

# Inflated population density of island antechinus: a case of allochthonous marine inputs leading to increased food availability?

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**Abstract.** Resource availability and other processes that affect maintenance, growth and decline of animal populations are central to ecology and conservation. This study quantified features indicative of population fitness and the availability of food resources for island and mainland populations of an insectivorous marsupial, the swamp antechinus (*Antechinus minimus*). The aim of the study was to test the hypothesis that colonial seabirds increase productivity of island habitats, ultimately providing greater food resources. The study found that antechinus biomass density was 4–13 times greater on the island site compared with the mainland site and was associated with higher recapture rates, suggesting that more individuals were surviving on the island during spring and summer months. An index of antechinus food availability (abundance and biomass of invertebrates) was also higher on the island site. Island antechinus also accessed marine food subsidies, in the form of seabird carrion, during the energetically demanding post-weaning growth period in spring and summer. Furthermore, based on soil nutrient and stable isotope analyses, there was strong evidence of nutrient enrichment from marine sources in the island ecosystem, commonly linked to increased productivity. Therefore, greater antechinus biomass and abundance on offshore islands are likely to be, in part, due to greater survival caused by higher availability of food resources.

**Additional keywords:** dynamics, ecology, productivity, seabirds, small mammal, stable isotope.

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## Introduction

The relative effects of resource availability, its partitioning and other processes that affect the maintenance, growth and decline of populations are central to ecology and conservation. Both resource availability and consumer density are considered to be a strong function of primary productivity. Generally, areas of high primary productivity provide sufficient resources to support large populations of consumers, whereas in areas of low primary productivity there are fewer resources and therefore fewer consumers (Persson *et al.* 1996).

Transported energy and nutrients from one ecosystem have been shown to increase the productivity of adjacent ecosystems (Polis *et al.* 1997; Spiller *et al.* 2010). A common instance where such divergent productivity occurs is between islands and neighbouring mainland habitats (Polis and Hurd 1996). Consumers living in terrestrial island habitats are known to take advantage of allochthonous resources that originate in more productive aquatic ones, and these inputs may subsidise consumer populations, permitting higher population densities than could be supported by terrestrial resources alone (Anderson and Polis 1999; Stapp and Polis 2003; Barrett *et al.* 2005; Pafilis *et al.* 2009). However, island consumers also generally have

fewer competitors and relaxed predation (Adler and Levins 1994) and it has been proposed that insular vertebrate populations may increase to such an extent that food may become more limiting than on the mainland (Case 1978).

Colonial seabirds and seals are powerful vectors of marine nutrients and can significantly increase the productivity of island ecosystems (Gillham 1960; Polis *et al.* 1997; Farina *et al.* 2003; Caut *et al.* 2012). Seabirds, in particular, provide nutrients, in the form of guano, discarded prey, egg remains and carcasses, which can increase greatly the concentration of nutrients in the soil and plant productivity of colony areas (Gillham 1960; Smith 1978; Anderson and Polis 1999; Bancroft *et al.* 2005; Fukami *et al.* 2006; Jones 2010). In turn, this can lead to an increase in the availability of food resources for terrestrial vertebrates such as lizards (Markwell and Daugherty 2002; Barrett *et al.* 2005; Pafilis *et al.* 2009) and small mammals (Drever *et al.* 2000; Stapp 2002; Stapp and Polis 2003; Wolfe *et al.* 2004).

The swamp antechinus (*Antechinus minimus*), a small (30–80 g) insectivorous marsupial, exhibits divergent interpopulation features between island and mainland sites (Sale *et al.* 2008, 2009). Populations on the mainland of Australia occur at low densities (typically below 10 animals ha<sup>-1</sup>)

in coastal localities from Wilsons Promontory in Victoria to Robe in South Australia (Menkhorst 1995; Bachmann and van Weenen 2001; Wilson *et al.* 2001). These contrast with high-density populations (often exceeding 100 animals  $\text{ha}^{-1}$ ) that occur on small islands in Bass Strait (Wainer 1976; Sale *et al.* 2006). Greater survival due to higher food availability on these islands has been proposed as one factor contributing to these large differences in population density (Sale *et al.* 2006). However, resource availability for the swamp antechinus has not been calculated nor have comparisons of population features indicative of a resource-rich environment been made (e.g. survival, seasonal mass) for island and mainland habitats.

This study tested the hypothesis that colonial seabirds increase productivity on Kanowna Island, providing greater food resources and ultimately influencing the insular population of the swamp antechinus. The three main aims of the study were: (1) to investigate features indicative of a subsidised population, such as population size, minimum survival, recruitment, animal movements and seasonal body mass; (2) to quantify invertebrate resource availability and small mammal biomass to assess resource availability and consumer density at each site; and (3) to examine whether nutrient enrichment from marine sources occurs on the island using soil nutrient testing and stable isotope analysis.

## Materials and methods

### Study sites

Two sites (one mainland and one island) were used (Fig. 1). The mainland site was on a coastal plateau (Urquhart Bluff) in the eastern Otway Ranges, ~100 km south-west of Melbourne, Victoria (38°26'S, 144°08'E). Surface sediments (Angahook Formation) at this site consist of shallow marine to coastal plain deposits of sandstone, conglomerate, shale, basalt and pyroclastic outcropping in cliff areas, likely to be formed during the Quaternary period. The soils are texture contrast Chromosols and Sodosols and gradational texture Dermosols. The plateau contains a diverse mosaic of vegetation communities consisting of low heathlands dominated by mid-storey species, including Australian oak (*Eucalyptus obliqua*), prickly tea-tree (*Leptospermum continentale*) and understory species, such as thatch saw-sedge (*Gahnia radula*) and heath tea-tree (*L. myrsinoides*). Mean annual rainfall for the region is 600–800 mm and drought conditions were apparent during the period of the study. The site has not been burnt since the Ash Wednesday fires in 1983. Although the site was located within 400 m of the ocean, there was no history of nesting seabirds at the site.

The island site was on Kanowna Island (part of the Anser Island Group) located in northern Bass Strait 5 km south-west of Wilsons Promontory (39°09'S, 146°18'E). The geology of the site consists of Palaeozoic granites and deep Quaternary sand deposits with resulting coarse-grained sandy soils with varying amounts of incorporated organic matter. Vegetation consists predominantly of short tussock grassland (*Poa poiformis*) with smaller patches of low heath (<2 m high) dominated by coastal tea-tree (*L. laevigatum*), coastal beard heath (*Leucopogon parviflorus*), seaberry saltbush (*Rhagodia baccata*) and white correa (*Correa alba*). The island experiences maritime

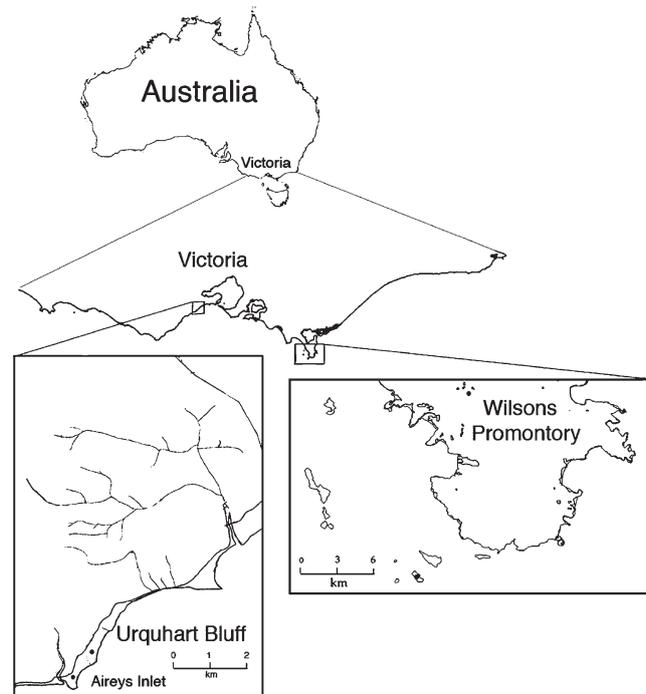


Fig. 1. The study sites located in Victoria with inlays of the eastern Otway Ranges and Wilsons Promontory.

conditions and is frequently exposed to strong south-easterly winds. Mean annual rainfall at the nearest weather station, Wilsons Promontory Lighthouse (#085096, Bureau of Meteorology) since 1873, was 1052 mm; however, orographic effects of the mainland range mean that rainfall on the island is considerably lower. Annual rainfall in the years 2003, 2005, 2006 and 2007 was below average, and 2004 received slightly above average rainfall. Over 100 000 pairs of burrow-nesting seabirds are present on Kanowna Island from November to March each year, together with a breeding colony of 15 000 fur seals (Kirkwood *et al.* 2010).

### Animal capture and handling

Elliott aluminium traps (100 × 100 × 300 mm) (Elliott Scientific, Upwey, Victoria, Australia), baited with a mixture of rolled oats, peanut butter and golden syrup, were used to capture animals. Each site (~1.5 ha) consisted of a similar trapping design of 100–150 traps positioned 10–15 m apart in a rectangular pattern. Captured animals were marked using a pattern of nicks along the ear margin for identification, weighed ( $\pm 0.5$  g) and measured ( $\pm 0.1$  mm). Trapping was conducted at four life-history stages: before breeding (autumn, April to June), during lactation (winter, August to September), during weaning (spring, November to December), and during the growth period (summer, January to March). Field data collected from 2005 to 2007 were supplemented with data on body mass and population features incorporated from previous work (Sale *et al.* 2006, 2008; B. A. Wilson, unpubl. data).

The direct enumeration of the number of individuals captured was used to obtain estimates of seasonal population size of the swamp antechinus (and other small mammals). Direct

counts of individuals are acknowledged as underestimates but have been found to be relatively robust indices when comparing populations within species (Hilborn *et al.* 1976; Slade and Blair 2000). Minimum survival, defined as the proportion of animals that were recaptured in the following season, was calculated for the duration of the study. During spring, minimum survival of juveniles was estimated as the proportion of juveniles captured from the total number of pouch young counted during winter. Available data (2001–07 for the mainland and 2003–07 for the island) were pooled for both sites. This was undertaken to reduce erroneous estimates of survival based on small numbers of animals on the mainland and to increase the likelihood of sound site-specific estimates of survival. Recruitment was assessed seasonally over this same period by comparing the proportion of new individuals (both male and female) to the number of resident (marked) individuals.

Given that the biomass of animals per unit area more accurately reflects total energy requirements of the population rather than animal numbers only, the total biomass of small and medium-sized mammals (both insectivorous and herbivorous) was estimated at both sites. This was calculated seasonally at each site as the mean total mass of all individuals present (per hectare) for each species. Although herbivorous small mammals are unlikely to compete directly for food resources with the insectivorous swamp antechinus, they were included in the analysis as they may compete for habitat (e.g. nest sites).

The average distance between recapture locations can be used as an index of animal movement and home-range size (Slade and Russell 1998), which may be influenced by resource availability. Therefore the average distance between recapture locations of individuals was compared for both sites between 2005 and 2007 for both males and females.

A linear mixed model was used to compare body mass using site, gender and season as main factors with interactions between these factors also performed. Two sample *t*-tests were used to compare average distance between recapture locations, as well as the frequency of occurrence of, and the number of individuals within, different arthropod groups, for the island and mainland habitats.

#### *Soil nutrient analysis and prey availability*

Soil nutrient levels were tested from the A horizon (the top 10 cm of surface soil) during November 2005 at each site. Approximately 250 g of soil was collected from 15 soil cores (10 cm deep  $\times$  2.5 cm diameters) at random points within a 5 m  $\times$  5 m quadrat and combined into a composite sample. Ammonium and nitrate N concentrations were measured using a Lachat Flow Injection Analyser (Pro-Tech Group, Coolumb Beach, Queensland, Australia) (Searle 1984). Available phosphorus and potassium were calculated using the Colwell method (Rayment and Higginson 1992). Extractable sulfur was extracted in 0.1 M KCl at 40°C and measured using inductively coupled plasma spectrometry (Blair *et al.* 1991). The percentage of organic carbon in the soil was measured using the techniques outlined by Walkley and Black (1934). Electrical conductivity, and pH in calcium chloride and in water were measured using the methods of Rayment and Higginson (1992). Comparisons of

soil nutrient concentrations between the island and mainland sites were undertaken using Mann–Whitney U-tests.

Pitfall sampling is commonly used to estimate invertebrate abundance and potential food availability for insectivorous mammals (Stratham 1982; Gilfillan 2001; Miller *et al.* 2003; Allison *et al.* 2006). This method provides a useful index of food availability for the swamp antechinus, since surface-active arthropods contribute most to their diet (Allison *et al.* 2006; Sale *et al.* 2006). Pitfall traps (15–20) were set 10 m apart within each site during each season. Traps consisted of embedded 250-mL cylindrical plastic containers with their rims sitting flush to the surface soil. A plywood lid was placed 40 mm above each trap to minimise disturbance by larger animals. Each trap contained a solution of 50 mL ethanol and 70% glycol. Pitfall traps were set over four nights and captured invertebrates were transferred into vials containing 70% ethanol. Individual arthropods from pitfall traps were counted and sorted to Order then oven-dried at 50°C. The overall dry biomass of each pitfall trap was weighed to the nearest  $\pm 0.01$  g.

Because pitfall sampling measures only the abundance of active surface-dwelling invertebrates, there are limitations in using pitfall sampling in isolation (Greenslade 1964; Luff 1975). Soil sampling was also undertaken to estimate the relative abundance of ground-dwelling invertebrates at each site. Soil samples, consisting of two soil volumes, measuring 250 mm  $\times$  250 mm to a depth of 100 mm, were collected and sieved onto a white sheet, and the invertebrates collected and stored in ethanol. Because the island site is a nesting habitat for numerous burrowing seabird species, repeated soil sampling for ground-dwelling invertebrates was not undertaken to avoid disturbing the site and damaging nesting burrows. Consequently, comparisons of the number of ground-dwelling invertebrates between sites were limited to the spring of 2005. Invertebrates occupying the shoots and roots of tussock grasses were not sampled to minimise disturbance to the site.

Pooled measures of invertebrate availability (biomass and abundance) were used as seasonal estimates of total food availability. Data for the arthropod biomass and the number of invertebrates per pitfall trap were log-transformed because of the variances between groups. Transformed data were compared using two-way analysis of variance (ANOVA) for comparisons of site and season. Seasonal comparisons of mean invertebrate biomass between sites (island and mainland) were undertaken using l.s.d. (least significant difference) mean separation tests (Steel and Torrie 1960). Two-sample *t*-tests were used to compare the frequency of occurrence and abundance of arthropod groups at each site.

#### *Stable isotope analysis*

The stable isotope ratios  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  (expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) are widely used to investigate trophic relationships within ecosystems (Peterson and Fry 1987). In terrestrial systems, plants differ in  $\delta^{13}\text{C}$  depending on the photosynthetic pathway.  $\text{C}_3$  plants have relatively low  $\delta^{13}\text{C}$  ( $< -28\%$ ) compared with  $\text{C}_4$  and CAM plants ( $-12$  to  $-13\%$ ; Peterson and Fry 1987).  $\delta^{13}\text{C}$  based on marine phytoplankton ( $-19$  to  $-24\%$ ) are intermediate between the two terrestrial pathways (Mizutani and Wada 1988; Anderson and Polis 1998; Stapp *et al.* 1999). The presence of

seabird guano-derived N can be clearly distinguished from terrestrial sources of N by the  $\delta^{15}\text{N}$  of plants and their consumers, because soils fertilised by seabird guano are enriched with  $\delta^{15}\text{N}$  (Stapp *et al.* 1999). Plant, arthropod and vertebrate tissues were collected on both the island and mainland sites to determine whether marine nutrients were being incorporated into the island food webs.

For each plant sample, at least three newly formed plant leaves were collected. Whole insects were also collected either by hand or using pitfall traps, and 30–70 mg of fur was plucked from the rump region of the swamp antechinus using forceps. Samples were immediately sealed in air-tight bags and frozen. Frozen plant and invertebrate samples for isotope analysis were oven-dried for 48 h at 60°C, and then finely ground. The animal fur was washed in a 2:1 chloroform:methanol solution to remove lipids, air-dried and then cut into fine fragments. Ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined using a continuous-flow mass spectrometer with an Anca-SI preparation system. Isotopic signatures are reported as the ratio of the sample to that of a known standard:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where  $X$  is the heavy isotope of interest and  $R$  is the ratio of the heavy to light isotope. Comparisons of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between sites were undertaken using two-sample  $t$ -tests and the non-parametric Kruskal–Wallis test.

Isotopic values obtained from the consumer's tissue can be used to reveal temporal shifts in their diets. This is because the isotopic ratios in the consumer's tissue are related to those of its food source in a predictable manner. Metabolically inactive tissues such as hair do not reabsorb or turnover nutrients. Therefore, their stable isotope ratios reflect the diet of individuals during the limited period when the tissue was formed (Roth 2002; Mizukami *et al.* 2005). Therefore, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the fur of the swamp antechinus collected from the island in early spring and in the autumn were compared to determine whether a dietary shift to include seabird products occurred. On the basis of the moulting patterns of the closely related dusky and agile antechinus (*A. swainsonii* and *A. agilis*) (Leeson and Wallis 1986), it was predicted the swamp antechinus would have two moults, a spring (early) moult and summer (late) moult. Hence, hair samples collected during early spring would have grown when seabirds were absent, and represented diet during winter, while hair collected during autumn would have grown during the summer, when seabird products were a potential food source for the antechinus.

All data were analysed using SPSS 14.0 and 17.0 (SPSS, Inc., Chicago, IL, USA). Mean data are presented with standard errors and differences, significant at  $P \leq 0.05$ .

## Results

### Population characteristics

The seasonal numbers of individuals were far greater in the island habitat than the mainland (Table 1). The mean number of individuals was lowest during winter, when only females were present, for the island and mainland respectively ( $19.0 \pm 4.7$  versus  $7.0 \pm 2.8$ ). The island population had the highest number of individuals during summer ( $99.7 \pm 21.1$ ), whereas the highest

number of individuals at the mainland site occurred during autumn ( $14.1 \pm 3.1$ ).

Minimum seasonal survival differed between the sites, with at least twice as many island individuals being recaptured after birth until breeding in comparison to those on the mainland (Fig. 2a). Disappearances of females are more likely to represent mortality than dispersal. Consequently, the difference in recapture rates between the sites is likely to indicate greater survival of females and lower dispersal (and potentially greater survival) of males on the island site.

The relative proportion of immigrant (new) individuals showed similar patterns, with a large influx of new animals entering the population during spring. However, during the summer and autumn the mainland population had a greater influx of new male and female individuals, relative to the island (Fig. 2b). This was particularly apparent for island males, for which new individuals represented less than 25% during summer and autumn compared with 38% and 67% during summer and autumn for mainland males. The average distance between recapture locations differed significantly between sites, with mainland animals moving significantly greater distances. This was consistent for both males ( $56.9 \pm 8.8$  versus  $25.6 \pm 1.9$ ;  $t_{113} = 5.14$ ,  $P < 0.001$ ) and females ( $48.6 \pm 3.5$  versus  $20.7 \pm 1.8$ ;  $t_{148} = 7.56$ ,  $P < 0.001$ ).

Overall body mass did not differ significantly between island and mainland sites ( $P = 0.12$ ). However, there were significant differences between sex (males heavier than females;  $P < 0.001$ ) and season (adding mass over time;  $P < 0.001$ ). There was also a significant interaction of site  $\times$  season ( $P = 0.02$ ), and of most relevance to this study was the significant interaction between site  $\times$  season  $\times$  sex ( $P = 0.02$ ). In spring, the body masses of males and females were similar between sites ( $27.6 \pm 0.5$  versus  $31.9 \pm 1.7$  and  $23.8 \pm 0.8$  versus  $25.9 \pm 1.7$ ). However, during summer both males and females were heavier on the island, with males showing the greatest difference ( $48.1 \pm 0.6$  versus  $39.7 \pm 3.8$  and  $35.5 \pm 0.9$  versus  $30.0 \pm 2.5$ , respectively). By autumn body mass was similar between the sites for males and females ( $57.4 \pm 0.8$  versus  $57.8 \pm 1.7$  and  $34.1 \pm 0.8$  versus  $34.7 \pm 1.6$ , respectively). There was also considerable interannual variation of seasonal body mass for both males and females on the mainland, with mean seasonal mass often varying more than 30% between years. The degree of interannual variation was far lower on the island site, with seasonal means varying less than 15%.

Whereas the swamp antechinus was the only terrestrial mammal present on the island site, bush rats (*Rattus fuscipes*), swamp rats (*R. lutreolus*), white-footed dunnarts (*Sminthopsis leucopus*) and house mice (*Mus domesticus*) were present at the mainland site. Despite the lower species diversity on Kanowna Island, the biomass ( $\text{g ha}^{-1}$ ) of the swamp antechinus was 2–4 times greater than the biomass for small to medium-sized terrestrial mammals and 4–13 times the biomass of the swamp antechinus compared with the mainland site (Fig. 3).

### Prey availability and allochthonous marine inputs

The mean numerical abundances of invertebrates (individuals captured per pitfall trap), grouped by Order, on the island site was significantly greater ( $P < 0.05$ ) for beetles (Coleoptera),

**Table 1. Number of individual swamp antechinus and other small mammals captured in similar-sized trapping areas (~1.5 ha) at the island (2003–07) and mainland (2001–07) sites**

Site	Taxon	Season			
		WinterRange (mean ± s.e.)	SpringRange (mean ± s.e.)	SummerRange (mean ± s.e.)	AutumnRange (mean ± s.e.)
Island	<i>A. minimus</i>	10–32 (19.0 ± 4.7)	64–137 (99.7 ± 21.1)	49–114 (84.7 ± 19.0)	93–99 (96.0 ± 3.0)
Mainland	<i>A. minimus</i>	3–18 (7.0 ± 2.8)	3–19 (11.8 ± 3.3)	3–39 (9.8 ± 5.1)	0–27 (14.1 ± 3.1)
	Other <sup>A</sup>	8–9 (8.3 ± 0.3)	1–8 (4.0 ± 1.8)	1–5 (2.6 ± 1.2)	2–9 (6.0 ± 2.1)

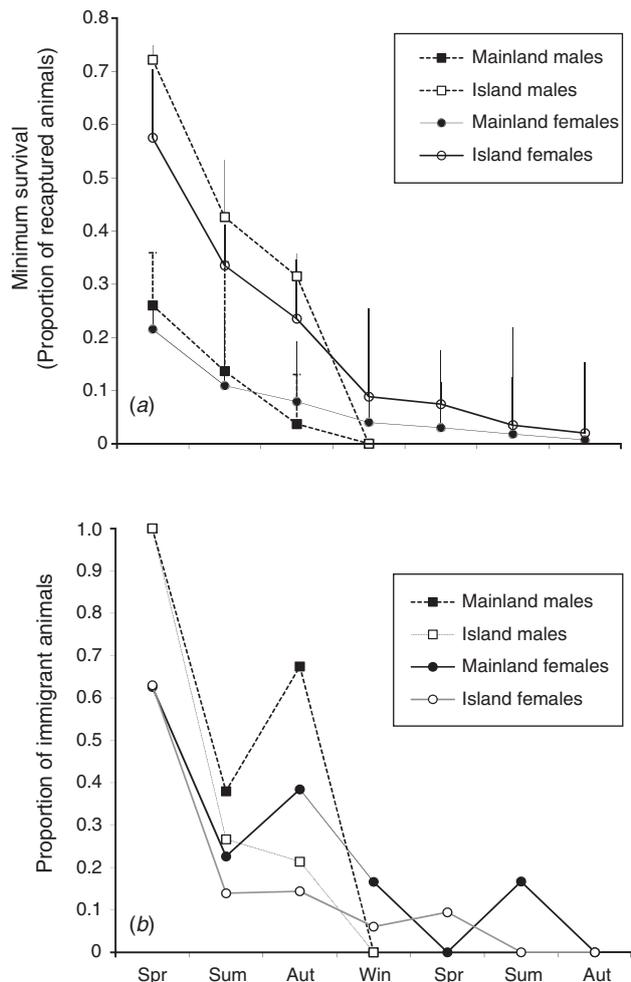
<sup>A</sup>Comprising bush rats (*Rattus fuscipes*), swamp rats (*R.lutroolus*), white-footed dunnarts (*Sminthopsis leucopus*) and house mice (*Mus domesticus*).

earwigs (Dermaptera), spiders (Araneae), cockroaches (Blattodea), flies (Diptera), mites (Acarina), caterpillars (Lepidoptera), worms (Oligochaeta) and grasshoppers (Orthoptera) than the mainland site. The only invertebrate category that was significantly more abundant on the mainland site was ants (Hymenoptera, Formicidae;  $P < 0.05$ ). Although subsurface invertebrates were encountered in the soil samples, abundances were far lower compared with the catches of pitfall traps. Worms, spiders, beetle larvae and centipedes were the most

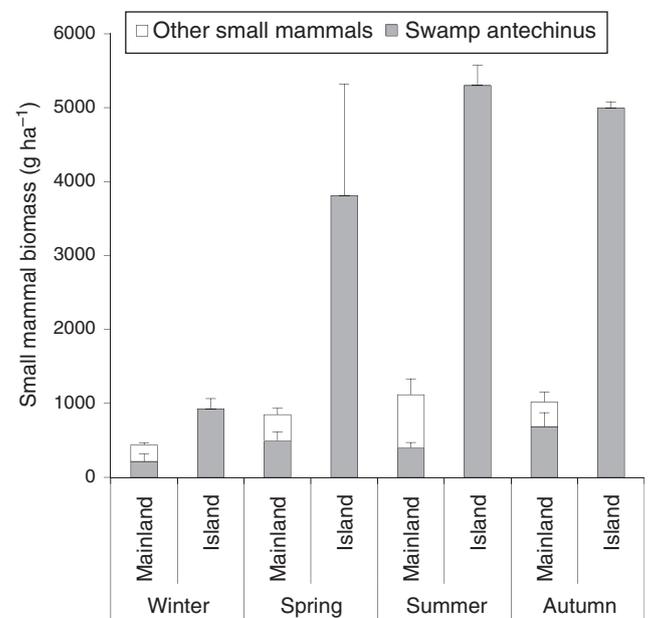
frequent invertebrates in soil samples. More invertebrates were collected from the island soil in comparison to the soil from the mainland site ( $3.4 \pm 0.8$  versus  $2.8 \pm 0.7$ ), although the difference was not significant (Mann–Whitney U-test,  $z = 0.7$ ,  $P > 0.05$ ).

Mean invertebrate biomass (all invertebrates pooled) collected in pitfall traps was significantly greater at the island site than at the mainland site, with more than twice the invertebrate biomass ( $0.27 \pm 0.04$  g pitfall<sup>-1</sup> versus  $0.13 \pm 0.02$  g pitfall<sup>-1</sup>;  $F_{1,110} = 18.1$ ,  $P < 0.001$ ). There was also a significant difference in invertebrate biomass between seasons ( $F_{3,110} = 12.5$ ,  $P < 0.001$ ), with greater biomass in spring compared with winter (Fig. 4a). However, a significant site × season interaction occurred for the invertebrate biomass ( $F_{3,110} = 2.7$ ,  $P < 0.05$ ). This interaction resulted from the almost three-fold higher invertebrate biomass collected in spring on the island compared with the mainland ( $0.49 \pm 0.1$  g pitfall<sup>-1</sup> versus  $0.17 \pm 0.05$  g pitfall<sup>-1</sup>;  $P < 0.05$ ) whereas in summer there were no differences in invertebrate biomass between sites ( $0.28 \pm 0.06$  g pitfall<sup>-1</sup> versus  $0.23 \pm 0.03$  g pitfall<sup>-1</sup>;  $P > 0.05$ ).

The number of invertebrate individuals (all invertebrate orders pooled) captured per pitfall trap differed significantly between sites ( $F_{1,110} = 6.1$ ,  $P < 0.001$ ), with more invertebrates



**Fig. 2.** (a) Seasonal mean minimum survival (proportion of recaptured animals) and (b) proportion of immigrant individuals for the swamp antechinus (males, dashed lines; females, solid lines) from the island (white symbols) and mainland (black symbols) sites.



**Fig. 3.** Mean biomass density (g ha<sup>-1</sup>) of small mammals at the island (white columns) and mainland (grey columns) sites.

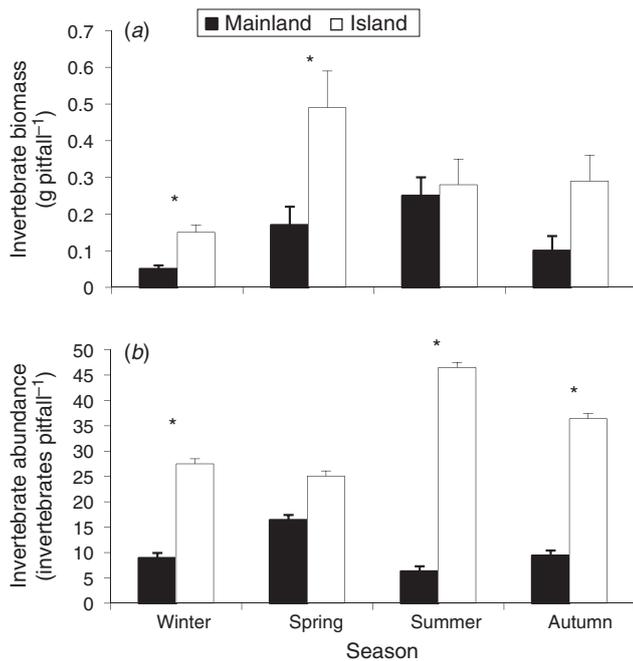


Fig. 4. (a) Mean ( $\pm$  s.e.) seasonal invertebrate biomass (dry weight g pitfall<sup>-1</sup>) and (b) mean ( $\pm$  s.e.) invertebrate abundance (n pitfall<sup>-1</sup>), at the island (white columns) and mainland (black columns) sites.  $n=117$ ; an asterisk indicates  $P \leq 0.05$ .

captured on the island than on the mainland ( $31.6 \pm 2.2$  invertebrates pitfall<sup>-1</sup> versus  $9.9 \pm 1.0$  invertebrates pitfall<sup>-1</sup>). Unlike the biomass of arthropods, season had no significant impact on the number of invertebrates per pitfall ( $F_{3,110}=0.3$ ,  $P>0.05$ ). However, there was a significant site  $\times$  season interaction ( $F_{3,110}=7.7$ ,  $P<0.001$ ) for invertebrate numbers (Fig. 4b). The basis for the interaction was the more than seven-fold increase in the number of invertebrates collected on the island in summer compared with the mainland ( $46.5 \pm 4.0$  versus  $6.3 \pm 2.0$ ;  $P<0.05$ ), yet there were no significant differences in numbers between sites in the spring ( $25.1 \pm 3.0$  versus  $16.4 \pm 2.0$ ;  $P>0.05$ ). Invertebrate numbers were also greater on the island in autumn ( $36.4 \pm 4.0$  versus  $9.4 \pm 2.0$ ;  $P<0.05$ ) and in the winter ( $27.5 \pm 2.0$  versus  $8.9 \pm 2.0$ ;  $P<0.05$ ).

Concentrations of nitrate-N, ammonium-N, phosphorus, potassium and sulfur in soil samples were 7–307 times greater on the island than the mainland (Table 2). For example, the concentration of ammonium-N in the island soil was  $472.5 \pm 70.6$  mg kg<sup>-1</sup>, whereas the concentration on the mainland site was only  $4.5 \pm 0.4$  mg kg<sup>-1</sup> (Mann–Whitney U-test,  $z=2.1$ ,  $P<0.05$ ).

Stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated the presence of marine nutrients in the island terrestrial food web, which was absent from the mainland site, and that the marine nutrients are passed up the food chain. The  $\delta^{13}\text{C}$  of hair samples differed significantly ( $t_{50}=4.9$ ,  $P<0.001$ ) between sites ( $-21.1 \pm 0.1\text{‰}$  versus  $-22.2 \pm 0.2\text{‰}$  for the island and mainland respectively), while the  $\delta^{15}\text{N}$  values of island individuals reached extreme values compared with those on the mainland ( $23.5 \pm 0.5\text{‰}$  versus  $5.3 \pm 0.1\text{‰}$ ;  $t_{50}=17.7$ ,  $P<0.001$ ).

Table 2. Mean plant-available soil nutrients from soil samples ( $n=8$ ) at the island and mainland sites, with Mann–Whitney tests for site comparisons

\*,  $P<0.05$

Soil nutrients	Sites		z
	Mainland ( $\pm$ s.e.)	Island ( $\pm$ s.e.)	
Nitrate Nitrogen (mg kg <sup>-1</sup> )	1.0 ( $\pm 0$ )	104.7 ( $\pm 24.9$ )	2.1*
Ammonium Nitrogen (mg kg <sup>-1</sup> )	4.5 ( $\pm 0.4$ )	472.5 ( $\pm 70.6$ )	2.0*
Phosphorus Colwell (mg kg <sup>-1</sup> )	3.0 ( $\pm 1.4$ )	921.5 ( $\pm 72.7$ )	2.0*
Potassium Colwell (mg kg <sup>-1</sup> )	59.0 ( $\pm 4.9$ )	446.0 ( $\pm 22.3$ )	2.0*
Sulfur (mg kg <sup>-1</sup> )	8.5 ( $\pm 1.0$ )	58.4 ( $\pm 7.9$ )	1.7
Organic Carbon (%)	3.5 ( $\pm 0.7$ )	8.1 ( $\pm 0.6$ )	2.0*
Conductivity (dS m <sup>-1</sup> )	0.1 ( $\pm 0.02$ )	0.5 ( $\pm 0.05$ )	2.0*
pH Level (CaCl <sub>2</sub> ) (pH)	3.8 ( $\pm 0.04$ )	4.0 ( $\pm 0.1$ )	1.0
pH Level (H <sub>2</sub> O) (pH)	4.7 ( $\pm 0.04$ )	4.9 ( $\pm 0.1$ )	1.0

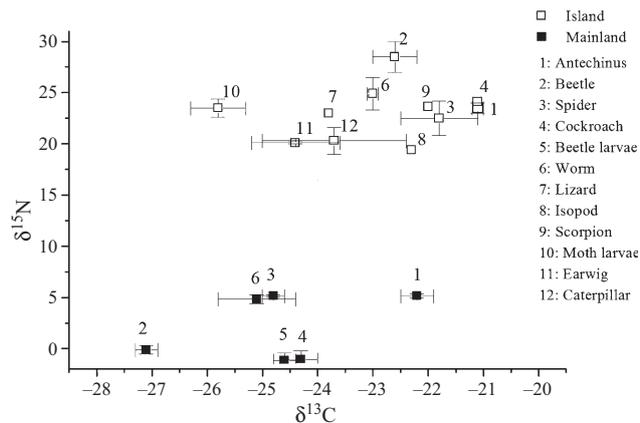
Similarly, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in whole arthropods collected from the island and mainland was also significantly different, with significant enrichment of  $\delta^{13}\text{C}$  ( $-23.3 \pm 0.3\text{‰}$  versus  $-25.2 \pm 0.3\text{‰}$ ;  $t_{34}=3.7$ ,  $P<0.001$ ) and  $\delta^{15}\text{N}$  ( $22.7 \pm 0.8\text{‰}$  versus  $1.8 \pm 0.9\text{‰}$ ;  $t_{34}=16.7$ ,  $P<0.001$ ) (Fig. 5).

The  $\delta^{13}\text{C}$  values of antechinus fur did not differ significantly between spring and autumn ( $-21.1 \pm 0.1 \pm 0.8\text{‰}$  versus  $-21.0 \pm 0.1\text{‰}$ ;  $t=0.6$ ,  $P>0.05$ ). However,  $\delta^{15}\text{N}$  values were significantly lower during autumn ( $22.4 \pm 0.6\text{‰}$  versus  $24.7 \pm 0.8\text{‰}$ ;  $t=2.1$ ,  $P<0.05$ ), indicating a possible dietary shift between spring and autumn. During summer swamp antechinuses on the island site were seen feeding on seabird carcasses.

## Discussion

The study found that a nutrient-rich island site with a greater abundance and biomass of invertebrates sustains a dense island population of the swamp antechinus, with 4–13 times the antechinus biomass of a mainland site. This supports the hypothesis that the island has greater productivity and available food resources for the swamp antechinus. MacArthur *et al.* (1972) coined the phrase ‘excess density compensation’ to describe such a situation, where the aggregate density of a given taxon is higher on islands than in equivalent mainland habitats. If mortality of *Antechinus* is the principal factor determining population size, because of a slow intrinsic rate of population increase, with annual breeding and associated male die-off (Wood 1970; Cockburn 1997), any factor that increases survival will increase the population density of *Antechinus*. Therefore higher survival and reduced emigration recorded in the island population are proposed to be the primary causes of the inflated population density.

High island population densities may be attributable to confounding site differences such as vegetation characteristics, soil type, rainfall or differing species interactions, such as predatory release (MacArthur *et al.* 1972). Indeed, high island population densities are often attributed to lower predation, resulting in reduced mortality relative to mainland populations (see reviews by Gliwicz 1980; Adler and Levins 1994). However, although introduced foxes (*Vulpes vulpes*) and cats (*Felis catus*) and native predators, such as snakes, are absent from the island



**Fig. 5.** Stable isotope ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of fur from swamp antechinus and invertebrate prey tissues at the island (white squares) and mainland (black squares) sites during summer.

habitat, avian predators such as brown falcons (*Falco berigora*) and Australian kestrels (*F. cenchroides*) were observed in greater numbers than on the mainland. The grassland habitat of the island affords little protective cover and avian predation was regularly observed, indicating that predatory release of antechinus was unlikely to occur in the island habitat. In addition, population density estimates of the swamp antechinus in the nearby heath habitat on Wilsons Promontory (<10 km from the island), were comparable to those for Urquhart Bluff (Sale and Arnold 2009). This habitat has a similar geological history and rainfall pattern to the island. Therefore confounding site differences are unlikely to be the primary cause for the divergent population densities of the swamp antechinus.

An important factor known to regulate population density is environmental resource availability (Hansen and Batzli 1978; Dickman 1989; Boutin 1990). In the present study, the biomass and numerical abundance of surface invertebrates was significantly higher on the island site, indicating that the island antechinus had more food available. In turn, more food could lead to higher survival and smaller movements of swamp antechinus on the island, resulting in higher population densities on the island.

Additional food resources for the antechinus on the island are likely to result, both directly and indirectly, from the presence of colonial seabirds on the island. Extensive research on seabird colonies has shown a significant positive effect on the productivity of island ecosystems (Smith 1978; Polis and Hurd 1996; Huxel and McCann 1998; Stapp and Polis 2003; Bancroft *et al.* 2005; Caut *et al.* 2012), including increased biomass/availability of invertebrates (e.g. Sánchez-Piñero and Polis 2000; Markwell and Daugherty 2002; Caut *et al.* 2012). In the present study, the concentrations of plant-available forms of nitrogen (nitrate-N and ammonium-N), phosphorus and potassium were up to 100 times higher in the island topsoil than in the nutrient-deficient soils in the mainland habitat. There was strong evidence that this nutrient enrichment was from seabirds, and these effects penetrated into areas adjacent to seabird colonies, perhaps via nutrient leaching. The  $\delta^{15}\text{N}$  values for terrestrial plants and invertebrates on the island greatly exceeded levels found in

mainland samples and are indicative of marine-derived nitrogen (Mizutani and Wada 1988; Farina *et al.* 2003; Stapp and Polis 2003; Fukami *et al.* 2006; Caut *et al.* 2012).

The present study also indicates that antechinus benefited directly from seabirds during spring and summer, with the consumption of seabird carrion. This is supported by the significant change in  $\delta^{15}\text{N}$  values between winter and summer, indicating a potential dietary shift. Winter hair was more enriched in  $\delta^{15}\text{N}$  and is likely to indicate a guano–plant–insectivore pathway. In contrast, significantly lower  $\delta^{15}\text{N}$  values in antechinus fur during autumn may have resulted, in part, from the consumption of seabird tissues or eggs, which have comparatively lower  $\delta^{15}\text{N}$  values (e.g. 8–12  $\delta^{15}\text{N}$  ‰; Minami *et al.* 1995), during the period of fur growth. The observations of island antechinus consuming seabird carrion and the presence of feathers in antechinus scats during the fledging of seabird chicks, as determined by faecal analysis (Sale 2008), supports this proposition.

It has been proposed that with fewer competitors and relaxed predation, island populations increase to such an extent that food may become relatively more limiting for consumers on islands than on the mainland Case (1978). Palkovacs (2003) extended this prediction and proposed that high intraspecific competition on islands may eventually result in a reduction in growth. However, there was no evidence that the swamp antechinus on Kanowna Island was experiencing any food shortages as a result of intense intraspecific competition, with body mass and growth comparable to, or greater than, that of the mainland.

The unique life history of *Antechinus* means that lower food resources and increased predation risks associated with foraging in suboptimal environments may limit their capacity to survive. This is particularly evident when the spring flush of insect prey, which historically has been predictable, is interrupted by drought (Rhind 2002; Parrott *et al.* 2007; Sale *et al.* 2008). In the present study, there was considerable interannual variation in seasonal body mass of animals in the mainland habitat (particularly during spring and summer), but the island population had a more stable body mass. Potentially, marine inputs may subsidise and maintain a more stable spring and summer food supply between years, irrespective of climatic conditions. Seabirds also directly provide additional food resources (discarded prey items, broken eggs and carrion) during this energy-demanding growth period of the swamp antechinus. The fact that island individuals were significantly heavier than mainland individuals during summer supports this proposition.

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