

Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California

Sarah A. Millus and Paul Stapp

Abstract: Nesting seabirds alter habitat and food availability for insular rodent populations; in turn, rodents can reduce seabird nest success by consuming eggs and chicks. Predation by deer mice (*Peromyscus maniculatus elusus* Nelson and Goldman, 1931) is considered a significant threat to reproductive success of Xantus' Murrelet (*Synthliboramphus hypoleucus* (Xantus de Vesey, 1860)), a small, burrow-nesting seabird that breeds off the coast of southern California and Baja California. We live-trapped mice in and out of seabird colonies on Santa Barbara Island, California, USA, to determine the effects of seabirds on mouse populations. We used stable isotope analysis to determine if mice fed on murrelet eggs and chicks. Mouse densities increased significantly on all sites from winter to summer, but there were no significant differences in densities between areas with and without seabirds. Although mice were abundant in murrelet colonies, mouse populations appeared to be affected more by habitat factors than seabird populations: areas with greater rock cover supported higher densities, fewer juveniles, and larger adults in winter and spring, whereas grassland sites had high densities and more reproductive adults in summer. We found no evidence of consumption of murrelet chicks or eggs, suggesting that eggs are not a major component of the diet of most mice. However, mice can still have a significant impact on local murrelet productivity because few eggs are laid each season relative to the high numbers of mice present.

Résumé : Dans les îles, les oiseaux marins nicheurs modifient l'habitat et la disponibilité de la nourriture pour les populations de rongeurs; en retour, les rongeurs peuvent réduire le succès de nidification des oiseaux marins en dévorant des œufs et des poussins. La prédation par les souris du crépuscule (*Peromyscus maniculatus elusus* Nelson et Goldman, 1931) est considérée comme une menace significative au succès reproductif du guillemot de Xantus (*Synthliboramphus hypoleucus* (Xantus de Vesey, 1860)), un petit oiseau marin qui niche dans des terriers au large des côtes du sud de la Californie et la Basse-Californie. Nous avons fait du piégeage vivant de souris à l'intérieur et à l'extérieur de colonies d'oiseaux marins sur l'île de Santa Barbara, Californie, É.-U., afin de déterminer l'effet des oiseaux marins sur les populations de souris. Une analyse des isotopes stables nous a permis de déterminer si les souris se nourrissaient d'œufs et de poussins de guillemots. Les densités de souris augmentent à tous les sites de l'hiver à l'été, sans qu'il n'y ait de différences significatives de densité entre les sites avec ou sans oiseaux marins. Bien que les souris soient abondantes dans les colonies de guillemots, les populations de souris semblent plus affectées par les facteurs de l'habitat que par les populations d'oiseau marin; les zones avec une couverture rocheuse plus étendue ont de plus fortes densités, moins de jeunes et de plus grands adultes en hiver et au printemps, alors que les zones herbeuses ont de fortes densités et plus d'adultes reproducteurs en été. Nous ne trouvons aucune indication de consommation d'œufs ou de poussins de guillemots, ce qui laisse croire que les œufs ne constituent pas un élément majeur du régime alimentaire de la plupart des souris. Néanmoins, les souris peuvent avoir un impact significatif sur la productivité locale des guillemots parce qu'un petit nombre d'œufs est pondu chaque saison par rapport aux grands nombres de souris qui sont présentes.

[Traduit par la Rédaction]

Introduction

Seabirds can have significant effects on the flora and fauna of islands where they roost and nest. Deposition of large amounts of guano increases soil nutrients (Mizutani and Wada 1988) and can lead to increases in primary productivity (Polis et al. 1997; Anderson and Polis 1999; Garcia et al. 2002), with concomitant increases in abundance of some arthropods (Polis and Hurd 1995, 1996; Sánchez-

Piñero and Polis 2000; Orgeas et al. 2003). Guano-fertilized plants and associated invertebrates, as well as the carrion, eggs, and chicks left by seabirds on islands, can provide food for terrestrial vertebrates such as lizards (Hews 1993; Markwell and Daugherty 2002; Barrett et al. 2005) and both native and introduced rodents (Murray 1980; Drever et al. 2000; Stapp 2002; Stapp and Polis 2003). Seabirds therefore may benefit insular rodent populations either directly, by providing higher quality food resources such as eggs and chicks, or indirectly, by increasing abundance of terrestrial food resources.

If seabird colonies represent areas of abundant food and high-quality habitat, rodents may be more abundant in colonies compared with other available insular cover types. Conversely, rodent population densities on islands may be affected more by other habitat factors, including the avail-

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ability of overhead cover provided by rocky outcrops (Kaufman et al. 1983) and areas under shrubs or other vertical cover (Kotler 1984; Kotler et al. 1991; Stapp and Van Horne 1997; Jensen et al. 2003), or by the availability of higher quality food resources (Cole and Batzli 1979; Taitt 1981; Doonan and Slade 1995). Studies of rodent populations and diets in seabird colonies and in similar areas without seabirds are necessary to distinguish the effects of seabirds versus local habitat factors.

Santa Barbara Island (SBI), in the Channel Islands off southern California, USA, is inhabited by a single rodent, an endemic subspecies of deer mouse (*Peromyscus maniculatus elusus* Nelson and Goldman, 1931). SBI also provides important nesting habitat for several species of seabirds, including the largest United States population of Xantus' Murrelet (*Synthliboramphus hypoleucus* (Xantus de Vesey, 1860)), a small, burrow-nesting seabird that breeds exclusively on islands off the coast of southern California and Baja California. Between 1977 and 1991, the breeding population of Xantus' Murrelet on SBI declined by approximately 30% (Sydeman et al. 1998), leading this species to be listed as threatened by the State of California (Carter et al. 2005). Although deer mice and murrelets have likely coexisted for thousands of years on SBI, egg predation by mice is considered the greatest threat to Xantus' Murrelets on land (Murray et al. 1983; Drost and Lewis 1995; Sydeman et al. 1998), in part because threats in the marine environment are difficult to study and mitigate. Deer mice are known to prey on seabirds elsewhere (e.g., Blight et al. 1999; Drever et al. 2000); evidence that mice consume murrelet eggs on SBI is based primarily on eggshell fragments and the absence of other terrestrial predators that could enter nest burrows. Removal of mice from one murrelet colony on SBI resulted in a decrease in egg predation and increased murrelet productivity (Millus et al. 2007). To date, however, no studies have directly examined the population ecology of deer mice in murrelet colonies, or examined the diet of colony mice for seabird remains, which would strengthen the contention that deer mice are a major predator of murrelet eggs.

We examined the effects of seabirds and habitat factors on deer mouse populations on SBI. We used mark-recapture methods to compare densities and demographic characteristics of mouse populations in seabird colonies and in other cover types on the island. Based on the population ecology of deer mice, we hypothesized that population densities would be highest in areas with seabird colonies and their associated food resources, and in areas with more available cover, such as shrubs and rocks. We also conducted carbon and nitrogen stable isotope analysis of mouse tissues to determine whether mice prey on seabirds, especially murrelets, and to determine the relative importance of seabirds versus other food sources to mouse diets. Stable isotope analysis has become an important tool for investigating the relative contributions of marine versus terrestrial prey in diets of consumers in coastal and insular environments (Schoeninger and DeNiro 1984; Peterson and Fry 1987; Kelly 2000). We predicted that isotopic signatures of deer mice living in seabird colonies would be relatively enriched compared with those of mice from other areas, reflecting consumption of seabird tissue and (or) the indirect effects of guano on isotopic signatures of terrestrial prey (Stapp et al. 1999).

Materials and methods

Santa Barbara Island (33°28'N, 119°2'W) is the smallest of the California Channel Islands, measuring only 2.6 km². It is located 64 km southwest of Los Angeles and 39 km west of Santa Catalina Island, and is one of four islands that compose the Channel Islands National Park. The climate is Mediterranean, with a mild wet season from October through April and a long dry season. Its coastline is characterized by steep, sloping rocky cliffs with a few small, rocky beaches. There are isolated, extensive patches of native giant coreopsis (*Coreopsis gigantea* (Kellogg) Hall) and coastal pricklypear (*Opuntia littoralis* (Engelm.) Cockerell) on sea slopes. The interior of the island is dominated by non-native plants, mostly annual grasses such as oats (*Avena* L.), brome (*Bromus* L.), and barley (*Hordeum* L.), which are remnants of farming and ranching that occurred on the island in the early 20th century, and the common iceplant (*Mesembryanthemum crystallinum* L.), which was introduced to the island in the late 19th century (Philbrick 1972). Deer mice are the only terrestrial, nonvolant mammals on SBI.

In 2003, deer mice were live-trapped on 10 sites (each 0.24 ha) representing five different cover types on SBI, with 2 trapping sites in each cover type: murrelet colonies, rocky areas without murrelets (hereafter, murrelet controls), colonies of Western Gulls (*Larus occidentalis* Audubon, 1939), non-native grasslands, and areas dominated by coreopsis. Grids measured 60 m × 40 m, with two small (15.2 cm × 5.1 cm × 6.4 cm) Sherman traps placed at 10 m intervals for a total of 48 traps per grid. Grids were >150 m apart and were therefore considered independent. Because of hazardous terrain and fewer murrelet nest sites, one pair of murrelet colony and control grids measured only 40 m × 30 m, with 12 trapping stations for a total of 24 traps per grid. Additional details on field methods are provided in Millus (2006).

Each grid was trapped three times in 2003: prior to (PRE, 19 February – 30 March), during (MID, 26 May – 3 June), and after (POST, 6–19 August) the seabird breeding season (peak egg laying, fledging: murrelets — April, June; gulls — May, July/August; Murray et al. 1983; Schreiber 1970). Each trapping session lasted three consecutive nights. Inclement weather prevented trapping of one of the gull grids during the PRE trapping session. Individuals were weighed, identified by sex, age, and reproductive status, and marked with a uniquely numbered aluminum ear tag. Densities on each grid were calculated for each trapping period using standard mark-recapture methods (CAPTURE; Otis et al. 1978) in DENSITY (Efford 2004). This approach fits models to capture-recapture data to estimate population size based on capture probabilities and individual capture histories. The mean maximum distance moved by all individuals captured was added to the area of the trapping grid to estimate the effective trapping area. Density was calculated for each grid for each trapping period by dividing population size by effective trapping area.

To determine diet of mice in and out of murrelet colonies, eight mice from one murrelet colony and one control site were trapped during the murrelet breeding season (MID; May 2003) and euthanized with an overdose of CO₂. These mice were sacrificed to obtain samples of tissues with differ-

ent metabolic turnover rates, which provide estimates of diet at different times during an individual's life (Stapp 2002; Tieszen et al. 1983). Liver, thigh muscle, and toe samples were taken from each sacrificed individual and stored in separate vials in 70% ethanol in a standard laboratory freezer at -10 °C. Turnover rates of these tissues correspond to diet changes on the order of weeks (liver) to months (bone) (Tieszen et al. 1983). Samples of possible prey items (seeds, leaves, arthropods) were also collected opportunistically from these sites. We also collected muscle tissue from murrelet and gull chicks, as well as murrelet egg tissue.

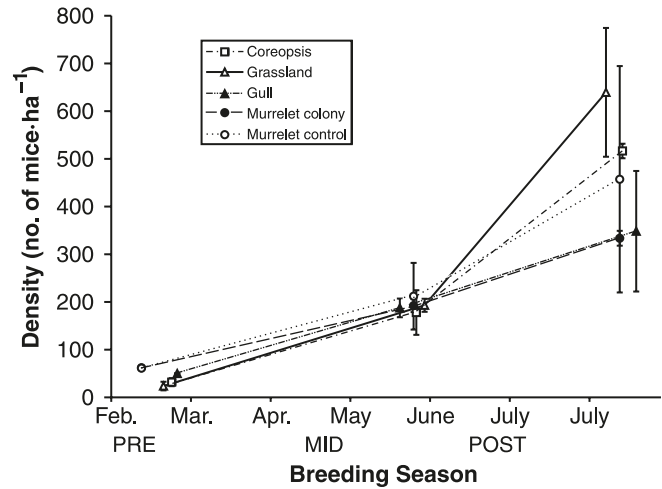
Tissue samples were dried at 50 °C for ≥24 h and ground using a mortar and pestle. Subsamples (1–2 mg) were weighed in a Mettler Toledo MT/UMT balance accurate to 0.001 mg. Samples were analyzed for stable carbon and nitrogen isotope ratios using a Europa Hydra 20–20 isotope ratio mass spectrometer at the University of California, Davis. Isotopic composition was expressed as the ratio of the heavy to light isotope relative to a standard, using the delta (δ) notation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C and ^{15}N , R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, and the units are parts per thousand (‰). We compared isotopic signatures of mouse tissues to those of potential terrestrial prey items and seabird tissue to determine which food sources likely contributed most to mouse diets.

Stomach contents of mice that died accidentally during trapping were examined to complement diet estimates from stable isotope analysis. Stomach contents were removed and placed into separate vials containing 95% ethanol and then frozen until analyzed. Occurrence of items in stomach was analyzed visually using a dissecting microscope and placed into broad categories, such as vegetation, seeds, and insects. All research on live animals was approved by the Institutional Animal Care and Use Committee at California State University Fullerton and with permission from California Department of Fish and Game and the National Park Service, and was performed humanely following guidelines of the American Society of Mammalogists (1998).

To quantify vegetation and substrate (habitat) characteristics on each grid during the study period, we estimated percent cover of vegetation and substrate and plant species richness in spring (April) and summer (August) 2003. Transects (10 m) were established in random directions from six randomly chosen trap stations. Percent cover and species richness were measured in a single 0.3 m² quadrat, at 2 m intervals along the transect. Percent cover was estimated visually for rock, bare ground, litter, and all plant species at each point for a total of 30 points per site. Vegetation data collected at the species level were categorized into vegetation structural classes. Means for each category (rock, bare, litter, forbs, grass, shrub, number of species) were calculated for each site. We measured habitat characteristics in both spring and summer to account for the changes in plant communities from the wet winter–spring to the dry summer season.

Statistical analyses were performed using SAS version 9.0 (SAS Institute Inc. 2005). Repeated-measures analysis of variance (ANOVA) was used to determine if densities and demographic traits (proportion of juveniles and subadults, proportion of adult females, proportion of reproductive

Fig. 1. Mean (± 1 SE) abundance of deer mice (*Peromyscus maniculatus elusus*) in five cover types before (PRE), during (MID), and after (POST) the seabird breeding season on Santa Barbara Island in 2003 ($n = 2$ grids per cover type).



adults, proportion of reproductive adult females, and mean adult male mass) of mouse populations differed among cover types and over time. One-way ANOVA was used to determine if stable isotope values differed among mouse tissue types. We used Student's t tests to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of mouse tissues and prey items between colony and control sites. Principal components analysis (PCA) was used to reduce vegetation and substrate variables to a few composite variables that best described the variation in habitat characteristics among sites. Habitat variables with eigenvectors >0.3 were considered to be significantly associated with a principal component (McGarigal et al. 2000). Habitat, density, and mass data were log-transformed to satisfy assumptions of parametric tests; proportional demographic data were arcsine square root transformed prior to analysis.

Results

Relationships between mouse populations and habitat types

The number of individual mice captured on each grid ranged from 5 to 31 during PRE trapping, from 11 to 62 during MID trapping, and from 38 to 106 during POST trapping (Millus 2006). Based on our mark–recapture modeling (Otis et al. 1978), in most cases (22 out of 30 grid sampling period combinations) the probability of capture did not differ among individuals or over time; therefore, the null model M_0 was used to estimate population density (Millus 2006). We found evidence of significant variation in capture probability over time on five grid sampling period combinations and based on previous capture history on two grid sampling period combinations, and used the corresponding models (M_t and M_b , respectively) to estimate density for those cases. Because few individuals were captured on gull grid during PRE trapping, we used the number of individuals caught as our estimate of population size. Estimates of variation in density estimates $[(\text{SE} \times \text{density})/\text{density}]$ ranged from 8.2% to 61.3%, with a mean of 21.1% (Millus 2006).

Mouse densities increased significantly in all cover types

Table 1. Vegetation and substrate characteristics on trapping grids used to capture deer mice (*Peromyscus maniculatus elusus*) on Santa Barbara Island in spring and summer 2003.

| Variable | Spring | | Summer | |
|------------------|--------|-------|--------|-------|
| | PC1 | PC2 | PC1 | PC2 |
| Eigenvector | | | | |
| Percent bare | 0.46 | 0.08 | 0.53 | 0.05 |
| Percent grass | -0.56 | 0.11 | -0.49 | 0.34 |
| Percent rock | 0.38 | -0.49 | 0.46 | 0.24 |
| Percent forb | 0.29 | 0.03 | -0.11 | -0.23 |
| Percent shrub | 0.48 | 0.21 | 0.50 | 0.12 |
| Percent litter | 0.12 | 0.59 | 0.04 | -0.63 |
| Species richness | 0.05 | 0.60 | -0.04 | 0.60 |
| Eigenvalue | 3.06 | 2.08 | 2.72 | 2.21 |
| Percent variance | 44 | 30 | 39 | 32 |

Note: Eigenvectors are from principal components analysis (PCA) of percent cover and plant species richness on each of 10 grids, which was run separately for each season. Percent variance is the amount of original variation explained by each PCA axis (PC1, PC2).

between PRE and POST trapping (ANOVA, $F_{[1,15]} = 204.14$, $p < 0.0001$; Fig. 1). There were no differences in mean densities among cover types ($F_{[4,15]} = 2.27$, $p = 0.196$); however, the significant interaction between cover type and time ($F_{[4,15]} = 3.52$, $p = 0.032$) suggested that populations responded differently in different cover types over time. Densities increased most dramatically on grassland grids and least on the murrelet and gull grids. Densities were similar for replicate grids within each habitat type ($F_{[5,15]} = 1.61$, $p = 0.218$) and over time.

Mean mass of adult males decreased over time ($F_{[1,14]} = 21.49$, $p < 0.001$), but there were no significant differences among cover types ($F_{[4,14]} = 2.74$, $p = 0.149$). The proportion of adult females did not differ among cover types or over time ($p > 0.086$); however, the significant interaction term between cover type and time ($F_{[4,14]} = 6.10$, $p = 0.005$) reflected an increase in the proportion of adult females on gull and grassland grids during POST trapping. There were no significant differences among cover types over time in the proportion of adults that were in breeding condition, the proportion of adult females in breeding condition, or in the proportion of juveniles ($p > 0.235$).

The density of mice in seabird colonies (murrelet and gulls combined) did not differ from the pooled densities of mice in areas without seabirds over time ($F_{[1,18]} = 3.07$, $p = 0.118$). During POST trapping, mean densities on grids without seabirds (537.8 ± 78.4 mice·ha⁻¹, $n = 6$) were higher than on seabird colony grids (340.9 ± 52.2 mice·ha⁻¹, $n = 4$), but the change in densities over time did not differ on and off colonies (cover type \times time interaction: $F_{[1,18]} = 3.59$, $p = 0.074$). Demographic characteristics of mouse populations were similar between seabird and nonbird areas ($p > 0.10$).

Mouse populations and habitat characteristics

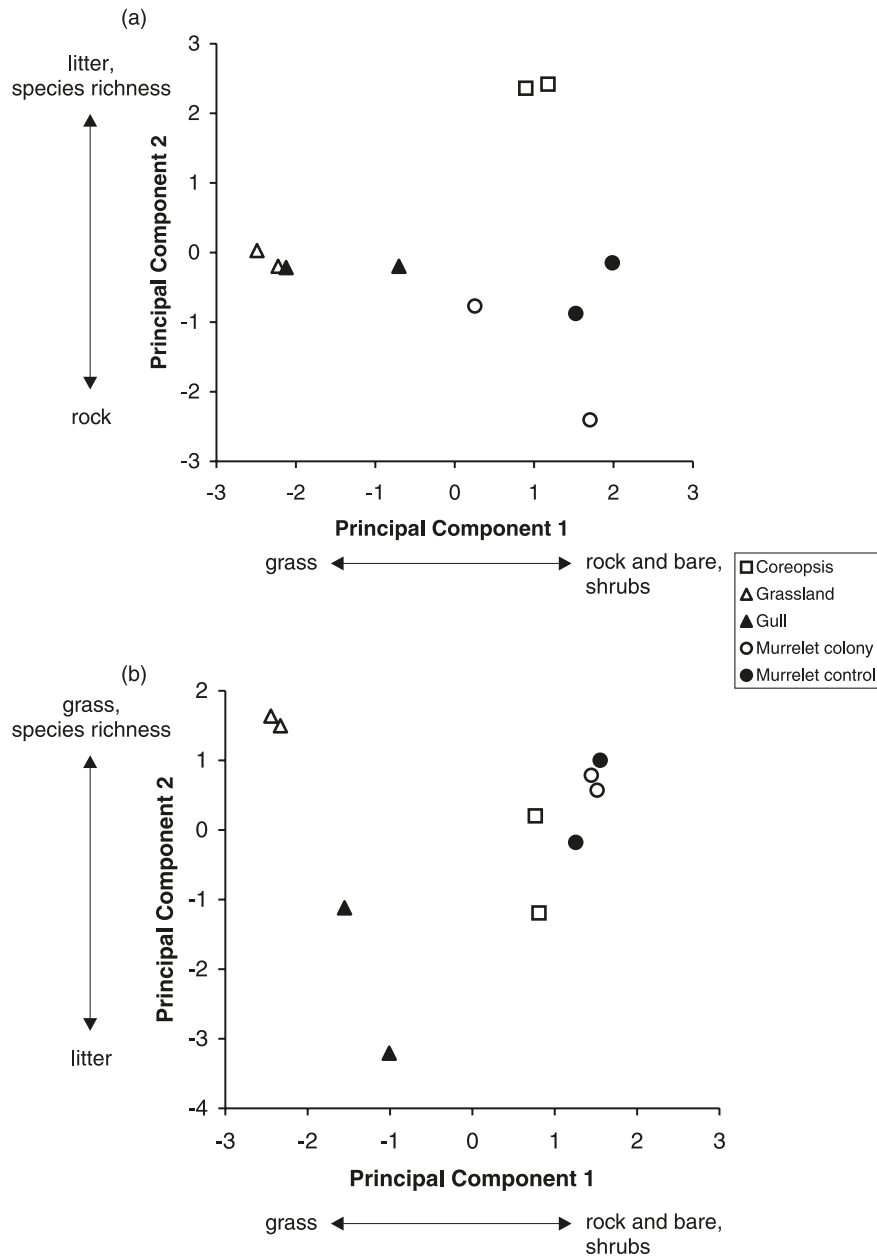
PCA conducted on habitat variables measured in spring resulted in two composite axes (PC1, PC2) with $\lambda > 1$, which explained 44% and 30%, respectively, of the total sample variation in habitat measurements (Table 1). PC1 was positively correlated with bare and rocky ground and shrub cover and negatively correlated with grass cover. PC2

was positively correlated with litter cover and species richness and negatively correlated with rock cover. Murrelet colony, murrelet control, and coreopsis sites were dominated by bare, rocky ground and shrubs (high values for PC1; Fig. 2a), whereas grassland and gull sites had high grass cover, little rocky ground, and few shrubs (low values for PC1). Coreopsis sites had higher litter cover and species richness than all other sites (high values for PC2).

For habitat variables measured in summer, the first two principal components also had $\lambda > 1$ and explained 39% and 32% of the sample variation, respectively (Table 1). The interpretation of PC1, based on eigenvector loadings, was similar in summer to that in spring. During summer, PC1 was positively correlated with bare and rocky ground and shrub cover and negatively correlated with grass cover. The interpretation of PC2 changed, however, in that PC2 was positively correlated with grass and species richness and negatively correlated with litter in the summer compared with in the spring (Fig. 2b). During the summer, murrelet colony, murrelet control, and coreopsis sites continued to be dominated by bare and rocky ground and shrubs (high PC1). By summer, gull sites were covered mostly with litter (dry annual grasses), whereas grasslands continued to have high grass cover and high species richness (high PC2).

Study grids were originally chosen to represent discrete cover types, and for most cover types, only two suitable, independent sites could be found on this small island. As a result of low replication and high variability among sites, power was low and discrete cover-type categories tended to be poor predictors of variation in mouse population density and demographic characteristics. Relationships between mouse populations and habitat characteristics were more apparent when vegetation and substrate variables were treated as continuous factors (Table 2). During PRE trapping, several population variables were significantly correlated with spring PC1. Mouse population densities increased with the amount of rock and shrub cover, i.e., on murrelet colony, murrelet control, and coreopsis sites ($r = 0.68$, $p = 0.032$; Fig. 3) compared with grass-dominated sites. The proportion of females in the population and body mass of adult males also increased with PC1 ($r = 0.74$, $p = 0.022$;

Fig. 2. Principal component scores of mean habitat characteristics on each trapping grid used to capture deer mice (*Peromyscus maniculatus elusus*) in (a) spring and (b) summer 2003 on Santa Barbara Island. Points represent means of random transects for each site ($n = 2$ grids per cover type).



$r = 0.88$, $p = 0.002$, respectively). Sites that had little rock and shrub cover and high grass cover, i.e., gull and grassland sites, had more juveniles than rocky or shrubby sites ($r = -0.83$, $p = 0.003$). Neither the proportion of reproductive adults nor the proportion of breeding adult females was significantly correlated with habitat variables in spring.

By summer (POST), after the seabird breeding season had ended, mouse densities were high (>300 mice·ha⁻¹) on all grids. There were no significant correlations between August mouse densities and habitat variables in summer ($r < 0.35$, $p > 0.30$), although demographic variables were significantly related to habitat characteristics. The proportion of the adults and adult females that were in breeding condition increased with grass cover ($r = -0.85$, $p = 0.002$ and

$r = -0.83$, $p = 0.003$, respectively) and decreased with the amount of rock and shrub cover (Fig. 4). Neither the proportion of juveniles nor mass of adult males were significantly correlated with habitat variables in summer.

Rodent diets

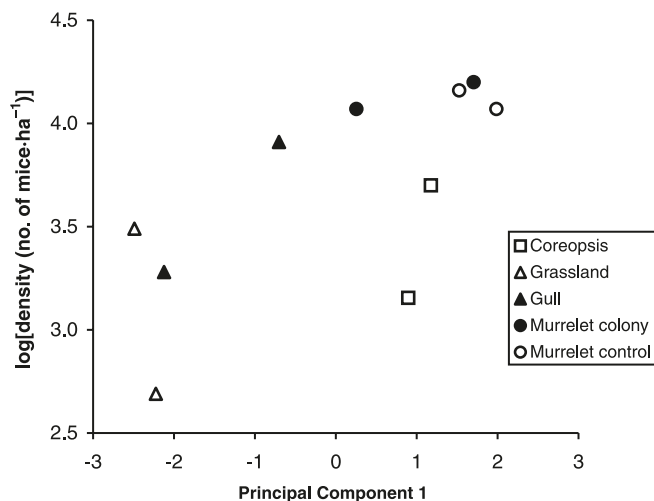
Muscle, liver, and bone tissues of sacrificed deer mice from murrelet colony and control grids differed only in their carbon isotope signatures. Bone tissue was most enriched and liver tissue was the least enriched in ¹³C for both colony and control mice. Bone was significantly more enriched than liver, but not muscle, for mice from the control site ($F_{[2,20]} = 4.64$, $p = 0.022$). A similar pattern was found for $\delta^{13}C$ values for colony mice: bone was more enriched than liver,

Table 2. Pearson correlations between deer mice (*Peromyscus maniculatus elusus*) population variables and composite variables (PC1, PC2) representing habitat characteristics on grids during spring (PRE) and summer (POST) 2003 ($n = 10$ grids).

| Variable | Density (mice·ha ⁻¹) | Proportion of juveniles | Proportion of adult females | Proportion of reproductive adults | Proportion of reproductive adult females | Mean adult male mass (g) |
|--|----------------------------------|-------------------------|-----------------------------|-----------------------------------|--|--------------------------|
| Spring (PRE) | | | | | | |
| PC1 | 0.68** | -0.83*** | 0.74** | 0.48 | -0.18 | 0.88*** |
| PC2 | -0.46 | -0.15 | 0.06 | 0.38 | 0.02 | -0.14 |
| Density | — | -0.63** | 0.80*** | 0.49 | 0.30 | 0.60* |
| Proportion of juveniles | — | — | -0.89*** | -0.76** | -0.31 | -0.64* |
| Proportion of females | — | — | — | 0.77** | 0.26 | 0.60* |
| Proportion of reproductive adults | — | — | — | — | 0.50 | 0.27 |
| Proportion of reproductive adult females | — | — | — | — | — | -0.54 |
| Summer (POST) | | | | | | |
| PC1 | -0.34 | -0.50 | -0.79*** | -0.85*** | -0.83*** | -0.18 |
| PC2 | 0.33 | -0.26 | -0.26 | -0.25 | -0.34 | -0.40 |
| Density | — | 0.28 | 0.23 | 0.19 | 0.18 | 0.14 |
| Proportion of juveniles | — | — | 0.20 | 0.26 | 0.30 | -0.26 |
| Proportion of females | — | — | — | 0.93*** | 0.93*** | 0.73** |
| Proportion of reproductive adults | — | — | — | — | 0.99*** | 0.56* |
| Proportion of reproductive adult females | — | — | — | — | — | 0.58* |

Note: PC1 and PC2 were generated from principal components analysis of percent cover of vegetation and substrate and plant species richness measured on each grid. Mass and density data were log-transformed, while proportional data were arcsine square root transformed. *, $p \leq 0.10$; **, $p \leq 0.05$; ***, $p \leq 0.01$; relationships were considered statistically significant if $p \leq 0.05$.

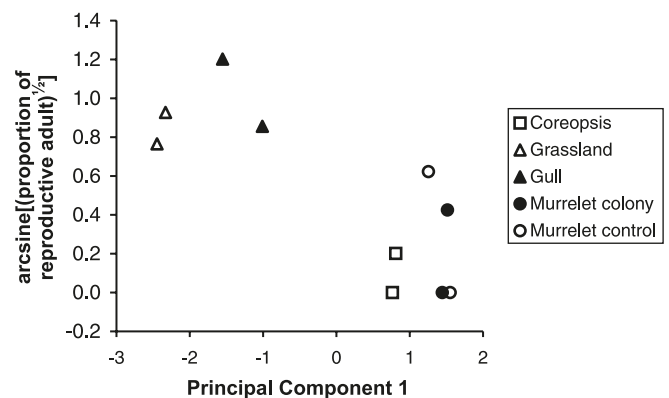
Fig. 3. Relationship between spring habitat characteristics (PC1) and deer mouse (*Peromyscus maniculatus elusus*) densities prior to the seabird breeding season (PRE) on Santa Barbara Island in February and March 2003.



which was the same as muscle ($F_{[2,20]} = 3.25$, $p = 0.059$). There were no significant differences in $\delta^{13}\text{C}$ values between colony and control mice for any of the three tissues examined ($p > 0.50$), indicating that mice consumed prey items with similar isotopic signatures in both areas. Tissue $\delta^{15}\text{N}$ values of colony and control mice were also similar ($p > 0.80$).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of potential food sources for mice on colony and control sites varied widely (Fig. 5). Plants had a wide range of $\delta^{13}\text{C}$ values, reflecting differences in their photosynthetic pathways; species with CAM and C_4 photosynthesis were significantly more enriched in ^{13}C than those that used C_3 photosynthesis (Wilcoxon rank-sum test,

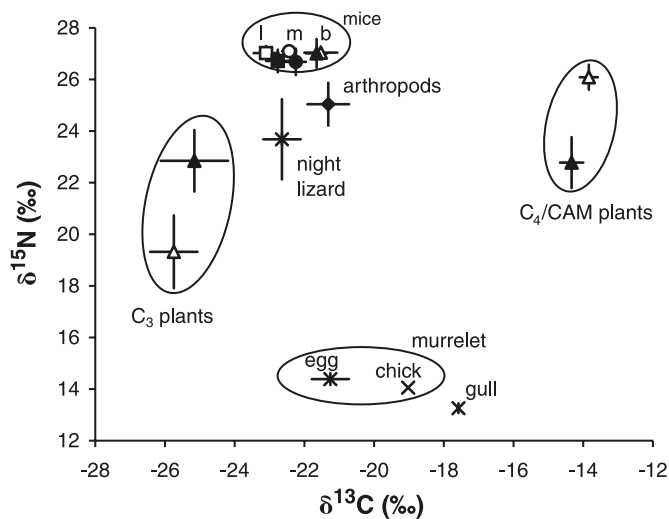
Fig. 4. Relationships between summer habitat characteristics (PC1) and proportion of adult deer mice (*Peromyscus maniculatus elusus*) that were in breeding condition during trapping conducted after the seabird breeding season (POST) on Santa Barbara Island in August 2003.



$U = 286$, $p < 0.0001$). $\delta^{15}\text{N}$ values were similar between colony and control sites for all plant species sampled. Arthropods had high $\delta^{15}\text{N}$ values and similar isotope signatures on colony and control sites for both $\delta^{13}\text{C}$ (Student's t test, $t = -1.23$, $p = 0.246$) and $\delta^{15}\text{N}$ ($t = 0.86$, $p = 0.410$). Seabird tissues were depleted in ^{15}N compared with other potential food sources sampled, e.g., plants and arthropods, from colony and control sites. Although $\delta^{13}\text{C}$ values were similar between mouse and seabird tissues, mean $\delta^{15}\text{N}$ values of mouse tissues were 11‰ higher than those of murrelet eggs and chicks.

Our stomach contents analysis ($n = 39$) was intended to be descriptive and complement results of isotope analyses. Plant material was found in stomachs of mice from all habitats (Table 3). Insect remains were found in mice from

Fig. 5. Mean (± 1 SE) stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures of deer mice (*Peromyscus maniculatus elusus*) sacrificed from the Xantus' Murrelet (*Synthliboramphus hypoleucus*) colony and control sites and potential food items. Solid symbols represent samples taken from the colony site, whereas open symbols represent samples taken from the control site. Symbols for mouse tissue ($n = 8$ each): l, liver; m, muscle; b, bone. C_3 and C_4/CAM represent plants with different photosynthetic pathways. Sample size for terrestrial prey items ranged from 2 to 11; murrelet eggs (9), murrelet chick (1), gull chick (1).



all habitats except gull colonies and composed the majority of identifiable matter from grassland mice (83% of stomachs). Unidentified starchy material was found in all mice except those from the murrelet controls and was probably digested grass seeds (Murray 1980). Unidentified animal material was also found in stomachs of mice from coreopsis and murrelet control habitats and may have belonged to terrestrial snails (Murray 1980), although no shell parts were found. Bones, apparently from a mouse, were found in one stomach from one control site. Shell fragments from a crustacean and a passerine feather were found in stomachs of two different mice from a coreopsis site.

Discussion

Mouse-habitat relationships

As is typical of many *Peromyscus* populations in seasonal environments, population densities increased dramatically on all cover types on SBI between winter and summer. The extremely high densities (>300 mice-ha⁻¹) attained by mice in August 2003 are part of a pattern of boom and bust that seems to characterize deer mouse populations on this small island (Drost and Fellers 1991; Schwemm and Coonan 2001), but are an order of magnitude higher than for *Peromyscus* populations elsewhere (Terman 1968, 1993). Previous studies on SBI have sampled in one or two vegetation types, but we found that population densities and demographic characteristics varied over time and among the five cover types we sampled. Early in spring 2003, when mouse densities were relatively low island-wide, areas with rocky and shrubby cover supported higher densities of mice and larger adults, whereas grassland areas had lower densities

and consisted mostly of juveniles and smaller adults. At low population densities, individuals are expected to occupy the most productive habitat types, where fitness is relatively high (Van Horne 1983). Higher habitat quality is also associated with a higher proportion of adults, as well as heavier adults (Van Horne 1981). The higher densities of larger adult mice in rocky and shrubby cover types in early 2003 suggest that these areas represent higher quality habitat than grassland sites. There were few breeding individuals at any sites in early spring, and no differences in breeding among sites, presumably because we trapped prior to the onset of the peak April-June mouse breeding season (Collins et al. 1979; Murray 1980).

We speculate that areas with rock and shrub cover represent higher quality habitat for deer mice for several reasons. First, food resources may have been more plentiful and of superior quality in these areas than elsewhere, which can contribute to higher densities and larger body size (Cole and Batzli 1979; Taitt 1981; Dobson 1995; Nupp and Swihart 1998). Forbs (rockdaisy (*Perityle* Benth.), mayweed (*Matricaria* L.), fiddleneck (*Amsinckia* Lehm.)) and shrubs (buckwheat (*Eriogonum* Michx.), *Coreopsis*, saltbush (*Atriplex* L.)) were likely the main sources of vegetation for deer mice during the early spring on rocky and shrubby sites. The grass species (*Avena*, *Hordeum*, *Bromus*) that were predominant on grassland sites had not seeded by early spring (S. Millus, personal observation). Second, overhead cover associated with rocky and shrubby areas reduce risk of predation from raptors, mainly Barn Owls (*Tyto alba* (Scopoli, 1769)) and American Kestrels (*Falco sparverius* L., 1758), the only known predators of mice on the island. Mice prefer areas where they can best avoid predators, including rocky outcrops (Kaufman et al. 1983) and areas under shrubs (Kotler 1984; Kotler et al. 1991; Stapp and Van Horne 1997), and such areas on SBI may have been preferred because they provided better overhead protection. Rocky and shrubby areas also tended to support more adults, which are expected to be socially dominant to juveniles. Because aggression from adults can prevent juveniles from using high-quality habitats (Lidicker 1975; Van Horne 1981; Wolff 1989 and references therein), juveniles may have been forced to settle in grassland areas in spring 2003.

Unlike spring trapping (PRE), population densities of mice were high in all cover types during summer trapping (POST). Trap saturation may partly explain why we detected no cover-type-related differences in population density during POST trapping. Capture success was high in all cover types (mean = 73%), with most traps filled each morning and often with multiple individuals. Our estimates of density, therefore, may be conservative, which could obscure real differences in abundance among cover types in summer. Despite similarities in population density among cover types in summer, there were clear differences in reproductive effort between grassy and rocky and shrubby areas. Reproductive activity had all but ceased on rock and shrub sites by August, while breeding activity was significantly higher on grassy sites into the summer. Mice typically reduce breeding activity in response to high density (Terman 1965, 1993; Montgomery 1989; Montgomery and Dowie 1993), a phenomenon that has been observed on SBI (Drost and Fellers 1991). Dramatic reductions in breeding can result from

Table 3. Frequency of occurrence (%) of food items from stomachs collected from deer mice (*Peromyscus maniculatus elusus*) on Santa Barbara Island in 2003 and 2004.

| Cover type | <i>n</i> | Seeds | Vegetation | Adult insects | Insect larvae | Bird | Hair | Unknown animal | Bait | Unknown | Empty |
|------------|----------|--------|------------|---------------|---------------|--------|--------|----------------|--------|---------|--------|
| Coreopsis | 18 | — | 50 (9) | 39 (7) | 17 (3) | <1 (1) | 22 (4) | 17 (3) | — | 28 (5) | 0 |
| Grassland | 6 | — | 67 (4) | 83 (5) | 33 (2) | — | 17 (1) | — | 17 (1) | 33 (2) | 17 (1) |
| Gull | 4 | — | 25 (1) | — | — | — | 25 (1) | — | — | 25 (1) | 25 (1) |
| Murrelet | | | | | | | | | | | |
| Colony | 6 | 17 (1) | 33 (2) | 33 (2) | — | — | 33 (2) | — | 33 (2) | 33 (2) | 33 (2) |
| Control | 5 | 20 (1) | 40 (2) | 40 (2) | — | — | — | 100 (5) | — | — | 0 |
| All sites | 39 | 5 (2) | 46 (18) | 41 (16) | 13 (5) | <1 (1) | 21 (8) | 21 (8) | 8 (3) | 26 (10) | 10 (4) |

Note: *n* is the number of mice and values in parentheses are the number of stomachs containing the item.

behavioral and physiological responses to high densities, such as increased aggression (Batzli 1977; Chapman et al. 2000) and increased production of androgens (Cowell et al. 1998). It is possible that mice on rocky and shrubby areas may have responded to high population densities by decreasing reproduction, although the mechanism is not known. The failure of mice in grassy areas to curtail reproduction at high densities, however, could not be explained. During an extended study of mouse populations on SBI, Drost (1989) reported moderately high levels of breeding activity in grassland areas when reproduction had ceased in coreopsis shrub habitats, but densities were always lower in grassland areas.

Effects of seabirds on deer mice and vegetation

Differences in mouse populations across cover types on SBI could not be directly attributed to seabirds. Neither densities nor demographic traits of the mice in seabird colonies were significantly different from those of populations outside colonies, either when considering sites using broadly defined habitat categories or by pooling sites based on the presence or absence of seabirds (gulls, murrelets). Seabird colonies, especially the rocky cliffs used by murrelets, seemed to provide suitable habitat for deer mice, but this may reflect more the relationship between mouse densities and habitat characteristics than presence of seabirds per se. We note that unlike the structurally similar grassland sites, mouse densities did not increase in gull colonies during summer. Adult and juvenile gulls were present on these sites through the summer and, although they are largely diurnal, they are known to prey on mice opportunistically (e.g., Ruiz and Simeone 2001). We have no evidence, however, that gull predation caused mouse mortality on gull colonies. Food resources or disturbance or mortality associated with nesting seabirds therefore did not appear to influence mouse populations directly.

Nonetheless, seabirds may affect deer mouse populations on SBI indirectly. The high $\delta^{15}\text{N}$ values (>25‰) of mouse tissues from seabird colonies suggest that mice consume plant and animal materials that are ultimately derived from marine nutrients. Stable isotope ratios of plant and arthropod tissues from murrelet and gull colonies were consistently enriched in ^{15}N , suggesting that plants on seabird colonies derive nitrogen from guano, which serves as a source of nutrients that subsequently move into consumers such as

mice (Stapp et al. 1999). We found evidence of guano ^{15}N enrichment in plants collected from areas >100 m outside of existing colonies (Millus 2006), suggesting that seabird nesting was widespread on the island prior to human disturbance (farming, introduction of exotic vertebrates) and that the indirect impacts of seabirds on SBI food webs were extensive and persistent.

Stable isotope results indicate that seabird eggs or chicks did not contribute substantially to the diet of deer mice in either murrelet or gull colonies. Although $\delta^{13}\text{C}$ values were similar between mice and seabirds, all mouse tissues had $\delta^{15}\text{N}$ values that were much higher (11‰) than would be expected (3‰–5‰) if mice had consumed seabirds (Tieszen et al. 1983; Schoeninger and DeNiro 1984; Post 2002). Similarly, $\delta^{15}\text{N}$ values of bone tissue from tails of mice caught on gull colonies were ~12‰ more enriched than gull chick muscle (Millus 2006), suggesting that mice also did not consume gull chicks.

Fasting and starvation can elevate $\delta^{15}\text{N}$ values by ~2‰ for muscle and liver tissues (Hobson et al. 1993); however, it is unlikely that nutritional stress accounted for the elevated $\delta^{15}\text{N}$ values observed in deer mice from SBI. All sacrificed mice appeared to be in good health and some individuals had substantial subcutaneous fat (Millus 2006). Instead, the high $\delta^{15}\text{N}$ values of mouse tissues from colony and control sites suggested that mice fed primarily on terrestrial (albeit guano-fertilized) material, primarily plants and arthropods. These food resources are likely important island-wide: isotope analysis of tail tissues of mice revealed similar diets across the different habitats that we studied (Millus 2006), with exotic grasslands having significantly lower $\delta^{15}\text{N}$ values which likely reflected the removal of guano-derived nutrients as a result of intensive, historical tilling of the soil. Deer mice consume a variety of plant parts, including seeds, and invertebrates on SBI (Collins et al. 1979; Murray 1980). Plants and arthropods are an abundant and predictable food source compared with seabird tissues, which represent a highly seasonal and sparse food source with high searching and handling times (cf. Murray 1980). Our analysis of gut contents supports this conclusion; stomachs of most mice contained largely plants and insects. Interestingly, isotopic signatures of mice (Fig. 5) suggest that they might also eat island night lizards (*Xantusia riversiana* Cope, 1883), which were common in colony and control areas.

Effects of deer mice on seabirds

By analyzing stable isotope signatures of liver, muscle, and bone tissues, we were able to estimate the diet of deer mice during the period when eggs and chicks of Xantus' Murrelets would have been available on SBI (April–May). Regardless of which mouse tissue we examined, however, we found no evidence from our stable isotope analyses that deer mice consumed any seabird tissue. This result was somewhat unexpected because native *Peromyscus* are considered to be important nest predators of alcids elsewhere, including Ancient Murrelets (*Synthliboramphus antiquus* (J.F. Gmelin, 1789); Gaston 1992), Marbled Murrelets (*Brachyramphus marmoratus* (J.F. Gmelin, 1789); Bradley and Marzluff 2003), Cassin's Auklets (*Ptychoramphus aleuticus* (Pallas, 1811)), and Rhinoceros Auklets (*Cerorhinca monocerata* (Pallas, 1811); Blight et al. 1999; Drever et al. 2000). Predation by Keen's mouse (*Peromyscus keeni* Merriam, 1897) was responsible for 32% of egg loss in an insular population of Rhinoceros Auklets, greater than all other single causes of nest failure (Blight et al. 1999). On the same island, Drever et al. (2000) used stable isotope analysis to show that eggs of Cassin's Auklets and Rhinoceros Auklets provided the majority of protein for mice. Our own experiments on SBI (Millus et al. 2007) suggested that local removal of deer mice reduces rates of egg loss in murrelet colonies.

Although it is difficult to know the exact fate of all nests on SBI because National Park Service biologists only checked nests every 5th day, the fate of eggs could usually be determined. In 2003, egg mortality attributed to mice was relatively low (15%), compared with a mean of 40% ($\pm 5\%$) each year between 1993 and 2002 (Millus et al. 2007). Given the small number of eggs (~12) that were presumed to be eaten in 2003 (Millus et al. 2007), and the large number of mice present while murrelets were on the island, it is perhaps not surprising that we found no evidence of murrelet tissues in the diets of the relatively few mice we sampled. Evidence of broken murrelet eggs may be the work of a few mice that happen upon eggs opportunistically. The relatively large size of Xantus' Murrelet eggs (54 mm \times 37 mm; Drost and Lewis 1995) may also limit egg predation by small mammals, as has been suggested elsewhere (DeGraaf and Maier 1996; Craig 1998; Bradley and Marzluff 2003). Regardless of the limited ability of mice to open murrelet eggs, or that murrelet tissue currently does not seem to constitute a major portion of mouse diets on SBI, deer mice could still have a significant impact on local murrelet reproductive success because so few (42–90) eggs are laid each season relative to the large numbers of mice present (Millus et al. 2007). Given the long evolutionary history of coexistence of murrelets and deer mice on SBI, egg predation has probably always occurred, but probably did not pose a significant threat to murrelet populations until other factors, including changes in food availability and mortality rates of juveniles and adults at sea, reduced population sizes.

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