

Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island

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Abstract. Apex predators can suppress the foraging activity of mesopredators, which may then result in cascading benefits for the prey of those mesopredators. We studied the interactions between a top predator, the Barn Owl (*Tyto alba*), and their primary prey, an island endemic deer mouse (*Peromyscus maniculatus elusus*), which in turn consumes the eggs of seabirds nesting on Santa Barbara Island in California. Scripps's Murrelets (*Synthliboramphus scrippsi*), a threatened nocturnal seabird, arrive annually to breed on this island, and whose first egg is particularly vulnerable to predation by mice. We took advantage of naturally occurring extreme variations in the density of mice and owls on the island over 3 years and predicted that (1) mouse foraging would decrease with increasing predation risk from owls and moonlight and (2) these decreases in foraging would reduce predation on murrelet eggs. We measured the giving up densities of mice with experimental foraging stations and found that mice were sensitive to predation risk and foraged less when owls were more abundant and less during the full moon compared to the new moon. We also monitored the fates of 151 murrelet eggs, and found that murrelet egg predation declined as owl abundance increased, and was lower during the full moon compared to the new moon. Moreover, high owl abundance suppressed egg predation even when mice were extremely abundant. We conclude that there is a behaviorally mediated cascade such that owls on the island had a positive indirect effect on murrelet egg survival. Our study adds to the wider recognition of the strength of risk effects to structure food webs, as well as highlighting the complex ways that marine and terrestrial food webs can intersect.

Key words: apex predators; barn owls; deer mice; giving up densities; indirect interactions; mesopredators; murrelets; predation; risk effects; seabirds; trophic cascade.

INTRODUCTION

Widespread declines in top predator populations across many different ecosystems has led to increased recognition of their role in controlling mesopredators via intraguild predation (Prugh et al. 2009). The resulting increases in the density of mesopredators can be an urgent conservation issue if they subsequently impact vulnerable prey species (Courchamp et al. 1999, Ritchie and Johnson 2009). Island food webs with relatively simple communities may be particularly prone to these effects (Schoener and Spiller 2010), and provide compelling examples of ecological cascades when top predators are removed (Terborgh et al. 1997, Terborgh et al. 2001). For instance, the introduction of both invasive rats (*Rattus* spp.) and their predators, feral cats, has been implicated in the decline or extinction of many island species, including seabirds (Townsend et al. 2006, Medina et al. 2011). The subsequent removal of cats from some islands to protect seabirds has instead led to intensified predation by rats or by mice on seabird eggs and chicks (Rayner et al. 2007, Wanless et al. 2007, Angel et al. 2009, Jones and Ryan 2010). In this way, the top predator may have indirect

positive effects on prey through its impacts on a mesopredator. However, with few exceptions, the “mesopredator release” (Soulé et al. 1988) that results from the loss of top-down control has largely been construed to be a density-mediated effect (Ritchie and Johnson 2009).

But density alone may not always predict predation rates (Abrams 1993, Schmidt and Ostfeld 2003), in part because predators influence their prey through both consumptive and nonconsumptive risk effects (Schmitz et al. 2004). Mesopredators respond to the risk of predation with strategies that help them avoid being killed by predators. For example, mice and other nocturnal rodents reduce or otherwise alter their activity patterns and foraging with changing moonlight (Prugh and Golden 2014), and with increasing predator numbers (Orrock and Fletcher 2014). The behavioral decisions made by prey are not inconsequential and involve costs that can directly impact their fitness (Morris and Davidson 2000), which can equal or even exceed the consumptive effects on prey demography (Werner and Peacor 2003, Preisser et al. 2005). Anti-predator behavior may also have cascading impacts throughout food webs (Lima and Dill 1990), such as when these predator-mediated changes in foraging benefits either resource prey or plants (e.g., wolves-elk-aspen; Ripple and Beschta 2007).

Predator control on islands has been a largely successful conservation strategy (Jones et al. 2016), and is expanding

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to increasingly larger islands and to islands with more complex food webs involving multiple invasive species (Glen et al. 2013, Sutherland et al. 2014). However, recommendations for optimal predator control programs are often exclusively focused on mitigating potential density mediated effects of mesopredators (e.g., Bode et al. 2015), while the potential for behaviorally mediated cascades are rarely considered. Given the complexity of predator effects, and to avoid unexpected outcomes from species removals (Zavaleta et al. 2001, Rayner et al. 2007, Bergstrom et al. 2009, Brodier et al. 2011), it is important to consider both the potential effects of changes in anti-predator behavior as well as density prior to initiating predator control.

We evaluated the potential conservation impact of a top predator, the Barn Owl (*Tyto alba*), on a nocturnal seabird via the effects on a mesopredator, an island deer mouse (*Peromyscus maniculatus elusus*) on Santa Barbara Island in California. These endemic deer mice are omnivorous predators of ground-nesting birds on the island (Collins et al. 1979). One vulnerable species is a threatened, small (~165 g) nocturnal seabird, the Scripps's Murrelet (*Synthliboramphus scrippsi*; formerly known as the Xantus's Murrelet, *Synthliboramphus hypoleucus scrippsi*). Mice depredate 8–70% of all murrelet eggs laid in a given year (Drost and Lewis 1995, Nur et al. 2013). Barn Owls are the primary predator of mice on the island and mice are the only extant mammal on the island. This resident breeding population of owls is demographically isolated from the mainland (Huang et al. 2016), and their population rises and falls (from ~3 to 30+ individuals) in accordance with rainfall driven patterns in the abundance of mice (Drost and Fellers 1991). We took advantage of these naturally occurring extreme variations in the density of mice and owls on the island to examine how changes in predation risk for mice influenced murrelet egg survival. We predicted that (1) mice would reduce their foraging activity with increased predation risk from owls and moonlight and (2) these reductions in foraging would also decrease murrelet egg predation.

MATERIALS AND METHODS

Study system and habitat

Santa Barbara Island (33°29' N, 119°02' W) is located about 63 km from the nearest mainland location, and at 2.6 km² it is the smallest of five islands comprising the Channel Islands National Park. Scripps's Murrelets are IUCN listed as Vulnerable (BirdLife International 2016), and this island hosts one of their largest breeding colonies in the US (475–650 pairs, ~20% of total world breeding population; D. Whitworth, *personal communication*). In addition to Barn Owls, other nocturnal raptors include the wintering Burrowing Owl (*Athene cucularia*). Diurnal raptors present during the murrelet breeding season include American Kestrels (*Falco sparverius*) and Peregrine Falcons (*Falco peregrinus*; Collins and Jones 2015). The vegetation on the island consists mostly of

non-native annual grasses (*Avena* spp., *Bromus* spp., and *Hordeum* spp.), interspersed with patchily distributed low growing native shrubs and cacti (e.g., *Leptosyne gigantea*, *Eriogonum giganteum* var. *compactum*, and *Opuntia* spp.; Junak et al. 1993). These patches of shrub cover generally become more common towards the shoreline of the island and within the five small canyons that are located on the south and east sides of the island. The shoreline consists primarily of steep sea cliffs, the two tallest of which rise up to nearly 193 and 171 m from the ocean below.

Owl abundance

To quantify owl abundance in different areas across the island, we set up 200 m line transects ($n = 23$) systematically located along the island perimeter and across the island using ArcGIS 10.0 (ESRI 2011). Barn owls on the island concentrate their activity close to their roost sites with extensively overlapping home ranges (Thomsen et al. 2014), which led to marked differences in local abundance of owls across the island. In 2011, all transects were surveyed 3–4 times each over three nights in mid-April. In 2012 and 2013, when we also collected data on mouse foraging activity, all transects were surveyed over three consecutive nights beginning during the last 2 weeks in April. All surveys were conducted on nights with winds <15 knots, no precipitation or fog, and were done under similar moonlight conditions (waxing gibbous). We counted the number of owls seen at night with a spotlight (72 lumens) while hiking with a handheld GPS (Global Positioning System) unit for navigation. Counts of owls were then averaged for each transect for each year.

Mouse abundance

We also established 10 sites where we used track tubes to obtain a relative index of mouse abundance from 2011 to 2013 (see Appendix S1 for details) as well as to confirm the presence of mice near the foraging stations. Each site consisted of nine track tubes that were placed in a 3 × 3 grid formation with 7 m spacing. Track tubes were deployed before nightfall in all grids during the new moon phase in April, May, July, and August of each year except for July 2013. The following day, we recorded the number of track tubes in each grid with mouse tracks. In 2011 and 2012, we also used our track tube methods within two sites that are used by the National Park Service for long-term mouse mark-recapture studies in the spring and fall months (Fellers et al. 1988). We found significant positive correlations between our track tube index and mouse density (mice/ha) calculated by Stanley (2012) in the NPS sites ($r = 0.64$, $n = 13$ site nights, $P = 0.02$; see Appendix S1).

Giving up densities

We studied the impact of Barn Owls and moonlight on the activity and foraging behavior of deer mice by measuring the amount of food remaining in experimental

foraging patches (called the “giving up density;” GUD). The GUD represents how mice balance the benefits of foraging in that patch against the costs such as predation risk, metabolic, and missed opportunities (Brown 1988). To measure the mouse giving up densities, we created experimental foraging stations ($n = 36$) out of 2.4 L round plastic containers (15 cm height \times 15 cm diameter) with removable translucent lids. Two 5-cm diameter holes were drilled into opposing sides to allow mice to enter the stations while excluding potential entry by granivorous birds. Six study sites were selected, spaced at least 300 m apart, each one in association with both a mouse track tube grid and a line transect for measuring nearby owl abundance. Two of these sites were within the murrelet nest monitoring plots that we used to examine egg fate. Within a site, we placed three pairs of foraging stations at least 30 m apart, which is approximately the radius of a deer mouse home range on the island (Collins et al. 1979). This spacing reduced the chances of individual mice foraging at multiple stations. For each pair, one container was placed under natural cover (“sheltered;” either under a rocky overhang or native shrub depending on the habitat available at each site) and another placed within 2 m out in the open with no cover (“exposed”). This paired design of sheltered and exposed containers at each station allowed us to compare how GUDs changed in response to predation risk by examining the relative differences in the amount of seeds remaining between paired containers (Brown and Kotler 2004), as well as examine patterns in the absolute amounts of foraging that gives rise to those differences (Brown 1988).

All foraging containers were filled with a mixture of 1 L sifted dried sand and 7.5 mL roasted hulled sunflower seeds (mean total seeds = 64.83 ± 2.8 ; $n = 12$). On the following day, the uneaten seeds were sifted out and counted before the container was refilled with new seeds. In both 2012 and 2013, we began the foraging experiment on the next full moon in late May/early June after conducting the owl surveys. Giving up densities were collected over three consecutive nights during the full moon, and then again over three consecutive nights during the next new moon phase. Within each of these moon phases, the percent lunar illumination changed very little between nights (maximum difference between nights $\leq 5\%$; US Navy 2013). Foraging stations were also removed completely from sites between moon phase treatments to prevent habituation by the mice to a new food source. On the first night of the study in 2012, a small number of station pairs ($n = 6$) had yet to be deployed, so no data were collected for those stations until the following two nights. In 2013, only five of the six study site locations were used because mice were not present and no foraging data were obtained from one site.

Murrelet nest monitoring

We investigated patterns of murrelet egg depredation by mice during three consecutive breeding seasons

(2011–2013) using data collected by the National Park Service (NPS, *unpublished data*). Murrelet nests were monitored using a standard protocol in two plots, Cat Canyon and Landing Cove, which are separated by ~ 2 km (Lewis et al. 1988, Howard et al. 2014). Murrelets nest on the ground inside shallow rocky crevices or underneath native shrubs, and exhibit high nest site fidelity. Eggs that have been depredated by mice are distinguished by characteristic teeth marks left on the eggshells, and the hatching success or failure of each egg can be reliably determined based on such eggshell evidence (Lewis et al. 1988, Millus et al. 2007). Deer mice have also been observed to open and consume murrelet eggs with nest site cameras (NPS, *unpublished data*). Within each plot, murrelet nest sites were individually marked and followed every year, with nest checks beginning in early March prior to the initiation of most nests. Thereafter, all nest sites were checked every 4–7 d throughout the breeding season, (March–June), so that the timing of nest initiation and changes in nest status between check intervals was known. We excluded from our analyses any nest site locations where the timing of nest initiation could not be determined. This resulted in a sample size for each year of 42, 46, and 63 nests, respectively.

Statistical analyses

We examined whether moon phase (full/new), owl abundance (mean number of owls detected on the nearest adjacent transect), and microhabitat (exposed/sheltered) influenced the giving up densities of mice with general linear mixed models. First, we analyzed the relative differences between the paired foraging containers (log-transformed $x + 1$ difference in the number of seeds remaining between exposed and sheltered containers) to test whether owl abundance and moonlight influenced the perceived predation risk by mice. Foraging station ID was included as a random effect in this model. Only foraging stations where we observed foraging activity in at least one container in a pair were used in this analysis, and we also excluded cases ($n = 9$ stations) where mice had consumed all of the seeds in both stations in a pair. Next, we also examined whether microhabitat, moon phase, and owls influenced absolute GUD amounts in each foraging container. In this analysis, we used the mean proportion of uneaten seeds (logit transformed $x + 0.5$) for the three nights over each moon phase condition for 2012 and 2013 in each individual foraging container as our response variable with foraging station ID as a random effect. Both analyses are useful and provide complementary data on foraging patterns; the first isolates the effect of predation risk on GUDs by controlling for other costs (e.g., metabolic and missed opportunities; Brown and Kotler 2004), and the second allows examination of how those foraging patterns occurred between the sheltered and exposed microhabitats.

In both analyses, we started with fully parameterized models that included all two-way interactions between

explanatory variables and then progressively removed fixed terms until reaching a final model containing only significant terms ($P < 0.05$) and the random effects (Crawley 2014). None of the two-way interactions we examined were significant (all $P > 0.05$); therefore none were retained in the final models. Mouse density could also potentially influence GUDs (Davidson and Morris 2001). Therefore, we also checked whether mouse abundance, as measured by the mean annual track tube index for each site (see Appendix S1), influenced GUDs by including this as an additional covariate in both analyses. Mouse abundance was not significant (all $P > 0.22$) in either of the two models and therefore not retained.

Murrelets generally lay two eggs in a clutch, the first of which is then left unattended by both adults for about 8 d (Murray et al. 1983, Drost and Lewis 1995). Most instances of egg depredation happen during this initial neglect period (Murray et al. 1983), therefore, we used the initial fate of the first egg during this vulnerable time period as our response variable. We modeled egg fate (intact or depredated) from 151 nest attempts as a function of moonlight (the proportion of the moon illuminated at midnight on the night prior to the nest check; US Navy 2013) and owl abundance (mean number of owls detected on the nearest adjacent transect) while controlling for plot ID in a generalized linear mixed model (GLMM; with binomial distribution and logit link) with nest site identity as a random effect. We started with a fully parameterized model, and then progressively removed fixed terms until reaching a final model using likelihood ratio tests. We did not include mouse abundance in this analysis because mouse abundance was positively correlated with owl abundance ($r = 0.54$), leading to issues with collinearity (Zuur et al. 2010). We also found no evidence that egg depredation increased as mouse abundance increased, as would be expected if egg predation by mice was density dependent. Finally, we also tested for an association of moon phase and egg fate with a Fisher's exact test using a subset of the murrelet nest data ($n = 66$) that was restricted

to when the proportion of moon illuminated was greater than 90% ("full") and less than 10% ("new"). These categories more closely resembled our data on mouse foraging that were collected during the brightest and darkest parts of the lunar cycle.

We used R 3.2.1 (R Core Team 2014) to conduct all statistical analyses. The general linear mixed effects models (LMM) were fit with the package "nlme" (Pinheiro et al. 2014), while the generalized linear mixed model (GLMM) of egg fate was fit with the package "lme4" (Bates et al. 2012).

RESULTS

Owl abundance on the line transects varied both spatially and among years. The mean number of owls detected per transect peaked in 2012 (mean = 0.9 ± 0.37 , range: 0–4.33), after increasing from 2011 (mean = 0.24 ± 1.01 , range: 0–1.33) and subsequently dropping in 2013 (mean = 0.09 ± 0.18 , range: 0–0.66). Mouse abundance followed a similar pattern. The annual track index (i.e., the mean number of track tubes that had mouse tracks each year) for all six sites where we collected giving up densities was 4.7 ± 0.9 , 5.0 ± 1.1 , and 3.2 ± 1.2 , for 2011, 2012, and 2013, respectively.

As predicted, we found that differences in GUDs between the paired foraging stations increased with increasing owl abundance ($\beta = 0.4 \pm 0.17$; $F_{1,98} = 5.59$; $P = 0.02$; Fig. 1A), and was greater during the full moon compared to the new moon ($\beta = -0.76 \pm 0.16$; $F_{1,98} = 20.47$; $P < 0.001$; Fig. 1B). Additionally, we also found that microhabitat, moonlight, and owl abundance influenced GUDs in individual foraging containers. Mice foraged less in the foraging stations out in the open than those under cover ($\beta = -1.38 \pm 0.24$; $F_{1,110} = 34.58$, $P < 0.001$) and foraged less during the full moon compared to the new moon ($\beta = -1.35 \pm 0.24$; $F_{1,110} = 33.16$, $P < 0.001$). Mice also foraged less with increasing owl abundance ($\beta = 1.03 \pm 0.23$; $F_{1,110} = 20.02$, $P < 0.001$).

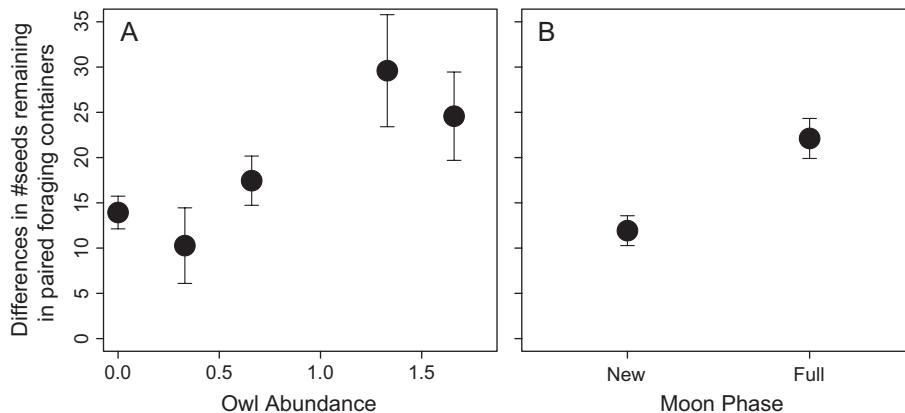


FIG. 1 Impacts of owl abundance (A) and moon phase (B) on perceived predation risk by deer mice on Santa Barbara Island. Data presented are the mean differences in foraging amounts (GUD_{exposed}-GUD_{sheltered}) between the paired foraging containers (mean \pm SE). Greater differences reflect increasing perceived predation risk.

Overall, 46 of the 151 eggs (30.5%) were found depredated by mice. Murrelet egg survival was strongly positively associated with owl abundance on the nearby transect (log odds = 7.33; 95% Wald CI: 1.37, 13.30, $\chi^2 = 32.06$, $P < 0.001$; Fig. 2) after controlling for the differences between nest monitoring plots (log odds = 2.67; Wald CI: 0.58, 4.76, $\chi^2 = 11.50$, $P < 0.001$). The probability of murrelet egg survival increased dramatically with each increase of a single owl observed, and quickly reached extremely low rates of egg predation (Fig. 2). The relationship between egg survival and moonlight was also positive (log odds = 0.31; 95% Wald CI: -1.31, 1.93), but the inclusion of this parameter did not improve the model ($\chi^2 = 0.15$, $P = 0.70$). When we examined the smaller subset of nests where eggs were laid during a full or new moon, rates of egg predation were 3.9 times higher during the new moon (17 of 44 eggs eaten) compared to the full moon (3 of 22 eggs eaten; Fisher's exact test, $P = 0.048$; Fig. 3).

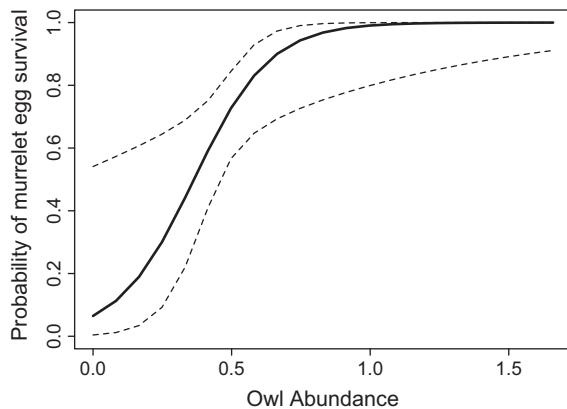


FIG. 2 Predicted probability of murrelet egg survival and owl abundance (probability and CI) after controlling for differences in survival between two murrelet monitoring plots.

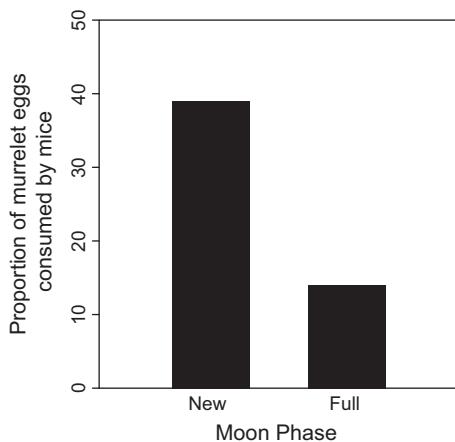


FIG. 3 Murrelet egg predation by deer mice during the new and full moon phases on Santa Barbara Island.

DISCUSSION

Island mesopredators can be a link between marine and terrestrial food webs (Stapp and Polis 2003, Suraci et al. 2014), and our study demonstrates that the strength of this connection can also be influenced by predation risk. Specifically, our results suggest that owls can indirectly benefit murrelets through a behaviorally mediated cascade. Deer mice were sensitive to predation risk and foraged less with increasing owl abundance and less during the full moon compared to the new moon (Fig. 1). Murrelet egg predation was consequently lower with increasing owl abundance, and lower during the full moon compared to the new moon (Figs. 2 and 3). Similarly, predators in a variety of communities can induce behaviorally mediated cascades on resource prey, ranging from the effects of hawks on hummingbird nest success (Greeney et al. 2015), to leopards and wild dogs on the spatial distribution of savanna trees (Ford et al. 2014). Our study, however, emphasizes that this can also have consequences for vulnerable species on islands.

Two factors may contribute to strong interactions between owls and mice. First, interactions between native prey and their predators are likely to be particularly strong because long histories of coexistence enables the development of anti-predator adaptations that naïve prey may lack (Salo et al. 2007, Li et al. 2014, Carthey and Banks 2016). Mice have been present on the Channel Islands in southern California a considerable time (perhaps 500,000 ybp; Ashley and Wills 1987), and on Santa Barbara Island, Barn Owls are their main predator. Similarly, on nearby San Miguel Island, deer mice also altered their foraging activity in response to endemic island foxes as they increased in abundance following their successful reintroduction to the island (Orrock and Fletcher 2014). Second, even the presence of a single owl can trigger anti-predator behavior in rodents, and they continue to adjust their foraging activity in response to the presence of additional owls (St. Juliana et al. 2011). At peak densities, we often would observe 10 or more individual owls in a small area and the overall estimated population of Barn Owls is among the highest reported in the literature.

Furthermore, the strong effect of predation risk was far more important than changes in deer mouse abundance in explaining variation in mouse foraging. Similar patterns have been observed elsewhere, where mouse foraging behavior, and not mouse density, predicts nest predation in birds (Schmidt et al. 2001, Schmidt and Ostfeld 2003). Here, despite the expectation that higher densities of mice should increase murrelet nest predation rates (Clotfelter et al. 2007, Millus et al. 2007), we found no evidence that our index of mouse abundance was associated with higher rates of egg depredation. In fact, the reverse was true. In the murrelet plots, the relationship between mouse and owl abundance was positive, resulting in egg survival increasing as both mouse and owl abundance increased. Barn Owl population dynamics tend to

be strongly driven by densities of their prey (Hone and Sibly 2002), and they breed rapidly in response to increased prey densities (Drost and Fellers 1991). This suggests that the indirect effect of owls on foraging behavior was the main driver of egg predation rather than a direct effect of predation on mice. Moreover, murrelet nest success over a 30-yr period was unrelated to interannual changes in mouse densities (Schwemm and Martin 2005, Nur et al. 2013). Thus, our results suggest that high owl abundance can suppress egg predation even when mice are abundant. Similarly strong effects have been demonstrated experimentally in other systems where the mere threat of predation can induce behaviorally mediated cascades even in the controlled absence of density-mediated effects (Beckerman et al. 1997).

Both owl abundance and moonlight strongly influenced mouse foraging patterns (Fig. 1A, B), and accordingly, we did find differences in egg survival between the new and full moon phases. Similarly, songbird nest predation decreased during the full moon when mice modified their nocturnal behavior to avoid predation by owls (Schmidt 2006). Interestingly, Schmidt (2006) also observed that the proportion of moonlight across the entire lunar cycle was not a good predictor of nest fate. Therefore, it is possible that there are more complex patterns of state-dependent foraging by mice over the entire lunar cycle that we did not capture by comparing foraging only during the extremes in moonlight (Kotler et al. 2010). In addition, relatively few murrelets tended to lay eggs closer to the full moon (Fig. 3) and nearly two-thirds (99 of 151) of the nests were initiated when the moon was illuminated at 50% or less. This pattern of moonlight avoidance may be a tactic to escape predators of adult seabirds on breeding colonies (Mougeot and Bretagnolle 2003, Shoji et al. 2011).

We have focused our attention here on positive indirect effects of owls on murrelet breeding success, but owls are also important predators of adult murrelets in some years (S. K. Thomsen et al., *unpublished manuscript*). The magnitude of murrelet predation by owls appears to be strongly related to differences in mouse density (S. K. Thomsen et al., *unpublished manuscript*), which suggests that murrelets are among those species of conservation concern that are impacted by apparent competition (DeCesare et al. 2010). This has prompted serious consideration of management interventions to reduce the owl population on the island (Nur et al. 2013). A recent effort to model murrelet population trends revealed that a reduction in adult mortality from owl predation could reverse a population decline, but only if egg predation is held constant or varies randomly (Nur et al. 2013). Our results suggest that egg predation is not fixed, and does increase considerably with reduced owl abundance. Even small reductions in the average number of eggs eaten by mice each year could have a substantial influence on murrelet population dynamics (Sydeman et al. 1998, Nur et al. 2013). Additional modeling approaches that address both the positive and negative effects of owls and mice on

murrelets are therefore needed and should incorporate these tradeoffs explicitly (Sabo 2008). For example, if antagonistic interactions between mesopredators and top predators are not appropriately considered, it is possible that management recommendations could actually exacerbate declines of threatened prey (Nishijima et al. 2014, Prugh and Arthur 2015).

Changes to predator-prey relationships, including those resulting from widespread apex predator loss (Ripple et al. 2014), can play an important role in contributing to population declines. Indirect interactions are a crucial component of understanding predator-prey dynamics that threaten species, especially on islands, as is demonstrated when management interventions focused on mitigating density mediated effects occasionally lead to unintended consequences (Zavaleta et al. 2001, Bergstrom et al. 2009). Our study therefore underscores the need to consider the potential impacts of behaviorally mediated indirect interactions for effective conservation decision-making.

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