

Influence of pulsed resources and marine subsidies on insular rodent populations

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Inputs of marine resources contribute to high consumer densities on small, barren islands in the arid Gulf of California, Mexico. Episodes of rainfall associated with El Niño Southern Oscillation (ENSO) events, however, stimulate plant growth and seed production and replenish soil detritus and seed banks. We studied the effects of marine inputs and pulsed ENSO resources on rodent populations on islands before, during and after the strong 1997–1998 ENSO event. Stable isotope analysis was used to determine rodent diets. During dry years, *P. maniculatus* consumed marine prey near shore and on small islands, and were much more abundant in these areas than farther inland and on larger islands. Captures were particularly concentrated near shore on three islands inhabited by *Chaetodipus ruidinoris*, a granivore that was numerous in inland areas. Following the ENSO, *Peromyscus maniculatus* increased in abundance by 408%, compared to only 160% for *C. ruidinoris*, and new individuals invaded inland areas. *P. maniculatus* populations declined sharply the following year, however, whereas *C. ruidinoris* populations remained relatively stable. In response to ENSO conditions, *P. maniculatus* ate more seeds on islands with *C. ruidinoris* than on islands without *C. ruidinoris*. *P. maniculatus* also increased less markedly and declined more quickly in abundance where *C. ruidinoris* was present. We speculate that *P. maniculatus* is capable of rapid numerical response to resource pulses but depends on marine foods during dry years. *C. ruidinoris* is restricted to islands with sufficient seed resources, but maintains stable populations by exploiting low-density seeds and caching seeds from wet years. On islands with both species, *C. ruidinoris* restricts *P. maniculatus* to near-shore areas via interference, but spillover consumption of seeds by subsidized *P. maniculatus* may limit the response of *C. ruidinoris* to ENSO resources. Combined with differences in life history and dispersal abilities, these ecological factors help explain the distinct biogeographic distributions of these rodents on Gulf islands.

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The evolution and ecology of desert communities are strongly influenced by the patchy and ephemeral nature of resources (Polis 1991). Because of their characteristically low and unpredictable primary productivity, energy flow through deserts and other extreme environments is often dependent on resources produced from outside the local system, that is, allochthonous materials carried by the wind, biotic vectors, or in coastal deserts, via inputs from the ocean (Swan 1963,

Borkhamm 1987, Polis and Hurd 1996). In situ primary productivity in arid regions is strongly influenced by precipitation (Rosenzweig 1968), and plants respond quickly both vegetatively and in seed production to even modest rainfall events (Gibbs and Grant 1987, Dillon and Rundel 1990). This flush of resources is critical in deserts, not only for the immediate increase in productivity, but because resources produced during these periods remain in the system long after an event

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has passed, in the form of litter and seed banks or in consumer tissues (Noy-Meir 1973, 1974). Such inputs in both space and time permit a diversity and abundance of life that would otherwise not be possible based on local, annual productivity.

On barren islands in the Gulf of California, Mexico, marine resources are a major source of energy and nutrients to terrestrial food webs. During dry years that characterize the region, allochthonous resources from a rich marine environment contribute more to insular food webs than terrestrial plant productivity (Polis and Hurd 1996). These resources arrive via shore drift of algae and carrion or are transported by seabirds, and fuel rich and diverse assemblages of scavengers and their predators in littoral and supralittoral areas and in seabird colonies (Polis and Hurd 1996, Sánchez Piñero and Polis 2000). Seabirds also provide nitrogen and phosphorus to soil through the tons of guano they deposit in roosting areas, which enhances establishment and growth of plants (Anderson and Polis 1999), and ultimately herbivore and predator populations. Through these direct (detritus and carrion input) and indirect (guano fertilization) effects, the ocean effectively subsidizes terrestrial food webs on Gulf islands.

The dynamics of insular ecosystems in the Gulf are strongly influenced, however, by changes in plant productivity during periods of high rainfall such as those that accompany El Niño Southern Oscillation (ENSO) events in the Pacific Ocean (Philander 1990). ENSO events have strong effects on marine ecosystems from Australasia to the Americas (Quinn et al. 1978, Barber and Chavez 1983, Allan 2000, Glantz 2001), with dramatic consequences for terrestrial communities (Gibbs and Grant 1987, Wright et al. 1999, Grant et al. 2000). On Gulf islands, increased precipitation stimulates growth and seed production of perennial plants and makes nutrients in guano-enriched soil available to annual plants, leading to an explosive increase of vegetative cover on islands with seabird colonies (Polis et al. 1997, A. Subalusky, unpubl.). In response, insects such as aerial herbivores (Polis et al. 1997) and plant detritivores (Sánchez Piñero and Polis 2000) increase dramatically in abundance, leading to large increases in spider populations (Polis et al. 1998). For many populations, these increases are short-lived; however, the effects of wet-year pulses of terrestrial resources may persist after the resumption of dry conditions as temporal subsidies in the form of plant litter and seeds, or in the bodies of long-lived animals.

Here we describe results of four years of field work to determine the combined effects of marine resources and ENSO-related changes in terrestrial resources on rodents on islands in the central Gulf of California. Small mammal populations in arid and semi-arid environments are strongly affected by changes in pro-

ductivity resulting from ENSO-related rainfall (Brown and Heske 1990, Meserve et al. 1995, Lima et al. 1999) as well as seasonal variation in precipitation (Brown 1973, Whitford 1976). Rodents potentially play important ecological roles on Gulf islands through their burrowing activities, by eating and caching seeds, and as predators of arthropods and other small vertebrates. Two species inhabit islands in our study area in and near Bahía de los Angeles, Baja California (Stapp 2002). *Peromyscus maniculatus*, a small (22 g) omnivorous murid, is found throughout North America and in a wide range of habitats. *Chaetodipus rudinoris* (20 g; formerly *C. baileyi*, Riddle et al. 2000) is one of several heteromyid rodents in the region and is primarily granivorous (Reichman 1975). The two species have very different biogeographic distributions on Gulf islands: *Peromyscus maniculatus* inhabits 10 of 18 islands in the area, whereas *C. rudinoris* is only found on three islands and never without *P. maniculatus*. Lawlor (1983) reported a similar distributional pattern for *Peromyscus* and *Chaetodipus* species on islands throughout the Gulf, which he attributed to the generalist habits of *Peromyscus* and the scarcity of seeds for *Chaetodipus* on most islands. Except for Lawlor's work (Lawlor 1971, 1982) and a few autecological studies (Vaughan and Schwartz 1960, Smith 1992), little is known of the ecology of mammals on these small, barren islands.

We live-trapped rodents on 6–10 islands in the Gulf to track changes in insular rodent populations before, immediately after and for three years following one of the strongest ENSO events of the century, in the winter of 1997–1998 (Changnon 2000, Glantz 2001). Diets were determined using stable isotope analysis, which allowed us to quantify changes in the contributions of marine and terrestrial prey to rodent tissue over time. We hypothesized that ENSO-related terrestrial resources would result in an increase in populations of both species, especially *C. rudinoris*, which depends on seed production. We also predicted that the influx of terrestrial foods would increase dietary and spatial overlap and affect interactions between these species on islands where they co-occur. For example, high densities of subsidized *P. maniculatus* might depress seed availability for *C. rudinoris* and reduce the latter's numerical response to increased seed production. Alternately, if *C. rudinoris* exploited seeds more effectively, it could monopolize and exclude *P. maniculatus* from consuming seeds. *Peromyscus maniculatus* populations might still increase because of ENSO-related increases in arthropod prey, but the magnitude of the increase would be lower than on islands lacking *C. rudinoris*, where *P. maniculatus* would have greater access to seeds as well as arthropods and marine-based foods.

Materials and methods

Field studies

Field work was conducted on islands in and near Bahía de los Angeles (28° 55' N, 113° 30' W) between 1997 and 2001. The islands are steep and rocky and have little vegetation (1–5% cover); perennial shrubs (*Atriplex barclayana*, *Viscainoa geniculata*, *Lycium* spp., *Bursera* sp.) and cacti (*Pachycereus pringlei*, *Opuntia* sp.) are the dominant plants. The area is one of the driest in North America, with mean annual precipitation of only 59 mm (Reyes-Coca et al. 1990). Between September 1997 and March 1998, however, a strong ENSO event in the Pacific brought 131 mm of rain, ending a 30-month drought during which only 38 mm of rain fell (Ing. Manuel Colima, Comisión Nacional del Agua, in litt). Plant cover in March 1998 ($\bar{x} \pm 1$ se: $15.63 \pm 1.00\%$, $n = 14$ islands) was three times higher than in the previous spring ($5.19 \pm 0.81\%$, $n = 11$ islands; F. Sánchez Piñero, unpubl.), largely as a result of an increase in annual plants (*Amaranthus watsonii*, *Chenopodium murale*, *Perityle emoryi*, *Cryptantha* sp.). Reproductive activity of *Atriplex barclayana*, one of the most common perennial shrubs on the islands, also increased dramatically; nearly three times as many individuals produced flowers and/or seeds in 1998 as in 1997 (A. Subalusky, unpubl.). In the three years following the 1997–1998 ENSO event (April 1998–April 2001), annual precipitation averaged only 27 mm (Ing. Manuel Colima, Comisión Nacional del Agua, in litt).

P. maniculatus inhabits nine of the 14 islands in the bay and one (Blanca) of four islands in nearby Bahía Las Animas; *C. ruidinoris* is present only on Pata, Mitlán, and Smith (Fig. 1). Except for four islands (Piojo, 0.57 km²; Cabeza de Caballo, 0.77 km²; Ventana, 1.41 km²; Smith, 9.13 km²), all were < 0.20 km² in area and most were 2–3 km offshore. Four islands (Blanca, Coronadito, Flecha, Piojo) were used by seabirds (Brown Pelicans, Yellow-footed Gulls, Double-Crested Cormorants) as roosting or nesting areas. Thus, islands inhabited by *P. maniculatus* were classified by the presence of seabirds (SB, $n = 4$), the presence of *C. ruidinoris* (WC, $n = 3$), and the absence of both seabirds and *C. ruidinoris* (NC, $n = 3$). *C. ruidinoris* is absent from all SB islands in the bay.

The remote location and extreme environmental conditions were significant constraints on field work. During most trips to the area, one or two researchers camped on islands and visited islands by sea kayak. The intense heat and the distance between islands limited the number of islands and traps that could be monitored concurrently without causing large numbers of trap-related deaths. Nesting islands could only be visited outside the seabird breeding periods, which lasted from March–June. Islands were usually trapped once from May–July each year and also in October–November 1998. Six islands (Coronadito, Flecha, Ven-

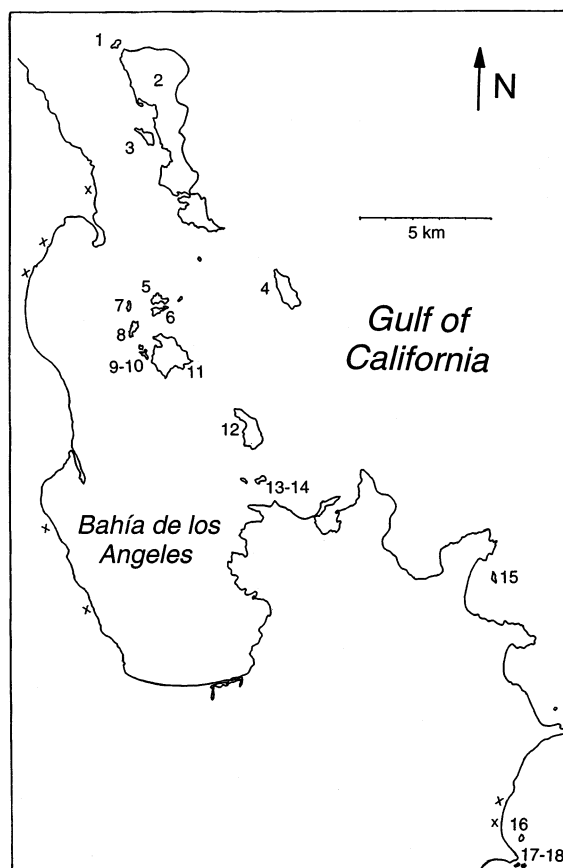


Fig. 1. Map showing the location of islands in the study area in the Gulf of California, México. *Peromyscus maniculatus* was present on 10 islands: Coronadito (1), Smith (2), Mitlán (3), Piojo (4), Pata (5), Bota (6), Flecha (8), Ventana (11), Cabeza de Caballo (12), and Blanca (16). *Chaetodipus ruidinoris* inhabited Smith (2), Mitlán (3), and Pata (5). Mice were absent from Jorobado (7), Llave (9), Cerraja (10), Gemelos West and East (13–14), Pescador (15), and Las Animas Norte and Sur (17–18). Mainland trapping sites are denoted by an “X”.

tana, Pata, Mitlán, Smith) were trapped in all 5 years of the study, Bota was trapped in 4 years (1998–2001), Blanca in 3 years (October 1998, 1999 and 2000), and Piojo only in October 1998 and in 2000. Cabeza de Caballo was omitted from all analyses because mice were not found there until 2000. Two sites on the mainland were trapped once in May–July each year and in October 1998, although sites differed among years.

One rectangular live-trapping grid was established at or near landings on each island to estimate relative abundance and collect tissue samples for stable isotope analysis. Trap lines were 15 m apart, with traps spaced at 25 m intervals along each line. Grids originated in the supralittoral zone and extended perpendicular to shore for 125 m inland. Traps were set farther inland on large islands (Smith, Ventana, Piojo, mainland) but captures in these traps are omitted here so as to stan-

standardize trapping effort and area. In 1997, grids consisted of 36 large Sherman traps (six lines of six traps) set for three consecutive nights. In 1998 and subsequent years, grids were reduced to 24 traps (four lines of six traps). Limited boat access and extremely steep terrain of some islands (Mitlán, Blanca) required us to set traps in pairs of transects (18–24 traps) and for only two nights. In Autumn 1998, all sites were only trapped for two consecutive nights. Except for the rocky seabird islands, the first two rows of traps were situated in a narrow band of coastal vegetation (*Salicornia subterminalis*, *Batis maritima*, *Frankenia palmeri*) immediately above the supralittoral zone, which graded into desert scrub vegetation farther inland.

Traps were baited with peanut butter and oats each night and closed at or before dawn the next morning to prevent mortality from heat and ants. Each captured individual was weighed, measured and given a uniquely numbered ear tag. In 1997 and 1998, a small (2–3 mm) distal piece of tail tissue was collected from a subset of mice for isotope analysis following protocols approved by the Animal Use and Care Committee at the University of California, Davis. Tail tissue (mostly bone and cartilage) was stored in separate vials in 75% ethanol and then frozen upon returning to the laboratory. All individuals were released at their location of capture. To aid in determination of rodent diets, tissue samples of potential invertebrate prey were collected by hand or in pitfall traps and stored in ethanol. Algae and seed and leaf tissue of plants were also collected and dried.

We used the number of unique individuals captured per unit trapping effort (individuals per 100 trap-nights, TN; discounted by 0.5 TN for each sprung trap that was empty) as an index of relative abundance. Individuals were placed into distance categories based on the location of first capture (mean capture location provided same results); captures were then pooled by trap row and divided by trapping effort to estimate relative abundance at different distances from shore (0–25 m, 50–75 m, 100–125 m). These values were then used to calculate the proportion of individuals captured at different distance categories on each island, which were used to compare spatial distribution of captures among islands that differed in relative abundance.

The time elapsed between most trapping sessions (approximately 1 year) exceeded the expected life-span of most individuals, which precluded precise calculations of survival rates. Rates of recaptures between trapping sessions were therefore used to estimate relative survival rates. Relative survival rate between two trapping periods was calculated as the fraction of individuals tagged and alive during the first trapping session that were recaptured or known to be alive during the second trapping session. This approach assumes no migration and equal trapping probabilities among islands and years.

Laboratory analyses

Tissue samples were dried for 12–24 h at 50°C, ground and weighed and placed in tin capsules. Stable carbon (C) and nitrogen (N) isotope ratios were determined using a Europa 20–20 continuous-flow isotope ratio mass-spectrometer connected to a Europa C–N analyzer at the Stable Isotope Facility at the University of California, Davis. Isotope values were expressed as the isotopic ratio ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) of the sample relative to a standard in parts per 1000 (‰):

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

where X is ^{13}C or ^{15}N and R is the ratio of heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$). The lab standard for estimating $\delta^{13}\text{C}$ was beet sucrose (–23.83‰ vs Pee Dee Belemnite, calibrated against NIST 22 at –29.73‰) and for $\delta^{15}\text{N}$, ammonium sulfate (1.33‰ vs air, calibrated against IAEN1 and IAEN2; D. Harris, University of California, Davis, pers. comm.).

Statistical analyses

Repeated-measures nested analysis of variance (ANOVA) was used to test the effects of the presence or absence of *C. ruginoris*, and the effects of seabirds (SB) on temporal patterns of abundance and spatial distribution of *P. maniculatus*. Differences in stable isotope signatures between species, years, and location relative to the shore were tested using ANOVA. Proportions were arcsine-square root transformed prior to analysis; relative abundance estimates were log-transformed. Unless indicated otherwise, values presented are means \pm 1 standard error of the mean. All statistical analyses were performed using SAS (SAS Institute 1989).

Results

Shifts in rodent diet

The stable carbon and nitrogen isotope signatures of plant and invertebrate foods potentially available to rodents are given in Table 1. Plants using C_3 and C_4/CAM photosynthesis differ in their $\delta^{13}\text{C}$ signatures, and representatives of both groups were found on Gulf islands. In general, $\delta^{13}\text{C}$ values for marine-derived prey were enriched in ^{13}C relative to C_4/CAM plants and much lower than those of terrestrial consumers and C_3 plants. Nitrogen signatures of both plants and terrestrial consumers were strongly influenced by the presence of seabirds. On islands lacking seabird colonies, plants had much lower $\delta^{15}\text{N}$ than similar plants on SB islands, reflecting the contributions of guano-derived N

Table 1. Stable C and N signatures of potential food items of rodents on islands in the Gulf of California, Mexico. Values are means \pm 1 SE, with sample size in parentheses (sample size same for C and N). Prey were collected on islands with and without seabird colonies and in the littoral zone of islands and the adjacent mainland.

| Prey type | Carbon $\delta^{13}\text{C}$ (‰) | | Nitrogen $\delta^{15}\text{N}$ (‰) | | Taxa included |
|--------------------------------|----------------------------------|------------------------|------------------------------------|------------------|---|
| | Seabirds | No seabirds | Seabirds | No seabirds | |
| TERRESTRIAL | | | | | |
| Seeds and leaves | | | | | |
| C_3 plants | -22.27 ± 0.34 (5) | -23.22 ± 0.81 (9) | 27.22 ± 3.00 | 9.54 ± 2.00 | Amaranthaceae, Asteraceae, Onagraceae, Scrophulariaceae, Solanaceae, Zygophyllaceae |
| C_4/CAM plants | -13.67 ± 0.33 (12) | -14.76 ± 0.63 (10) | 28.03 ± 1.88 | 14.03 ± 1.15 | Aizoaceae, Cactaceae, Chenopodiaceae |
| Herbivores | -16.04 ± 1.11 (11) | -18.00 ± 1.34 (10) | 32.37 ± 1.30 | 14.65 ± 2.62 | Acrididae, Anobiidae, Curculionidae, Ptinidae, Psycidae |
| Detritivores | -18.20 ± 0.93 (13) | -19.85 ± 0.70 (15) | 29.39 ± 0.77 | 14.13 ± 1.90 | Lepismatidae, Tenebrionidae |
| Predators | -16.19 ± 0.75 (13) | -19.63 ± 0.41 (6) | 25.75 ± 1.08 | 16.16 ± 1.19 | Agelenidae, Araneidae, Lycosidae |
| MARINE | | | | | |
| Algae | -11.55 ± 1.50 (7) | | 12.57 ± 0.42 | | Sargassaceae, Ulvaceae |
| Littoral invertebrates | -12.13 ± 0.43 (34) | | 14.13 ± 0.41 | | Muricidae, Cancridae, Diogenidae, Gammaridae, Ligiidae, Tenebrionidae, Histeridae |
| Fish carrion | -14.51 ± 0.51 (5) | | 17.21 ± 0.59 | | Serranidae |

in the soil (Anderson and Polis 1999, Stapp et al. 1999). The $\delta^{15}\text{N}$ values of herbivores, plant scavengers and predatory arthropods on SB islands were similarly enriched (Table 1). On SB islands, $\delta^{15}\text{N}$ of spiders was lower than that of herbivores and detritivores, presumably because these spiders included some marine-derived prey, with lower $\delta^{15}\text{N}$, in their diets (Stapp et al. 1999).

Isotope analyses of rodent tissues suggested that, in 1997, the diet of *P. maniculatus* living close to shore was similar across islands (Fig. 2a, Table 2). Comparing these

values to potential prey in Table 1, the relatively high $\delta^{13}\text{C}$ ($> -14\text{‰}$) and intermediate $\delta^{15}\text{N}$ values (14–18‰) of near-shore mice were consistent with a diet of littoral invertebrates. Littoral prey were also important foods in inland areas of SB and WC islands in 1997 (Fig. 2b), suggesting that mice living inland on these small islands traveled to and foraged near the ocean. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were significantly lower in inland areas of Ventana (NC) than in inland areas of other islands in 1997 (Fig. 2b, Table 2), which is consistent with a diet of seeds and terrestrial arthropods.

Fig. 2. Shifts in stable isotope signatures of *Peromyscus maniculatus* (filled symbols) and *Chaetodipus ruidinoris* (open squares) between dry 1997 and the wet 1998 El Niño year in: a) areas 0–25 m from shore, and b) areas ≥ 50 m inland. Each point represents the mean for one island. Lines connect means for islands sampled in both 1997 and 1998; for clarity, standard errors are only given for islands sampled in both years [(Coronadito (SB); Pata, Smith (WC); Ventana (NC)]. Letters denote significant differences (ANOVA, $P < 0.05$) between years on seabird islands (SB; a, b), islands with *C. ruidinoris* (WC; c, d; results for *C. ruidinoris* italicized) and islands with neither seabirds nor *C. ruidinoris* (NC; e, f).

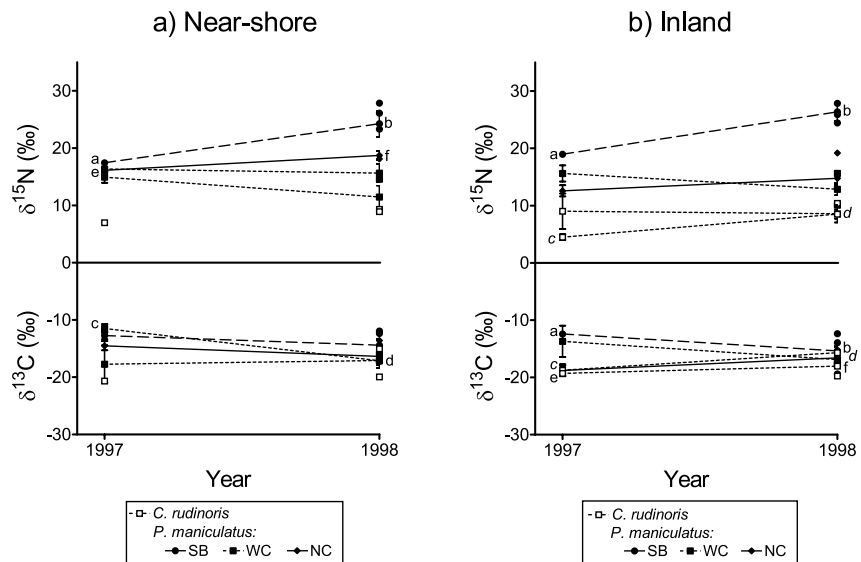


Table 2. Results of analysis of variance tests to determine differences in stable carbon and nitrogen isotope signatures of *P. maniculatus* among islands with seabird colonies (SB), islands with *C. rudinoris* (WC) and islands with neither seabirds nor *C. rudinoris* (NC). Island types sharing an underline were not significantly different from one another (Tukey's HSD multiple comparison test, $P \leq 0.05$; n.s. = not significant).

| | F | d.f. | P | Tukey HSD |
|--------------|-------|-------|--------|-----------------|
| 1997 Dry | | | | |
| Nearshore | | | | |
| Carbon | 0.38 | 2, 11 | 0.694 | n.s. |
| Nitrogen | 3.01 | 2, 11 | 0.091 | n.s. |
| Inland | | | | |
| Carbon | 20.79 | 2, 13 | 0.0001 | <u>SB WC NC</u> |
| Nitrogen | 21.83 | 2, 13 | 0.0001 | <u>SB WC NC</u> |
| 1998 El Niño | | | | |
| Nearshore | | | | |
| Carbon | 3.54 | 2, 30 | 0.042 | <u>SB NC WC</u> |
| Nitrogen | 36.86 | 2, 30 | 0.0001 | <u>SB NC WC</u> |
| Inland | | | | |
| Carbon | 1.65 | 2, 53 | 0.201 | n.s. |
| Nitrogen | 79.34 | 2, 53 | 0.0001 | SB NC WC |

In contrast to the omnivorous habits of *P. maniculatus*, the consistently low $\delta^{15}\text{N}$ signature of *C. rudinoris* (Fig. 2) indicated that it ate primarily plant material and presumably, seeds. On the three islands (WC) where they occurred together, $\delta^{15}\text{N}$ values of *C. rudinoris* were significantly lower than those of *P. maniculatus*, both in coastal and inland locations and before and after the 1998 ENSO (ANOVA, $P < 0.05$). In 1997, both coastal and inland *P. maniculatus* had significantly higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than *C. rudinoris*. By 1998, the two species apparently used an isotopically similar C source ($F = 0.24$, d.f. = 1, 15, $P = 0.629$ near shore; $F = 0.01$, d.f. = 1, 30, $P = 0.915$ inland), but $\delta^{15}\text{N}$ of *P. maniculatus* was still significantly higher than that of *C. rudinoris* in both near-shore ($F = 5.80$, d.f. = 1, 15, $P = 0.029$) and inland locations ($F = 10.75$, d.f. = 1, 30, $P = 0.003$). Mean $\delta^{15}\text{N}$ of *P. maniculatus* on islands inhabited by *C. rudinoris* (WC) was significantly lower than that on all other island types (Fig. 2b, Table 2), which is consistent with an increase in the consumption of seeds, and hence, greater dietary overlap with *C. rudinoris* on these islands during the ENSO year. On NC islands, $\delta^{15}\text{N}$ signatures of inland *P. maniculatus* in 1998 were higher than on WC islands, indicating that terrestrial arthropods were more important on islands without *C. rudinoris*. There was a slight but significant increase in $\delta^{15}\text{N}$ between years near shore on NC islands (Fig. 2a), but marine prey apparently continued to be consumed by coastal mice on NC islands in 1998. Carbon signatures of inland *P. maniculatus* were similar among islands in 1998, but the large differences among islands in $\delta^{15}\text{N}$ reflected the contributions of guano to plants and consumers on SB islands (Fig. 2b). The enriched $\delta^{15}\text{N}$ values of *P. maniculatus* from both inland and coastal locations of these islands suggested

increased consumption of terrestrial resources, presumably seeds from guano-fertilized plants, and the significant decline in $\delta^{13}\text{C}$ of inland mice suggested that mice took advantage of the pulse of C_3 annuals on these islands.

The direct and indirect effects of marine-derived resources on the diet of *P. maniculatus* are particularly evident by comparing $\delta^{15}\text{N}$ values of tissues collected in 1998 at different distances from shore on Ventana, a large NC island, with those from Piojo, a similar-sized island with a large nesting colony of Brown Pelicans (Fig. 3). Near shore, *P. maniculatus* from both islands appeared to consume littoral prey. The proportion of land-based foods increases in mice captured farther inland, as indicated by the significant decrease ($r^2 = 0.66$, $P = 0.003$) and increase ($r^2 = 0.52$, $P = 0.002$) in $\delta^{15}\text{N}$ on Ventana and Piojo, respectively. On Ventana, isotope signatures of *P. maniculatus* were consistent with a diet of insects and seeds (Table 1). On Piojo, the elevated $\delta^{15}\text{N}$ values also suggested consumption of terrestrial resources, but the nitrogen in these foods ultimately originated from seabird guano.

Effects on relative abundance and survival

Populations of the two species were affected differently by the 1997–1998 ENSO event. On average, *P. maniculatus* increased by 408% between May 1997 and May 1998 (Fig. 4, Table 3), but numbers then fell by 41% between 1998 and 1999. Although population responses varied among islands, changes in abundance of *P.*

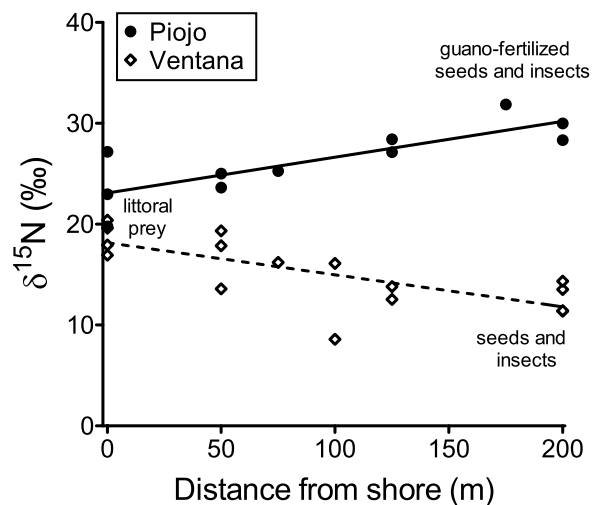


Fig. 3. Direct and indirect effects of marine resources on the diet of *P. maniculatus*, as demonstrated by changes in $\delta^{15}\text{N}$ values with increasing distance from shore on Piojo, a seabird nesting island, and Ventana, a large island lacking seabirds, in 1998. Each point is one individual. Lines are significant linear regressions ($P \leq 0.003$) for Piojo (solid) and Ventana (dashed) values. Broad diet categories are based on $\delta^{15}\text{N}$ values in Table 1.

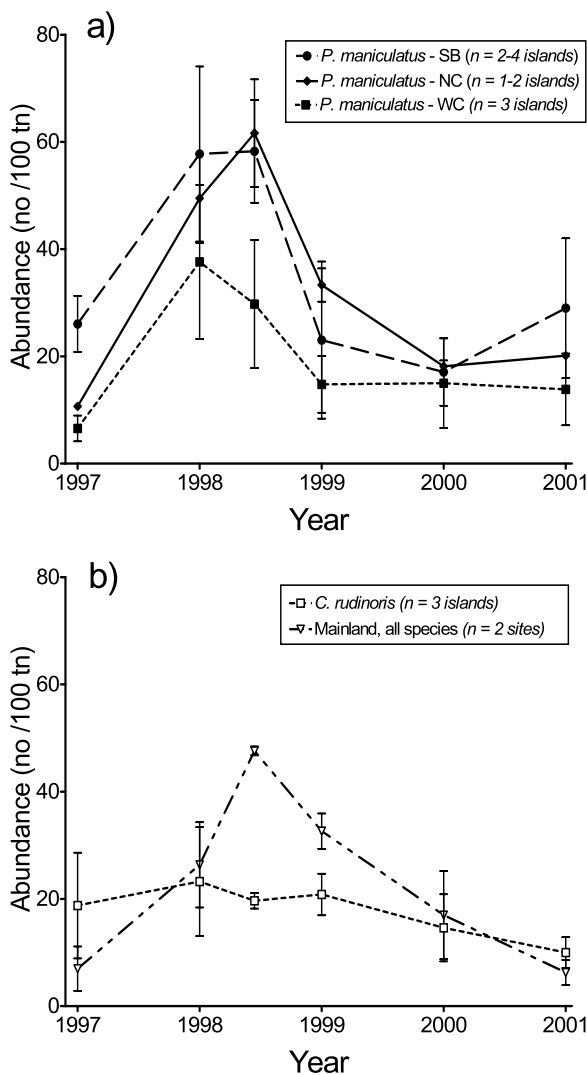


Fig. 4. Temporal variation in the abundance (individuals/100 trap-nights) of a) *P. maniculatus* on islands with seabirds (SB), with both species (WC) and islands without seabirds inhabited only by *P. maniculatus* (NC); and b) *C. rudinoris* on Gulf islands, from 1997–2001. Estimates of the combined abundance of all nocturnal rodents captured on two mainland sites each year are provided in b) for comparison. Values are means \pm 1 SE of the number of islands (n), in parentheses.

maniculatus tended to be more pronounced on islands it shared with *C. rudinoris* (WC) than on those where it occurred alone. On WC islands, *P. maniculatus* abundance was 572% (\pm 181%; n = 3) higher in 1998 than 1997, and declined sharply by 58% (\pm 16%) in 1999. On other islands, *P. maniculatus* increased by only 243% (\pm 118%; n = 3) in 1998 and declined by only 31% (\pm 16%; n = 5) by 1999. The greatest post-ENSO decline (89%) was recorded on Flecha, a small SB island where the largest number of *P. maniculatus* were captured in 1998 (Table 3). *P. maniculatus* remained

scarce on Flecha, and much lower than other SB and NC islands, until 2001.

Comparing all years, *P. maniculatus* was significantly more abundant in May and October 1998 than in 1997 and all subsequent years (repeated-measures nested ANOVA, overall model: $F = 10.31$, d.f. = 18, 27, $P = 0.0001$; YEAR effect: $F = 12.72$, d.f. = 5, $P = 0.0001$; Tukey HSD multiple comparison test, $P < 0.05$). *Peromyscus maniculatus* was consistently less numerous on islands with *C. rudinoris* than on those where it occurred alone, and populations returned more quickly to dry-yr levels on islands with *C. rudinoris* (Fig. 4, Table 3). However, there was no statistically significant difference between islands with and without *C. rudinoris* in patterns of abundance of *P. maniculatus* over time ($F = 4.30$, d.f. = 1, $P = 0.077$). This result reflected the consistently high densities of *P. maniculatus* near shore; there was no difference in the number of *P. maniculatus* captured ≤ 25 m from shore between island types ($F = 1.45$, d.f. = 1, $P = 0.267$). However, *P. maniculatus* was significantly less abundant in inland areas of WC islands than on NC and SB islands ($F = 11.05$, d.f. = 1, $P = 0.013$). Although *P. maniculatus* tended to reach its highest densities on small SB islands (Fig. 4, Table 3), there was no significant relationship between the presence of seabirds and *P. maniculatus* abundance (repeated-measures ANOVA, overall model: $F = 12.23$, d.f. = 18, 24, $P = 0.0001$; SB effect: $F = 1.72$, d.f. = 1, $P = 0.231$).

Compared to *P. maniculatus*, the increase in abundance of *C. rudinoris* between 1997 and 1998 was modest (160%). *C. rudinoris* populations were larger on two islands (Mitlán, Smith) in 1998, but decreased by 57% on Pata, the WC island with the largest number of *C. rudinoris* in 1997 and the most *P. maniculatus* in 1998. Unlike *P. maniculatus*, there was relatively little change (a 10% increase) in abundance of *C. rudinoris* between 1998 and 1999. In fact, *C. rudinoris* numbers, on average, were relatively stable for the entire study period (repeated measures ANOVA, overall model: $F = 2.52$, d.f. = 7, 10, $P = 0.090$). Island populations of *C. rudinoris* also differed markedly from those on the mainland, which were dominated numerically by *Chaetodipus* species (*C. arenarius*, *C. rudinoris* and *C. spinatus* represented $74.52 \pm 3.98\%$ of captures; n = 12 sites). Rodent abundance on mainland sites peaked in October 1998, then declined gradually before returning to pre-El Niño levels in 2001 (Fig. 4). Mainland sites differed among years, therefore no statistical tests were conducted.

Of the 484 *P. maniculatus* tagged on seven islands between 1997 and 2000, 7% (34 individuals) were captured a yr later and only 1.4% (7) were present > 1 yr, with one mouse captured 2.5 years after it was first caught. A total of 124 *C. rudinoris* were tagged on three islands during the same period; 4.8% (6 mice) were present 1 yr later, 3.2% (4) between 1–2 years later, and another 3.2% (4) were re-captured 2–3 years after their

Table 3. Numbers of *P. maniculatus* and *C. rudinoris* captured on Gulf islands, 1997–2001. See text for details of trapping methods. Values in parentheses are numbers of individuals that were recaptured from an earlier session; missing values denote periods prior to ear-tagging or islands where rodents were not permanently marked. Island types: SB, seabird-colony islands; WC, islands with *C. rudinoris*; and NC, islands with neither seabirds nor *C. rudinoris*.

| Island | Area (km ²) | Type | 1997 | May 1998 | Oct 1998 | 1999 | 2000 | 2001 |
|-----------------------|-------------------------|------|------|----------|----------|---------|--------|--------|
| <i>P. maniculatus</i> | | | | | | | | |
| Blanca | 0.03 | SB | – | – | 21 | 24 | 18 | – |
| Bota | 0.09 | NC | – | 28 | 22 (12) | 21 (8) | 12 (3) | 13 (4) |
| Coronadito | 0.10 | SB | 33 | 29 (1) | 22 (6) | 26 (9) | 20 (0) | 29 (5) |
| Flecha | 0.16 | SB | 5 | 50 | 34 (17) | 6 (0) | 5 (1) | 11 (0) |
| Pata | 0.18 | WC | 10 | 42 (0) | 24 (2) | 13 (6) | 22 (5) | 18 (5) |
| Mitlán | 0.19 | WC | 3 | 10 | 12 | 10 (7) | 5 (0) | 6 (0) |
| Piojo | 0.57 | SB | – | – | 21 | – | 11 | – |
| Ventana | 1.41 | NC | 11 | 36 (1) | 32 (15) | 25 (12) | 14 (8) | 14 (0) |
| Smith | 9.13 | WC | 2 | 12 (0) | 5 (0) | 3 (1) | 2 (1) | 2 (0) |
| <i>C. rudinoris</i> | | | | | | | | |
| Pata | 0.18 | WC | 39 | 8 (0) | 9 (2) | 14 (4) | 7 (2) | 9 (3) |
| Mitlán | 0.19 | WC | 6 | 15 | 10 | 13 (5) | 12 (5) | 6 (1) |
| Smith | 9.13 | WC | 3 | 9 (0) | 8 (2) | 10 (6) | 5 (3) | 3 (2) |

initial capture. These estimates do not account for right-censored nature of the data, and thus may slightly underestimate the proportion that were present > 1 yr, especially for *C. rudinoris*. They suggest, however, that the vast majority (88–92%) of individuals probably live ≤ 1 yr, and that *C. rudinoris* tends to be longer-lived. Interspecific differences in survival are also suggested by recapture rates between trapping sessions (Table 4). Relative survival rates of *P. maniculatus* were consistently lower than those of *C. rudinoris*, especially on islands where the two species co-occur (Table 4). Most mortality associated with the rapid post-ENSO decline in *P. maniculatus* on WC islands occurred between May and October 1998. After 1998, annual survival rates of *P. maniculatus* were relatively constant and fairly low, whereas *C. rudinoris* individuals were present considerably longer (Table 4). Averaging across all 5 years of the study for each island, the mean annual survival rate of *C. rudinoris* was significantly higher ($26.70 \pm 6.00\%$, $n = 3$ islands) than that of *P. maniculatus* ($10.56 \pm 2.76\%$, $n = 7$; $F = 8.17$, $d.f. = 1, 8$, $P = 0.021$).

We conducted a multiple regression analysis to assess the relative importance of seabirds, shoreline effects, plant diversity (species richness; P. West, unpubl.), and the presence of *C. rudinoris* as determinants of the relative abundance of *P. maniculatus* on islands during dry years. The mean dry-yr abundance of *P. maniculatus* was calculated for each island, as there was no significant difference in abundance among dry years (1997, 1999–2001; ANOVA: YEAR effect: $F = 2.45$, $d.f. = 3$, $P = 0.096$). These means were used as the response variable in a stepwise multiple regression analysis which included coded independent variables for the presence of seabirds and of *C. rudinoris*, log-transformed values of island area as an index of shoreline effects, and log-transformed plant species richness. Island area was the only variable selected in the model (α -value to enter = 0.10); mice reached highest densities

on small islands and abundance declined significantly with island area ($r^2 = 0.71$, $P = 0.004$). The effects of island area on *P. maniculatus* abundance apparently were less important during the 1997–1998 ENSO. For May 1998, none of the variables met the criteria for entry into the model, and for October 1998, the presence of *C. rudinoris* was the only variable to explain significant variation in *P. maniculatus* abundance ($r^2 = 0.52$, $P = 0.029$).

Spatial distribution

During dry years (1997, 1999–2001), more *P. maniculatus* were captured near shore than farther inland (Fig. 5). This was the case on islands with (WC) and without *C. rudinoris* (NC, SB) although captures of *P. maniculatus* were more concentrated near shore and less numerous inland on the three WC islands. *C. rudinoris* showed the opposite trend, with fewest numbers of captures within 25 m of shore and higher numbers of captures inland (Fig. 6).

The ENSO event had a brief but significant effect on the local distribution of both species. In May 1998, proportionately more *C. rudinoris* were captured near shore, so that there was no significant difference in the fraction of captures among distance classes ($d.f. = 2, 6$, $F = 3.04$, $P = 0.123$; Table 5, Fig. 6). By October 1998, *C. rudinoris* were again rare near the shore, and captured in greatest numbers far inland ($d.f. = 2, 6$, $F = 12.92$, $P = 0.007$; Fig. 6). The distribution of captures of *P. maniculatus* in 1998 also differed from 1997 and subsequent dry years. During the increase in abundance in May 1998, *P. maniculatus* invaded inland areas, and the proportion of captures did not differ significantly among distance classes, nor between islands with and without *C. rudinoris* ($d.f. = 10, 10$, $F = 1.33$, $P = 0.329$;

Table 4. Relative survival rates of island populations of *P. maniculatus* and *C. rudinoris*, estimated as the percentage of individuals that were tagged and alive during the first trapping session that were recaptured or known to be alive during the second trapping session. Separate estimates are provided for *P. maniculatus* on islands with and without *C. rudinoris*. Values are means \pm 1 SE, with the number of islands in parentheses.

| Species | May 1997–May 1998 | May 1998–October 1998 | October 1998–May 1999 | May 1998–May 1999 | May 1999–June 2000 | June 2000–May 2001 |
|-----------------------------|---------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------------|
| <i>P. maniculatus</i> | | | | | | |
| <i>C. rudinoris</i> present | 0 (2) | 6.61 \pm 1.73 (2) | 37.30 \pm 10.58 (3) | 9.56 \pm 7.11 (2) | 19.49 \pm 11.12 (3) | 9.09 \pm 9.09 (2) |
| <i>C. rudinoris</i> absent | 3.91 \pm 0.88 (2) | 40.61 \pm 6.74 (4) | 25.99 \pm 9.27 (4) | 13.27 \pm 4.83 (4) | 12.98 \pm 4.63 (4) | 14.58 \pm 8.59 (4) |
| Combined | 1.95 \pm 1.19 (4) | 29.27 \pm 8.35 (6) | 30.83 \pm 6.76 (6) | 12.03 \pm 3.65 (6) | 15.77 \pm 5.05 (7) | 12.75 \pm 6.03 (6) |
| <i>C. rudinoris</i> | 0 (2) | 35.00 \pm 15.00 (2) | 43.33 \pm 3.33 (3) | 16.67 \pm 16.67 (2) | 34.61 \pm 10.19 (3) | 33.93 \pm 8.93 (2) |

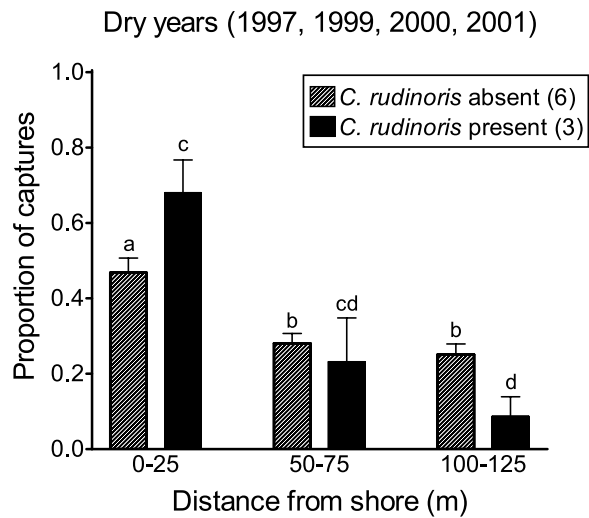


Fig. 5. Spatial distribution of captures of *P. maniculatus* on Gulf islands with and without *C. rudinoris* during dry years (1997, 1999–2001), expressed as the proportion of individuals captured at different distances from shore (mean \pm 1 SE). Within an island type, means sharing letters among distance categories are not statistically different (ANOVA of island means, Tukey HSD, $P < 0.05$). Sample size (number of islands) in parentheses.

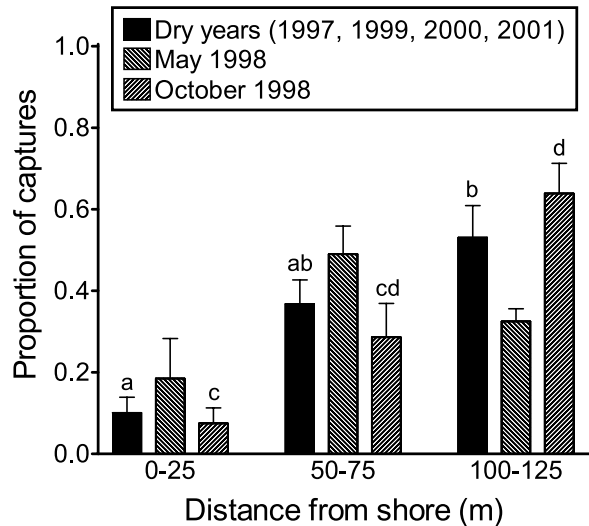


Fig. 6. Spatial distribution of captures of *C. rudinoris* on Gulf islands during dry years (1997, 1999–2001) and immediately after the 1997–1998 ENSO event, expressed as the proportion of individuals captured at different distances from shore (mean \pm 1 SE). For a given time period, means sharing letters among distance categories are not statistically different (ANOVA, Tukey HSD, $P < 0.05$, $n = 3$ islands).

Table 5, Fig. 7a). By October 1998, *P. maniculatus* remained at high densities regardless of proximity to shore on islands without *C. rudinoris*, but had returned to the dry-yr pattern near shore on WC islands (Fig. 7b).

Table 5. Results of repeated-measures analysis of variance to test differences in the spatial distribution of *P. maniculatus* and *C. rudinoris* on Gulf islands, expressed as the proportion of captures in three distance classes of traps (0–25, 50–75, 100–125 m) in relation to the shore. CKIND is a categorical variable denoting the presence/absence of *C. rudinoris*; YEAR denotes the 5 years of the study; and DISTANCE is a categorical variable representing the three distance classes.

| Species | d.f. | Type III SS | F | P |
|--------------------------|------|-------------|-------|--------|
| a) <i>P. maniculatus</i> | | | | |
| MODEL | 30 | 6.361 | 2.44 | 0.002 |
| CKIND | 1 | 0.068 | 13.54 | 0.008 |
| YEAR | 3 | 0.002 | 0.01 | 0.994 |
| DISTANCE | 2 | 4.141 | 23.83 | 0.0001 |
| ISLAND(CKIND) | 7 | 0.035 | 0.06 | 1.000 |
| YEAR × CKIND | 3 | 0.007 | 0.03 | 0.994 |
| YEAR × DISTANCE | 6 | 0.715 | 1.37 | 0.241 |
| CKIND × DISTANCE | 2 | 1.330 | 7.65 | 0.001 |
| YEAR × DISTANCE × CKIND | 6 | 0.733 | 1.41 | 0.227 |
| ERROR | 59 | 5.125 | | |
| b) <i>C. rudinoris</i> | | | | |
| MODEL | 11 | 2.727 | 4.19 | 0.002 |
| YEAR | 3 | 0.020 | 0.11 | 0.953 |
| DISTANCE | 2 | 2.168 | 18.18 | 0.0001 |
| YEAR × DISTANCE | 6 | 0.559 | 1.56 | 0.201 |
| ERROR | 24 | 1.431 | | |

Discussion

The pulse of terrestrial resources associated with El Niño precipitation has a profound effect on the ecology of islands in the Gulf of California. Like other animals that inhabit these islands (Polis et al. 1997, 1998), rodent populations benefit from ENSO resources, but the two species responded differently. During dry years typical of the region, *P. maniculatus* and *C. rudinoris* seem to occupy distinct niches. Stable isotope analysis demonstrated that *C. rudinoris* is primarily granivorous, whereas *P. maniculatus* is an omnivore and takes advantage of marine-derived prey as well as terrestrial arthropods and seeds. The benefits of marine subsidies are suggested by patterns of abundance of *P. maniculatus* in dry years, both island-wide and on a local scale. *P. maniculatus* reached its highest densities on small islands, which have a relatively large amount of coastline and therefore, potentially more marine inputs, per unit area. Many small islands are also used by roosting and nesting seabirds, which contribute nutrients and energy to these islands as carrion and nitrogen for

plants. Within an island, *P. maniculatus* was usually most numerous near shore and in close proximity to littoral prey (Fig. 5); although on small islands, even individuals living inland return to the shore to forage (Stapp et al. 1999). Captures of *P. maniculatus* were especially concentrated near shore on islands with *C. rudinoris*, which was more abundant inland. The relative scarcity of *P. maniculatus* in inland areas of these otherwise similar islands suggests interference by *C. rudinoris*. The exact mechanism by which *C. rudinoris* might influence habitat use and activity of *P. maniculatus* is not known, but heteromyid rodents such as *C. rudinoris* are often territorial and aggressive toward other rodents (Jones 1993).

Effects of El Niño events on rodent populations

The 1997–1998 ENSO event brought significant changes in the population density and spatial distribution of *P. maniculatus*. On average, *P. maniculatus* were

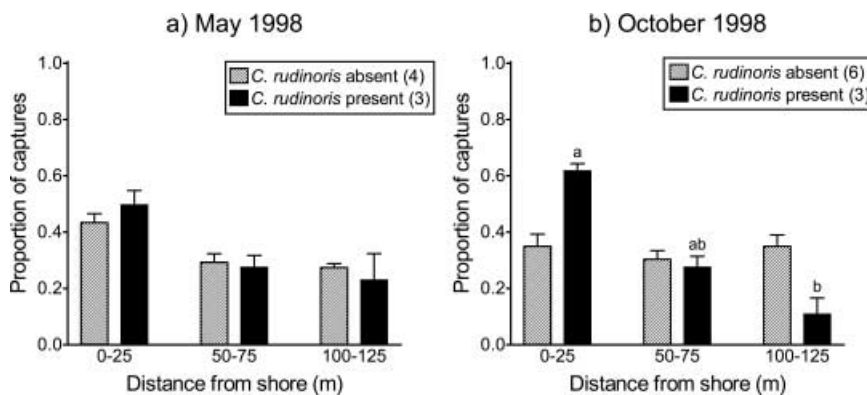


Fig. 7. Spatial distribution of captures of *P. maniculatus* on Gulf islands with and without *C. rudinoris* in a) May and b) October 1998, expressed as the proportion of individuals captured at different distances from shore (mean + 1 SE). Within an island type, means sharing letters among distance categories are not statistically different (ANOVA, Tukey HSD, $P < 0.05$). Sample size (number of islands) in parentheses.

four times more abundant in 1998 than in dry 1997, and with the pulse of reproduction, individuals moved into inland habitats. On islands inhabited by *C. rudinoris* (WC), the invasion of inland habitats was very short-lived; by autumn 1998, *P. maniculatus* were again significantly more abundant near shore on WC islands. This pattern contrasts with the spatial distribution of *P. maniculatus* on NC and SB islands, where it was captured in similar numbers at all distances from shore throughout the year. The magnitude of increase was also affected by the presence of *C. rudinoris*: *P. maniculatus* increased by 572% on WC islands but by only 273% on islands lacking *C. rudinoris*. One possible explanation for the large increase in *P. maniculatus* on WC islands may be related to seed availability. The three islands inhabited by both species have relatively high plant species diversity (P. West, unpubl.), and thus a greater variety of seeds. Isotope analysis indicated that *P. maniculatus* increased its consumption of seeds on WC islands, as well as on SB islands, where the growth of annual plants was most pronounced. On other islands, *P. maniculatus* apparently ate mostly arthropods in both 1997 and 1998 (Fig. 2). The increased consumption of seeds, combined with the invasion of inland habitats, resulted in greater dietary and spatial overlap with *C. rudinoris* at a time when seeds were plentiful.

The sharp decline in abundance of *P. maniculatus* in 1999 (Fig. 4) demonstrated that island resources are usually not sufficient to sustain ENSO levels of productivity during dry years. The exact cause of the decline is not clear, though the drastic reduction in abundance on islands such as Flecha (Table 3), where mice apparently switched to a diet of seeds and where predators are absent, suggests food limitation. Steep population declines also occurred on islands inhabited by *C. rudinoris* (Fig. 4, Table 3), where isotopic signatures suggested that *P. maniculatus* also ate primarily seeds. On WC islands most of the remaining *P. maniculatus* retreated to shore by late 1998, where they presumably survived on marine-based prey (Fig. 2a). Conversely, *P. maniculatus* was able to maintain somewhat larger populations in 1999 on most NC islands, where isotope signatures suggested that arthropods comprised most of their diet. Terrestrial predators (rattlesnakes *Crotalus mitchelli*) are absent from all but the largest islands, but owls (*Bubo virginianus*) were seen or heard on some islands, so predation cannot be completely ruled out as a source of mortality.

Compared to *P. maniculatus*, the increase in *C. rudinoris* from 1997 to 1998 was much less marked (160%; not statistically significant), and included a 57% decline in capture success on one island where *P. maniculatus* was especially abundant in 1998. The surprisingly small increase in *C. rudinoris* numbers suggests that *P. maniculatus* took advantage of the newly abundant seeds and were more effective at converting these resources into

offspring. This may reflect the relatively conservative life history (e.g. low reproductive potential, long life span; Paulson 1988) of *C. rudinoris* and other heteromyids compared to murid rodents (Whitford 1976). For example, more than one-third (37%) of individual *P. maniculatus* captured were in reproductive condition and breeding individuals were captured during all months, whereas only 7% of *C. rudinoris* individuals were reproductive and then, only in early summer. With a predicted litter size of 4.7 and potentially four litters per year (Millar 1989), annual reproductive potential of *P. maniculatus* is 2.4–4.8 times higher than that of *C. rudinoris* (assuming a litter size of 4 and one-two litters per year for the latter; Paulson 1988, Jones 1993). Other studies in desert and semi-arid environments have shown that omnivorous and/or granivorous murids contribute most to rodent population outbreaks associated with ENSO events (Pearson 1975, Whitford 1976, Péfaur et al. 1979, Jiménez et al. 1992, Meserve et al. 1995). However, large eruptions have been reported in desert heteromyid communities as well (Brown and Harney 1993).

The comparatively large increase in *Chaetodipus* populations on the mainland (Fig. 4), where *Peromyscus* was extremely rare, indicates that *P. maniculatus* may limit the potential increase of *C. rudinoris* on islands, but also underscores the inherently low primary productivity of these small, rocky islands. Unfortunately, no islands in the bay are inhabited solely by *C. rudinoris*, and therefore it is not possible to determine directly the effects of *P. maniculatus* on *C. rudinoris* populations, nor to estimate the potential population growth of *C. rudinoris* in the absence of competitors. Another explanation for the relative stability of insular *C. rudinoris* populations is that individuals were able to utilize seeds stored during ENSO periods to survive during dry years. *C. rudinoris* often inhabits rocky or gravelly soils (Paulson 1988) and may be particularly effective at exploiting seeds at low densities in these substrates, which they then hoard in large belowground caches. Like other desert animals that feed on plant materials (Louw and Seely 1982, Sánchez Piñero and Polis 2000), *C. rudinoris* populations may depend upon the renewal of resource pools during episodic events of high precipitation and the subsequent increase in productivity. The restricted distribution of *C. rudinoris* on Gulf islands implies that it and other specialized granivores may be particularly susceptible to periods of extended drought, such as those that may accompany future climate change or the loss of plant diversity as a result of human disturbance.

Pulsed resources and spatial subsidies

Whereas seeds produced during wet years act as a temporal subsidy to insular *C. rudinoris*, the proximity

of the ocean provides an important spatial subsidy to *P. maniculatus* populations, inputting energy and nutrients that allows *P. maniculatus* to persist and maintain high numbers on a broader range of islands than would be possible based on land resources alone. Small islands ($\leq 0.2 \text{ km}^2$), which receive relatively more marine inputs, support the highest population densities; in terms of breeding activity of adults, populations on these islands also are more than twice as productive as those on larger islands (P. Stapp, unpubl.). Frustrated dispersal and the absence of predators and competitors undoubtedly also contribute to high densities of *P. maniculatus* on many small islands. *Peromyscus maniculatus* populations tend to be more variable than those of *C. rudinoris* because the greater reproductive potential of *P. maniculatus* permits a stronger numerical response to ENSO resources, even if the increase is short-lived and most of the offspring produced disappear shortly afterward. The ability of *P. maniculatus* to use a wide range of terrestrial and marine resources allows it to persist on small islands, and its habit of foraging in littoral habitats increases the probability of encountering potential rafting sources, so that *P. maniculatus* is probably better at dispersing over water than *C. rudinoris*. On islands where the two species co-occur, we speculate that *C. rudinoris* is competitively superior to *P. maniculatus* in harvesting limited seed resources during dry years, and behaviorally restricts *P. maniculatus* mostly to near-shore habitats. However, consumption of seeds by high densities of marine-subsidized *P. maniculatus* may ultimately reduce the availability of seeds to *C. rudinoris*, and hence, their ability to take greater advantage of ENSO-related resource pulses, such as that observed in mainland populations. In experimental studies, rates of seed removal from artificial trays are much higher in near-shore areas, where *P. maniculatus* is abundant, than farther inland (P. Stapp, unpubl.). Moreover, higher-level predators such as snakes may be attracted to areas of high *P. maniculatus* abundance, which, on islands such as Smith, may ultimately result in higher mortality for *C. rudinoris*. The importance of these indirect effects depend upon a number of as yet unknown factors, including relative renewal rates of resources, consumer functional and numerical responses, and species differences in their vulnerability to predators. Additional experimental studies are necessary to untangle these relationships.

As in many other systems (Ostfeld and Keeling 2000), the pulse of resources associated with episodic events such as ENSO climatic changes alter the strength of interactions between species, here briefly in favor of *P. maniculatus*, but their greatest impact on the system may be in the residual effects on consumers such as *C. rudinoris* that rely on plants and other terrestrial resources. The scarcity of these resources in most years ultimately limits the suitability of these small islands for

sustaining vertebrate granivores and herbivores and therefore, their diversity, whereas generalists like *P. maniculatus* that can use both marine and land prey are persistent and widespread. Although chance events and history undoubtedly contributed to the biogeographic distribution of rodents on Gulf islands, these patterns ultimately are best understood in the light of interspecific differences in natural history and ecology, processes that we can study today.

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