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Burrowing Owl (*Athene cunicularia*) Diet and Abundance at a Stopover and Wintering Ground on Southeast Farallon Island, California

Sara Lee Chandler
San Jose State University

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BURROWING OWL (*ATHENE CUNICULARIA*) DIET AND ABUNDANCE
AT A STOPOVER AND WINTERING GROUND
ON SOUTHEAST FARALLON ISLAND, CALIFORNIA

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Sara L. Chandler

December 2015

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The Designated Thesis Committee Approves the Thesis Titled

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by

Sara L. Chandler

APPROVED FOR THE DEPARTMENT OF ENVIRONMENTAL STUDIES

SAN JOSÉ STATE UNIVERSITY

December 2015

Dr. Lynne Trulio	Department of Environmental Studies
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Dr. Rachel O'Malley	Department of Environmental Studies
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James Tietz	Point Blue Conservation Science
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ABSTRACT

BURROWING OWL (*ATHENE CUNICULARIA*) DIET AND ABUNDANCE AT A STOPOVER AND WINTERING GROUND ON SOUTHEAST FARALLON ISLAND, CALIFORNIA

by Sara L. Chandler

On the Farallon Islands the burrowing owl (*Athene cunicularia*) is a native migrant and predator of the non-native house mouse (*Mus musculus*) and the native ash storm-petrel (*Oceanodroma homochroa*). Burrowing owl predation on the ash storm-petrel is 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 prey upon storm-petrels, a species of conservation concern. In 2009, the U.S. Fish and Wildlife Service proposed eradication of the house mouse from the Farallon Islands in order to reduce owl predation on and aid recovery of the storm-petrel. From September 2010 to May 2011, I conducted daily owl surveys and a pellet study of burrowing owls on Southeast Farallon Island, the largest island. The goal was to document burrowing owl abundance, overwintering duration, and seasonal changes in diet composition prior to any mouse eradication effort. During my study I counted 23 owl migrants; a subset of these owls overwintered an average of 118 days. Insects were most numerous, but mice and storm-petrels comprised 98% 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. It is likely that mouse eradication would result in fewer owls overwintering and subsequently reduce impacts to the storm-petrel population.

DEDICATION

I dedicate this thesis to the many colleagues, interns, friends, and family who have supported me along the way:

Thank you, Jim, and my Farallon family, for teaching me about Island life, for staring at the rocks with me, and for sharing your daily experiences, no matter how small. Thank you, Lynne, for taking me under your wing and providing guidance and lift when I needed it. Thank you, dear Friends, for enthusiastically dissecting pellets (especially the stinky ones) with me, and for always cheering me on. Thank you, loving Parents, for your amazing generosity, for providing warm clothing and flea powder, and for never giving up on me. Thank you, Ed, for being my greatest champion, for holding my hand, for being so very patient, and for braving the Pacific to bring me home. Finally, I thank you, Rosalee, for carrying me to the end, even as I carried you! May you always have angels and owls watching over you.

For all of You, I am so grateful.

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Introduction

The introduction of non-native species has caused a range of ecological impacts, including the reduction of native species diversity (Clout & Russell, 2008; Fritts & Rodda, 1998). Examples of this occur in a variety of habitats all over the world, resulting in great biological and economic damage (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). Some infamous cases include the introduction of the European rabbit to Australia (Williams, Parer, Coman, Burley, & Braysher, 1995), the Indian mongoose to Hawaii (Hays & Conant, 2007; Kear & Berger, 2010), and the brown treesnake to Guam (Fritts & Rodda, 1998). In addition to ecological havoc, non-native species cause billions of dollars a year in economic damage (Pimentel, Lach, Zuniga, & Morrison, 2000; Vitousek et al., 1997).

The capacity for an introduced species to cause such devastation is often attributed to the alteration or introduction of predator-prey relationships, where the exotic species has a great ecological advantage over the native fauna (Fritts & Rodda, 1998). The introduction of the brown treesnake to Guam epitomizes this phenomenon (Fritts & Rodda, 1998). The treesnake is responsible for the extirpation of nearly all of Guam's native bird species and one of its three native mammal species (Fritts & Rodda, 1998). The native fauna were particularly susceptible to predation because they had not evolved strategies or defenses in tandem with the brown treesnake (Fritts & Rodda, 1998). Due to the large number of endemic and naïve species, oceanic island ecosystems are especially vulnerable to imbalances in predator-prey relationships caused by introduced species (Fritts & Rodda, 1998).

Sudden changes in predator-prey interactions may lead to extensive changes in the food web and subsequent losses in biodiversity (Clout & Russell, 2008; Sandlund, Schei, & Viken, 2001; Vander Zanden, Casselman, & Rasmussen, 1999). Trophic interactions within an ecosystem can be complex; introduced species may disrupt ecosystems by filling empty niches, competing with existing species in the same trophic level, or severely reducing and possibly eliminating species within a trophic level (Clout & Russell, 2008; Sandlund et al., 2001; Vander Zanden et al., 1999). 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, Estes, Miller, & Honnold, 2005).

Introduced species can elicit predator responses that further alter predator-prey interactions, the food web, and interacting species dynamics. A predator species may respond to increased availability of prey by consuming greater quantities of prey or consuming prey at a higher rate, called a functional response (Smith, R. L., 1996). Prey switching is one such type of predator response (Murdoch, 1969; van Baalen, Krivan, van Rijn, & Sabelis, 2001), whereby the predator shifts to a different prey based on prey availability or the predator's prey preference.

The burrowing owl (*Athene cunicularia*), ash storm-petrel (*Oceanodroma homochroa*), and house mouse (*Mus musculus*) are three interacting species of management concern on the Farallon Islands (Farallones, or Islands), which are part of the Farallon National Wildlife Refuge managed by the U.S. Fish and Wildlife Service (USFWS). Both the burrowing owl and the ash storm-petrel, a small seabird, are native

and 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, McIver, & McChesney, 2008; Gervais, Rosenberg, & Comrack, 2008). The Farallones are believed to support approximately half of the world's breeding population of ashy storm-petrels (Carter et al., 2008).

The burrowing owl may be affecting the seabird's population on the Islands. Some researchers have hypothesized that the abundance of house mice induces the burrowing owl to remain on the Farallones longer and in greater abundance than it naturally would if the mice were not present (Buffa, 2003; Irwin, 2004; USFWS, 2013b). Subsequently, the burrowing owls that stay through winter until early spring prey on the ashy storm-petrel when the mouse population crashes in the winter (Irwin, 2004; USFWS, 2013b; Witmer & Jojola, 2006). At this time the storm-petrels become more available as they return to the Island in greater numbers to breed. The burrowing owl may be exhibiting a predator response such as prey switching. Predation pressure exerted on the ashy storm-petrel by the burrowing owl may have population-level consequences for the storm-petrel (Buffa, 2003; Carter et al., 2008; Nur, Bradley, Salas, & Jahncke, 2014; Witmer & Jojola, 2006): reduced adult survival, high predation rates, and future population declines, if this predation were to continue at observed rates (Nur et al., 2014).

These trophic interactions pose a challenging management problem for USFWS, which, as steward of the Farallones and in partnership with Point Blue Conservation Science (Point Blue, formerly PRBO Conservation Science), actively manages the Islands to restore breeding bird populations to historic numbers (USFWS, 2002).

Currently, USFWS is considering a plan to remove the house mouse from the Farallones. The strategy aims to restore ecological balance to the Islands by removing the owl's main prey in the fall and thereby minimize predation of ashy storm-petrels by burrowing owls.

On Southeast Farallon Island (SEFI, or Island), I conducted a nine-month diet study of the burrowing owl from September 2010 to May 2011. To determine the strength of the interactions between the burrowing owl and its prey, I estimated how many burrowing owls stopped on the Island in the fall and winter and how long they stayed. I also investigated if the burrowing owl exhibited prey switching behavior. None of the previous research has quantified both burrowing owl diet and abundance on the Island in depth. My research provides USFWS with baseline conditions on the trophic interactions between the burrowing owl, ashy storm-petrel, and house mouse on the Farallones. The results of this study will help USFWS determine if mouse eradication would be an effective management strategy for achieving its conservation goals on SEFI. In addition, this research will add to the body of knowledge about burrowing owl diet during the non-breeding season, how it changes from fall and winter to spring, and its composition within a unique island ecosystem.

Related Research

Winter Ecology of the Western Burrowing Owl

In general, data are lacking for migratory burrowing owls across their range during the winter, but a few researchers have studied the burrowing owl's winter migration movements, behavior, and diet. Attempts to determine migration movements of burrowing owls have historically relied primarily on band recoveries. This strategy has yielded very few band re-sights or recoveries, however (Harman & Barclay, 2007). In 2010, Holroyd, Trefry, and Duxbury conducted a telemetry study in order to discover where burrowing owls that breed in central Canada wintered. In the three-year study, 125 burrowing owls that originated from the Canadian Great Plains (Alberta and Saskatchewan) were banded and fitted with radio transmitters. Researchers then searched for the owls by plane and on the ground in southern Texas, along the Gulf Coast, and in central Mexico, where Canadian owls were suspected to go during the winter (Holroyd et al., 2010).

Of the 125 burrowing owls with transmitters, the researchers were only able to relocate eight live owls and one dead owl. The owls were found between Houston, Texas and Michoacán, Mexico (Holroyd et al., 2010). These owls were located in cultivated or shrubby habitats with areas of low vegetation within one kilometer of the roost, and any roosts identified were highly variable, including a mammal burrow, a woodpile, culverts or pipes, and vegetation (Holroyd et al., 2010). In general, the wintering habitat of the burrowing owls was much more diverse than their breeding habitat in Canada.

In order to better inform management of burrowing owls during the non-breeding

season, a group of researchers studied the winter budget of burrowing owls in the Imperial Valley, California (LaFever, LaFever, Catlin, & Rosenberg, 2008). LaFever et al. (2008) observed a total of 28 owls, including male and female, paired and unpaired, and resident and non-resident individuals. During the breeding season, at least one owl at each burrow was fitted with a radio transmitter and banded; the sex was determined by the presence or absence of a brood patch, as well as behavior. LaFever et al. conducted observations in October and November 2002 and followed an “instantaneous” sampling scheme, where each individual owl’s activity was recorded every 15 seconds within a 15-minute period (LaFever et al., 2008). If the owl was out of sight, either radio telemetry or a burrow scope was used to determine whether the owl was in its burrow or away from the burrow.

Although LaFever et al. (2008) expected the time budgets to be more similar between both males and females during the winter, they found that some of the differences between the sexes remained even in the non-breeding season. For example, female owls still tended to spend more time in the burrow than males, and males tended to exhibit more alert behavior and spend more time away from the burrow (LaFever et al., 2008). The researchers suggested that the behavioral differences between the sexes during the winter might be beneficial to the owl pair in the following breeding season. The females may stay in the burrow in order to conserve energy and physical condition for future breeding, and the males may maintain alertness so as to protect their mate. This study provided important documentation of how much time wintering owls spend in the burrow.

Pellet studies are a traditional method of 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 show the burrowing owl to be an opportunistic and generalist feeder, with a relatively diverse diet throughout its range and across seasons. In a recent study, Trulio and Higgins (2012) examined the diet of urban burrowing owls in the Santa Clara Valley, California. The Santa Clara Valley is located south of San Francisco, and Trulio and Higgins' burrowing owl diet study is currently the only study proximal to SEFI. In this study, owls were identified by walking transects; then the owl pellets were collected and analyzed for both the breeding and non-breeding seasons.

Trulio and Higgins (2012) found that while insects – especially earwigs, grasshoppers, and beetles – were the most numerous prey in the owls' diet, rodents – especially Botta's pocket gopher (*Thomomys bottae*), California vole (*Microtus californicus*), and the house mouse – made up the majority of the prey biomass in both breeding and non-breeding seasons. Similarly, Hall, Greger, and Rosier (2009) found that the most common prey items for a year-round population of burrowing owls in south central Nevada were crickets, grasshoppers, and beetles; rodents, particularly kangaroo rats, however, were the most important component of the diet.

Rodents have been shown to be important in the diet of burrowing owls in several other studies as well. Littles, Williford, Skoruppa, Woodin, and Hickman (2007) conducted a study of wintering burrowing owls in Texas and found that rodents, such as

northern pygmy mice (*Baiomys taylori*) and fulvous harvest mice (*Reithrodontomys fulvescens*), were particularly important. In this study, even though insects dominated the owls' diet in quantity, small mammals and birds accounted for the majority of the prey biomass. Arthropods made up 98 percent of the total prey items consumed and primarily included crickets, as well as Lepidopteran larvae, beetles, spiders, and earwigs (Littles et al., 2007). Only 2 percent of all prey items consisted of vertebrates; vertebrates, however, comprised 71 percent of the total prey biomass.

Similar results have been reported for populations of burrowing owls in the Imperial Valley of California (Coulombe, 1971), Oregon and Washington (Green, 1983), New Mexico (Best, 1969), southern Texas (Williford, Woodin, Skoruppa, & Hickman, 2009), Utah (Smith, D. G. & Murphy, 1973), Colorado (Marti, 1974), Iowa (Errington & Bennett, 1935), and Oklahoma (Tyler, 1983), as well as in other parts of the world. In these and previously mentioned studies, burrowing owls, both breeding and non-breeding, were shown to be opportunistic predators; they included a wide variety of prey items in their diet. The owls consumed a high percentage of arthropods – especially insects – by quantity. Some studies showed that vertebrate prey – particularly rodents – were generally consumed with much lower frequency, but made up a greater portion of the total prey biomass (Littles et al., 2007; Marti, 1974; Poulin & Todd, 2006). Birds were a smaller proportion of the diet, or occurred incidentally. These results were also true for studies of burrowing owls near the ends of their range in Saskatchewan, Canada (Haug, 1985; Poulin & Todd, 2006), in Chile (Schlatter, Yanez, Nunez, & Jaksic, 1980), and in Patagonia (Andrade, Nabte, & Kun, 2010).

Only one unpublished study has looked at burrowing owl wintering diets on SEFI. Mills (2006) conducted a diet study of all migratory owls – including burrowing owls – that arrived on SEFI between 1994 and 2004. This study suggested that burrowing owls seasonally switch from eating mice to eating birds (Mills, 2006); the burrowing owl switched primarily to ashy storm-petrels, but occasionally included a Cassin’s auklet. Insects were also a part of the burrowing owl’s diet. While this study provided valuable information on owl prey choices, the sample size of pellets was relatively small and unevenly distributed over the 10-year time period; the majority of pellets were collected between 2000 and 2003, and some years were represented by a single pellet. In addition, pellets prior to 2000 were not collected in a standardized fashion (Mills, 2006).

Prey Switching

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, as long as that alternate species becomes more abundant or is more energetically profitable (Smith, R. L., 1996).

Many authors provide examples of prey switching in both the laboratory and the field. Heidarian, Fathipour, and Kamali (2012) tested whether a predatory thrips (*Scolothrips longicornis*) exhibited prey switching when offered two life stages of a spider mite (*Schizotetranychus smirnovi*) within a laboratory environment. The experimental results showed that the thrips preferred spider mite larvae when the larvae were more abundant compared to the nymphs, but switched to preying upon nymphs

when the nymphs were more abundant and the larvae less abundant (Heidarian et al., 2012). This study demonstrated prey switching behavior: The thrips showed a clear functional response, preferring whichever was the more abundant prey (Heidarian et al., 2012; Murdoch, 1969). These results support early prey switching models that predict prey switching behavior as a function of density of prey (van Baalen et al., 2001); when prey density falls below a threshold, predators will switch to alternative prey (Murdoch, 1969).

In a field study near Chicago, Illinois, researchers observed a combination of prey switching and prey selectivity in coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) after a severe ice storm caused a decrease in abundance of their primary prey (Randa, Cooper, Meserve, & Yunger, 2009). Randa et al. (2009) examined the scat of coyotes and red foxes and estimated prey abundance, both before and after the ice storm. Both predators consumed a greater number of eastern cottontail rabbits (*Sylvilagus floridanus*) and voles (*Microtus* spp.) prior to the storm, but after the storm their scat showed more white-tailed deer (*Odocoileus virginianus*), ring-necked pheasant (*Phasianus colchicus*), and squirrel (*Sciuridae*) prey. Their diets included a disproportionately larger number of voles and squirrels than was available as well (Randa et al., 2009). Randa et al. suggested that the coyotes and red foxes switched to more available prey when their preferred prey diminished, but still showed preference for their main prey if it was energetically beneficial for them to do so.

In some cases, prey switching can have drastic impacts upon the alternative prey population. One example was documented on Santa Barbara Island, a part of the Channel

Islands National Park, off the coast of southern California. There a population of resident barn owls (*Tyto alba*) switched to preying upon the winter population of burrowing owls after a cyclic decline in the barn owl's main prey, the deer mouse (*Peromyscus maniculatus*) (Drost & McCluskey, 1992). Deer mice were the only terrestrial mammalian prey available on Santa Barbara Island, and burrowing owls were a winter migrant to this Island, arriving in the fall and overwintering until spring. The deer mouse population fluctuates dramatically every few years; during these declines the resident barn owls switch to preying upon a wider variety of fauna and include other birds, reptiles, and invertebrates in their diet (Drost & McCluskey, 1992).

In 1984 and 1987, after crashes in the deer mouse population on Santa Barbara Island, the barn owl population showed signs of food stress and starvation. The barn owls switched to predation upon burrowing owls as an alternative prey species, as was evident in the pellets and prey remains at the barn owls' roosts. In previous years, the burrowing owl population was estimated to be between 13 and 18 individuals; during the two years of low mouse abundance, however, up to 10 burrowing owls were killed in each of those years. Only one or two were observed on the island after intense searches of burrowing owl roosts in 1987 (Drost & McCluskey, 1992). Drost and McCluskey (1992) concluded that burrowing owls were extirpated or nearly extirpated from the island by barn owls by spring of 1987. Reasons for this unusual extirpation of an alternative prey species were attributed to the island being an isolated system with a low diversity of available prey, as well as the already low abundance of the burrowing owls on the island. Also, the open habitat on Santa Barbara Island may not have provided

enough escape cover for the burrowing owls (Drost & McCluskey, 1992).

Interacting Species of Concern

Interacting species are species whose “presence or absence [...] influences the distribution or abundance of [...] other species” (Soulé et al., 2005). A widely recognized term for strongly interacting species is “keystone species,” used to describe species that have a prominent role in shaping the structure or function of an ecosystem (Paine, 1969). Interactions can be characterized by the type of ecological interaction; predation is one type of interaction that is well studied with respect to predator-prey relationships and trophic cascades or effects (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. There are several examples of this type of species interaction in the literature: the predation of northern abalone (*Haliotis kamtschatana*) by northern sea otter (*Enhydra lutris kenyoni*) (Chadès, Curtis, & Martin, 2012), of Chinook salmon (*Oncorhynchus tshawytscha*) by killer whale (*Orcinus orca*) (Williams et al., 2011), of San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) by island fox (*Urocyon littoralis*) (Roemer & Wayne, 2003), and of least tern (*Sterna antillarum browni*) by burrowing owl (Garcia & Conway, 2010). All species, both predators and prey, were listed as endangered, threatened, or species of conservation concern. As environmental changes, driven largely by development and habitat loss, increase, more wildlife

populations are at risk, and it becomes more likely that one protected species will threaten the viability of another through ecological interactions (Soulé, Estes, Berger, & Del Rio, 2003; Soulé et al., 2005). Optimal solutions for balancing management of protected species, especially strongly interacting species, seem to favor ecosystem-based management (EBM), which considers the ecosystem as a whole rather than focusing on a more traditional single-species management strategy. In the case of the northern sea otter and the northern abalone, both species became endangered due to intense overhunting and subsequent overfishing, respectively (Chadès et al., 2012). By modeling potential recovery strategies, Chadès et al. (2012) concluded that the best management and recovery solutions include measures to protect and manage both species simultaneously, rather than focusing on each separately. This entailed a combination of anti-poaching enforcement of abalone and removal of the sea otters above a certain population threshold (e.g., 50-70% of carrying capacity) (Chadès et al., 2012).

Similarly, an EBM approach is necessary to recover populations of endangered Chinook salmon and southern resident killer whales in the Salish Sea, located along the coastal waters of southwestern British Columbia, Canada. Williams, R. et al. (2011) modeled the consumption of Chinook salmon necessary to fulfill the energetic requirements of the southern resident killer whale. Through these models, the authors found that the goals for conserving these species separately were in conflict with each other. Specifically, any recovery in this killer whale population was expected to dramatically reduce Chinook populations given the high energetic requirement per whale and the degree of diet specialization. For the southern resident killer whale, prey

switching is unlikely to occur due to the whale's intense consumption of Chinook salmon (Williams et al., 2011); Chinook salmon make up 83% of the killer whale's diet (Williams et al., 2011) and appear to be selected even when they are far less abundant than other salmon species (Ford & Ellis, 2006). Therefore, in order to effect southern resident killer whale recovery in the Salish Sea, Chinook salmon recovery must first be considered.

An example where a single-species management approach was implemented to the detriment of interacting species can be found with the San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) and island fox (*Urocyon littoralis*). In efforts to recover the species, predators of the endangered shrike, including the native island fox, were removed or excluded from areas of the island (Roemer & Wayne, 2003). The removal of the island fox (*U. littoralis*) subsequently contributed to the endangerment of the San Clemente island fox (*U. l. clementae*), a subspecies of the island fox that was state-listed as threatened (Roemer & Wayne, 2003). Because the San Clemente island fox and one other subspecies were not included in the federal listing for island fox, they do not benefit from any type of recovery measures available for the other four subspecies listed (Roemer & Wayne, 2003). An analysis by Roemer and Wayne (2003) concluded that an EBM approach in this case would have identified a key conservation component – the restoration of suitable habitat for both the shrike and the fox. This component was not addressed in the shrike recovery efforts, however. Roemer and Wayne suggested that an EBM approach for conservation of protected species not only minimizes or avoids conflicting conservation goals between interacting species, but also is economically more

efficient.

In another example, burrowing owls are a problem predator for the California least tern, another species of concern. The California least tern is a small seabird that is listed as endangered under both the Federal and California Endangered Species Acts. At the Naval Base Coronado, located along the coast near San Diego, California, both breeding and non-breeding burrowing owls were documented preying upon both chicks and adults in California least tern colonies (Roemer & Wayne, 2003). In a 5-year review of the California least tern, USFWS found that groups of colonies or clusters along the San Diego coast supported approximately 38% of the total tern population (Garcia & Conway, 2010).

Until recently, the naval base implemented single species management, using anti-predator measures to control burrowing owl predation on the terns. From 1991 to 2011, an approximate minimum of 65 “problem” owls were trapped and removed (non-lethally and lethally) from the naval base (USFWS, 2006). The continuous removal of burrowing owls from the naval base may have contributed toward the cumulative decline of the owls within San Diego County (Garcia & Conway, 2010), especially the coastal areas. The naval base once supported the largest numbers of burrowing owls in San Diego County, an estimated population of 20 to 50 pairs of owls in the mid-1990s. Between 2009 and 2011, however, only one pair of owls was documented at the base (Wilkerson & Siegel, 2010).

In an effort to address the decline in burrowing owls, a new management plan was developed to simultaneously increase the owl population on the naval base up to 15 pairs

– which is still lower than historic numbers – while still implementing measures to deter problem owls from preying upon California least terns. The plan takes an ecosystem-based approach by supporting a stable burrowing owl population while still protecting California least tern populations (Garcia & Conway, 2010).

Objectives

The USFWS is considering a plan to eradicate the non-native house mouse from the Farallones, with the goal of returning the ecosystem to a more natural one, both in character and function (USFWS, 2013b). A significant benefit of mouse eradication would be to increase storm-petrel populations. Recent population modeling predicts that reduced burrowing owl predation would relieve predation pressure on the storm-petrel, significantly and positively impacting the population (Nur et al., 2014).

In compliance with the National Environmental Policy Act, a Draft Environmental Impact Study for the mouse eradication plan was released for public review in September 2013 (USFWS, 2013b). In preparation for this effort, several background studies were conducted on SEFI to determine the population cycle (Irwin, 2004) and diet of the house mouse (Jones & Golightly, 2006), as well as the proportions of mice and birds in the diets of all species of owls on the Island (Mills, 2006). In addition, monitoring the ashy storm-petrel and burrowing owl populations has been and is currently a part of regular ongoing studies on SEFI (Nur et al., 2014). More current and in-depth baseline information on burrowing owl ecology on the Farallones was still needed, however.

Locating and monitoring individual burrowing owls at their diurnal roosts has been challenging, given the innumerable rocky crevices and burrows all over the Island that serve as refuges for roosting owls. Determining how many owls actually overwintered on SEFI versus how many were just passing through during the fall was difficult (Tietz, 2009a). For this reason, in 2009 and 2010, biologists working for the

USFWS attached transmitters to a number of burrowing owls in order to track the owls to their roost locations (Tietz, 2010).

The focus of this research was to conduct a more in-depth investigation into burrowing owl diet on SEFI, and to contribute to the overall baseline dataset on the burrowing owl prior to any potential implementation of a mouse eradication plan. Specifically, the objectives of this study were to obtain an estimate of wintering burrowing owl abundance and to describe the composition of the burrowing owl diet on SEFI. Abundance estimates were used to quantify predation pressure on the ash storm-petrel (J. R. Tietz, personal communication, June 16, 2010), and the diet study was important for quantitatively documenting the burrowing owl's prey switching behavior on SEFI.

This study provides valuable information on the interaction of the burrowing owl and ash storm-petrel, as predator and prey, with the exotic house mouse as a contributing factor. In addition, the study contributes to the knowledge of the migratory stopover and wintering ecology of the burrowing owl. The results from this burrowing owl study may be used to further conservation efforts for the burrowing owl and for the ash storm-petrel population on SEFI (Nur et al., 2014).

My research examined burrowing owl diets for the duration of the overwintering period on SEFI. I tracked the species eaten, the changes in the diet over time, and the diets for individual owls. By comparing the biomass of mice versus storm-petrels eaten across seasons, I examined whether prey switching was occurring. I also examined whether the owls were foraging opportunistically – as they are known to do in central

California (Trulio & Higgins, 2012) and throughout other parts of their range (Haug & Didiuk, 1993) – by determining if the owls were consuming mice in proportion to their seasonal abundance, i.e. availability in the environment. Finally, I compared diet changes over time for individual owls to determine whether prey consumption patterns were consistent among all owls. In conjunction with an estimate of the burrowing owl abundance on SEFI over time, the answers to these diet questions are designed to improve the understanding of how burrowing owl dietary habits affect the ashy storm-petrel population on SEFI, and how introduced mice influence the burrowing owl abundance on the Farallones.

To meet these objectives, I addressed the following research questions and hypotheses.

Research Questions

1. What is the estimated number of burrowing owls that stopped over or overwintered on SEFI during my research?
2. How long during the non-breeding season are burrowing owls observed on SEFI?
3. What is the diet of the burrowing owls on SEFI during the winter season?
4. Do burrowing owls switch from house mouse to storm-petrel prey between fall and spring seasons? (H_01)
5. Do burrowing owls exhibit density-dependent prey selective behavior with house mice? (H_02)

Null Hypotheses

H₀1: The biomass of mice eaten per pellet per owl and the biomass of storm-petrels eaten per pellet per owl do not differ significantly between the fall and spring seasons.

H₀2: The number of mice eaten per pellet is not correlated with mouse abundance, as measured by trap success from mouse-trap data.

Study Area

Location

SEFI is located 48 km (30 miles) from San Francisco off the coast of Central California (Figure 1). Measuring 28 hectares (70 acres; G. McChesney, personal communication, August 19, 2010), SEFI is the largest of the Farallones, a small group of rocky islands within the Farallon National Wildlife Refuge.

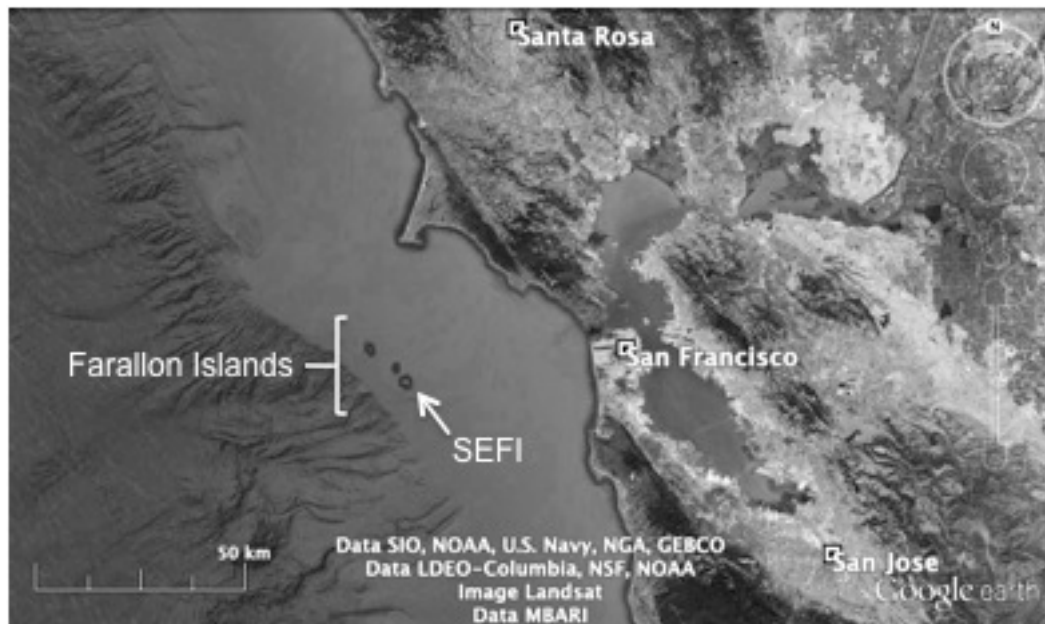


Figure 1. Location of SEFI within the Farallon Islands, off the Central California coast. Satellite imagery from Google Earth, 2015.

The Farallones sit along the edge of the continental shelf in the Pacific Ocean. SEFI is characterized by two hills that rise from the center up to 90 meters high, and a wide, flat marine terrace that extends up to 365 meters out from and around the hills like an apron. The apron is widest from the southeast to the western portions of the Island (Figure 2). The slopes are rocky and consist of crumbling granite that is replete with

fissures, crevices, and caves. The flat terrace is spongy and topped with dark, reddish fine soils riddled with seabird burrows.



Figure 2. Aerial photograph showing SEFI, Maintop Island, and adjacent islets. Satellite imagery from Google Earth, 2014.

There are several historic structures on SEFI, including the lighthouse, Powerhouse, North Landing boathouse, Carpenter's Shop, and two houses built in the 1800s that are currently used for housing researchers. In addition to the buildings, a paved cart path and a few established trails generally allow good pedestrian access.

The northeast slopes and flats, and some of the north-facing slopes at the north end of the Island, are more difficult to access due to the steep terrain (Figure 3). These

areas are also part of a conservation zone where access is restricted so as to prevent spread of non-native weeds and to minimize disturbance to sensitive marine and avian wildlife. Access to the conservation areas is limited to brief visits at select times of the year; however, much of these areas was visible from either Shubrick Point or the Lighthouse.

Similarly, Maintop Island (also known as West End Island), which is separated from SEFI by a narrow channel (Figure 3), and the surrounding islands were not included in the regular study area due to difficult access and sensitive wildlife concerns.

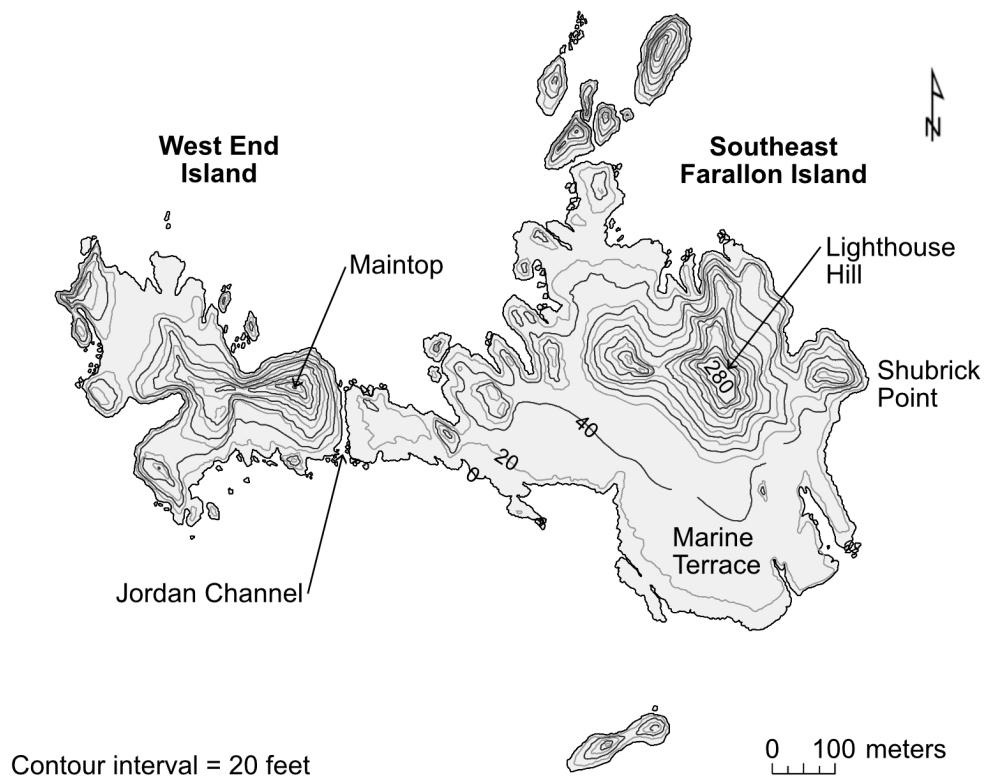


Figure 3. Topographic map of SEFI, West End (Maintop) Island, and adjacent islets. Used with permission from Point Blue, 2015.

Vegetation

The vegetation on SEFI is a mix of native and non-native species. In the spring, the native plant commonly known as maritime goldfield or “Farallon weed” (*Lasthenia maritima*) and the non-native New Zealand spinach (*Tetragonia tetragonioides*) enrobe the Island in a deep emerald green (Figure 4). The goldfields die back or are pulled out by nesting seabirds in the summer, however. By fall, when the burrowing owls arrive, the Island appears brown and bare, except for patches of perennial spinach (Figure 4).



Figure 4. Differences in seasonal vegetation coverage on the Marine Terrace, SEFI. Spring (left) versus fall (right). Photographs by Sara Chandler, 2011 and 2010, respectively.

Historical Context to the Present

There is a long history of human disturbance on the Farallones: Russian fur traders hunted fur seals to near extirpation in the first half of the 19th century, and egg traders gathered up seabird eggs, especially murre eggs, to sell in San Francisco during the mid- to late-1800s (White, 1995). Between 1877 and 1881, much of the infrastructure and buildings were constructed on SEFI to accommodate the keepers of the

“Light,” or lighthouse, and the families of the keepers. U.S. Coast Guard personnel took over lighthouse maintenance in 1939 and monitored the light until 1970 when it became automated. The U.S. Navy also had a presence on the Island, operating a weather station and then a radio station on the island from 1905 through the end of World War II (White, 1995). At one point the number of human inhabitants was almost 80 persons (White, 1995).

Human visitors brought several domesticated and exotic species to the Island, including dogs, cats, goats, donkeys, rabbits, and the house mouse (White, 1995). Attitudes toward the Island and its resources shifted to a conservation focus, however; by the 1970s the USFWS had removed all introduced animals – except the mice – from the Island (White, 1995). The house mouse remains the only introduced vertebrate on the Island.

SEFI as an Important Seabird Colony

The Farallones are a migratory stop for many land birds, and they support the largest seabird colony in the contiguous United States. Several species of seabirds breed on SEFI, including gulls, auklets, and both Leach’s (*Oceanodroma leucorhoa*) and ashly storm-petrels. SEFI provides breeding habitat for slightly fewer than 5,000 individual ashly storm-petrels, approximately half of the world’s population (Carter et al., 2008). Breeding seabirds generally begin to arrive to SEFI in numbers in the spring to defend nesting territories; the seabird population can number several thousand birds at the peak of breeding season (Carter et al., 2008; USFWS, 2002).

Study Species

Burrowing owl. The burrowing owl (*Athene cunicularia*) is a new-world owl of prairies and open grasslands that utilizes underground burrows for nesting and shelter. The western subspecies of the burrowing owl (*A. c. hypugaea*) ranges across portions of Canada and throughout much of the western United States and Mexico (Poulin, Todd, Haug, Millsap, & Martell, 2011). While the burrowing owl is a much-studied species, the majority of studies have focused on the ecology of the owl during its breeding season; few have addressed the non-breeding or winter ecology of the western burrowing owl (Gervais, et al., 2008; Poulin et al., 2011).

Burrowing owl natural history and status in California. A small, long-legged owl measuring up to 19-25 cm tall and weighing approximately 150-170 g, the burrowing owl is active both during the day and night (Poulin et al., 2011; Haug & Didiuk, 1993). During the breeding season, the burrowing owl generally inhabits short grasslands and open plains, and nests in burrows typically created by fossorial mammals such as ground squirrels, badgers, and prairie dogs (Poulin et al., 2011). Burrowing owls are generally considered to be generalist foragers, feeding opportunistically on a variety of prey items, especially rodents and other small mammals, insects and other invertebrates, birds, and amphibians (Poulin et al., 2011). An early account of burrowing owls in the Imperial Valley, California, notes carrion as a food source as well (Coulombe, 1971).

The burrowing owl is recognized as a California Species of Special Concern (Gervais et al., 2008) and is federally protected under the Migratory Bird Treaty Act (USFWS, 2013a). Over the last 50 years, populations of the burrowing owl have been

declining throughout much of their range in North America (Poulin et al., 2011). In California, the overall decline has been less than in other locations (e.g. Canadian prairie), but local declines and extirpation from some regions have been documented (Gervais et al., 2008). Censuses conducted by the Institute for Bird Populations from 1991 to 1993, and from 1993 to 2007, revealed burrowing owl populations in California to be extremely fragmented, with local populations disappearing, especially those along the central and southern coast (DeSante, Ruhlen, & Scalf, 2003; Wilkerson & Siegel, 2010). Certain areas, such as the San Francisco Bay Area and the Bakersfield regions, have seen a severe decline in burrowing owl population numbers between 1993 and 2007 (Wilkerson & Siegel, 2010). The 2006-2007 surveys noted an alarming decline of 27.9% of the population in the San Francisco Bay Area Interior Region (Wilkerson & Siegel, 2010). Furthermore, Christmas Bird Count (CBC) data reflected a 1.2 percent per year decline in the wintering population of Burrowing Owls in California (Sheffield, 1997).

Burrowing owls on the Farallones. The burrowing owl is a migrant to the Farallones; most owls arrive in the fall, with some overwintering or staying over until spring (Tietz, 2009a). It is not known for certain 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 (Buffa, 2003; Holroyd et al., 2010). Observations of burrowing owls on the Farallones have been recorded as early as the late 19th century and have been documented in bird survey data up to the present day (Richardson, Pyle, Burnett, & Capitolo, 2003).

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 and have not been thoroughly surveyed for owls. On the Farallones the burrowing owls are primarily nocturnal, mostly hunting at night and roosting during the day. SEFI is pockmarked with innumerable rocky crevices on their slopes and natural burrows dug by Cassin's and Rhinoceros auklets, small- to medium-sized burrowing seabirds, respectively. Burrowing owls roost in these crevices and burrows (Figure 5), in addition to old sea caves. On SEFI there is an abundance of roosting habitat for the burrowing owl.



Figure 5. Photos of burrowing owl roosts on SEFI. On the left is an owl roost in a Cassin's auklet burrow, and on the right is a roost in a rock crevice. Photographs by Sara Chandler, 2010.

Prior to 2007, the presence of burrowing owls on SEFI had been recorded during daytime counts for all migrant birds on SEFI, which are conducted daily by Point Blue biologists in the fall. Starting in 2007, focused daytime surveys for burrowing owls and their roosts occurred daily in the fall and a few days per week during the winter (and into spring as well); these surveys improved the daily estimate of burrowing owl abundance (Tietz, 2010). Also starting in 2007, Point Blue biologists began focused efforts to capture and band burrowing owls. In the fall of 2008, 11 burrowing owls were detected (Chiang, 2008), and in the fall of 2009, the burrowing owl total was 15 (Tietz, 2010).

Upon arrival in September, the owls prey primarily on the non-native house mouse, which is at its highest density in the fall. During the winter and spring months – when mice are relatively scarce – burrowing owls consume avian prey, particularly the ashy storm-petrel (Irwin, 2004; Mills, 2006), as well as other birds and invertebrates (Mills, 2006). It is not known whether burrowing owls overwintered on the Farallones prior to the introduction of the house mouse, but their presence on SEFI and predation on storm-petrels is considered to have a long-term impact on the ashy storm-petrel population (Buffa, 2003; Nur et al., 2014).

Ashy Storm-Petrel. The ashy storm-petrel is a diminutive seabird, measuring only 17.8-25.0 cm in length and 38.1-39.6 g (38.85 g average) in mass (Ainley, 1995). The ashy storm-petrel population is estimated at 10,000 individuals worldwide (Carter et al., 2008), and approximately half the population breeds on the Farallones. This seabird is long-lived and slow-breeding; it can only produce one chick per year. The ashy storm-petrel spends all day foraging at sea and flies to the Island only at night to avoid

predation by western gulls. During the winter, ashy storm-petrel activity on the Island is fairly limited. The birds start attending nests in numbers in February and March, and chicks fledge from September to November (Ainley, 1995; Warzybok & Bradley, 2011). Considering the population as a whole, relatively few burrowing owls visit the Farallones every year; a single owl, however, can depredate dozens of adult storm-petrels each year, permanently removing these potential breeding birds from the population (Carter et al., 2008; Nur et al., 2014).

House Mouse. The ubiquitous house mouse was likely accidentally introduced to the Farallones by humans in the 1850s, but may have been introduced earlier (Jones & Golightly, 2006). On SEFI the house mouse measures an average of 16.2 cm (adults) in snout-to-tail length and 18.5 g in mass (Jones & Golightly, 2006). The diet of the house mouse on SEFI consists of native and non-native plants and invertebrates. Some food items appear to be seasonally important such as foxtail barley (*Hordeum murinum*) in the fall, beetle larvae in the winter, and maritime goldfields (*Lasthenia maritima*) in the spring (Jones & Golightly, 2006).

The house mouse population on SEFI is cyclic: The population builds during the summer, peaks in the fall, then declines severely in the winter to its lowest numbers in the early spring to early summer months (Irwin, 2004; Nur et al., 2014). During the fall season, the house mouse is so abundant that it is not uncommon to see mice moving about in the open during the day (personal observation). Island Conservation, a non-profit research and conservation organization, conducted mouse abundance trials during

fall 2010. The density of house mice was recorded at “ten times greater than reported densities in most island or mainland environments” (USFWS, 2013b).

Methods

Timing of Study

I conducted research on SEFI from September 2010 to May 2011, over periods that varied between 15 and 60 days at a time. I stayed on the Island for a total of 156 days, equaling approximately 22 weeks. While on SEFI, I worked closely with Point Blue biologists, who assisted with collection of data when I was absent.

Estimating Burrowing Owl Abundance

Surveys. The number of burrowing owls that migrated to SEFI was estimated by combining the number of burrowing owls observed during general landbird area searches as well as those observed during focused burrowing owl counts, with care taken to avoid double-counting. The general landbird area searches were conducted twice daily, once in the morning and once in the afternoon, by Point Blue biologists as part of regular fall bird monitoring on SEFI, from August to December. During these area searches, Point Blue biologists systematically surveyed the Island on foot, dividing the Island into unit areas and counting and recording all birds observed within each area (Tietz, 2009b).

In addition to the Point Blue surveys, I conducted focused surveys for burrowing owls daily, weather permitting, from September to May. I surveyed the accessible parts of the Island, walking the established trails and scanning known roosts, rocky crevices, and open areas with binoculars (10x magnification, 42 mm objective lens diameter). Generally, the surveys were conducted between 11:00 and 15:00, because previous research on the Island indicated that the owls were most likely to be standing outside their roosts during midday (J. R. Tietz, personal communication, June 16, 2010). During

all surveys, the total number of owls observed and their locations were recorded.

Additional data referenced. Since 2007, Point Blue biologists have captured and banded burrowing owls on SEFI in an effort to get an accurate count of the owls overwintering on the Island. All owls captured on SEFI receive a numeric USFWS metal (silver-colored) band on one leg (determined by whether the capture date was an even or odd date) and a blue-colored alphanumeric aluminum band (ACRAFT brand) on the leg opposite the USFWS band (Tietz, 2009a). The ACRAFT band is marked with a letter and a one- or two-digit number designed to more easily allow identification from a distance. During my study, both banded and unbanded burrowing owls were observed on the Island. If an owl had a visible leg band, the identification number and which leg was banded were recorded. If the owl was unbanded, Point Blue biologists attempted to capture it the next suitable night by setting up mist nets near its roost.

In addition to banding owls, in 2009 and 2010 Point Blue biologists used telemetry to determine the location of burrowing owl roosts and allow the biologists to more easily identify individual owls; this was especially useful if the owls were reclusive during the day and/or if they moved roosts (Tietz, 2009a). Point Blue biologists tracked many of the owls fitted with transmitters to their roosts, using a portable antenna and receiver. Because each transmitter had a unique frequency, an owl's presence on SEFI, and therefore its duration of stay, could also be determined.

During my study, I was able to use this telemetry data to find the roosts and search for owls and pellets at these locations, as well as determine how long an owl overwintered on the Island. Transmitters were removed from two owls (A56 and A81)

during the study period, however, and another owl (A55) never received a transmitter. For these three owls I relied solely on the visual detection data (daily counts) for the remainder of the study, and I approximated their length of stay by assuming the last known date of visual detection to be the last day on the Island.

Daily estimated total and abundance estimate. A daily total of burrowing owls was estimated for each day on the Island, beginning on the date the first owl of the fall season was observed, and ending when no more birds were observed on the Island. Any owls detected by Point Blue biologists during the general surveys were crosschecked with the focused owl survey data to avoid double counting, and then added to the daily total. All survey data were compiled into an electronic spreadsheet, and individual owls (if identifiable) and their roosts were tracked throughout the study period. Unknown or unmarked burrowing owls were assumed to be the same individual if seen at the same roost, or within the immediate vicinity, day after day.

The daily estimated total approximated the burrowing owl abundance at any point in time during the study. However, the total number of individuals for 2010-2011 was estimated by summing only the number of new owls arriving to the Island daily. This cumulative total is an estimate of the number of burrowing owls visiting SEFI from fall to spring, regardless of when they arrived, departed, or the duration of their stay.

It is likely that some owls went undetected during the daily counts. It is also likely that some owls were unknowingly double-counted, due to the fact that many of them were unmarked and not individually identified. Similarly, some owls may have been underestimated; owls thought to have been previous arrivals may have actually been

new arrivals.

Diet Study

Collection of pellets and prey remains. In order to determine the composition of the burrowing owl diet on SEFI, I collected burrowing owl pellets (Figure 6) and prey remains from burrows, from September 2010 through May 2011. The pellets were stored in a freezer for several months until transported off the Island. I then dissected the pellets, and I analyzed and recorded the contents.

The regurgitated owl pellets were collected from outside burrows or crevices that were known roosts of burrowing owls, many of which were banded and/or had transmitters. Burrowing owl pellets were collected from the roosts of these known owls and also from locations where the identity of the owl was unknown. Any burrowing owl pellets (identified by size and general shape) incidentally encountered at any time were collected as well.



Figure 6. Examples of burrowing owl pellets collected on SEFI. Photographs by Sara Chandler, 2011.

Pellets and prey remains were collected approximately every one to two weeks. Three of the banded owls (A52, A73, and B9) had roosts that were not easily accessible; I 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 Whirl-pak bag and labeled with the date, location, number of pellets, and identity of owl, if known.

Pellet dissection. To dissect the pellets, each sample (one collection event) was pulled apart with forceps in a shallow dish with some water. All notable parts (bones, exoskeletons, feathers, mandibles, etc.) of prey items and non-food objects (metal bands, plastic, thread, rock, and vegetation) were identified and recorded on a data sheet. I identified prey items visually as mammal, bird, or invertebrate, and then classified them to genus and species when possible (Bland & Jacques, 1978; Gaston, 2004; Sibley, 2000). 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 the species of bird was taxonomically identified visually 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, any feathers, wings, furcula, or feet were used to identify the species. In cases of a marked bird becoming prey, the unique identification number on the metal leg band identified individual birds even if no other bird parts were present.

To obtain an accurate count of prey items, I only used certain parts of a prey

animal to tally an individual animal for each Class. For instance, if a group of pellets yielded three lower mandibles (one left, two right) of a mouse and several assorted mouse bones, the number of mice recorded was two: The left and one right mandible were considered a pair from one mouse (unless they were noticeably unmatched), and the right mandible was counted as a another mouse eaten. I did not use the other bones to count individual prey items, but as a way to corroborate the number of prey estimated.

Birds were enumerated by the greatest number of identifiable parts, beginning with the most restrictive part. For example, a sample with two bills, three wings (one left, two right), and one furculum – all from the same bird species – would be conservatively tallied as two birds, because those parts at minimum would comprise no more than two birds. The two bills are the limiting factor – their presence alone indicates a minimum of two birds, given that birds only have one bill. If this example included three right wings, however, then I would record a total of three birds in the sample.

Invertebrates were more challenging to identify, given their inherently small size and even smaller body parts. I used an entomological key to identify insects to Class and Order (Bland & Jacques, 1978), and Alma Saucedo Mejia in the Department of Entomology at the California Academy of Sciences assisted with the invertebrate parts that were difficult to identify, especially those belonging to spiders and earwigs.

The approach to enumerating the invertebrates was similar to that for the other prey items – I used the most restrictive of the identifiable parts. For beetles (Coleoptera) only the heads were enumerated because they remained relatively whole in the pellets. Heads and mandibles were used to count crickets and grasshoppers (Orthoptera). Again,

I used a conservative approach, counting any two mandibles as one item, and determining the minimum possible count from the parts. For example, a sample with 21 loose cricket mandibles and four cricket heads (two with complete sets of mandibles and two with just one mandible each) would be tallied as 14 crickets total: the two complete heads would be counted as two crickets; the two incomplete heads and two loose mandibles would be counted as another two; and the remaining 19 mandibles would be counted as 9 pairs plus one incomplete pair, or 10 crickets.

For the moths and butterflies (Lepidoptera), the adult heads were counted and added to the number of larvae, with or without larval casings. A sample with two larvae and one empty larval casing would be counted as two larvae total, and a sample with one larva and two empty larval casings would also total two larvae. A sample with one larva, one empty casing, and one casing with a larva inside would total two larvae. Earwigs (Dermaptera) were enumerated by the tail (with pincers), centipedes (Lithobiomorpha) were tallied by the head, and the whole bodies of amphipods or marine invertebrates (Amphipoda), as well as pill bugs or isopods (Isopoda), were tallied.

Diet analysis.

Pellet analysis. When analyzing the contents of the pellets, samples from each owl were grouped into approximate two-week sampling periods. A period of two weeks was used because collection events at roosts were sometimes spaced up to two weeks apart. In addition, the pellets were grouped to minimize bias toward overestimation of prey items consumed. Burrowing owls can apportion a prey item over more than one

pellet; counting the quantity of prey items on a pellet-by-pellet basis – using prey remains within each individual pellet to estimate number of prey consumed per pellet – may result in a bias toward overestimation of the number of prey eaten (Green, 1983). Therefore, in order to enumerate prey items in a consistent manner, the pellets from the banded owls – from whom pellets were regularly collected – were grouped in a sampling period that encompassed either the first half or the second half of each month.

The pellets from unknown owls and the three banded owls that had difficult-to-access roosts were not assigned 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, the pellets collected were analyzed as one sample, without regard to when they were collected. The diet results from these three owls were added to the aggregate diet information for all burrowing owls during the study, but not to analyses of seasonal changes in diet. All the pellets from unknown owls were analyzed as one large group as well.

Ultimately, pellets from only eight of the 12 banded burrowing owls were used to detect differences in the owl diet over time. Owls excluded from this portion of the analysis included the three banded owls with difficult to access roosts, and one banded owl for which pellets were only collected over three sampling periods. Only owls contributing pellets in at least five sampling periods (approximately six weeks) were included. Most of the eight owls contributed pellets in ten or more sampling periods within the study.

Estimated Biomass. I 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, I referenced a study by Jones and Golightly (2006), using 18.5 g as the average mass for an adult mouse. For the ashy storm-petrel, I referenced the Birds of North America account for this species (Ainley, 1995). I averaged the mass during the courtship period in February with the mass during the egg-laying period in April to get 38.85 g, which was used as the biomass for the storm-petrel.

The other two prey groups for which I estimated biomass were the beetles and crickets. For the beetles, I used a mass of 0.2445 g, referencing another burrowing owl diet study in the San Francisco Bay area (Higgins, 2007). For the crickets I was unable to find a reference in the literature; in 2012, however, an entomologist conducting a field study on SEFI estimated the Farallon cricket mass to be an average of 0.25 g, which is the mass I used in my calculations (N. DiRienzo, personal communication, October 23, 2012).

For all prey species, biomass was calculated using whole animal weights; I essentially assumed all parts of a prey animal were consumed and had contributed toward the total energy gain to the owls (Steenhof, 1983). Determining biomass in this method results in an over-estimate of overall energy gain to the owl: 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, comprises relatively very little of the ingested prey (Tabaka, Ullrey, Sikarskie, DeBar, & Ku, 1996). In a nutrition study of prey of three raptor species, including great-horned owl,

researchers showed that the nutritional composition of the prey minus egested material is comparable to that of the whole prey (Tabaka et al., 1996). The researchers found that regurgitated pellets comprised only 2-8% of prey (dry weight), both mammalian and avian, consumed (Tabaka et al., 1996). The standard in raptor diet studies is to use the biomass based on whole prey weights, preferably from live animals collected locally and grouped by age and sex (Steenhof, 1983). I used average weights from local studies or the literature; this method did not account for prey demographic variability, but yielded a broad estimate of prey biomass. This level of precision, however, is acceptable for my research.

Mouse abundance. In my analysis, I referenced mouse abundance data collected at the same time as my study by Point Blue and Island Conservation. In November 2010, Island Conservation conducted three nights of field trapping, setting non-lethal mousetraps arranged along a trap line first delineated in a previous mouse abundance study on SEFI (Irwin, 2004). From December 2010 to April 2011, Point Blue biologists continued mouse abundance data collection monthly, following a similar protocol and trap line. In my study, I used the mouse-trap success (the number of traps that trapped at least one mouse) data from these efforts as an index for mouse abundance.

Statistical Analysis

I used Systat 13™ and ran 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. I used ANOVA to test whether the owls' diet varied between seasons: Fall season was defined from September 15, just before the owls started

arriving, to December 31; spring season was defined from January 1 to May 15, after the last owl had departed. I conducted ad hoc testing to compare the amounts of mice eaten in fall, mice eaten in spring, and storm-petrels eaten in spring. For the ANOVA, I compared the average biomass of mice (per pellet per owl) and the average biomass of storm-petrels (per pellet per owl) in each period.

The average number of pellets or biomass of prey per owl within each period was calculated by dividing the total pellets or biomass, respectively, by the number of owls contributing pellets within a given period. Up to eight of 12 banded owls contributed pellets consistently throughout the study, and the number of contributing owls varied per period. For some periods only two owls contributed pellets, and in others up to seven owls contributed.

Results

Abundance of Stopover and Overwintering Burrowing Owls on SEFI

From the daily estimate of new arrivals, the total number of burrowing owls migrating to SEFI was estimated to be 23 unique owls from fall 2010 to spring 2011. Over the study period, the average number of owls, including new arrivals, observed per day was six ($SE \pm 0.20$) (range = 1-11). December, January, and February averaged the greatest number of owls observed daily, while May averaged the least (Table 1). The greatest number of owls counted in one day was 11, observed in mid-January.

Table 1.

Highest and Lowest Monthly Means of Burrowing Owls Observed on SEFI from Fall 2010 to Spring 2011

Month	Mean	SE	Range
Highest Mean of Daily Totals			
December	8	± 0.32	1 - 10
January	8	± 0.22	4 - 11
February	8	± 0.13	7 - 10
Lowest Mean of Daily Totals			
May	1	± 0.13	0 - 1

Note: SE = standard error.

The greatest number of new owls that arrived to SEFI in one day occurred in September, with a total of four owls. The highest number of new arrivals in one month was 10 owls in October (Table 2). No new owls were observed arriving after March 9, 2011.

Table 2.

Number of New Arrivals and the Cumulative Total of Burrowing Owls Observed on SEFI

Month - Year	Number of New Arrivals	Cumulative Total Number of Owls
September - 2010	4	4
October -2010	10	14
November - 2010	1	15
December - 2010	1	16
January - 2011	4	20
February - 2011	0	20
March - 2011	3	23
April - 2011	0	23
May - 2011	0	23

Most of the owls that arrive to the Island are unbanded, although in 2010 three owls were returns, having been captured and banded on SEFI in previous years. Owl A42 was first captured on SEFI in 2009; A44 in 2008; and B9, who returned to the Island for the third year in a row in 2010, was banded in 2007 (Tietz, 2009b).

The new arrivals contributed cumulatively toward the total abundance of burrowing owls observed in the study (Table 2). The new arrivals are included in the daily counts averaged for each month (Figure 7). The change in density of the owls on SEFI throughout the fall and winter seasons is evident when looking at the greatest number of burrowing owls observed for each calendar week during my study (Figure 8).

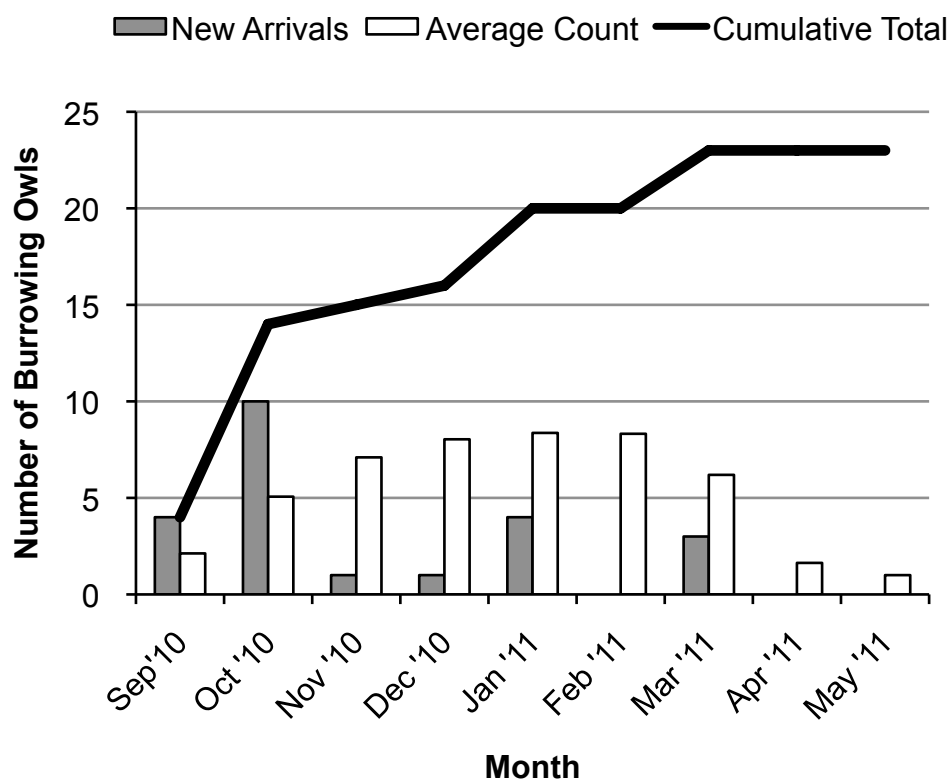


Figure 7. Number of new arrivals, average count, and cumulative total of burrowing owls by month. The average count shows the daily estimates averaged by month. The cumulative total is the sum of new arrivals observed during the study.

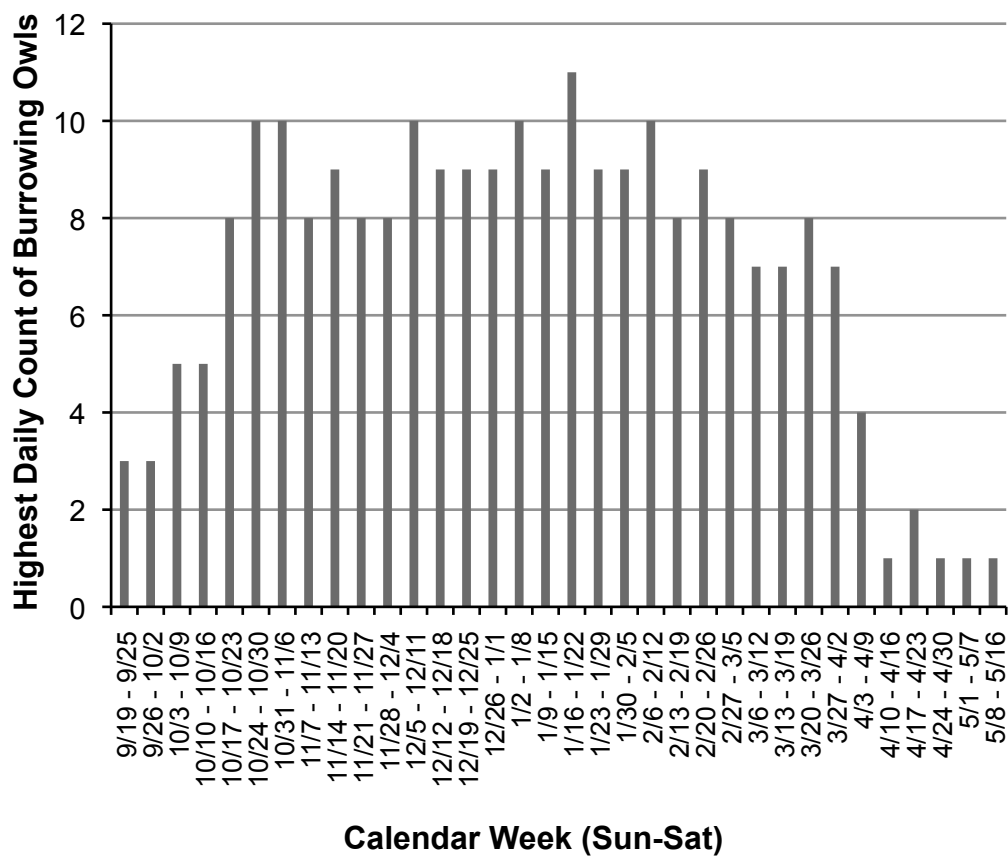


Figure 8. Highest daily count of burrowing owls observed within each calendar week of the study. The chart includes all burrowing owls observed.

Duration of Stay for Overwintering Burrowing Owls on SEFI

The average stay on SEFI for the 12 banded burrowing owls was approximately 118 (SE±17) days (Figure 9). One owl, with band code A70, was found dead after 154 days. Of the 11 owls fitted with transmitters, nine arrived in the fall (September through December) and stayed until spring (January or later). The owls typically occupied three to four roosts in the same general area for the duration of their stay on SEFI; one owl (A70) occupied up to 10 roosts, however, and relocated once to an entirely different area of the Island (Table 3).

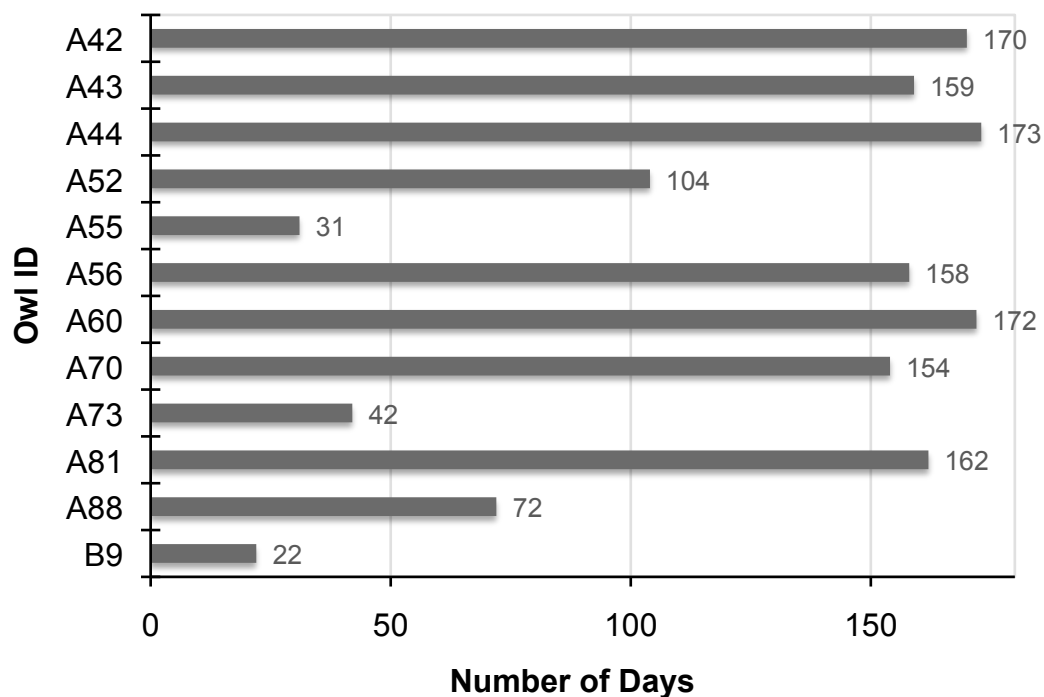


Figure 9. Estimated duration of stay for banded burrowing owls between fall 2010 and spring 2011 on SEFI. The average length of stay was 118 days.

Table 3.

Number of Roosts, Arrival and Departure Dates, and Transmitter Removal Dates for 12 Banded Owls

Owl	Roosts	First Sighting	Last Detected	Transmitter Removed ^a
B9	3	29-Oct-2010	19-Nov-2010	not removed
A88	3	22-Jan-2011	3-Apr-2011	not removed
A81	5	22-Oct-2010	1-Apr-2011	16-Mar-2011
A73	1	6-Dec-2010	16-Jan-2011	not removed
A70	10	28-Sep-2010	28-Feb-2011	not removed
A60	4	18-Nov-2010	8-May-2011	not removed
A56	1	15-Oct-2010	21-Mar-2011	16-Dec-2010
A55	2	7-Mar-2011	6-Apr-2011	no transmitter
A52	2	18-Nov-2010	1-Mar-2011	not removed
A44	3	18-Oct-2010	8-Apr-2011	not removed
A43	4	23-Sep-2010	28-Feb-2011	not removed
A42	3	12-Oct-2010	30-Mar-2011	not removed

Note. ^aPoint Blue Conservation Science, 2011.

Burrowing Owl Winter Diet on SEFI

I analyzed a total of 679 burrowing owl pellets (Table 4). Of these, 437 were collected from the roosts of 12 owls that were banded on SEFI. An additional 242 pellets were collected from other roosts or feeding locations; it was not known from which or from how many owls these pellets originated. The average number of pellets contributed per banded owl during each two-week period across all periods was five, and ranged from zero to nine (Figure 10). The number of banded owls that contributed pellets ranged from zero to seven in any one period (Figure 10, Table 4).

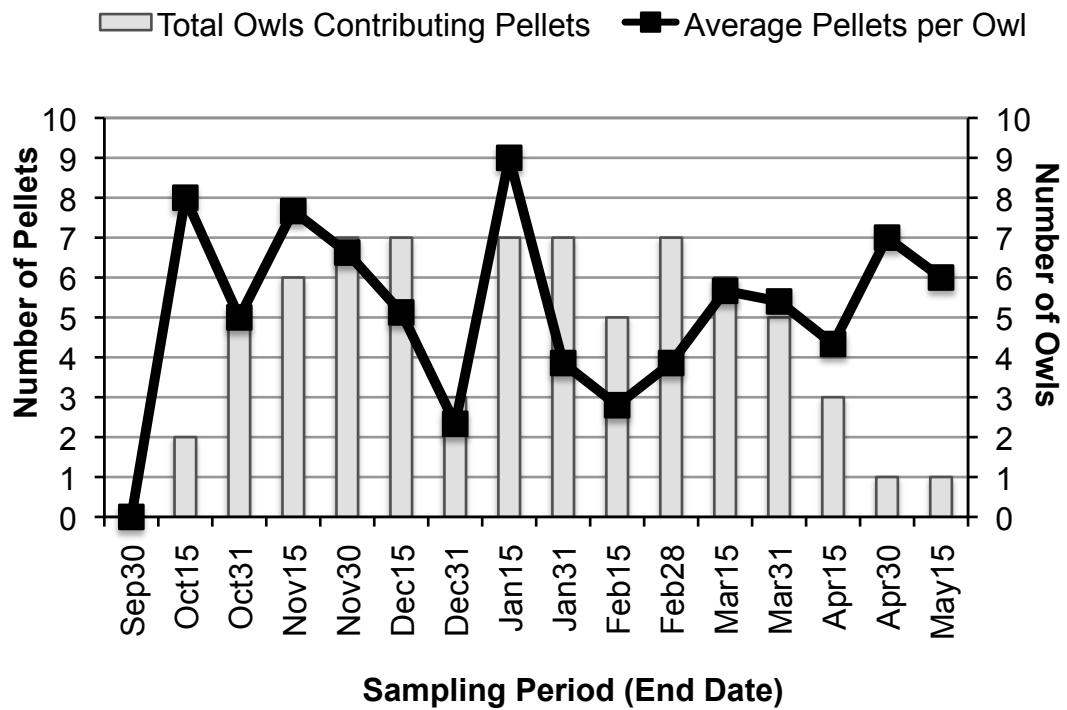


Figure 10. Average number of pellets per owl within each period. The line shows the average number of pellets per owl, and the columns show the number of owls contributing pellets in each period.

Table 4.

Number of Pellets Collected and Number of Owls Contributing Pellets on SEFI from Fall 2010 to Spring 2011

Sampling Period	Period of Collection	Pellets Collected	Owls Contributing Pellets
1	9/15 - 9/30	0	0
2	10/1 - 10/15	16	2
3	10/16 - 10/31	25	5
4	11/1 - 11/15	46	6
5	11/16 - 11/30	53	7
6	12/1 - 12/15	41	7
7	12/16 - 12/31	7	3
8	1/1 - 1/15	63	7
9	1/16 - 1/31	27	7
10	2/1 - 2/15	14	5
11	2/16 - 2/28	27	7
12	3/1 - 3/15	35	6
13	3/16 - 3/31	31	5
14	4/1 - 4/15	14	3
15	4/16 - 4/30	7	1
16	5/1 - 5/15	6	1
None	9/15 - 5/15	267	unknown

Note. The pellets from nine banded owls are shown by sampling period; for the three banded owls and unknown owls there was no sampling period.

The pellets and prey remains contained 1,625 prey items, 1,091 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 more than 90% of all prey items counted by number: beetles (32%), crickets (28%), mice (28%), and storm-petrels (5%) (Figure 11). In total, 12 orders were represented; however, I was unable to identify some birds and invertebrates to Order (Table 5).

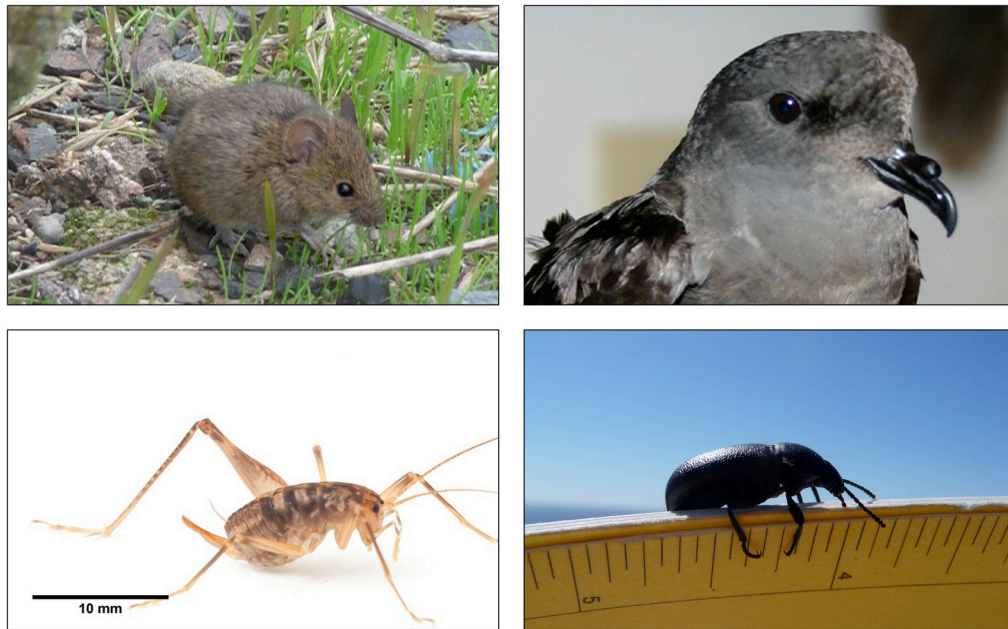


Figure 11. Photos of common burrowing owl prey items on SEFI. Shown clockwise from top left: House mouse, photograph by Sara Chandler, 2010; ashy storm-petrel, used with permission from Point Blue, 2015; Farallon cricket, used with permission from Nicholas DiRienzo, 2012; and beetle, photograph by Sara Chandler, 2010.

Table 5.

Burrowing Owl Prey Items by Taxonomic Rank

Prey Items			Number of Items	Percent of Total
Class	Order	<i>Genus species</i> (Common name)		
Vertebrates (Phylum: Chordata)			554	34
Mammalia	Rodentia	<i>Mus musculus</i> (House mouse)	452	27.8
Aves	Procellariiformes	<i>Oceanodroma homochroa</i> (Ashy storm-petrel) / <i>Oceanodroma leucorhoa</i> (Leach's storm-petrel)	86	5.3
	Charadriiformes	<i>Ptychoramphus aleuticus</i> (Cassin's auklet)	2	0.1
	Passeriformes			0.2
		<i>Sayornis nigricans</i> (Black phoebe)	1	
		<i>Regulus calendula</i> (Ruby-crowned kinglet)	2	
		<i>Zonotrichia albicollis</i> (White-throated sparrow)	1	
	Unknown Bird		10	0.7
Invertebrates (Phylum: Arthropoda)			1071	66
Arachnida	Araneae (Spiders)		6	0.4
Insecta	Orthoptera			28.1
	Suborder: Ensifera	<i>Farallonophilus cavernicolus</i> (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

Note. Percent of Total shown only by Order and summed by Phylum (in bold).

Prey Switching in the Burrowing Owl Diet on SEFI

Based on the number of mice and storm-petrels consumed by owls in each period, the burrowing owl diet noticeably shifts from primarily mice in the fall and early winter to storm-petrels in the early winter to early spring (Figure 12). From October through mid-November, and again in January, 100% of the owls contributing pellets consumed mice. Beginning in January, the percentage of owls consuming storm-petrels steadily increased. At the end of April through mid-May only one 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 (Figure 12).

While beetles and crickets were the most numerous of the prey items counted in the diet, they did not represent as much biomass in the owls' diet as compared to mice and storm-petrels, which comprised 98% of the total prey biomass (Table 6). As measured by prey biomass, mice provided the majority of energy gain in the fall, while storm-petrels provided half to a majority of energy gain in the winter and early spring, respectively (Figure 13). Beetles and crickets were present throughout most of the study period, but contributed much less to the diet in terms of energy gain.

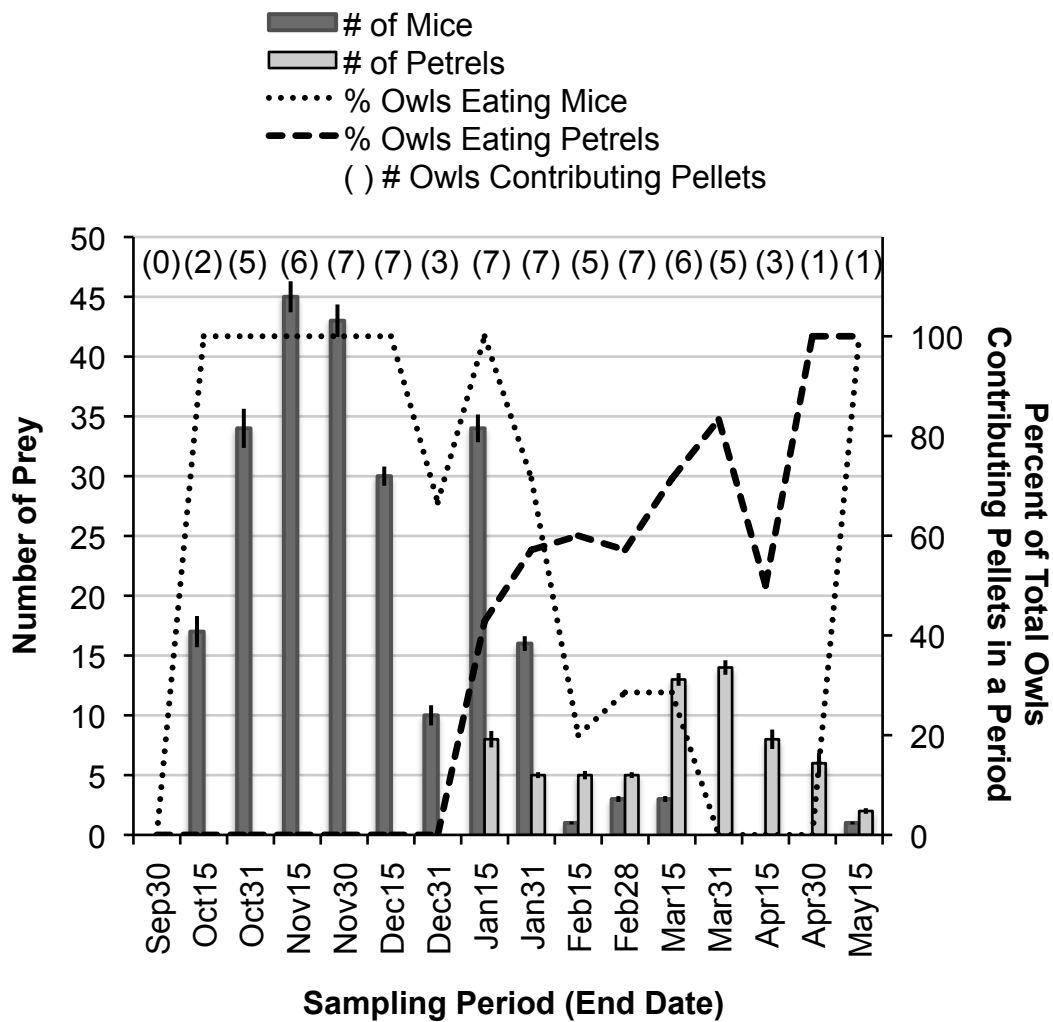


Figure 12. Number of mice and storm-petrels eaten, and the proportions of owls eating them, by period. Error bars show the standard error. The percentages of owls eating mice and of owls eating storm-petrels are depicted by dotted and dashed lines, respectively. The percentages are proportions of the total number of owls contributing pellets (shown in parentheses) within a period.

Table 6.

Biomass of Common Prey Items in the Study

Prey Item	Number of Prey Items	Average Mass (g) of Prey Item	Total Biomass (g)	Percent Biomass (%)
House mouse	452	18.5 ^a	8362	70
Storm-petrel	86	38.85 ^b	3341	28
Beetle	525	0.25 ^c	131	1
Cricket	456	0.25 ^d	114	1

Note. ^a Tietz, 2009b; ^b Jones & Golightly, 2006; ^c Ainley, 1995; ^d N. DiRienzo, personal communication, October 23, 2012.

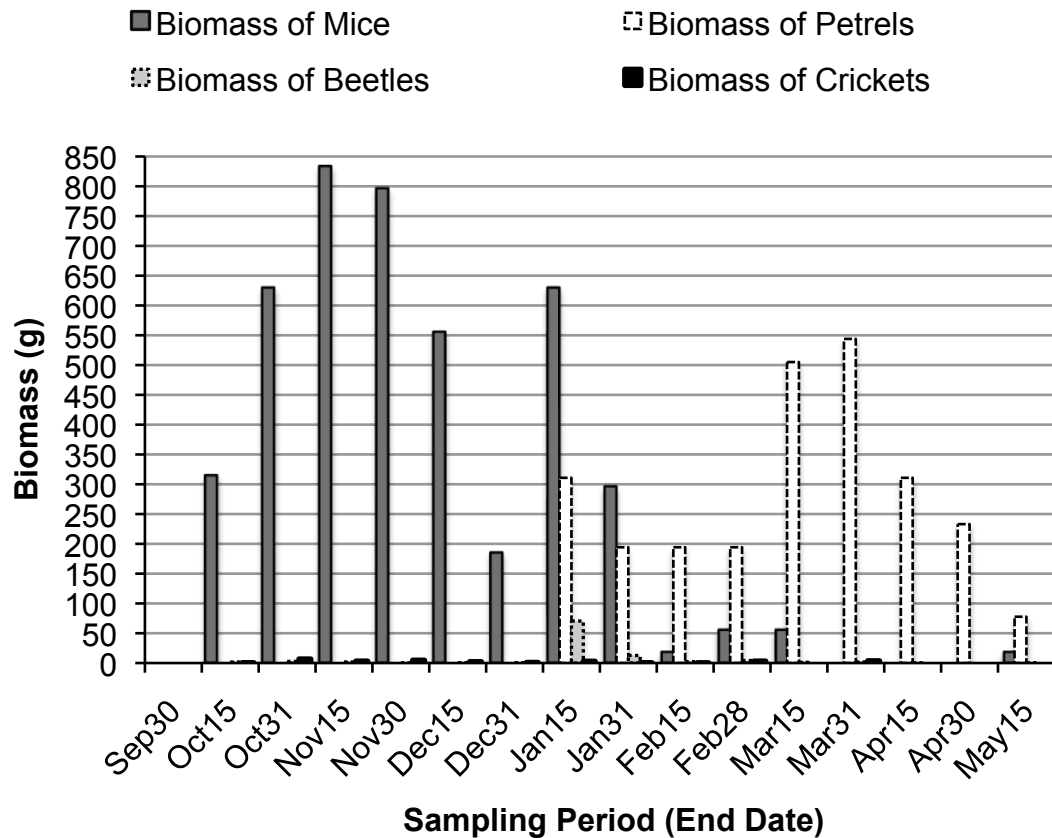


Figure 13. Prey biomass of four main types of prey, by period.

The transition from eating mice in the fall to eating storm-petrels in the spring is true both for owls as a group and for individual owls (Figure 14). 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 (A42, A70, A81, and A88) made a complete switch, with storm-petrels comprising up to 100% of the owls' diet for the remainder of their stay on SEFI. The remaining two owls (A56 and A60) still included mice in the diet until their departures in March and May, respectively, although storm-petrels made up the majority of their diet (Figure 14). For all owls except A44, the last diet data recorded for each owl coincides with the last time the owl was detected. A44 was detected on SEFI through early April, but no pellets were found for this owl from January onward.

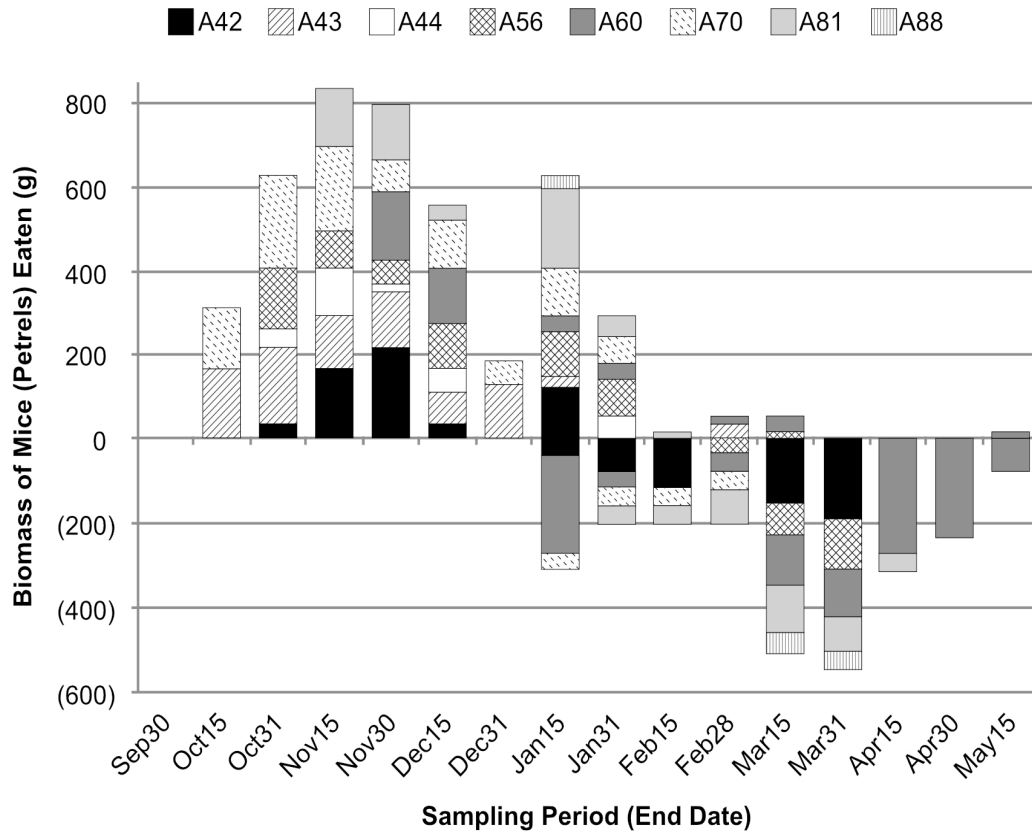


Figure 14. Biomass of mice and petrels eaten by individual owls, by period. The mouse biomass is displayed above the x-axis, while that of storm-petrels is shown below the x-axis.

There was a difference in prey biomass between seasons; therefore, I rejected H_01 . Results from the ANOVA indicated there was a significant change in the owls' diet between seasons. There was at least one difference among the means of biomass for mice consumed in the fall, mice consumed in the spring, and petrels consumed in the spring ($F_{(2,21)}=12.696$, $p<0.001$) (Figure 15). Post-hoc tests showed that the biomass of mice consumed in the spring was significantly less than the biomass of mice consumed in the fall ($p<0.001$), 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 ($p=0.494$).

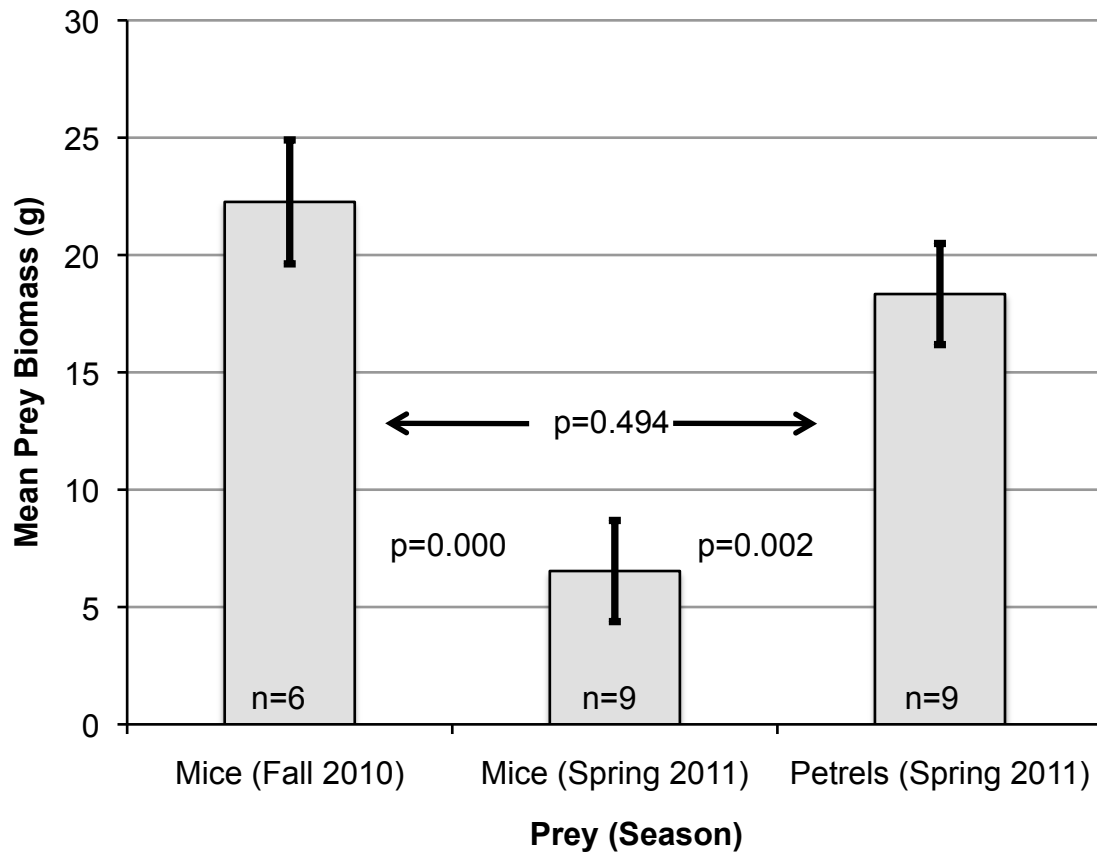


Figure 15. Mean prey biomass by season. The average biomass with standard error (SE) bars is shown for mice and storm-petrel prey in the fall and spring. Sample size (n) is shown for each variable, and p-values from Tukey's Test are displayed between the paired variable comparisons.

Density-Dependent Prey Selective Behavior in Burrowing Owls on SEFI

There was a correlation between mouse abundance and mouse prey; therefore, I rejected H_0 . Over a six-month period the number of mice per pellet was strongly and positively correlated with trapping success for mice ($R^2=0.792$, $p=0.017$) (Figure 16).

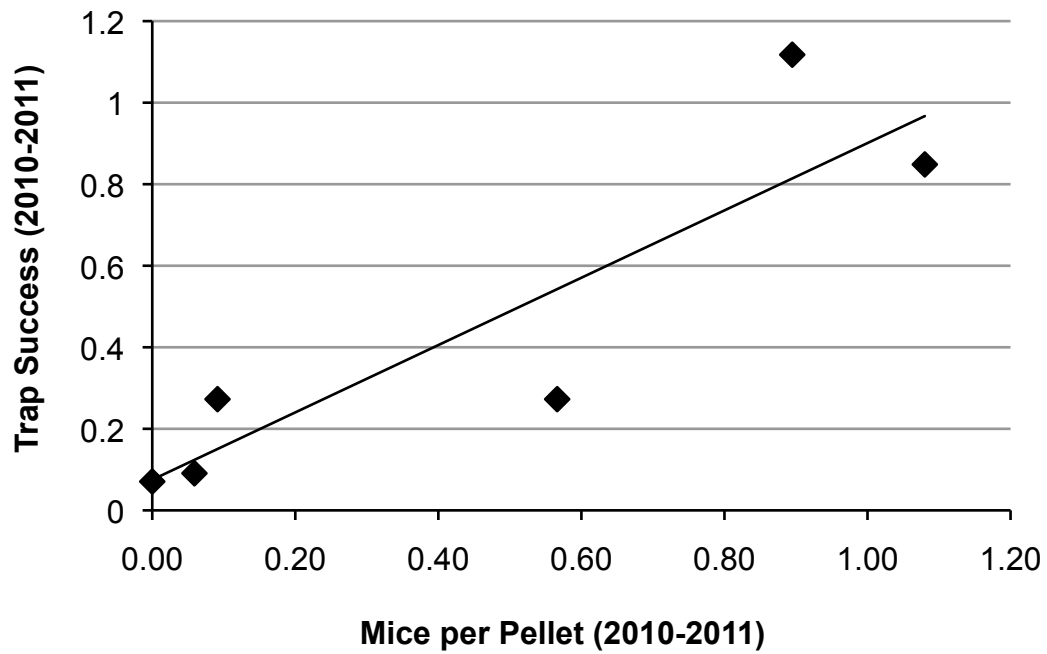


Figure 16. Regression line for mice per pellet, and mouse abundance as measured by trap success ($R^2=0.792$).

Discussion

I investigated some basic questions on wintering burrowing owls on SEFI in 2010-2011. Specifically, I wanted to know how many owls visited and overwintered on SEFI, how long they stayed, and what they ate during their stay. Furthermore, I wanted to know how important mice and storm-petrels were in the burrowing owl's diet on SEFI. The results of this study indicate a regular and stable burrowing owl presence on SEFI from fall to spring. I estimated the abundance of burrowing owl migrants on SEFI during fall 2010 to spring 2011 to be 23 owls. Considering only the fall period (September through December), the 16 owls observed during my study is a slightly higher but similar number than that of previous years' totals: 14 in fall 2008 (Tietz, 2009a) and 15 in fall 2009 (Tietz, 2010). The number of burrowing owls on SEFI has been relatively stable over this time period, although an unusually large influx of migrants, or irruption, occurred in more recent years: in fall 2012, a record 37 burrowing owls were captured and banded by Point Blue biologists (J. R. Tietz, personal communication, December 14, 2012). In fall 2013, however, a total of 16 owls were recorded (J. R. Tietz, personal communication, December 18, 2013); this was equal to the total of burrowing owls recorded at the time of my study (fall 2010) and is consistent with fall numbers in previous years. Therefore, the number of owls in this study likely represents the typical annual burrowing owl presence in the fall.

With the aid of telemetry data, the nine owls documented as arriving in fall and staying until spring provided an estimate of the overwintering owl population on SEFI in 2010-2011. The telemetry data in conjunction with dedicated owl monitoring throughout

the spring allowed for a more accurate determination of how long the owls stayed on the Island. In 2010-2011, the average stay was 118 days, with a maximum of 173 days recorded for owl A44. Without the telemetry data, however, estimates for stopover duration are more approximate. In the year (2009) prior to my study, when telemetry data and dedicated owl monitoring were limited due to fewer owls retaining the transmitters during the spring, the longest stopover duration for an owl was recorded to be a minimum of 159 days, but its total duration was unknown (Tietz, 2009b). The longest documented stopover for a burrowing owl (without telemetry) in 2008 was 134 days, relying solely on the resighting of bands and the assumption that the owls stayed at the same roosts throughout their stay (Tietz, 2009b). I found that the burrowing owls used few to several roosts and may move a relatively long distance from their previous roost, as was the case with owl A70. This owl in one instance moved roosts from the top of a south-facing slope to a cave with a northern exposure, over two ridges and approximately 200 meters away. Owl A70 notably had more than double the number of roost of any other owl, and also used roosts that not only varied in location but in size, aspect, elevation, and exposure.

A major focus of this study has been the investigation of the burrowing owl diet on SEFI, not only the composition of the diet, but also how the diet changes throughout the seasons and the resulting energetic and ecologic implications. The information from this study will hopefully help influence management decisions involving the burrowing owl on SEFI.

The burrowing owl diet on SEFI included a diversity of vertebrates and invertebrates. The variety and number of invertebrates in the owl diet on SEFI likely reflect the opportunistic foraging nature typical of burrowing owls; this diet is consistent with diet studies in other habitats (Hall et al., 2009; Littles et al., 2007; Trulio & 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 quantity, the total biomass contribution to the diet was only 2%. Vertebrates, in contrast, comprised 98% of the total biomass contribution to the burrowing owl diet. These results demonstrate that, on SEFI, invertebrates in the diet contribute very little toward the burrowing owl's energetic gain and are not a significant component of the diet.

The data do show that mice are an important energetic component of the burrowing owl's diet on SEFI, as they are in other parts of the owl's range (Hall et al., 2009; Littles et al., 2007; Trulio & Higgins, 2012). In terms of biomass, mice alone made up 70% of the total prey biomass, similar to results of previous burrowing owl diet studies (Littles et al., 2007; Trulio & Higgins, 2012). On SEFI, there was a strong positive correlation between mouse abundance and mice consumed, indicating that the owls consumed more mice prey when they were available, and fewer when they were scarce.

The seasonal differences in the burrowing owl diet on SEFI reflect the varying availability of prey throughout the seasons. We know from previous research that there is an abundance of mice on SEFI in the fall, followed by a marked decrease in the spring

(Irwin, 2004; USFWS, 2013b). This is evident in my study results, which showed a decrease in the biomass of mouse prey consumed between fall and spring. Also, in the spring, the prey biomass of mice was less than the prey biomass of storm-petrels, suggesting the owls switched from the less abundant mice to the more available storm-petrels as their primary prey.

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 beginning in late winter and early spring, as they attend to breeding sites on the Island (Ainley, 1995; USFWS, 2013b). As with the mice, it is possible that burrowing owls consumed storm-petrels in quantities that corresponded to their availability on SEFI. I also documented individual diet variation among the owls. One owl (A43) appeared to have departed the Island without ever having consumed a storm-petrel. By the end of February, when A43 left the Island, the other owls had already made the switch to storm-petrels. I found the majority of the owls, however, ate both mice and storm-petrels, suggesting that this was a population-wide phenomenon and not idiosyncratic behavior.

The burrowing owls switching from mice to storm-petrels in the diet appears similar to what Heidarian (2012) described in experiments with thrips and spider mite prey. The proportion of mice prey consumed in the fall is a positive function of abundance of mice on the Island, and therefore, Island density of mice, in the fall. Similarly, the proportion of storm-petrel prey consumed in the spring is also positively dependent upon storm-petrel abundance in the spring. These results suggest a functional

response is occurring. It is possible that mice, being the more abundant prey in the fall, made up a greater percentage of the biomass in the fall diet relative to their availability in the environment. Similarly, storm-petrels comprised a greater percentage of the biomass in the spring diet relative to their availability because prey switching behavior was occurring. Because abundance data were not available for storm-petrels in the fall and spring during the study period, however, prey switching theory as defined in a classical sense could not be tested. Despite this, my results do agree with other research findings from SEFI that indicate the burrowing owls' diet shifted significantly from one composed primarily of mice to that of storm-petrels (Nur et al., 2014).

The reasons for the diet shift, in addition to prey abundance, may include ease of prey capture. Perhaps storm-petrels were more easily caught by burrowing owls as they attended their breeding grounds in the spring. Energy gain may be a factor as well – the storm-petrels clearly provide a larger energy gain to the owls, with one storm-petrel averaging 38.85 g as compared to an average mass of 18.5 g for a mouse. In addition to what appears to be prey switching, prey selectivity may also be occurring with burrowing owls on SEFI, similar to what occurred with coyotes and foxes in the study by Randa et al. (2009). The data from my study show that mice were still an important component of the owls' diet in the spring, suggesting that prey switching behavior may be a necessary result of initially expanding prey selection to include storm-petrels when mice are most scarce (Murdoch, 1969; Randa et al., 2009). Perhaps these reasons, or a combination thereof, may explain the change in the owls' diet from mice to storm-petrels.

Mouse eradication on SEFI is one management option under consideration by

USFWS 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 diet on SEFI in the fall. As discussed, this is probably due to their availability and abundance during that time, or possibly due to the owls' preference, to some degree, for mice. In any case, the quantity of mice in terms of prey biomass is key for sustaining the owls from the fall months through early winter. Elimination of the mouse population on SEFI, therefore, will likely result in a lower carrying capacity and thereby reduce the burrowing owl presence on SEFI.

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 Farallones briefly, only a dozen or so owls overwinter, staying up to several months. Few of the owls that arrive on SEFI are returns (Chiang, 2008); the rest are migrants that essentially fill an available ecological niche every fall. Without mouse prey available, 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. As noted, invertebrates overall do not provide substantial prey biomass for burrowing owls, and therefore it is unlikely that burrowing owls could overwinter, being sustained solely by invertebrate prey. Also, there has been 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 to nest sites 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, they are mostly diurnal during stopover, so there would be little opportunity for the owls to capture them. While they might provide more consistent prey, the number of storm-petrels returning to the Island decline rapidly as their chicks fledge in October; this is when most of the burrowing owls arrive.

Therefore, the storm-petrels alone may not be abundant enough to sustain many overwintering burrowing owls. Cassin's auklets appear to be an uncommon prey item for the burrowing owl based on the results of my research and previous diet studies (Mills, 2006). 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; these owls may subsequently move on to other wintering grounds where prey may be more abundant.

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 (Buffa, 2003), and two burrowing owls were inexplicably found dead at the time of my study. Also, the owls may be forced to hunt more during daylight hours, which puts them at higher risk of predation by peregrine falcons on the Island. During my study period at least one burrowing owl, seen flying in the open 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 as well.

Whether the burrowing owls stay for a shorter length of time, or have a higher rate of mortality, the mouse eradication will likely limit the number of owls that overwinter on SEFI. Nur et al. (2014) predict that even a partial reduction in burrowing owl abundance (50-72%) will have dramatic positive impacts for Farallon storm-petrel populations. Successful removal of mice from the Farallones should, therefore, be an effective management strategy for recovering the ashy storm-petrel population.

Recommendations for Future Research

My first recommendation is for a follow up study that repeats my research questions post mouse eradication. Point Blue already tracks the number of owls arriving and overwintering annually on the Farallones, which will help determine how the migrant owl population changes in response to elimination of their main prey. By repeating the diet component of my study, wildlife managers will be able to determine how the owls' diet changes, and potentially identify alternative prey for the burrowing owl. It is possible that, post mouse eradication, the burrowing owl may prey more heavily on invertebrates, take some of the late nesting storm-petrels that continue to nest through fall, or prey upon more of the migrant songbirds that stop over on SEFI.

A second recommendation is to conduct more potential prey availability surveys in the fall, both before and after the mouse eradication. Invertebrate surveys and additional vertebrate surveys, including those for seabirds and salamanders, prior to and during mouse eradication may be useful to see which wildlife might be susceptible to increased owl predation. Post-eradication surveys might detect any changes in these prey populations as a result of the removal of mice and the probable increase in owl predation. These prey surveys are especially important for endemic species such as the Farallon cricket, and for the Cassin's auklet, another native seabird on the Farallones known to be occasional prey for the burrowing owl.

Conducting this research will help wildlife managers to better understand the winter ecology of the burrowing owl on SEFI and make more informed management decisions for the Farallones, especially pertaining to the owl's interaction with the ash

storm-petrel and the non-native introduced house mouse. Also, any additional research is a valuable contribution toward understanding and protecting both the burrowing owl and the ashy storm-petrel in California and across their ranges.

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