Burrowing Owl Diet at a Migratory Stopover Site and Wintering Ground on Southeast Farallon Island, California

J. Raptor Res. 50(4):391–403

BURROWING OWL DIET AT A MIGRATORY STOPOVER SITE AND WINTERING GROUND ON SOUTHEAST FARALLON ISLAND, CALIFORNIA

SARA L. CHANDLER
San José State University, 1 Washington Square, San José, CA 95162 U.S.A.

JAMES R. TIETZ[1] AND RUSSELL W. BRADLEY
Point Blue Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954 U.S.A.

LYNNE TRULIO
San José State University, 1 Washington Square, San José, CA 95162 U.S.A.

ABSTRACT.—On the Farallon Islands, 48 km west of the coast of central California, Burrowing Owls (*Athene cunicularia*) are a native migrant and a predator of the nonnative house mouse (*Mus musculus*) and the native Ashy Storm-Petrel (*Oceanodroma homochroa*). Previous research showed that Burrowing Owl predation on Ashy Storm-Petrels is likely unnaturally exacerbated by the abundance of house mouse prey in the fall, which may encourage more owls to overwinter. When the cyclic mouse population crashes in winter, the owls switch to preying upon the storm-petrels, a species of conservation concern. From September 2010 to May 2011, we conducted daily owl surveys and a diet study of Burrowing Owls on Southeast Farallon Island. One goal was to document seasonal changes in Burrowing Owl diet composition through collection and assessment of pellets. During our study period, 12 banded owls overwintered for an average of 118 d and contributed 64% of the 679 analyzed owl pellets. Insects were the most numerous prey item detected in pellets, but mice and storm-petrels made up 98.5% of the total prey biomass in the diet. Mouse consumption correlated positively with mouse abundance, and owls exhibited seasonal prey-switching behavior from mice to storm-petrels, when mouse abundance declined during the winter. Our findings suggest that a mouse eradication program on the Farallon Islands would result in fewer owls overwintering and subsequently reduce negative effects on the storm-petrel population.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *Ashy Storm-Petrel*; Oceanodroma homochroa; *house mouse*; Mus musculus; *diet*; *prey switching*.

DIETA DE *ATHENE CUNICULARIA* EN UN SITIO DE PARADA MIGRATORIA Y ZONA DE INVERNADA EN LA ISLA FARALLÓN SURESTE, CALIFORNIA

RESUMEN.—En las Islas Farallones, 48 km al oeste de la costa del centro de California, *Athene cunicularia* es una especie migratoria nativa, depredadora de la especie no nativa *Mus musculus* y de la especie nativa *Oceanodroma homochroa*. Estudios anteriores demostraron que probablemente *A. cunicularia* depreda sobre *O. homochroa* de forma exagerada debido a la abundancia de *M. musculus* en otoño, lo que puede alentar a más búhos a invernar en el lugar. Cuando la población cíclica de *M. musculus* colapsa en invierno, los búhos cambian de presa a *O. homochroa*, una especie de interés de conservación. De septiembre de 2010 a mayo de 2011, llevamos a cabo censos diarios de búhos y un estudio de dieta de *A. cunicularia* en la Isla Farallón Sureste. Uno de los objetivos fue documentar los cambios estacionales de la composición de la dieta de *Athene cunicularia* a través de la recolección y la evaluación de egagrópilas. En nuestro periodo de estudio, 12 búhos anillados permanecieron un promedio de 118 días durante el invierno y aportaron el 64% de las 679 egagrópilas de búhos analizadas. Los insectos fueron las presas más detectadas en las egagrópilas, pero *M. musculus* y *O. homochroa* compusieron hasta un 98.5% del total de la biomasa de las presas en la dieta. El consumo de *M. musculus* se correlacionó positivamente con la abundancia de dicha especie y los búhos

---

[1] Email address: jtietz@pointblue.org

exhibieron un comportamiento de cambio de presa estacional de *M. musculus* a *O. homochroa* cuando la abundancia de la primera disminuyó durante el invierno. Nuestros resultados sugieren que la realización de un programa de erradicación de *M. musculus* en las Islas Farallones disminuiría la cantidad de búhos que permanecen durante el invierno y subsecuentemente reduciría los efectos negativos sobre la población de *O. homochroa*.

[Traducción del equipo editorial]

The introduction of nonnative species has caused a range of economic and ecological effects, including the reduction of native species diversity (Vitousek et al. 1997, Fritts and Rodda 1998, Clout and Russell 2008). Due to the large number of endemic species, oceanic island ecosystems are especially vulnerable to imbalances in predator-prey relationships caused by introduced species (Fritts and Rodda 1998). Sudden changes in predator-prey interactions may lead to extensive changes in the food web and subsequent losses in biodiversity (Vander Zanden et al. 1999, Sandlund et al. 2001, Clout and Russell 2008). In some situations, the introduced species strengthens an interaction between native species, such as increasing predation of one upon another. For rare species, such interactions can threaten the survival of one or both species (Soulé et al. 2005).

Introduced species can elicit predator responses that further alter predator-prey interactions, the food web, and interacting species dynamics. Prey switching is one such type of predator response (Murdoch 1969, van Baalen et al. 2001), whereby the predator shifts to a different prey based on prey availability or the predator's prey preference. Prey switching is associated with a functional response to prey abundance. It is generally described as the circumstance when a predator has developed a search image, or "preference," for one prey species, but can switch to an alternate prey species if it becomes more abundant or is more energetically profitable (Smith 1996). In some cases, prey switching can have drastic effects upon the alternative prey population (Drost and McCluskey 1992).

Interacting species are species whose "presence or absence ... influences the distribution or abundance of ... other species" (Soulé et al. 2005). Management of interacting species, especially if one or more are special status or of conservation concern, can be a challenge. For example, in some wildlife or habitat management scenarios, protected species prey upon other protected species and managers are faced with conflicting strategies or are forced to choose a strategy that benefits one species over the other (Roemer and Wayne 2003, Garcia and Conway 2010, Chadès et al. 2012).

The Burrowing Owl (*Athene cunicularia*), Ashy Storm-Petrel (*Oceanodroma homochroa*), and house mouse (*Mus musculus*) are three interacting species of management concern on the Farallon Islands, which are part of the Farallon National Wildlife Refuge managed by the U.S. Fish and Wildlife Service (U.S.F.W.S. 2013). Both the Burrowing Owl and the Ashy Storm-Petrel, a small seabird, are native and are classified as California Species of Special Concern. This designation indicates the species are in decline, exist in small or fragmented populations, or are otherwise of conservation concern (Carter et al. 2008, Gervais et al. 2008). The Farallon Islands are believed to support approximately half of the world's breeding population of Ashy Storm-Petrels (Carter et al. 2008).

Burrowing Owls are negatively affecting storm-petrel populations on the Farallon Islands (Nur et al. 2013). The abundance of house mice likely induces Burrowing Owls to remain on the Farallon Islands longer and in greater abundance than they naturally would if the mice were not present (Irwin 2004, U.S.F.W.S. 2013, Nur et al. 2013). Subsequently, the Burrowing Owls that stay through winter until early spring (January–April) prey on the Ashy Storm-Petrel, when the mouse population crashes in the winter (Irwin 2004, Witmer and Jojola 2006, U.S.F.W.S. 2013, Mills 2016, Nur et al. 2013). In late winter and early spring (February–April), the storm-petrels become more available as they return to the Farallon Islands in greater numbers to breed. Burrowing Owls may exhibit a predator response such as prey switching. Predation pressure exerted on the Ashy Storm-Petrel by Burrowing Owls has population-level consequences for the storm-petrel (Witmer and Jojola 2006, Carter et al. 2008, Nur et al. 2013): reduced adult survival due to predation, and future population declines, if this predation were to continue at observed rates (Nur et al. 2013).

On Southeast Farallon Island (SEFI) we conducted a 9-mo study of the diet of the Burrowing Owl from September 2010 to May 2011. The primary objective of this study was to describe the composition of the Burrowing Owl diet on SEFI and quantitatively document whether this owl species exhibits prey switching behavior on SEFI.

METHODS

Study Area. SEFI is located 48 km west of San Francisco off the coast of central California. Measuring 28 ha, SEFI is the largest of the Farallon Islands, which is one of several islands that compose the Farallon National Wildlife Refuge. Topographically, it is characterized by a hill that rises from the center up to 90 m high, and a wide, flat marine terrace that extends outward from the base of the hill. The terrace is widest from the southeastern to the western portions of the island, and the seabirds have excavated numerous burrows within its friable soil. The hill is composed of crumbling granite cliffs that contain fissures, crevices, and caves, and rocky scree fields at its base. SEFI has a temperate, maritime climate, with wet winters and dry summers (average annual rainfall = 51 cm). The temperature is warmest in October, with an average air temperature of 16.1°C, and coldest in January, with an average air temperature of 11.4°C.

The northern and northeastern slopes and flats are more difficult to access due to steep terrain. These areas have only restricted access, to prevent the spread of nonnative weeds and to minimize disturbance to sensitive marine and avian wildlife. Access to these areas is limited to brief visits at select times of the year; however, these areas were mostly visible from either Shubrick Point or the lighthouse. West End Island, which is separated from SEFI by a narrow channel, and the surrounding islands were not included in the study area due to difficult access and sensitive wildlife concerns.

Study Species. In general, data are lacking for migratory Burrowing Owls during stopover and across their range during the winter, but a few researchers have studied the Burrowing Owl's winter migration movements, behavior, and diet (Harman and Barclay 2007, LaFever et al. 2008, Holroyd et al. 2010). Examining pellet remains has been a traditional method for describing owl diets, which are often used to answer questions about a predator's foraging ecology (Errington 1930). There are ample studies on the diet of Burrowing Owls across their range, including a few studies conducted during the winter. These studies indicated that the Burrowing Owl is an opportunistic and generalist feeder, with a relatively diverse diet throughout its range and across seasons (Poulin et al. 2011). In general, the owls consumed a high percentage of arthropods, especially insects, by quantity, but some studies showed that vertebrate prey, particularly rodents, although consumed with much lower frequency, made up a greater portion of the total prey biomass (Marti 1974, Poulin and Todd 2006, Littles et al. 2007, Hall et al. 2009, Trulio and Higgins 2012). Birds were a smaller proportion of the diet, or occurred only occasionally in pellets.

The Burrowing Owl is a migrant to the Farallon Islands, with most owls arriving in the fall (September–November), and some overwintering until spring (Richardson et al. 2003). It is not completely known where the Farallon Burrowing Owls originate, although researchers suspect, based on telemetry and band recoveries in California, that some migrate from the northwestern United States or southwestern Canada (Holroyd et al. 2010). Observations of Burrowing Owls on SEFI were recorded as early as the late 19th century and have been documented in bird survey data up to the present day (DeSante and Ainley 1980, Point Blue Conservation Science unpubl. data).

Burrowing Owls have been observed occasionally on West End Island but are primarily on SEFI, the largest of the islands and the most habitable for terrestrial wildlife. Although Burrowing Owls have not been found on the smaller islands, these islands are not easily accessed by researchers and have not been thoroughly surveyed for owls. On the Farallon Islands, Burrowing Owls are primarily nocturnal, mostly hunting at night and roosting during the day (Point Blue Conservation Science unpubl. data). SEFI is pockmarked with innumerable rocky crevices on its slopes and natural burrows dug by Cassin's Auklets (*Ptychoramphus aleuticus*) and Rhinoceros Auklets (*Cerorhinca monocerata*), providing an abundance of roosting habitat for Burrowing Owls.

The Ashy Storm-Petrel is a diminutive seabird (length = 18.9 cm, wing chord = 14.2 cm), with a population estimated at 10,000 individuals worldwide (Ainley 1995, Carter et al. 2008); approximately half the population breeds on the Farallon Islands. This seabird is long-lived and can only produce one nestling per year. The Ashy Storm-Petrel spends all day foraging at sea and flies to the island only at night, thus limiting predation by diurnal Western Gulls (*Larus occidentalis*). On the island, they acquire nest sites and mates, and tend to eggs or nestlings. During the fall and winter (August–February), Ashy Storm-Petrel abundance on the island is greatly reduced with the cessation of nesting activity. The birds start courtship at the colony on the island in February and March, and young fledge from September to November (Ainley 1995). In addition, Leach's Storm-Petrels (*Oceanodroma leucorhoa*) also nest on SEFI (length = 20.3 cm, wing chord = 15.1 cm; Ainley 1980, Howell 2012), but their population is estimated to be <5% of the Ashy Storm-Petrel population, based on mist-netting data, breeding bird monitoring, and nest-site searches with playbacks of both species (Point Blue Conservation Science unpubl. data). The International Union for Conservation of Nature (IUCN) classifies the Ashy Storm-Petrel as endangered, whereas the Leach's Storm-Petrel, which has a much larger global population, is considered to be of least concern (population categories defined by IUCN; BirdLife International 2016).

The house mouse was likely accidentally introduced to the Farallon Islands by humans in the 1850s, but may have been introduced earlier (Jones and Golightly 2006). On SEFI, the house mouse measures an average of 16.2 cm (adults) in snout-to-tail length (Jones and Golightly 2006). The house mouse population on SEFI is cyclic, such that the population builds during the summer, peaks in September and October, then declines severely in the winter to its lowest numbers from January to July (Irwin 2004, Nur et al. 2013). In field surveys conducted in 2010, the density of house mice at its peak was 1297 ± 224 individuals per hectare (95% CI: 799–1792), which is "ten times greater than reported densities in most island or mainland environments" (U.S.F.W.S. 2013).

Burrowing Owl Surveys and Marking. From August to December of 2010, we conducted general landbird area searches twice daily, once in the morning and once in the afternoon, as part of regular fall bird monitoring on SEFI. During these area searches, we systematically surveyed the island on foot, dividing it into unit areas, and counting and recording all birds observed within each area. In addition to the area searches, we conducted focused surveys for Burrowing Owls daily, weather permitting, from September 2010 to May 2011. We surveyed the accessible parts of the island and scanned known roosts, rocky crevices, and open areas with binoculars. Generally, the surveys were conducted between 1100 and 1500 H because previous research on the island indicated that the owls were most likely to be standing outside their roosts during midday (Point Blue Conservation Science unpubl. data). During all surveys, we recorded the total number of owls observed and their locations. We estimated the number of Burrowing Owls that migrated to SEFI by combining the number of Burrowing Owls observed during general landbird area searches with those observed during focused Burrowing Owl counts, with care taken to avoid double-counting.

From 2007–2011, we captured and banded Burrowing Owls on SEFI in an effort to get an accurate count of the owls overwintering on the island. We banded all owls captured on SEFI with a U.S.G.S. aluminum band on one leg and a blue alphanumerically coded aluminum band (ACRAFT, Edmonton, Alberta, Canada) on the other. Codes were one letter and a one- or two-digit number, and bands could be read from a distance with a spotting scope or binoculars. When we observed an owl with a visible leg band, we recorded the identification number and which leg was color-banded. We attempted to capture unbanded owls using mist nets near their roosts at night.

In addition to searching for roosting owls, we used telemetry to determine the location of Burrowing Owl roosts and to more easily identify individual owls, which was especially useful if the owls were reclusive during the day or if they moved between roosts. For 11 of the 12 owls we captured, we attached transmitters (Holohil, PD-2, Carp, Ontario, Canada) using a backpack-style harness (Rappole and Tipton 1991). The transmitters weighed <5 g, which is approximately 3% of the mass of a Burrowing Owl, and had a battery life of approximately 6 mo. We used a portable antenna and receiver (ATS, R4000, Isanti, MN U.S.A.) to track the owls to their roosts, where we searched for their pellets. Transmitters were removed from two owls during the study period because they appeared to adversely affect the owls' behavior.

Pellet Collection and Diet Analysis. Building on previous research by Mills (2016), we collected regurgitated pellets and prey remains from roosts, from September 2010 through May 2011, to determine the composition of the Burrowing Owl diet on SEFI. We collected most owl pellets from outside burrows or crevices that were known roosts of Burrowing Owls, whose identity was known from either their transmitter or band, but also from locations where the identity of the owl was unknown. This method differs from that of Mills (2016), who combined pellets from four different owl species for analysis. In our study, we also collected any

Burrowing Owl pellets (identified by size and general shape) incidentally encountered at any time.

We collected pellets and prey remains from individual owls approximately every 1–2 wk. Three of the banded owls had roosts that were not easily accessible, so we only collected pellets and prey remains from these roosts one or two times during the study. All the pellets and prey remains collected from one roost on a single day (one collection event) were placed in a plastic bag and labeled with the date, location, number of pellets, and identity of owl, if known.

To dissect the pellets, each sample (one collection event) was pulled apart with forceps in a shallow dish with some water. We identified all notable parts (e.g., bones, exoskeletons, feathers, mandibles, etc.) of prey items and nonfood objects (e.g., metal bands, plastic, thread, rock, and vegetation) and recorded them on a data sheet. We identified prey items visually as mammal, bird, or invertebrate, and then classified them to genus and species when possible (Bland and Jacques 1978, Sibley 2000, Gaston 2004). The house mouse is the Burrowing Owl's only available terrestrial mammalian prey and, therefore, easily identified by the presence of mouse mandibles and fur in the pellets. For avian prey, we identified the species of bird according to bill shape when possible. Storm-petrels characteristically have long slender bills with a distinctive hook at the tip, as well as a pungent, musky odor, which was evident in the owl pellets. If a bill was not present, we used feathers, wings, furcula, or feet to identify the species. When a banded bird was a prey item, the band number identified the individual, even if no other bird parts were present. We used an entomological key to identify insects to Class and Order (Bland and Jacques 1978), and Alma Saucedo Mejia of the Department of Entomology at the California Academy of Sciences assisted with identifications, particularly of spiders and earwigs. Pellets consisting entirely of insects may have been slightly less likely to be found, as they disintegrated rapidly after regurgitation. To accurately count prey items, we tallied the minimum number of individuals (MNI) using the greatest number of identifiable parts, beginning with the most restrictive part (Mollhagen et al. 1972, see Chandler 2016 for more details).

When analyzing the contents of the pellets, we grouped samples from each owl into approximate 2-wk sampling periods. We used a period of 2 wk because collection events at roosts were sometimes spaced up to 2 wk apart. In addition, we grouped the pellets to minimize bias toward overestimation of prey items consumed. Because Burrowing Owls can apportion a prey item over more than one pellet, counting prey items on a pellet-by-pellet basis may result in an overestimation (Green 1983). Therefore, in order to enumerate prey items in a consistent manner, we grouped the pellets from the banded owls (whose pellets were regularly collected) in a sampling period that encompassed either the first half or the second half of each month.

We did not assign the pellets from unknown owls and the three banded owls that had difficult-to-access roosts to a sampling period, as there was no way of consistently knowing when the pellets were egested. For each of the three banded owls with difficult-to-access roosts, we analyzed the pellets collected as one sample, without regard to when they were collected. We added the diet results from these three owls to the aggregate diet information for all Burrowing Owls during the study, but not to analyses of seasonal changes in diet. We analyzed all the pellets from unknown owls as one large group as well.

We used pellets from eight of the 12 banded Burrowing Owls to detect differences in the owl diet over time. Owls excluded from this portion of the analysis included the three banded owls with roosts that were difficult to access, and one banded owl for which pellets were only collected over three sampling periods. We included only owls contributing pellets in at least five sampling periods. On average, each of the eight owls contributed pellets in 8.3 (SE ± 1.0) sampling periods within the study.

Estimated Biomass. We estimated prey biomass by multiplying the total number of prey items for each main prey type by a reference mass from the literature or from a field resource. For the house mouse, we followed Jones and Golightly (2006), who used 18.5 g as the average mass for an adult mouse. For the Ashy Storm-Petrel, we referenced Ainley (1995) by averaging the species' mass during the courtship period in February with their mass during the egg-laying period in April, which equaled 38.9 g. Leach's Storm-Petrels at SEFI were slightly heavier, with an average mass of 39.5 g (Point Blue Conservation Science unpubl. data). Because the prey remains of Ashy and Leach's Storm-Petrel are indistinguishable and the difference in mass between them was only 0.6 g, we lumped them for the purposes of this study and used a mass of 38.9 g for all storm-petrels. For the beetles (*Coniontus* spp.), we weighed 34 adults to obtain an average mass of 0.11

g. For the Farallon camel cricket (*Farallonophilus cavernicolus*), we weighed 10 adults and six juveniles to obtain an average mass of 0.25 g.

For all prey species, we calculated biomass using whole-animal weights, essentially assuming all parts of a prey animal were consumed (Steenhof 1983). Determining biomass in this method results in an overestimate of overall energy gain because the owls do not digest the fur, feathers, bills, bones, elytra (beetle wings), mandibles (cricket jaws), and some whole feet and wings of birds. The undigested material in the pellets, however, represents relatively little of the ingested prey (Tabaka et al. 1996). In a nutrition study of three raptor species, including Great Horned Owl (*Bubo virginianus*), the nutritional composition of the prey minus the egested material was comparable to that of the whole prey (Tabaka et al. 1996); regurgitated pellets made up only 2-8% (dry weight) of mammalian and avian prey consumed (Tabaka et al. 1996). Researchers studying raptor diets typically estimate biomass based on whole prey weights, preferably from live animals collected locally and grouped by age and sex (Steenhof 1983). We used average weights from local studies or the literature, although we did not account for prey demographic variability.

Mouse Abundance. Following the protocol described by Irwin (2004), we estimated mouse abundance by trapping on three consecutive nights per month from November 2010 to April 2011. We baited 48 covered snap traps with peanut butter and oats and arranged them along four trap lines (12 traps per line) spread across the various island habitats. We used the mousetrap success data (the number of traps that caught at least one mouse) from these efforts as an index for mouse abundance (Nur et al. 2013).

Statistical Analysis. We used a regression analysis to determine if there was a relationship between the number of mice per pellet and mouse abundance (trap success), averaged by month. We used ANOVA to test whether the owls' diet varied between seasons. For the purposes of this test only, we defined the fall season as 15 September (just before the owls started arriving) to 31 December and the spring season as 1 January to 15 May (after the last owl had departed). We compared the average biomass of mice (per pellet per owl) and the average biomass of storm-petrels (per pellet per owl) in each period. We used Tukey's tests for pairwise comparisons of the biomass of mice eaten in fall, mice eaten in spring, and storm-petrels eaten in spring. All statistical analyses were performed using Systat 13.

We calculated the average number of pellets or biomass of prey per owl within each period by dividing the total pellets or biomass, respectively, by the number of owls contributing pellets within a given period. Eight of the 12 banded owls were consistently represented by pellets throughout the study, and the number of contributing owls varied per period, ranging from 0–7 owls.

RESULTS

We estimated the total number of Burrowing Owls migrating to SEFI was 23 unique owls from fall 2010 to spring 2011. Most of the owls that arrived on SEFI were unbanded, although in 2010 three owls were returns, having been captured and banded on SEFI in previous years. Nine of the other 20 owls were captured and banded. The average stay on SEFI for the 12 banded Burrowing Owls was approximately 118 d (SE $\pm$ 17), with a minimum stay of 22 d and a maximum stay of 173 d. Of the 11 owls fitted with transmitters, 10 arrived in the fall (September–December) and stayed until at least January. The owls typically occupied three to four roosts in the same general area for the duration of their stay on SEFI.

Burrowing Owl Diet on SEFI. We analyzed 679 Burrowing Owl pellets. Of these, 437 were collected from the roosts of 12 owls that were banded on SEFI. We collected an additional 242 pellets from other roosts or feeding locations; we did not know from which owl or from how many owls these pellets originated. The average number of pellets collected per banded owl during each 2-wk period across all periods was 5.2 (range = 0–9; Fig. 1). The number of banded owls that contributed pellets ranged from zero to seven in any one period (Fig. 1).

The pellets and prey remains contained 1625 prey items, 1091 of which were from the 12 banded owls, and 534 were from unknown owls. The Burrowing Owl diet included only one species of mammalian prey (house mouse), several species of avian prey, and invertebrates, especially insect and spider taxa. Four prey types accounted for >90% of all prey items by number: beetles (32%), crickets (28%), mice (28%), and storm-petrels (5%). In total, 12 orders were represented; however, some birds and invertebrates could not be identified to order (Table 1).

Prey Switching. Based on the number of mice and storm-petrels consumed by owls in each period, the

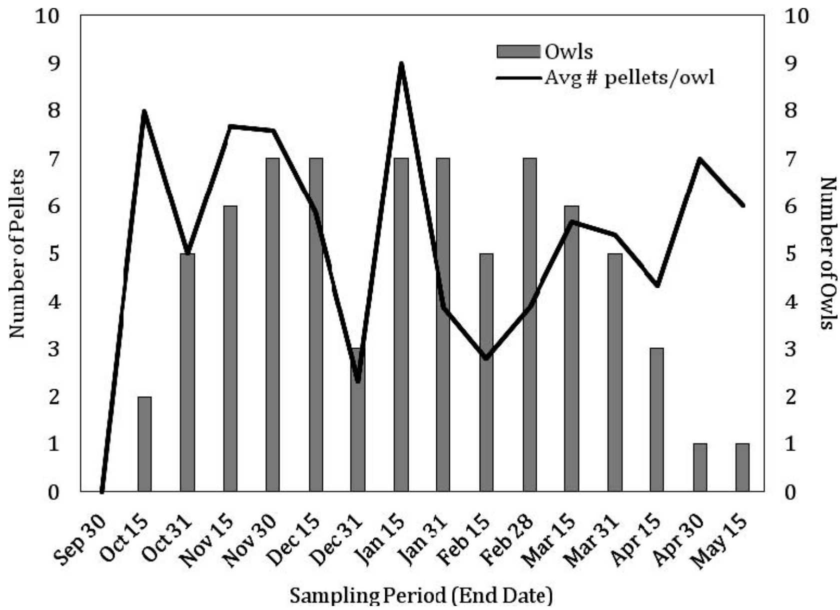

Figure 1. Number of owls and average number of pellets per owl within each period, 2010–2011. The line shows the average number of pellets per owl, and the columns show the number of owls contributing pellets in each period.

Burrowing Owl diet shifted noticeably from primarily mice from October to mid-January to storm-petrels from February to May (Fig. 2). From October through mid-November, and again in January, all owls consumed mice (Fig. 2). Beginning in January, the percentage of owls consuming storm-petrels steadily increased (Fig. 2). From late April to mid-May, only a single owl remained; this owl consumed only storm-petrels in the second half of April and both storm-petrels and mice in the first half of May (Fig. 2).

Although beetles and crickets were the most numerous of the prey items counted in the diet, they did not represent significant biomass in the owls' diet as compared to mice and storm-petrels, which made up 98.5% of the total estimated prey biomass (Table 2). By biomass, mice made up most of the diet in the fall, whereas storm-petrels made up half to most of the diet in the winter and early spring, respectively (Fig. 3). From November to April, the number of mice per pellet was strongly and positively correlated with trapping success for mice ($R^2 = 0.79$, $P = 0.017$). Beetles and crickets were present in the pellets throughout most of the study period, but contributed much less to the diet in terms of biomass.

The transition from eating mice in the fall to eating storm-petrels in the spring was identifiable both for owls as a group and for individual owls. Six of the eight (75%) uniquely marked owls exhibited a transition or switch in diet. During the month of January, mice and storm-petrels were consumed in similar quantities. Four of the owls made a complete switch, with storm-petrels composing nearly 100% of the owls' diet for the remainder of their stay on SEFI, whereas two owls continued to eat some mice, although storm-petrels made up the majority of their diet. For the two remaining owls that did not appear to switch, one contributed very few pellets after mid-December, so it is possible that we simply did not detect its diet change. Pellets of the other owl that did not switch consisted mostly of beetles in January and February until its departure on 28 February.

The owls' diet changed significantly between seasons ($F_{(2,21)} = 12.70$, $P < 0.001$). The biomass of mice consumed in the spring was significantly less than the biomass of mice consumed in the fall (Tukey's test; $P < 0.001$), and also less than the biomass of storm-petrels consumed in the spring ($P = 0.002$). The biomass of mice consumed in the fall and the biomass of storm-petrels consumed in the spring did not differ ($P = 0.49$).

Table 1. The number of prey items of each identified taxon and their percent of total consumed by Burrowing Owls (*Athene cunicularia)* on Southeast Farallon Island, CA, September 2010–May 2011. Percent of total shown only by order and summed by phylum (in bold).

Prey Items					
Phylum	Class	Order	Species (Common Name)	Number of Items	Percent of Total
Chordata (Vertebrates)				**554**	**34**
	Mammalia	Rodentia	*Mus musculus* (House mouse)	452	27.8
	Aves	Procellariiformes	*Oceanodroma homochroa* (Ashy Storm-Petrel) / *Oceanodroma leucorhoa* (Leach's storm-petrel)	86	5.3
		Charadriiformes	*Ptychoramphus aleuticus* (Cassin's Auklet)	2	0.1
		Passeriformes	*Sayornis nigricans* (Black phoebe)	1	0.2
			Regulus calendula (Ruby-crowned kinglet)	2	
			Zonotrichia albicollis (White-throated sparrow)	1	
		Unknown bird		10	0.7
Arthropoda (Invertebrates)				**1071**	**66**
	Arachnida	Araneae (Spiders)		6	0.4
	Insecta	Orthoptera			28.1
		Suborder: Ensifera	*Farallonophilus cavernicolus* (Farallon camel cricket)	456	
		Suborder: Caelifera (grasshoppers)		1	
		Dermaptera (earwigs)		3	0.2
		Coleoptera (beetles)		525	32.3
		Lepidoptera (moths and butterflies)		61	3.8
	Chilopoda	Lithobiomorpha (stone centipedes)		9	0.6
	Malacostraca	Superorder: Peracarida, Amphipoda (amphipods)		5	0.3
		Isopoda (isopods)		3	0.2
	Unknown arthropod			2	0.1

DISCUSSION

The Burrowing Owl diet on SEFI included a diversity of vertebrates and invertebrates. The variety and number of invertebrates in the owl diet likely reflect the opportunistic foraging typical of Burrowing Owls; this diet is consistent with diet studies in other habitats (Littles et al. 2007, Hall et al. 2009, Trulio and Higgins 2012). Invertebrate prey made up the majority of the owl diet in sheer number of prey items on SEFI. However, the data show that, while invertebrates made up 66% of the diet by frequency, their total biomass was only an estimated 1.5% of the diet. Vertebrates, in contrast, composed an estimated 98.5% of the total biomass contribution to the Burrowing Owl diet.

Mice are an important energetic component of the Burrowing Owl's diet on SEFI, as they are in other parts of this owl's range (Arana et al. 2006, Littles et al. 2007, Hall et al. 2009, Trulio and Higgins 2012). Mice made up an estimated 70.4% of the total prey biomass, which was similar to diets in studies in other regions (Littles et al. 2007, Trulio and Higgins 2012). On SEFI, there was a strong positive correlation between mouse abundance and mice consumed.

The seasonal differences in the Burrowing Owl diet on SEFI reflect the varying availability of prey throughout the seasons. Previous research indicated that mice are abundant on SEFI in the fall, but that populations undergo a marked decrease in the spring (Irwin 2004, U.S.F.W.S. 2013, Nur et al.

Table 2. The biomass in grams of the four most common prey items eaten by Burrowing Owls (*Athene cunicularia)* on Southeast Farallon Island, CA, 2010–2011.

PREY ITEM	NUMBER OF PREY ITEMS	AVERAGE MASS OF PREY ITEM (g)	BIOMASS (TOTAL; g)	BIOMASS (% OF TOTAL)
House mouse	452	18.5[a]	8362	70.4
Storm-petrel	86	38.85[b]	3341	28.1
Beetle	525	0.11	58	0.5
Cricket	456	0.25	114	1.0

[a] Jones and Golightly 2006.
[b] Ainley 1995.

2013). We found a decrease in the number and biomass of mouse prey consumed by owls from fall to spring. Also, in the spring, the biomass of mice consumed was much less than the biomass of storm-petrels consumed, suggesting the owls switched from decreasingly abundant mice to increasingly available storm-petrels as their primary prey. These results support those found by Mills (2016) in a multiyear study on the diet of Farallon owls in the early 2000s.

Although the relationship between storm-petrel abundance and storm-petrels eaten was not explicitly tested in this study, previous research has shown that storm-petrels increase in abundance on SEFI from February to April, as they initiate pre-breeding behavior and start attending breeding sites on the island (Ainley et al. 1974, 1990). This study showed that as storm-petrel numbers increased, they were increasingly preyed upon as mouse abundance dramatically decreased over the winter (Nur et al. 2013). We also documented individual diet variation among owls. One owl appeared to overwinter without ever having consumed a storm-petrel. In contrast, by the end of February, when that individual departed SEFI, all other owls had already made the switch to storm-petrels. The majority of the owls, however, ate both mice and storm-petrels, depending on the month, suggesting that this prey switching was a population-wide phenomenon.

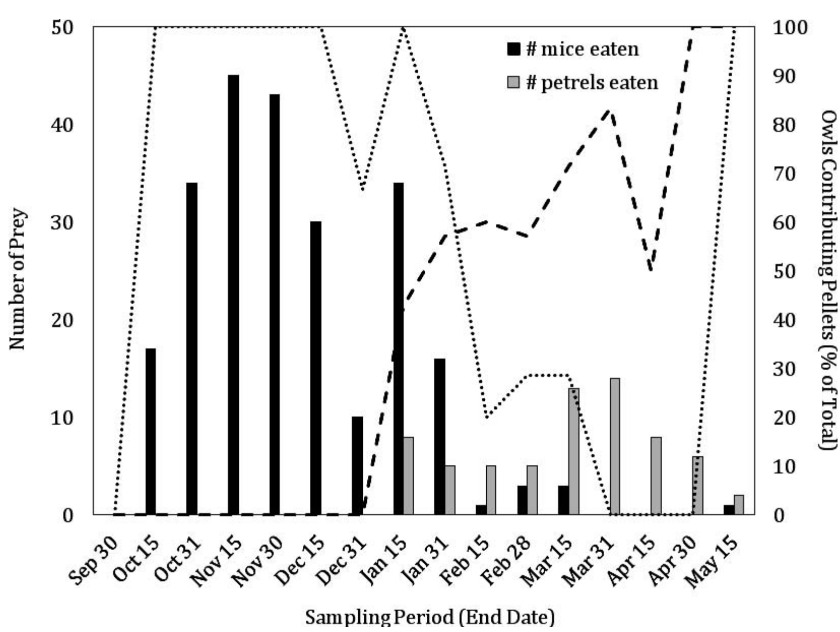

Figure 2. Number of mice and storm-petrels eaten, and the percentages of owls eating them, by period, 2010–2011. The percentages of owls eating mice and owls eating storm-petrels in each period are depicted by dotted and dashed lines, respectively.

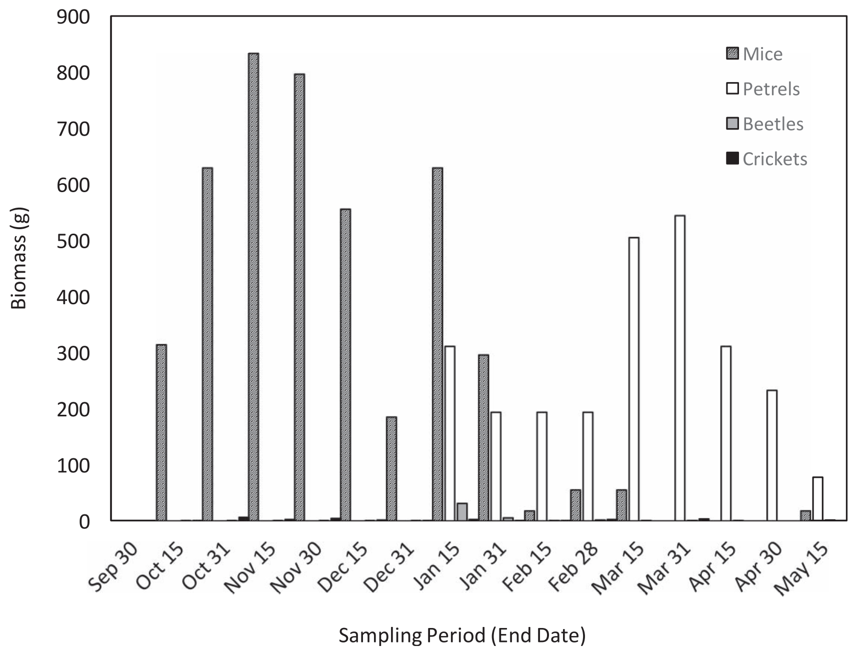

Figure 3. Prey biomass of four main types of prey, by period, 2010–2011. Note that insect biomass makes up such a small proportion of the owls' diet that the bars are very small at this scale.

Prey switching theory, as defined in a classical sense, could not be tested because abundance data were not available for storm-petrels in the fall and spring during the study period. However, previous research on SEFI has shown that Ashy Storm-Petrel colony attendance declines steadily by 85% from August to December before increasing again in February (Ainley et al. 1974, 1990). Moreover, our results agree with other research findings from SEFI that indicate seasonal shifts in the Burrowing Owls' diet from one composed primarily of mice in the fall to that of storm-petrels in the winter and spring (Nur et al. 2013, Mills 2016).

Mouse eradication on SEFI is one management option under consideration by U.S.F.W.S. to reduce Burrowing Owl predation upon storm-petrels, among other ecological benefits. Mice are a main prey species for the owl and are clearly important in the owl's diet on SEFI in the fall, most likely due to their great abundance and availability. Our findings suggest that eliminating the mouse population on SEFI is likely to reduce the number of Burrowing Owls that can be supported on SEFI in the fall and early winter before Ashy Storm-Petrel numbers increase.

One outcome of mouse eradication may be that the stopover duration for Burrowing Owls becomes shorter, resulting in fewer owls overwintering on SEFI. Although many owls visit the Farallon Islands briefly during migration, up to a dozen may attempt to overwinter and stay several months. Few of the owls that arrive on SEFI overwinter multiple years (Point Blue Conservation Science unpubl. data); the rest are migrants that essentially fill an available ecological niche every fall. Without mice available as prey, it is possible that the Burrowing Owls, upon arrival in the fall, will switch to an alternate prey. Whether other food sources, such as birds, amphibians, or invertebrates, are available in quantities to sustain an overwintering Burrowing Owl population is not known. However, our research indicated that invertebrates overall did not provide substantial prey biomass for Burrowing Owls, and there was no evidence of Burrowing Owls preying upon salamanders on SEFI.

The available alternate prey would then be avian, likely including migrant songbirds, a small proportion of storm-petrels that attend the colony year-round, and Cassin's Auklets, which are also present year-round. Because migrant songbird arrivals are erratic and their stopover durations and numbers are variable, they alone are unlikely to provide a reliable and consistent food source in quantities needed to sustain Burrowing Owls throughout the winter. Furthermore, the songbirds are mostly diurnal during their migratory stopover, so there would be little opportunity for the owls to capture them. Although they might provide more consistent prey, the number of storm-petrels returning to SEFI declines rapidly as nonbreeders stop attending in August and chicks fledge in September and October (Ainley et al. 1974, 1990); most of the Burrowing Owls arrive in October. Therefore, storm-petrels alone may not be abundant enough to sustain Burrowing Owls through the fall until storm-petrel numbers increase in February. Cassin's Auklets, which are common at SEFI year-round, appear to be an uncommon prey item for the Burrowing Owl (Table 1, Mills 2016); Mills' analysis found that predation of auklets was much higher by Barn Owls (*Tyto alba*) than Burrowing Owls. Cassin's Auklets (184 g) are likely a difficult prey item for Burrowing Owls (156 g) to handle due to the auklet's larger mass (10 times heavier than house mice and five times heavier than Ashy Storm-Petrels) and rapid flight to and from nest sites (Ainley et al. 2011, Poulin et al. 2011). With a smaller available prey base, more Burrowing Owls that arrive on SEFI in the fall may stop on the island for only a few days instead of a few months, and these owls may subsequently move on in search of other wintering grounds where prey may be more available.

Another outcome may be that some Burrowing Owls attempting to overwinter may die of starvation. There have been accounts of "emaciated owl carcasses" found on SEFI (DeSante and Ainley 1980), and two Burrowing Owls were inexplicably found dead during the time of this study. Also, the owls may be forced to hunt more during daylight hours, which puts them at higher risk of predation by Peregrine Falcons (*Falco peregrinus*) on SEFI. During our study period at least one Burrowing Owl, inadvertently flushed by a biologist during midday, was killed by a Peregrine Falcon. The remains of another Burrowing Owl were found far from its regular roosts; this bird may have been killed by a Peregrine Falcon as well.

If mouse eradication limits the number of owls that overwinter on SEFI by 50% or more, Nur et al. (2013) predict dramatic and positive impacts for Farallon Ashy Storm-Petrel populations. However, careful monitoring of owl responses to mouse removal from the Farallon Islands will be required to determine whether this management approach is an effective long-term management strategy for recovering the Ashy Storm-Petrel population on SEFI.

ACKNOWLEDGMENTS

We thank the many Farallon interns who helped collect data for this project. We also thank Jennifer Gorospe and Nandana Grace, who helped dissect pellets, and Phil Higgins at San José State University, who helped develop the pellet dissection methods. Additionally, we sincerely appreciate Alma Saucedo Mejia of the California Academy of Sciences, who helped identify invertebrate prey items. Research was conducted with permit approval by San José State University IACUC, California Department of Fish and Wildlife (SC-007343). Point Blue's Federal Banding Permit number is 09316, and this project's California Resident Scientific Collecting Permit number is 801168-03. Funding and impetus for this research were provided by Gerry McChesney and the U.S. Fish and Wildlife Service. The Environmental Studies Department at San José State University provided funding through a College of Social Sciences Research Grant. Point Blue Conservation Science and the Farallon Patrol provided logistical support. Additional funding for Point Blue's Farallon research was provided by the Bently Foundation, Baker Trust, Marisla Foundation, Mead Foundation, Campini Foundation, Bernice Barbour Foundation, Kimball Foundation, RHE Charitable Foundation, Volgenau Foundation, and Friends of the Farallones. This is Point Blue Conservation Science contribution number 2056.

LITERATURE CITED

AINLEY, D.G. 1980. Variation in Leach's Storm-Petrel. *Auk* 97:837–853.

———. 1995. Ashy Storm-Petrel (*Oceanodroma homochroa*). *In* A. Poole [ED.], The birds of North America online, No. 185. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/185 (last accessed 27 November 2015).

———, R.P. HENDERSON, AND C.S. STRONG. 1990. Leach's Storm-Petrel and Ashy Storm-Petrel. Pages 128–162 *in* D.G. Ainley and R.J. Boekelheide [EDS.], Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling system community. Stanford University Press, Palo Alto, CA U.S.A.

———, D.A. MANUAL, J. ADAMS, AND A.C. THORSEN. 2011. Cassin's Auklet (*Ptychoramphus aleuticus*). *In* A. Poole [ED.], The birds of North America online, No. 050. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/050 (last accessed 15 July 2016).

———, S.H. MORELL, AND T.J. LEWIS. 1974. Patterns in the life histories of storm-petrels on the Farallon Islands. *Living Bird* 13:295–312.

ARANA, M., M.L. RUÍZ-LUNA, S.S. MARIA, AND O. RAMIEREZ. 2006. Population fluctuations of the house mouse in a

Peruvian loma and the functional response of Burrowing Owls. *Austural Ecology* 31:956–963.

BIRDLIFE INTERNATIONAL. 2016. IUCN Red List for birds. http://www.birdlife.org (last accessed on 6 January 2016).

BLAND, R. AND H. JACQUES. 1978. How to know the insects, Third Ed. WCB McGraw-Hill, Dubuque, IA U.S.A.

CARTER, H.R., W.R. MCIVER, AND G.J. MCCHESNEY. 2008. Ashy Storm-Petrel (*Oceanodroma homochroa*). Pages 116–124 *in* W. Shuford, T. Gardali, and L. Comrack [EDS.], California bird Species of Special Concern: a ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. Studies of Western Birds Vol. 1. Western Field Ornithologists, Camarillo, CA U.S.A. and California Department of Fish and Game, Sacramento, CA U.S.A.

CHADÈS, I., J.M.R. CURTIS, AND T.G. MARTIN. 2012. Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. *Conservation Biology* 26:1016–1025.

CHANDLER, S.L. 2016. Burrowing Owl (*Athene cunicularia*) diet and abundance at a stopover and wintering ground on Southeast Farallon Island, California. M.S. thesis, San José State University, San José, CA U.S.A.

CLOUT, M.N. AND J.C. RUSSELL. 2008. The invasion ecology of mammals: a global perspective. *Wildlife Research* 35:180–184.

DESANTE, D.F. AND D.G. AINLEY. 1980. The avifauna of the South Farallon Islands, California. *Studies in Avian Biology* 4:1–104.

DROST, C.A. AND R.C. MCCLUSKEY. 1992. Extirpation of alternative prey during a small rodent crash. *Oecologia* 92:301–304.

ERRINGTON, P.L. 1930. The pellet analysis method of raptor food habits study. *Condor* 32:292–296.

FRITTS, T.H. AND G.H. RODDA. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics* 29:113–140.

GARCIA, V. AND C.J. CONWAY. 2010. A plan to conserve and manage Burrowing Owls on Naval Base Coronado, San Diego, CA. (Report #00246NR026). University of Arizona, Tucson, AZ U.S.A.

GASTON, A.J. 2004. Seabirds: a natural history. Yale University Press, New Haven, CT U.S.A.

GERVAIS, J.A., D.K. ROSENBERG, AND L.A. COMRACK. 2008. Burrowing Owl (*Athene cunicularia*). Pages 218–226 *in* W. Shuford, T. Gardali, and L. Comrack [EDS.], California bird Species of Special Concern: a ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. Studies of Western Birds Vol. 1. Western Field Ornithologists, Camarillo, CA U.S.A. and California Department of Fish and Game, Sacramento, CA U.S.A.

GREEN, G.A. 1983. Ecology of breeding Burrowing Owls in the Columbia Basin, Oregon. M.S. thesis, Oregon State University, Corvallis, OR U.S.A.

HALL, D.B., P.D. GREGER, AND J.R. ROSIER. 2009. Regional and seasonal diet of the western Burrowing Owl in south central Nevada. *Western North American Naturalist* 69:1–8.

HARMAN, L.M. AND J.H. BARCLAY. 2007. A summary of California Burrowing Owl banding records. Pages 123–131 *in* J.H. Barclay, K.W. Hunting, J.L. Lincer, J. Linthicum, and T.A. Roberts [EDS.], Proceedings of the California Burrowing Owl Symposium, Bird Populations Monographs No. 1. The Institute for Bird Populations and Albion Environmental, Inc.

HOLROYD, G.L., H.E. TREFRY, AND J.M. DUXBURY. 2010. Winter destinations and habitats of Canadian Burrowing Owls. *Journal of Raptor Research* 44:294–299.

HOWELL, S.N.G. 2012. Petrels, albatrosses, and storm-petrels of North America: a photographic guide. Princeton University Press, Princeton, NJ U.S.A.

IRWIN, J. 2004. Annual population cycle of house mice on Southeast Farallon Island and the effect on nesting seabirds. Farallon National Wildlife Refuge, Newark, CA U.S.A.

JONES, M.A. AND R.T. GOLIGHTLY. 2006. Annual variation in the diet of house mice (*Mus musculus*) on Southeast Farallon Island. Unpublished report. Department of Wildlife, Humboldt State University, Arcata, CA U.S.A.

LAFEVER, D.H., K.E. LAFEVER, D.H. CATLIN, AND D.K. ROSENBERG. 2008. Diurnal time budget of Burrowing Owls in a resident population during the non-breeding season. *Southwestern Naturalist* 53:29–33.

LITTLES, C. J., D. WILLIFORD, M.K. SKORUPPA, M.C. WOODIN, AND G.C. HICKMAN. 2007. Diet of western Burrowing Owls wintering in southern Texas. *Journal of Raptor Research* 41:307–313.

MARTI, C.D. 1974. Feeding ecology of four sympatric owls. *Condor* 76:45–61.

MILLS, K.L. 2016. Seabirds as part of migratory owl diet on Southeast Farallon Island, California. *Marine Ornithology* 44:121–126.

MOLLHAGEN, T.R., R.W. WILEY, AND R.L. PACKARD. 1972. Prey remains in Golden Eagle nests: Texas and New Mexico. *Journal of Wildlife Management* 36:784–792.

MURDOCH, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335–354.

NUR, N., R. BRADLEY, L. SALAS, AND J. JAHNCKE. 2013. Modeling the impacts of house mouse eradication on Ashy Storm-Petrels on Southeast Farallon Island. Appendix M in U.S.D.I. Fish and Wildlife Service, South Farallon Islands invasive house mouse eradication project: revised draft environmental impact statement. San Francisco Bay National Wildlife Refuge Complex. Fremont, CA U.S.A. https://www.fws.gov/uploadedFiles/Farallon_House_Mouse_Eradication_Revised_DEIS_compressed.pdf (last accessed 27 June 2016).

POULIN, R.G., E.A. HAUG, B.A. MILLSAP, AND M.S. MARTELL. 2011. Burrowing Owl (*Athene cunicularia*). *In* A. Poole [ED.], The birds of North America online, No. 061. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/061 (last accessed 31 March 2016).

——— AND L.D. TODD. 2006. Sex and nest stage differences in the circadian foraging behaviors of nesting Burrowing Owls. *Condor* 108:856–864.

RAPPOLE, J.H. AND A.R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.

RICHARDSON, T.W., P. PYLE, R. BURNETT, AND P. CAPITOLO. 2003. The occurrence and seasonal distribution of migratory birds on Southeast Farallon Island, 1968–1999. *Western Birds* 34:58–96.

ROEMER, G.W. AND R.K. WAYNE. 2003. Conservation in conflict: the tale of two endangered species. *Conservation Biology* 17:1251–1260.

SANDLUND, O.T., P.J. SCHEI, AND Å VIKEN. 2001. Introduction: the many aspects of the invasive alien species problem. Pages 1–7 *in* O.T. Sandlund, P.J. Schei, and Å. Viken [EDS.]. Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

SIBLEY, D.A. 2000. The Sibley guide to birds, First Ed. Knopf, New York, NY U.S.A.

SMITH, R.L. 1996. Ecology and field biology, Fifth Ed. HarperCollins, New York, NY U.S.A.

SOULÉ, M.E., J.A. ESTES, B. MILLER, AND D.L. HONNOLD. 2005. Strongly interacting species: conservation policy, management, and ethics. *BioScience* 55:168–176.

STEENHOF, K. 1983. Prey weights for computing percent biomass in raptor diets. *Raptor Research* 17:15–27.

TABAKA, C.S., D.E. ULLREY, J.G. SIKARSKIE, S.R. DEBAR, AND P.K. KU. 1996. Diet, cast composition, and energy and nutrient intake of Red-tailed Hawks (*Buteo jamaicensis*), Great Horned Owls (*Bubo virginianus*), and Turkey Vultures (*Cathartes aura*). *Journal of Zoo and Wildlife Medicine* 27:187–196.

TRULIO, L.A. AND P. HIGGINS. 2012. The diet of western Burrowing Owls in an urban landscape. *Western North American Naturalist* 72:348–356.

U.S. FISH AND WILDLIFE SERVICE (U.S.F.W.S.). 2013. South Farallon Islands invasive house mouse eradication project: revised draft environmental impact statement. San Francisco Bay National Wildlife Refuge Complex. Fremont, CA U.S.A. https://www.fws.gov/uploadedFiles/Farallon_House_Mouse_Eradication_Revised_DEIS_compressed.pdf (last accessed 27 June 2016).

VANDER ZANDEN, M.J., J.M. CASSELMAN, AND J.B. RASMUSSEN. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467.

VAN BAALEN, M., V. KRIVAN, P.C.J. VAN RIJN, AND M.W. SABELIS. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. *American Naturalist* 157:512–524.

VITOUSEK, P.M., C.M. D'ANTONIO, L.L. LOOPE, M. REJMANEK, AND R. WESTBROOKS. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21:1–16.

WITMER, G. AND S. JOJOLA. 2006. What's up with house mice?—a review. Pages 6–9 *in* R.M. Timm and J.M. O'Brien [EDS.], Proceedings of the 22nd Vertebrate Pest Conference, Berkeley, CA U.S.A.

Received 14 January 2016; accepted 21 June 2016.
Associate Editor: Stephen B. Lewis