton JL, Yang SY, Myers P (1975) Genetic and morphologic divergence among introduced rat populations (*Rattus rattus*) of the Galápagos archipelago, Ecuador. *Syst Zool* 24:296–310
- Peck DR, Faulquier L, Pinet P, Jaquemet S, Le Corre M (2008) Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel. *Anim Conserv* 11:65–74
- Pergams ORW, Ashley MV (2001) Microevolution in island rodents. *Genetica* 112–113:245–256
- Raia P, Meiri S (2006) The island rule in large mammals: paleontology meets ecology. *Evolution* 60:1731–1742
- Rodríguez C, Torres R, Drummond H (2006) Eradicating introduced mammals from a forested tropical island. *Biol Conserv* 130:98–105
- Rowe KC, Aplin K, Baverstock PR, Moritz C (2011) Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Syst Biol* 60:188–203
- Ruscoe WA, Norbury G, Choquenot D (2006) Trophic interactions between native and introduced animal species. In: Allen RB, Lee WG (eds) *Biological invasions in New Zealand*. Springer, Berlin, pp 247–263
- Russell JC, Clout MN (2004) Modelling the distribution and interaction of introduced rodents on New Zealand offshore islands. *Glob Ecol Biogeogr* 13:497–507
- Russell JC, Le Corre M (2009) Introduced mammal impacts on seabirds in the Îles Éparses, Western Indian Ocean. *Mar Ornithol* 37:121–128
- Russell JC, Clout MN, McArdle BH (2004) Island biogeography and the species richness of introduced mammals on New Zealand offshore islands. *J Biogeogr* 31:653–664
- Russell JC, Lecomte V, Dumont Y, Le Corre M (2009) Intraguild predation and mesopredator release effect on long-lived prey. *Ecol Model* 220:1098–1104
- Russell JC, Gleeson DM, Le Corre M (2011) The origin of *Rattus rattus* on the Îles Éparses, Western Indian Ocean. *J Biogeogr* (in press)
- Sánchez-Piñero F, Polis GA (2000) Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81:3117–3132
- Sax DR, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am Nat* 160:766–783
- Singleton GR, Leirs H, Hinds LA, Zhang Z (1999) Ecologically-based management of rodent pests—re-evaluating our approach to an old problem. In: Singleton GR, Hinds LA, Leirs H, Zhang Z (eds) *Ecologically-based rodent management*. ACIAR Monograph No. 59, Canberra, pp 17–29
- Stapp P, Polis GA (2003) Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos* 102:111–123
- Tamarin RH, Malecha SR (1971) The population biology of Hawaiian rodents: demographic parameters. *Ecology* 52:383–394
- Tollenaere C, Brouat C, Duplantier J-M, Rahalison L, Rahelinirina S, Pascal M, Moné H, Mouahid G, Leirs H, Cosson J-F (2010) Phylogeography of the introduced species *Rattus rattus* in the western Indian Ocean, with special emphasis on the colonization history of Madagascar. *J Biogeogr* 37:398–410
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecol Lett* 11:1351–1363
- Ventura J, López-Fuster MJ (2000) Morphometric analysis of the black rat, *Rattus rattus*, from Congreso Island (Chafarinas Archipelago, Spain). *Orsis* 15:91–102
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science* 277:494–499
- Yom-Tov Y, Yom-Tov S, Moller H (1999) Competition, coexistence and adaptation among rodent invaders to Pacific and New Zealand islands. *J Biogeogr* 26:947–958
- Zavaleta ES, Hobbs RJ, Mooney HA (2000) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol Evol* 16:454–459