INTRODUCTION

The introduction of non-native mammals is often a primary factor in the decline or extirpation of seabird populations on islands worldwide (Croxall et al. 2012). The Farallon Islands (hereafter, Farallon), an archipelago 48 km west of San Francisco, California, United States, have the highest diversity and density of nesting seabirds in North America south of Alaska, with 13 breeding species totaling about 500,000 individuals (Warzybok et al. 2014). The islands also have seasonally resident populations of owls and hawks, which prey on the seabirds there (DeSante & Ainley 1980), and reflect a high diversity of raptors on the adjacent mainland. Included in the region is one of North America’s largest resident and wintering Burrowing Owl Athene cunicularia populations (James & Espie 1997, Sheffield 1997). Studies on Southeast Farallon Island (SEFI) have indicated that mouse densities in the fall are one of the highest reported for any island in the world (Grout & Griffiths 2013). Trapping studies there indicate that the mouse population reaches its peak in October and a marked low point in April of each year (Irwin 2006; Point Blue Conservation Science, pers. comm.). Burrowing Owls arrive on the Farallones in October (DeSante & Ainley 1980, Richardson et al. 2003). At this time of year, most of the island vegetation has gone to seed and the mouse population is much more abundant and visible; as a result, these raptors find an abundant food supply. However, when the mouse population reaches its low point because of a combination of rains that flood burrows and a decreasing food supply (P. Pyle, pers. comm.), the owls lose their primary food source.

The purpose of my study was to test the hypothesis that between October and January, when the mouse population on SEFI is high, owl diet consists almost entirely of mice, and between February and June, when the mouse population is low, owls switch their diet from one that mainly consists of mice to alternative prey, including migrant passerine and breeding seabird species. On the basis of these results, I discuss the role of owl predation on certain seabird breeding populations on the Farallones.

STUDY AREA AND METHODS

This study was conducted at SEFI, which is part of the Farallon National Wildlife Refuge (Fig. 1; 48 km off the coast of San Francisco, California; 37°42′N, 123°00′W). It included analysis of owl pellets collected there in 2000–2003 (results are reported by calendar year). Since 1971, the US Fish and Wildlife Service and Point Blue Conservation Science (Petaluma, California) have monitored the annual reproductive success and conducted population estimates of the 13 seabird species nesting on these islands; these species include Ashy Oceanodroma homochroa and Leach’s storm-petrels Oceanodroma leucorhoa, as well as Cassin’s Auklets Ptychoramphus aleuticus. Before 2000, biologists opportunistically collected.

SUMMARY

I investigated diet of migratory owls on Southeast Farallon Island (SEFI), California, United States, including how diet changed in response to time of year and prey availability. I analyzed 523 pellets collected at SEFI from at least four different owl species during 2000–2003 (as well as 99 pellets for other time periods) and quantified the proportion of mice, insects and birds within pellets. The non-native House Mouse Mus musculus was the most abundant diet item across all four years, followed by birds and then insects. Examination of diet composition within each year revealed that between November and February owls primarily consumed mice, while they ate more birds between March and June. Between July and October, consumption of mice and birds was about equal. Previous mouse-trapping studies have shown an abundant mouse population on SEFI during autumn, when owls arrive, while winter mouse populations decrease in response to rains that flood burrows and lower food supplies. My study indicates that, as wintering owls lose a primary food source, they shift their diet from mice to other prey. Included in the shift were storm-petrels (Ashy Oceanodroma homochroa and Leach’s O. leucorhoa), mostly consumed by Burrowing Owls Athene cunicularia, as well as Cassin’s Auklets Ptychoramphus aleuticus, mostly consumed by Barn Owls Tyto alba. The presence of mice on SEFI may be indirectly affecting seabird populations by keeping migrating owls on the islands longer than they would stay if mice were absent.

Key words: Athene cunicularia, invasive species, Mus musculus, Oceanodroma homochroa, Oceanodroma leucorhoa, Ptychoramphus aleuticus, Southeast Farallon Islands, Tyto alba

SEABIRDS AS PART OF MIGRATORY OWL DIET ON SOUTHEAST FARALLON ISLAND, CALIFORNIA

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owl pellets on SEFI. In 2000, a comprehensive pellet collection effort was instituted, covering nine designated areas twice per month. These areas consist of natural crevices, caves and trees where pellets have historically been discovered. Collected pellets are individually stored in a plastic bag labeled with date and location. The owl species, if known, is recorded.

For the present study I analyzed 523 owl pellets collected between 2000 and 2003. Pellets came from at least four owl species: Barn (n = 102), Burrowing (n = 79), Long-eared (n = 11), Saw-whet (n = 99) and unknown owl species (n = 232). For the purposes of prey item comparison by owl species and groupings by month, an additional 99 pellets were included (from 1996–1999, before systematic pellet surveys began, and from a partial collection in 2004). Each pellet was examined for its contents, with presence of mice, insects and bird (if known) recorded. An attempt was made to determine bird species, although not to distinguish between Ashy and Leach’s storm-petrels, which are hereafter referred to as “petrels.” Biomass of the different prey items was not quantified. Pellet content results are reported as frequency of occurrence (FOO), i.e. percent of pellets containing a particular prey category.

To compare trends of mice caught in traps and mice caught by owls, I used trap data from a separate study. To determine whether seasonal fluctuations in the mouse population coincided with increased predation on storm-petrels, Irwin (2006) systematically trapped mice along four transects on SEFI (Lighthouse Hill, Marine Terrace, North Landing and Shubrick; Fig. 2) for three consecutive nights per month between March 2001 and March 2004. Results represented the proportion of successful trap nights per trap effort (“trap night” = each night a trap was set). Further details on trapping methods are described in Irwin (2006).

Statistical tests included linear regression analyses to illustrate relationships between parameters, and the relative fit of each regression analysis was evaluated using the coefficient of determination ($R^2$). All statistical tests were performed using STATA (StataCorp, 2011); $P$ values of 0.05 or less were assumed to be significant.
RESULTS

The predominant prey item found in pellets was mice (FOO 57.4%, Fig. 3), with up to seven mice in a single pellet from a Barn Owl. Birds of several species also occurred frequently (45.5% of pellets): Cassin’s Auklets (25.4%), petrels (9.6%), migrant passerines, and other unidentified avian species (10.5%, which may have included the above seabird species or others, but could not be identified because of decomposition). Insect parts were found in 16.6% of pellets. Pellet composition varied among owl species; Barn Owls took a greater number of Cassin’s Auklets than mice, and Burrowing Owls preyed on a greater number of petrels compared with other owl species, although mice remains still predominated (Table 1). Pellets from Long-eared and Saw-whet owls, present on SEFI in the winter (both species) and early spring (Saw-whet Owl), indicated that they took almost exclusively mice, which occur in greater abundance during these times of year (Long-eared = 91%, Saw-whet = 96% FOO; Table 1).

In comparing prey items among calendar years, in 2001 owl predation on mice was highest (FOO 94%) and predation on birds was lowest (14%; Fig. 3). In 2003, however, birds were found in 64% of pellets, which surpassed the FOO of mice by 23%. The percentage of pellets that contained insects was fairly similar across years (13% in 2000, 14% in 2002 and 15% in 2003). In 2001, however, insects were found in 38% of pellets.

In comparing frequency of occurrence among months, all years combined, mice were found in pellets at highest frequency (93.2% on average) during October–January, reaching a low point in April (25.5%) and in September (21.4%). Birds, including petrels, Cassin’s Auklets and unidentified species, were found in a low number of pellets collected between October and February (6.7%). Starting in March, however, when mice are presumably scarce or more difficult to find and more seabirds are found on the island, there was a sharp increase in the number of birds taken, and this level remained high through to September (69% average, March–September).

I also grouped pellet composition by seasons relevant to seabird breeding: November–February (all years combined, non-breeding season, few seabirds present), March–June (main breeding season) and July–October (continued breeding season of storm-petrels and Cassin’s Auklets and higher numbers of migrating passerines; Fig. 4). The first four-month grouping (November–February) had the highest FOO for mice (92.5%, n = 196) and the lowest for birds (8.0%, n = 17). In contrast, March through June had the greatest FOO of birds (61.9%, n = 223) and the lowest of mice (37.5%, n = 135). During the July through October period, similar frequencies of both birds and mice were eaten by owls (58.0%, n = 29, mice; 54.0%, n = 27, birds). These results are also apparent in Fig. 5, which shows a negative correlation between the frequency of mice in pellets and birds in pellets ($y = 1.09 - 1.05x$, $R^2 = 0.87$, $P < 0.0001$, $n = 12$).

There was a positive correlation between the frequency of mice caught in traps and the frequency of mice found in owl pellets, although this relationship was not significant ($y = 34.07 + 0.09x$, $R^2 = 0.04$, $P > 0.05$, $n = 12$; Fig. 6). Thus, trapping success of live mice during 2001–2004 demonstrated a population trend similar to the trend of mice found in pellets (Fig. 6), except for September (months combined across years), when 31.7% more mice were found in pellets than caught in traps. April was the month with the lowest

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**TABLE 1**

<table>
<thead>
<tr>
<th>Prey item</th>
<th>Frequency of occurrence, %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Barn owl</td>
</tr>
<tr>
<td>Mice</td>
<td>37.3</td>
</tr>
<tr>
<td>Insects</td>
<td>4.9</td>
</tr>
<tr>
<td>Petrels</td>
<td>2.0</td>
</tr>
<tr>
<td>Auklet</td>
<td>43.1</td>
</tr>
<tr>
<td>Unknown bird</td>
<td>22.5</td>
</tr>
</tbody>
</table>

Fig. 4: Seasonal frequency of occurrence of owl pellet contents (1996-2004) by four-month groupings: November through February (n = 148), March through June (n = 360), and July through October (n = 48).

Fig. 5: Regression analysis of frequency of occurrence of mouse and bird remains in owl pellets.
trapping success per trap night (1.2%), and September was the month with the lowest number of mice caught by owls (21.4% FOO).

DISCUSSION

The analysis of pellets from migrating and over-wintering owls on SEFI reveals some interesting details: (1) there is annual variability in owl diet overall — in 2001, mice and insects were more prevalent, and birds less prevalent, whereas in 2003 the opposite was true; (2) there is a seasonal pattern in prey consumption by SEFI owls — FOO of mice was highest in November–February, when birds were nearly absent, whereas in March–June, FOO of birds was higher than mice; and (3) there is a negative correlation between mouse and bird FOO, which suggests that when owls eat mice they eat few birds, and vice versa. This may indicate that mice are the preferred prey for owls (as it is the most prevalent prey when they first arrive at the island), but that when the mouse population declines they switch to birds. Last, (4) mice found in pellets and mice caught in traps show a similar trend, as was expected, although this relationship was not significant. This is perhaps explained by the low sample size of the mouse-trapping study. Similar conclusions were reached in a study that found a negative correlation between mouse abundance and owl predation index, after controlling for owl abundance (Nur et al., in press).

Owls occurring on SEFI mainly prey on mice and various species of birds. Average insect FOO was low (20%, 2000–2003), and the insect contribution to pellet-determined diet in terms of biomass is likely minimal (Chandler 2015). It is also unclear whether owls ingested insects or mice that had eaten insects. Coleopteran beetles are a common diet item of mice on the Farallon islands (Hagen 2003), and 89.1% of the insects recorded in pellets (mostly Coleoptera beetles) were found in pellets that also had mice. This may indicate that (1) owls were eating Coleopteran beetles; (2) owls were consuming mice that had previously eaten Coleopteran beetles; or (3) owls were eating both mice and beetles if both are abundant at similar times. In 2001, the FOO of insects was 38%, which was higher than in the study’s other years; November 2000-October 2001 was also the study time period. FOO of insects was 38%, which was higher than in the study’s other years; November 2000-October 2001 was also the study time period. FOO of insects was 38%, which was higher than in the study’s other years; November 2000-October 2001 was also the study time period. FOO of insects was 38%, which was higher than in the study’s other years; November 2000-October 2001 was also the study time period. FOO of insects was 38%, which was higher than in the study’s other years; November 2000-October 2001 was also the study time period.

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Storm-petrels are present on SEFI mainly from February through October (Ainley & Boekelheide 1990). Estimates of breeding populations of Ashy Storm-Petrels indicate a decline in numbers from the 1970s to the present (Sydeman et al. 1998, Warzybok & Bradley 2009), while evidence from a mark-recapture analysis indicates a decline of 42% over two decades, from an estimated 3,500–4,000 breeding birds in 1972 to approximately 2,000–2,400 birds in 1992 (Sydeman et al. 1998). Potential reasons for this decline include increased predation by gulls, mice and, most recently, owls (Ainley & Boekelheide 1990, Sydeman et al. 1998, Mills 2000, Warzybok et al. 2014), as well as population variation driven by changing oceanographic conditions (Carter et al. 2016). There are only two records of petrel chicks being eaten by a mouse at SEFI (R. Bradley, pers. comm.; Ainley & Boekelheide 1990). However, documentation of direct mouse predation on seabird eggs and chicks is difficult, given the secretive nesting habits of storm-petrels, the relatively few nests accessible enough for study and environmental conditions that make it challenging to use mouse-detection methods such as track plates or video cameras.

The Cassin’s Auklet population, measured both at-sea and on SEFI, has declined precipitously since the early 1970s (Adams 2008, Warzybok & Bradley 2009, Wolf et al. 2010). About 105,000 birds were estimated to breed on the Farallon in 1971 (Manuwal 1974). More recent estimates indicate a 73% decline, to an estimated 28,000 individuals in 2014 (Warzybok et al. 2014). In the region between Monterey Bay and Bodega Bay, at-sea numbers of this species have also decreased during recent decades (Oedekoven et al. 2006, Lee et al. 2007) and other changes (e.g. recovery of trophically competing cetaceans; Ainley & Hyrenbach 2010).

Cassin’s Auklets visit nest burrows year-round, although during the non-breeding season they visit burrows mainly on moonless,
dark nights, and are present at a lower density. However, during the breeding season (April–June/July), burrow visits occur regardless of light level (Ainley & Boekelheide 1990), which may account for the increased predation by Western Gulls Larus occidentalis (Nelson 1989) observed during the breeding season. However, both Cassin’s Auklets and petrels are primarily nocturnal at their breeding colonies, a behavior which, along with their small size, may account for the high predation rates by owls. Moreover, the populations of these seabirds at SEFI are large enough, and nesting habitat limited enough (Ainley & Boekelheide 1990), that their searches for burrows and nesting cavities may require increased effort, thus exposing potential recruits to increased predation risk. Although the extent of mouse predation on petrels and auklets needs to be further investigated, results of this and other studies suggest that mouse presence may contribute indirectly to the observed declines in these two species through their effect on mouse-eating birds such as Western Gulls (Nelson 1989) and Burrowing Owls.

Since 1968, Point Blue Conservation Science has recorded daily totals of all land birds year-round, from which annual numbers of arriving individuals and winter residents can be calculated (DeSante & Ainley 1980, Pyle & Henderson 1991, Richardson et al. 2003). From 1968 to 2000, a total of 271 Burrowing Owls arrived at SEFI during fall (mean 8.21/year, range 4–16; Point Blue Conservation Science, unpubl. data). A total of 92 owls were recorded as winter residents (mean 2.79/year, range 1–7), representing 33.9% of the fall arrivals of this species. Before 1973 there was a large population of introduced rabbits on SEFI (Ainley & Boekelheide 1990). The mean number of winter Burrowing Owl residents before 1973, the year when rabbits were removed, was much lower (1.67; 24.4% of fall arrivals) than after rabbits were removed (3.04; 35.7%). The difference in the number and proportion of wintering owls before and after 1973 supports the premise that rabbits suppressed mouse numbers through depletion of vegetation and annual seed crops (P. Pyle, pers. comm.), resulting in fewer wintering owls at SEFI before 1973.

The US Fish and Wildlife Service has been considering the eradication of the House Mouse from SEFI. Justification of this action will rest to some degree on documentation of any adverse effects of mouse presence on the natural ecology of the islands. Before eradication plans are implemented, however, all factors, both direct and indirect, must be considered. Indirect effects of introduced mammals on native populations should be examined when considering eradication efforts. The results of this study indicate that the presence of mice may be indirectly affecting petrel and auklet populations by keeping migrating Burrowing Owls on the islands for longer than they would naturally stay if the mice were absent. The loss of even small numbers of long-lived Ashy Storm-Petrel adults or potential recruits by owl predation can have a significant demographic impact. The removal of mice from SEFI may benefit not only the migrating owls, but also the seabird species that owls prey upon when the mouse population decreases. Without mice, the migrating owls might not remain on the Farallones, but continue their migration to wintering grounds with more food resources (USFWS 2013).

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