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## Marine resources subsidize insular rodent populations in the Gulf of California, Mexico

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**Abstract** Inputs of energy and nutrients from one ecosystem may subsidize consumers in adjacent ones, with significant consequences for local communities and food webs. We used stable isotope and faecal pellet analysis to quantify use of ocean-derived resources by small mammals on islands in the Gulf of California, Mexico. Rodents were live-trapped on grids originating near shore and extending 125–200 m inland to evaluate the extent to which rodents transport marine nutrients inland, and to determine whether marine foods subsidize island populations, permitting higher densities than would be possible based on terrestrial resources alone. Both faeces and stable carbon and nitrogen isotopes revealed that omnivorous mice (*Peromyscus maniculatus*) consume ocean-derived prey, including littoral and supralittoral invertebrates, and that their diets differed markedly from those of granivorous rodents (*Chaetodipus rudinoris*). On a small, seabird roosting island, marine prey were important in the diet of mice regardless of their proximity to shore, underscoring the pervasive influence of the ocean on small islands with relatively large coastline area. On a large island, however, consumption of marine foods declined sharply  $\geq 50$  m from shore, which suggests that mice are poor conduits of inland movement of energy and nutrients from the sea. Marine resources seemed to act as subsidies for omnivorous rodents: more *P. maniculatus* were captured near shore

than farther inland and there was an inverse relationship between island area and rodent abundance, suggesting that small islands with large amounts of marine inputs support the highest population densities. Patterns of local and island-wide abundance of *P. maniculatus* are likely the result of several interacting factors, including frustrated dispersal, competition with *C. rudinoris*, and the absence of predators. We speculate, however, that the availability of marine resources allows *P. maniculatus* to reach high densities and to persist on small islands in the Gulf despite low and unpredictable terrestrial productivity. Spatial trophic subsidies thus provide a possible mechanistic explanation for the widely reported inverse relationship between population density and island or habitat area.

**Keywords** *Chaetodipus rudinoris* · Island ecology · *Peromyscus maniculatus* · Spatial subsidies

### Introduction

Ecologists have long recognized that the dynamics of one system are closely linked to processes occurring in adjacent or even distant environments (Odum 1971; Hansson 1977). Studies of aquatic and coastal environments in particular have demonstrated that productivity of streams, lakes and estuaries is influenced by inputs from the adjoining land (e.g., Minshall 1967; Hansler 1975; Ward 1989), and reciprocal flows from water to land can provide substantial amounts of nutrients and energy to terrestrial food webs (e.g., Bouchard and Bjorndal 2000; Nakano and Murakami 2001). Consumers living in terrestrial habitats take advantage of allochthonous resources that originate in more productive aquatic ones, and these inputs may subsidize consumer populations, permitting higher densities than could be supported by land resources alone. Subsidized consumers influence the abundance and dynamics of resources and other consumer populations through a variety of direct and indirect effects

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that remain poorly understood (Polis et al. 1997a; Fagan et al. 1999).

Trophic subsidies and their food web effects should be important in all heterogeneous landscapes, but the large differences in productivity between marine and terrestrial systems make coastal, and especially, island environments model systems for studying trophic linkages. For more than a decade, our research group has studied the effects of the ocean on small islands in the Gulf of California, where the contrast in productivity between sea and land is particularly striking. The region is one of the driest in North America, receiving on average only 59 mm of precipitation annually (Reyes-Coca et al. 1990) and, as a consequence, plant productivity is extremely low  $<100$  g dry mass  $m^{-2}year^{-1}$ ; (Polis and Hurd 1996). The islands are surrounded, however, by a rich marine environment fed by upwelling in the northern Gulf. In addition to ameliorating the physical environment, the ocean contributes nutrients and energy to the islands in the form of algal wrack and animal carcasses that wash ashore, supporting diverse communities in the littoral zone (Polis and Hurd 1996). Seabirds are a second major conduit of marine inputs to islands where they roost and nest. Food scraps, addled eggs and dead chicks fuel scavenger food webs, and even on islands lacking significant nesting colonies, roosting seabirds contribute large amounts of nitrogen, phosphorus and other nutrients via their guano. Guano-fertilized soils support higher productivity and higher nutritive quality of plants (Anderson and Polis 1999), which are key resources for many detritivores (Sánchez Piñero and Polis 2000) and form the base of terrestrial food webs (Stapp et al. 1999). Island consumers thus may be subsidized directly, via shore drift or carrion or indirectly, through the effects of guano fertilization on plants or by the consumption of subsidized prey.

Polis and Hurd (1996) argued that the amount of marine input to an island via shore drift is proportional to the length of its coastline and hence, its perimeter. Assuming that the relative impact of the ocean is highest close to shore, a small island, with a relatively large perimeter-to-area ratio, should be more affected by marine inputs than a larger island with the same basic shape. Island size is also important because seabirds often prefer to nest and roost on small, predator-free islands (Sánchez Piñero and Polis 2000). On these islands, inputs from seabirds may be more pervasive than those associated with shore drift because birds deposit nutrients island-wide and beyond the immediate shore. Shore drift may penetrate core interior areas indirectly, however, through the movements and/or dispersal of subsidized consumers.

In earlier studies, we showed that a variety of terrestrial animals consume and are apparently subsidized by marine resources (Polis and Hurd 1996; Anderson and Polis 1998; Rose and Polis 1998; Sánchez Piñero and Polis 2000). Omnivorous rodents (*Peromyscus maniculatus*) use both marine and terrestrial foods depending on their availability (Stapp et al. 1999) and are good candidates for determining how allochthonous resources

affect insular populations and food webs. These rodents are highly mobile and have great reproductive potential, which makes them potentially important vectors of inland transport of ocean nutrients. Islands inhabited by *P. maniculatus* vary in size and seabird activity, and therefore in the nature and amount of marine inputs. This variation is expected to influence the contributions of marine foods to mouse diets and may be manifest in patterns of population density within and among islands if marine foods subsidize rodent populations. Understanding the relationship between marine inputs and *P. maniculatus* density is necessary to evaluate the effects of these rodents on their terrestrial prey and other species.

In this paper we address two central questions. First, to what degree do mice use marine resources and are they major conduits for the movement of marine materials from shore to the island interior? Stable carbon and nitrogen isotopes are increasingly used to examine trophic connections between marine and terrestrial systems (Peterson and Fry 1987; Hobson 1999), and we compared isotopic signatures of rodents captured along a gradient from shore to inland to estimate the degree of penetration of marine nutrients via rodents. Second, do marine resources subsidize rodent populations; that is, are mice more abundant near shore than in inland areas, and do islands with more marine inputs support larger, more productive populations? We live-trapped rodents at different distances from shore and on islands that differed in size, and hence, in the amount of marine input expected via shore drift and the presence of seabirds.

## Materials and methods

### Field studies

Our study area is located in the Midriff region of the Gulf of California, near Bahía de los Angeles (28°55'N, 113°30'W), Baja California, México. The islands in the bay are very rocky and vegetation cover on the islands is sparse (1–4% plant cover) and dominated by perennial shrubs (*Atriplex barclayana*, *Viscainoa geniculata*, *Lycium* spp., *Bursera* sp.) and cacti (*Pachycereus pringlei*, *Opuntia* sp.). Annual plants (*Amaranthus watsonii*, *Chenopodium murale*, *Perityle emoryi*, *Cryptantha* spp.) are more abundant during wet El Niño Southern Oscillation events, which bring heavy winter rains every 3–8 years (Polis et al. 1997b). Between March 1995 and August 1997, the area received only 38 mm of precipitation (Comision Nacional del Agua, Gerencia Regional de la Peninsula de Baja California, unpublished data).

Live-trapping surveys revealed the presence of rodents on 10 of 18 small islands in the vicinity of Bahía de los Angeles (Stapp 2002a). *Peromyscus maniculatus* (22 g) was captured on all 10 islands, whereas *Chaetodipus ruidinoris* (formerly *C. baileyi*; Riddle et al. 2000), a similar-sized (20 g) granivore, was found on only 3 islands (Pata, 0.18 km<sup>2</sup>; Mitlán, 0.19 km<sup>2</sup>; Smith, 9.13 km<sup>2</sup>), all of which were inhabited by *P. maniculatus*. Here we report results from field work on 6 islands in Bahía de los Angeles in May and June 1997. These islands ranged in area from 0.10 km<sup>2</sup> to 9.13 km<sup>2</sup>; most were roughly elliptical or round in shape and situated 2–3 km offshore. Seabirds, notably yellow-footed gulls (*Larus occidentalis*) and double-crested cormorants (*Phalacrocorax auritus*), roost or nest in small numbers on two small islands (Coronado, 0.10 km<sup>2</sup>; Flecha, 0.16 km<sup>2</sup>). Land predators were absent on all of these islands except Smith, which is inhabited by rattlesnakes (*Crotalus*

*mitchelli*), but shrikes, owls and other raptors move freely between the islands and mainland (P. Stapp, personal observation).

Rectangular live-trapping grids were established on islands to estimate relative abundance and collect diet samples. Trap lines were 15 m apart, with traps spaced at 25-m intervals along each line. Grids originated in the supralittoral and extended inland perpendicular to the shore for 125–200 m, depending on island size. Grids consisted of 36 large Sherman traps (six lines of six traps each) on the small islands and 54 traps (six lines of nine traps) on the two largest islands (Smith; Ventana, 1.41 km<sup>2</sup>). Two sites on the adjacent mainland were also trapped using the larger grid design. Sites were selected to be as similar as possible: grids were located on relatively flat, gravelly landings at the base of small canyons, all beach substrates were cobble and the first two rows of traps were situated in a band of coastal vegetation (*Salicornia subterminalis*, *Batis maritima*, *Frankenia palmeri*) just above the supralittoral zone, which then graded into scrub vegetation 20–50 m farther inland. The two seabird roosting islands (Coronadito, Flecha) were steep and rocky and lacked landings and coastal vegetation, therefore grids originated as close to shore as possible.

Traps were set for three consecutive nights on most islands and the mainland. Limited boat access and steep terrain required us to set traps in pairs of transects (18–24 traps) and for only two nights on two islands (Mitolán and Flecha). Traps were baited each evening with peanut butter and oatmeal and then closed at dawn the next morning to prevent mortality from heat and ants. Individuals were weighed, measured and given a uniquely numbered ear tag. Mice with swollen testes or teats, with a perforate vagina, or that were obviously pregnant were classified as being in breeding condition. We collected a small (2–3 mm) piece of tail tissue from a subset of individuals for stable isotope analysis, following protocols approved by the Animal Use and Care Committee at the University of California, Davis. Tail tissues consisting of bone, cartilage and skin were stored separately in 75% ethanol and then frozen upon returning from the field. We also collected faecal pellets from coastal and inland mice from three islands (Ventana, Coronadito for *P. maniculatus*; Pata for *C. rudinoris*) to corroborate stable isotope results. All individuals were released immediately at their location of capture.

We used the number of different individuals captured per unit trapping effort (individuals per 100 trap-nights (TN)) as an index of abundance of mice on islands. Captures were pooled by trap rows and divided by trap effort to estimate abundance at four different distances from shore (0–25 m, 50–75 m, 100–125 m, 150–175 m, 175–200 m). To determine whether marine resources resulted in higher abundance near shore among islands with different population densities, we classified individuals into distance classes based on the location where they were first captured, and then compared the proportion of individuals among the four different distance categories using analysis of variance (SAS 1989). Proportions were arcsine-square root transformed prior to analysis; abundance estimates were log-transformed. Unless indicated otherwise, values presented are means  $\pm$  1 SE.

#### Laboratory analyses

Mouse tissue samples were oven-dried for 12–24 h at 50°C, ground and weighed. Stable carbon (C) and nitrogen (N) isotopic ratios were determined using a Europa continuous-flow isotope ratio mass-spectrometer connected to a Europa gas analyzer at the Ecosystem Sciences Division at University of California Berkeley, USA. Isotopic signatures are usually expressed as the ratio of the heavy to light isotopes (<sup>13</sup>C/<sup>12</sup>C, <sup>15</sup>N/<sup>14</sup>N) and then reported as the ratio of the sample to that of a known standard, (in parts per thousand):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$$

where  $X$  is the heavy isotope of interest and  $R$  is the ratio of the heavy to light isotope. Standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were PeeDee Belemnite carbonate and atmospheric N, respectively.

Because little ( $\sim 1\%$ ) C fractionation occurs during digestion and assimilation,  $\delta^{13}\text{C}$  of a consumer's tissues are similar to those of its prey, making  $\delta^{13}\text{C}$  a useful index of integrated diet (Schoeninger and DeNiro 1984; Peterson and Fry 1987). In terrestrial systems, plants differ in  $\delta^{13}\text{C}$  depending on the photosynthetic pathway used; C<sub>3</sub> plants have relatively low ( $\delta^{13}\text{C} < -28\%$ ) compared to C<sub>4</sub> and CAM plants ( $-12$  to  $-13\%$ ; Peterson and Fry 1987; Herrera et al. 1993).  $\delta^{13}\text{C}$  values based on marine phytoplankton ( $-19$  to  $-24\%$ ) are intermediate between those based on land plants, whereas intertidal organisms feeding in benthic algal food webs have  $\delta^{13}\text{C}$  signatures similar to or more enriched than those of C<sub>4</sub> plants ( $-11$  to  $-15\%$ ; Stapp et al. 1999). Nitrogen is also a useful diet marker in our system because soils fertilized by seabird guano are enriched in <sup>15</sup>N, so that the presence of guano-derived N can be clearly distinguished from terrestrial sources in the  $\delta^{15}\text{N}$  values of plants and their consumers in both wet and dry years (Stapp et al. 1999).  $\delta^{15}\text{N}$  has also been used widely to identify feeding relationships because  $\delta^{15}\text{N}$  increases predictably by 3–5‰ with each stepwise increase in trophic position (Minagawa and Wada 1984; Schoeninger et al. 1983). In general, consumers feeding on marine-derived prey were expected to have higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than those eating purely terrestrial resources.

Faecal pellets collected from a given individual were combined and a sub-sample of the homogenized pellets was mounted on a slide following the methods described in Hansen et al. (1974). Recognizable structures were identified to ordinal or familial level using a reference collection. The proportional representation of plant and animal material was estimated by tallying the number of occurrences of each known item at a fixed point on 20 random microscopic fields (Sparks and Malechek 1968), which provided an estimate the percentage composition by volume of invertebrate and plant matter in rodent diets. Faecal analyses were conducted by staff of the Composition Analysis Laboratory, Fort Collins, Colo., USA.

## Results

### Use and transport of marine resources

Nearly all faeces of *P. maniculatus* contained a mixture of animal and plant material (Table 1), confirming that this species is truly omnivorous. *P. maniculatus*' diet was very different on the two islands from which pellets were collected. Seeds made up a greater proportion of the diet of mice on Coronadito than on Ventana, where invertebrates were eaten much more often. Adult Coleoptera and larval Lepidoptera were the most commonly identified terrestrial arthropods in faeces. Of plant materials, *P. maniculatus* consumed mostly seeds of Compositae and grasses on Coronadito, and *Agave cerulata*, *Atriplex* spp. and *Cammissonia cardiophylla* on Ventana. By comparison, *C. rudinoris* ate a broader variety of plants, including seeds or other parts of *Atriplex barclayana*, *Agave* spp., *Opuntia alcahes*, *Aristida adscensionis*, *Lotus strigosus* and unidentified Compositae. *Chaetodipus rudinoris* is considered to be granivorous, but 57% (8/14) consumed some animal material, especially those living close to shore (Table 1), and invertebrates constituted a greater proportion of diet of coastal *C. rudinoris* than those captured farther inland ( $t=2.45$ ,  $df=12$ ,  $P=0.031$ ).

*Peromyscus maniculatus* faeces contained fragments that could be tentatively identified as littoral or marine invertebrates, such as amphipods, isopods and mollusks.

**Table 1** Frequency of occurrence and percent composition by volume of items in faeces of insular *Peromyscus maniculatus*. Frequency of occurrence is the percentage of individuals that consumed a particular prey type. Coronadito is a small seabird roosting island; Ventana is a large island without seabirds. Diet

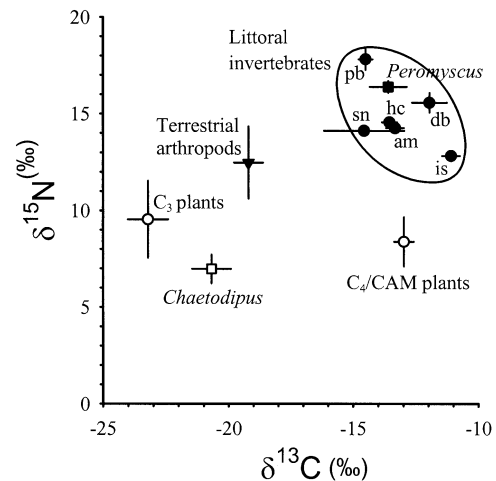
	N	Littoral invertebrates		All invertebrates		Seeds		All plants		
		Frequency	Percent volume	Frequency	Percent volume	Frequency	Percent volume	Frequency	Percent volume	
<i>Peromyscus maniculatus</i>										
Coronadito										
Coast	9	66.7	17.6±7.2	77.8	27.7±10.9	88.9	65.2±13.6	100	71.8±10.7	
Inland	12	41.7	16.6±6.9	83.3	36.9±9.1	100	53.8±10.9	100	62.5±9.3	
Ventana										
Coast	10	0	0	100	56.9±8.6	70.0	24.5±10.5	100	43.1±8.6	
Inland	12	8.3	0.6±0.6	100	54.9±8.6	83.3	24.3±7.6	100	45.1±8.6	
<i>Chaetodipus rudinoris</i>										
Coast	6	16.7	0.6±0.6	100	34.4±11.3	100	43.5±13.9	100	65.6±11.3	
Inland	8	0	0	25.0	7.0±4.8	100	61.5±13.8	100	93.0±4.8	

There were no significant differences between coastal and inland mice in the amount of littoral prey consumed on either island *t*-tests, ( $P>0.37$ ); fragments of littoral prey were rare in faeces from Ventana at both distances, and were found in similar proportions in pellets of mice near shore and inland on Coronadito (Table 1). More of Coronadito mice ate littoral prey (48%) than on Ventana (5%;  $\chi^2=11.70$ ,  $df=1$ ,  $P=0.001$ ), including four captured  $\geq 100$  m from shore, and these items contributed more to mouse diets on Coronadito ( $t=3.41$ ,  $df=20.2$ ,  $P=0.003$ ). Littoral prey comprised 35.7±6.1% of the diet of the 10 *P. maniculatus* from Coronadito that ate these foods.

Faeces provide dietary information from at most one to a few meals, and thus may not reflect the relative importance of particular prey items over longer time periods. Stable C and N analysis of tissues of mice demonstrated that marine invertebrates are important food items of coastal *P. maniculatus* (Fig. 1). Isotopic signatures of mice collected 0–25 m from shore were similar to those of invertebrates collected from littoral zone and were very different from those of plants (the most common supralittoral plant, *Salicornia subterminalis*, is a  $C_3$  species) and terrestrial arthropods. In contrast, the isotopic signature of *C. rudinoris* indicated a diet of  $C_3$  and  $C_4$ /CAM seeds.

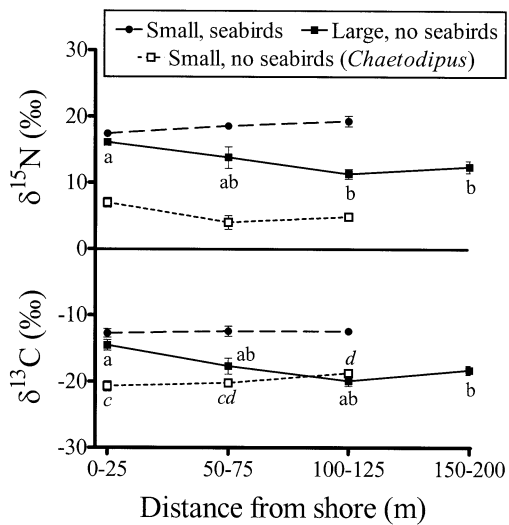
Patterns in isotopic signatures of *P. maniculatus* suggested that the degree of penetration of marine resources via rodent tissues differed depending on island size (Fig. 2). On large Ventana, C and N signatures were enriched near shore but dropped off significantly at distances farther inland ( $\delta^{13}C$ :  $df=3$ , 11,  $F=7.24$ ,  $P=0.006$ ;  $\delta^{15}N$ :  $df=3$ , 11,  $F=4.33$ ,  $P=0.030$ ). Isotopic signatures of inland *P. maniculatus* suggested that they ate a mixture of terrestrial arthropods and seeds. On Coronadito, however, there were no significant differences in isotopic signatures between coastal and inland areas ( $\delta^{13}C$ :  $df=2$ , 9,  $F=0.08$ ,  $P=0.926$ ;  $\delta^{15}N$ :  $df=2$ , 9,  $F=3.31$ ,  $P=0.084$ ). Signatures of inland mice on Coronadito were similar to those near

composition of *Chaetodipus rudinoris* collected from one small island with no seabirds (Pata) is provided for comparison. Coastal and inland samples were collected from individuals captured 0–25 m and >25 m from shore, respectively. Values are means ±1 SE, with  $n$  = number of individuals



**Fig. 1** Stable carbon and nitrogen isotopic signatures of *Peromyscus maniculatus* ( $n=14$ ) and *Chaetodipus rudinoris* ( $n=4$ ) captured 0–25 m from shore on islands in the Gulf of California. Values are means ±1 SE. Plants included seeds and leaf material from six  $C_3$  plants (*Asclepias*, *Nicotiana*, *Perityle*, *Viscainoa*, *Mojavea*, *Encelia*;  $n=9$ ) and two  $C_4$ /CAM plants (*Atriplex*, *Opuntia*;  $n=5$ ) collected on four islands (Smith, Ventana, Pata, Mitlán). Terrestrial arthropods ( $n=7$ ) consisted of three spiders, three silverfish and a grasshopper collected from Smith and Ventana. Littoral invertebrates included predatory beetles (*pb*;  $n=3$ ), detritivorous beetles (*db*;  $n=3$ ), hermit crabs (*hc*;  $n=4$ ), isopods (*is*;  $n=8$ ), amphipods (*am*;  $n=5$ ), and snails (*sn*;  $n=4$ ). See Stapp et al. (1999) for preservation and preparation methods

shore and higher than those of inland mice on Ventana (Fig. 2), suggesting that shore-derived prey were important across this small island. By comparison, isotopic signatures of *C. rudinoris* from Pata were less enriched than those of *P. maniculatus* on the other islands, which is consistent with a mostly granivorous diet. Carbon isotopic signatures of *C. rudinoris* captured near shore were significantly lower, and N signatures slightly higher

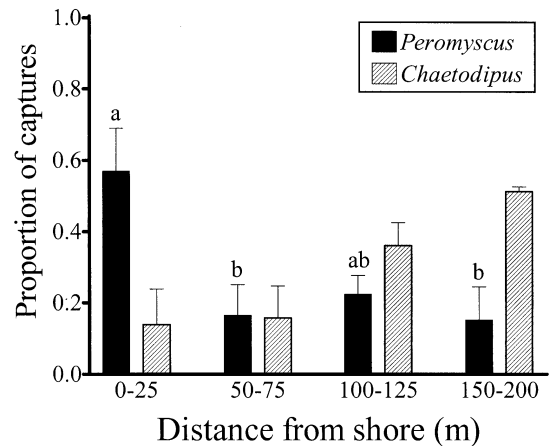


**Fig. 2** Stable carbon and nitrogen isotopic signatures (mean $\pm$ 1 SE) of tissues of *P. maniculatus* captured at different distances from shore on a small, seabird roosting island Coronadito, (0.10 km<sup>2</sup>) and a large island without seabirds (Ventana, 1.41 km<sup>2</sup>). Isotopic signatures of *C. rudinoris* tissues from Pata (0.18 km<sup>2</sup>), a small island with no seabirds, are provided for comparison. Means in the same series that have the same letter were not significantly different (Tukey multiple comparison tests,  $P>0.05$ ). Sample size ranged from three to six individuals for a given distance category

( $\delta^{13}\text{C}$ :  $df=2, 11, F=4.41, P=0.039$ ;  $\delta^{15}\text{N}$ :  $df=2, 11, F=3.78, P=0.057$ ), than those of individuals captured farther inland. This implies a diet comprised more of  $\text{C}_3$  plants (e.g., *Salicornia*) or their associated arthropods, as seen in their faeces (Table 1), or differences in N metabolism between inland and near-shore populations (cf. Ambrose 1991).

#### Effects of marine resources on rodent abundance

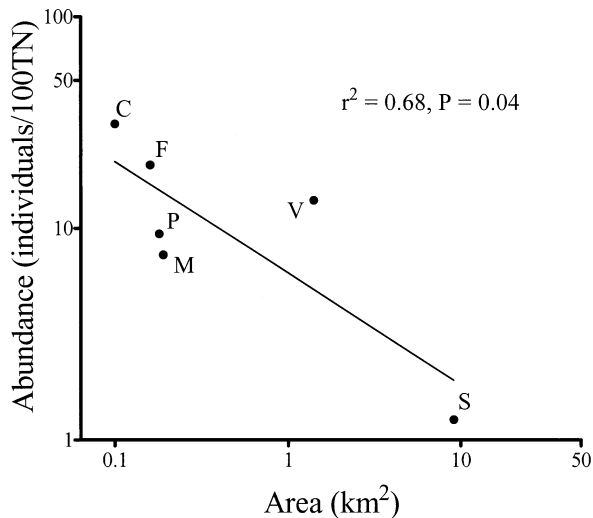
Patterns in captures of mice suggested that marine inputs subsidized *P. maniculatus*, both locally and on an island-wide basis. On average, nearly 60% of mice were captured in traps near the supralittoral zone, and capture rates declined significantly with increasing distance from shore (Fig. 3;  $df=3, 18, F=4.20, P=0.020$ ). By comparison, *C. rudinoris* were generally more abundant in the island interior, although there was no significant difference in the distribution of individuals with distance ( $df=3, 7, F=2.53, P=0.141$ ). A higher fraction of *P. maniculatus* were captured near shore on large ( $>1 \text{ km}^2$  in area) islands than on small ( $<0.2 \text{ km}^2$ ) islands (0.64 vs 0.54) and mice were distributed nearly equally among all three distance classes on Coronadito. However, analysis-of-variance models that included a binary categorical variable for island size (Small, Large) did not explain any significant variation in number of individuals captured across distance classes overall model: ( $df=7, 14, F=1.95, P=0.137$ ; Distance $\times$ Size interaction,  $F=0.71, P=0.560$ ). An analysis of covariance with distance class and island



**Fig. 3** Distribution of captures of *P. maniculatus* and *C. rudinoris* at different distances from shore, expressed as a mean proportion ( $\pm$ 1 SE) of all individuals captured on a given island, excluding recaptures. Means in the same series that have the same letter were not significantly different (Tukey multiple comparison tests,  $P>0.05$ ). Sample size was six and three islands for *P. maniculatus* and *C. rudinoris*, respectively, for the first three distance classes and two islands for both species for the last distance class (150–200 m)

area as continuous variable showed no significant interaction between distance and area ( $F=2.04, P=0.155$ ). The proportion of individuals captured 0–25 m from shore was inversely related to overall abundance (Pearson  $r=-0.94$ ), which suggests that where rare, *P. maniculatus* tended to be more concentrated near shore.

Abundance of *P. maniculatus* was negatively related to island area: small islands, with a relatively high proportion of coastline area, support denser populations than larger ones ( $r^2=0.68, P=0.044$ ; Fig. 4). Because most islands were roughly similar in shape, island area was strongly correlated with island perimeter-to-area ratio (Pearson  $r=-0.99$ ). Shoreline effects were also confounded with those of seabirds because Coronadito and Flecha, the only two roosting islands, were both small. On average, *P. maniculatus* was three times more abundant on the two seabird islands ( $25.6\pm 5.6$  individuals/100 TN) than on islands without seabirds ( $7.9\pm 2.6, n=4$ ), but this difference was not significant statistically ( $t=-1.79, df=4, P=0.148$ ). *Peromyscus maniculatus* also tended to be more abundant when alone ( $21.6\pm 5.2$  individuals/100 TN,  $n=3$ ) than in the presence of *C. rudinoris* ( $6.1\pm 2.5, n=3$ ;  $t=2.23, df=4, P=0.090$ ). An analysis of covariance to test the combined effects of island area and the presence of *C. rudinoris* on *P. maniculatus* indicated significant main effects area ( $F=45.54, P=0.021$ ; *C. rudinoris*:  $F=47.41, P=0.020$ ), but no interaction between them ( $F=3.70, P=0.194$ ). *Chaetodipus rudinoris* was much more abundant on the two smaller islands ( $26.7\pm 10.1$  individuals/100 TN) than on Smith (2.8 individuals/100 TN). Neither species was captured at the two mainland sites. The pooled relative abundance of all species (*P. eremicus*, *Neotoma lepida*, *C. spinatus*, *C. arenarius*) captured on the mainland ( $7.0\pm 4.1$  individuals/100 TN) was similar to



**Fig. 4** Relationship between island area and abundance individuals/100 (TN, trap-nights) of *P. maniculatus*. Note the logarithmic scale of both axes. Island codes: C Coronadito, F Flecha, P Pata, M Mitlán, V Ventana, S Smith

the combined density of *P. maniculatus* and *C. rudinoris* on Smith, the largest island (6.3 individuals/100 TN).

Demographic characteristics of *P. maniculatus* populations also differed with island size. Significantly more mice were in breeding condition on small islands ( $98.2 \pm 1.9\%$ ,  $n=4$ ) than on the two large ones ( $16.7 \pm 16.7\%$ ;  $\chi^2=3.87$ ,  $P=0.049$ ). On average, juveniles made up a greater proportion of individuals captured on small islands ( $10.5 \pm 3.8\%$ ,  $n=4$ ) than on large islands (0%,  $n=2$ ), although the difference was not statistically significant ( $\chi^2=2.18$ ,  $P=0.140$ ). There was no significant difference in sex ratio among islands ( $\chi^2=0.21$ ,  $P=0.643$ ), which did not differ overall from 50:50 ( $\chi^2=0.02$ ,  $df=1$ ,  $P=0.903$ ).

## Discussion

### Use and transport of marine resources

Our results suggest that omnivorous rodents on Gulf islands use and are subsidized by resources from the ocean. Stable C and N isotopes revealed that littoral prey are important in the diet of *P. maniculatus* living close to shore but even mice captured in the interior of small islands consumed marine-based foods (Fig. 2). These conclusions were generally supported by faecal analysis, a more conventional method of quantifying diet, although littoral prey were less common in faeces than expected based on stable isotopes. Diets of omnivores such as *P. maniculatus* are highly variable over time, and large numbers of faecal samples are therefore necessary to estimate diet composition reliably. Highly digestible items may contribute much energy and protein to support growth and tissue development, but are often difficult to

identify in faeces and their importance may be underestimated. In contrast, isotopic signatures of tail tissue reflect the assimilation of nutrients into tissues over a much longer period (weeks to months, vs hours for faeces) and are not biased by differences in preservation or detectability. Isotopes offer less taxonomic resolution than methods such as gut or faecal analysis, but in systems where diet sources are isotopically distinct, stable isotopes provide an integrated measure of the relative contributions of different sources that complements traditional methods.

Our finding that small mammals such as *P. maniculatus* living in coastal areas prey upon or scavenge littoral prey is not new (e.g., McCabe and Cowan 1945; Koepcke and Koepcke 1952; Osborne and Sheppe 1971; Thomas 1971; Stewart et al. 1989; Navarrete and Castilla 1993), although much past evidence is anecdotal. From a mouse's perspective, marine resources may be less readily depleted than terrestrial foods because new material is continually washing ashore, and because prey have numerous refuges in the littoral zone. Although the abundance of this prey varies temporally with marine productivity and wave action, we speculate that marine resources are more predictable in space and time than many terrestrial foods in our desert system. The ability of *Peromyscus* to eat marine prey may in part explain its widespread distribution among islands in the Gulf and elsewhere (McCabe and Cowan 1945; Grant 1970; Redfield 1976; Adler et al. 1986). *Peromyscus* inhabits 77% of the islands surveyed off Baja California, (compared to only 27% and 35% for herbivorous *Neotoma*) and granivorous (*Chaetodipus*, *Dipodomys*) rodents, respectively (Lawlor 1983). Lawlor (1983) attributed the scarcity of granivores on Gulf islands to be a consequence of insufficient seed production on small islands with few plant species. Indeed, the two small islands inhabited by *C. rudinoris* have relatively high plant diversity for their size (P. West, University of Arizona, unpublished data). Unlike *C. rudinoris*, which depends on ephemeral seed production and seed caches, insular *P. maniculatus* populations may be buffered from vagaries of terrestrial productivity by a rich supply of marine-derived foods.

The importance of marine inputs in rodent diets, however, and the degree to which these inputs penetrate inland via mice, differed among islands of different size (Fig. 2). On Coronadito, a small roosting island, *P. maniculatus* apparently ate littoral prey at all distances from shore, and not seeds or insects associated with plants, which have distinctly enriched  $\delta^{15}\text{N}$  values on islands fertilized by seabird guano (Stapp et al. 1999). In contrast, consumption of littoral prey on Ventana was largely restricted to the areas immediately adjacent to shore (Fig. 2), which suggests that mice are less effective vectors of inland transport of marine nutrients on large islands such as Ventana and presumably, the peninsula. This conclusion is supported by data on movement patterns of *Peromyscus*: mean ( $\pm$  SE) distances between captures were significantly longer on small ( $23.8 \pm 1.8$  m,

$n=117$  individuals) than large islands ( $15.9\pm 2.2$  m,  $n=86$  individuals), and a significantly greater proportion of mice captured near shore moved inland on small islands (35%) than on large ones (12%; P. Stapp, unpublished data).

#### Effects of marine resources on rodent abundance

Marine inputs can have significant indirect effects on interior populations, however, if net productivity is higher near shore and if coastal populations act as a source of dispersers. Our limited sampling did not allow us to compare the productivity of interior versus coastal populations but our results clearly show that *P. maniculatus* were most abundant near shore and on islands expected to have the highest marine inputs, either from the shore or from direct and indirect effects of seabirds. Others have reported high coastal densities of small mammals, including *Peromyscus* (McCabe and Cowan 1945; Thomas 1971; Herman 1979), *Mus* (Berry and Tricker 1969; Efford et al. 1988; Rowe-Rowe and Crafford 1992) and shrews (*Crocidura*, Spencer-Booth 1963; *Sorex*, Stewart et al. 1989), but ours is one of the first to link high coastal or insular densities to the consumption of marine prey. Population densities of small mammals are generally higher on islands than adjacent mainland sites (Gliwicz 1980; Adler and Levins 1994) and a negative relationship between density and area has been reported for both oceanic and freshwater islands as well as isolated habitat 'islands' on land (Smith and Vrieze 1979; Crowell 1983, Tellería et al. 1991; Nupp and Swihart 1996). These studies and our results contrast with general conclusions of reviews by Conner et al. (2000) and Bowers and Matter (1997), who reported either a positive or no significant relationship between density and size of habitat patches for most mammals.

High insular population densities are the result of decreased immigration combined with higher reproductive success and/or lower mortality relative to mainland populations (Gliwicz 1980). Several hypotheses have been proposed to explain high insular densities, including frustrated dispersal and competitive or predatory release (MacArthur et al. 1972), and all of these factors may apply to insular rodent populations in the Gulf of California. For example, frustrated dispersal could lead to the accumulation of subordinate individuals along shore, but the few juveniles and sub-adults that were captured in this study were caught in equivalent proportions among distance categories. The negative relationship between overall abundance and the proportion of captures near shore also indicated that, where rare, *P. maniculatus* tended to be most concentrated near shore, suggesting an affinity for supralittoral habitats. We have attributed high shore densities of *P. maniculatus* to abundance of littoral prey but *P. maniculatus* may also prefer shrubby vegetation associated with the supralittoral zone on many landings. This would not explain the high densities of *P. maniculatus* on the small, mostly barren

seabird islands but the rocky substrates on these islands may provide adequate refuge in the absence of significant shrub cover.

The apparent preference of *P. maniculatus* for shoreline areas also seems to be reinforced by the presence of *C. rudinoris*; on the three islands occupied by both species, on average 82% of *P. maniculatus* individuals were captured within 25 m of shore. Accounting for island size, *P. maniculatus* tended to be less abundant on islands it shared with *C. rudinoris* than where it occurred alone. Competition between the two species therefore may influence their local distributions, especially in wet years when shared foods are more plentiful (P. Stapp and G. Polis, unpublished data). Predation by rattlesnakes may also contribute to the lower abundance of both species on Smith, the largest island in the bay, where total abundance of rodents was low and similar to that on the predator-rich peninsula.

Although we did not directly manipulate marine inputs, the association between consumption of marine foods and relative abundance suggests that ocean resources fuel higher productivity of coastal and insular *P. maniculatus* populations and allow mice to persist despite extremely low terrestrial productivity. In addition to supporting higher densities, small islands contained more individuals that were reproductively active and a greater proportion of juveniles than on larger islands, suggesting subsidized populations may also be more productive. Direct estimates of the amount of marine inputs to each island are not available but small islands have a greater proportion of their area near the productive shore, and others have invoked this high secondary productivity to explain dense consumer populations in coastal and insular environments (Case 1975, Nilsson 1977, Bengtson and Bloch 1983, Polis and Hurd 1996). Obviously, shoreline effects cannot explain all cases of high insular population densities (e.g., herbivorous mammals; Gliwicz 1980), but the large amount of prey near shore may be more important for insular insectivores and omnivores than has been previously appreciated. By analogy, the abundance of resources in edge areas may in part explain the high densities of omnivorous mammals in small terrestrial islands (cf. Nupp and Swihart 1996).

#### Conclusions

Our results should be considered somewhat tentative because our work was limited to one season in a single year and a relatively small number of islands, but they nonetheless add to growing evidence of the potential contributions of marine resources to insular and coastal food webs in Baja California and worldwide (Polis et al. 1997a). A wide range of land-based consumers use marine foods but most also rely on terrestrial items, including arthropods, seeds and plant litter. Spillover predation by high densities of subsidized consumers may have significant effects on alternate terrestrial prey. *Peromyscus maniculatus*, for example, eats tenebrionid

beetles and may depress beetle numbers locally and on an island-wide basis (P. Stapp and F. Sánchez Piñero, unpublished data). Consumption of seeds by *P. maniculatus* may also reduce seed availability for *C. rudinoris* and other granivores. The indirect food-web effects of marine subsidies will likely vary with temporal variation in terrestrial productivity as well; *P. maniculatus*' diet consists primarily of terrestrial foods such as arthropods and seeds during wet El Niño years (Stapp et al. 1999).

The increasing recognition of the inter-connections between the land and ocean also have important implications for the conservation of insular faunas. Introduced predators pose a major threat to native species on islands and many of the most significant predators may be subsidized directly or indirectly by resources from the ocean. Mice and rats, for example, have been implicated in the declines of native terrestrial species (e.g., Towns 1991; Cree et al. 1995; Palmer and Pons 1996) as well as breeding seabirds (Atkinson 1985). Introduced rodents consume marine-based prey (Efford et al. 1988; Navarrete and Castilla 1993, Stapp 2002b), which may buffer their populations during lean times, e.g., outside seabird nesting seasons. Moreover, cats introduced to control rodents are among the most significant seabird predators (Anderson et al. 1989; McChesney and Tershy 1998). To the extent to which commensal species depend on human habitats or foods, the activities of humans themselves effectively subsidize these and other exotic predators and contribute to the destruction of native faunas. The consequences of these and other trophic subsidies are not unique to islands (e.g., Boarman 1992; Crooks and Soule 1999), but studies of insular systems can provide valuable insights that can be broadly applied to the conservation of increasingly fragmented terrestrial landscapes as well as insular communities.

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