Direct and indirect interactions between owls, mice and nocturnal seabirds: integrating marine and terrestrial food webs

by

Sarah K. Thomsen

B.A., Hampshire College, 2006

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Summer 2017

Approval

Name:	**Sarah K. Thomsen**
Degree:	**Doctor of Philosophy (Biological Sciences)**
Title:	***Direct and indirect interactions between owls, mice and nocturnal seabirds: integrating marine and terrestrial food webs***
Examining Committee:	**Chair:** Eirikur Palsson Assistant Professor

David Green
Senior Supervisor
Professor

Ron Ydenberg
Supervisor
Professor

Patricia Baird
Supervisor
Research Associate

Elizabeth Elle
Internal Examiner
Professor

Laura Prugh
External Examiner
Assistant Professor
School of Environmental and Forest Sciences
University of Washington

Date Defended/Approved: July 31, 2017

Ethics Statement

Abstract

Climate variability in semi-arid ecosystems can influence species interactions from the bottom-up, and through these perturbations we can gain insight into both direct and indirect interactions in food webs. In this thesis, I studied the effects of ENSO-driven rainfall pulses and drought on the interactions between a top predator, the Barn Owl (*Tyto alba*), a mesopredator, an island endemic deer mouse (*Peromyscus maniculatus elusus*), and a threatened nocturnal seabird, the Scripps's Murrelet (*Synthliboramphus scrippsi*). On Santa Barbara Island in the Channel Islands National Park in California, adult breeding murrelets are killed by owls, but their eggs are eaten by mice, which is the main cause of reduced murrelet nest success. First, I assessed how owl predation on murrelets varies with the availability of mice, the primary prey of owls. I found that heavy rainfall years drive the irruptions in the mouse population that precede peaks in owl abundance, which results in high murrelet predation by owls when the mouse population subsequently crashes. Next, I examined evidence for positive indirect effects of owls on murrelets through their influence on mouse foraging behavior. I found that mouse foraging was strongly suppressed as the abundance of owls increased, and survival of murrelet eggs was also positively related to owl abundance. I also examined how both the terrestrial and marine environments influenced overall murrelet nest success over a span of 21 years. I found that the severity of drought was the most important variable determining nest success, which suggests that during severe droughts, mice consume substantially more eggs when there are fewer terrestrial resources and also less risk from predation. Climate-driven indirect interactions with predators therefore influences both survival and nest success of murrelets on this island. Finally, I developed a mathematical model of island community dynamics to assess whether owl management might benefit murrelets given projected changes to rainfall patterns in this region. I found no evidence that managing the owl population would enhance murrelet abundance, demonstrating the importance of considering both direct and indirect effects of predators when evaluating potential conservation strategies.

Keywords: ecological cascades; climate variability; predator-prey interactions; Scripps's Murrelets; semi-arid islands; indirect interactions

Acknowledgements

First, I thank my supervisor Dr. David Green and my committee members, Dr. Patricia Baird and Dr. Ron Ydenberg. In the beginning, our committee meetings were often massive affairs lasting well over 3 hours long. But I am so grateful that they contributed their expertise and clearly were hooked by my interest and enthusiasm for the murrelets, mice, and owls of Santa Barbara Island. I am so glad that David suggested I roll up from the M.Sc. program, and really cannot thank him enough for everything.

I am very grateful for those that provided the funding for this research. It was provided in part by the Montrose Trustee Council, the National Fish and Wildlife Foundation and also with in-kind support from the National Park Service. I thank all of the excellent staff of the Channel Islands National Park and the California Institute of Environmental Studies for their support and assistance over the years. I am particularly deeply grateful for the support of Jennifer Boyce, Annie Little, Scott Hall, and Frank Gress.

I will always immensely appreciate the expert, dedicated field assistance (and friendship) contributed by Caitlin Kroeger and Spencer Plumb. Tons of other folks also helped with data collection on the island, and I am forever grateful for our time spent together on (and off!) the island, in particular: Christy Hand, Sasha Auer and Kevin Barnes, Kris and Renee Robison, Simon Avery, Helen Fitting, Marie-Eve Jacques, Caty Carter and Andrew Yamagiwa. I also thank Dr. Nina Karnovsky, Charles Drost, Sean Carr, Nick Giese, Jim Howard, Eden Wynd, Paige Martin, and many others.

Several people had pivotal roles in the development of the project over the years. First, I thank Dr. Pete Bloom, who generously contributed his expertise with Barn Owls and lent me equipment for capturing owls in the early days. I also am enormously grateful for the assistance and support of Darrell Whitworth, Harry Carter (*in memoriam*), and David Mazurkiewicz. I also warmly thank Laurie Harvey for all of her support. I also am extremely grateful that Dr. Paul Collins at the Santa Barbara Museum of Natural History helped me identify landbird species in the owl pellets and provided temporary lab space for sorting out prey remains. I also would like to thank Dr. R. Fetecau, Dr. Nadav Nur and Dr. Sean Cox for helpful discussions about modeling approaches. I thank Tim Coonan and Thomas Stanley for sharing NPS data on deer mice.

I also appreciate the dedicated work of the small army of undergraduates who helped with the owl pellet dissection for at least one semester or longer: Jillian Neri (4+ semesters), Kate Gibson (3 semesters), Preeti Nagra (3 semesters), Jennie Harvey, Alfonso Ocampo, Lyndsey Drozdowski, Amanda Smith, Samantha Chan, Severin Vaillancourt, Agathe Lebeau, Vincent Fung, Sarah Warda, Elaine Wu, Cindy Wu, Eve Ho, Kendra Munn, James Chang, Taylor Ockerman, and Amber Burnett. I am truly grateful for my time with each of them during the tedious and important task of sorting and identifying tens of thousands of tiny bones.

I'd also like to thank everyone in the CWE and all other grad students at SFU (from DGSC, statsbeerz, etc.) that I've met over the years. I deeply appreciate all the conversations I've shared over coffee/beers with so many people during this time. I especially appreciate all my fellow Green Lab inhabitants—those of us that understand how exciting it was to see random sunshine streaming into our basement windows!! I thank Marinde Out for generously contributing her amazing artistic talents for Figure 2-3. I also could not have done this without my 'Hampshire College family' and Emma Moline.

Finally, I'd like to thank my family. My parents have supported me relentlessly over the years as I've pursued my passions and would continually bounce between different remote islands and field sites. My brother and sister-in-law have also provided a temporary home for me in Portland many, many times over the years and provided a much-needed oasis of family time, good beer, and kitty cats. It has been the most fun seeing my nephews, Henry and Noah, grow up.

I do believe that the muscle-memory of hiking the island trails at night will never leave me. Neither will I forget all the times I stood atop the edges of sturdy cliffs, with the moon and stars above, and with murrelets hidden in the dark and only their cheerful trills heard from the ocean below.

> "*i suri wa, yuqire!*"
>
> translation from Chumash: (*it will continue indefinitely), (hooray!*)

Table of Contents

List of Tables

List of Figures

Chapter 1.

General Introduction

Changes to predator-prey dynamics have been increasingly recognized for their potential role in contributing to species declines (e.g. DeCesare et al. 2009; Zarnetske et al. 2012). Top predators, in particular, can have an important role in structuring food webs, but also tend to be relatively more susceptible than other community members to a range of threats (Estes et al. 2011; Ripple et al. 2014). The loss of top predators can fundamentally alter food webs (Terborgh et al. 1997, 2001), because predators not only affect prey through killing and consumption, but can also influence the behavior or other traits of their prey as well (Schmitz et al. 2004; Werner and Peacor 2003; Preisser et al. 2005). Either of these density or trait-mediated interactions potentially also have cascading indirect impacts through food webs (Lima and Dill 1990; Peacor and Werner 1997), which can lead to positive indirect effects for species that gain protection from the top predator through trophic cascades or knock-on effects (Ripple et al. 2016). However, often these indirect effects that are mediated by top predators tend to be far less visible than direct effects (Estes et al. 2011).

One potentially important mechanism for elucidating top-down direct and indirect pathways is to examine changes to trophic interactions that result from a bottom-up ephemeral superabundant resource (Yang et al. 2008). A resource pulse can trigger a sequence of effects from the bottom-up, followed by top-down effects by predators and consumers (Ostfeld and Keesing 2000). The pulse itself can be as varied as seed or fruit masts, insect outbreaks, or drought-breaking rainfall in arid ecosystems (reviewed in Yang et al. 2010). Once the pulse subsides, predators may switch to alternative prey and possibly influence key demographic parameters. For example, across much of eastern North America, oak (*Quercus* spp.) acorn masts have been linked with subsequent increases in the abundance of white-footed mice and eastern chipmunks, which then increases songbird predator populations, which may reduce bird productivity once mouse populations decline (Clodfelter et al. 2007, Schmidt and Ostfeld 2008).

These and other seemingly diverse food webs are linked by current ecological theory by having the same or similar ecological modules embedded within them (Bascompte and Melián 2005), and resource pulses may help increase our understanding of these fundamental ecological interactions. For example, in one-predator two-prey modules, an increase in the density of the preferred prey species can enhance predator density, which can then suppress the population of the alternative prey (i.e. apparent competition; Holt 1977). For systems influenced by resource pulses, once the primary prey densities decline, prey switching by generalist predators can lead to an increase in predation on alternative prey (Holt and Kotler 1987; Yang et al. 2008). If the decline of the primary prey is severe enough, predation on the alternative prey could even lead to its extinction (i.e. hyperpredation; Courchamp et al. 2000, Roemer et al. 2002, Kristan and Boarman 2003). However, in a related module type, the primary prey can actually have an additional trophic role as a mesopredator with direct negative effects on the alternative prey (a case of intraguild predation; Holt and Polis 1997). In such systems, the top predator may have positive indirect effects on alternative prey through its effect on the mesopredator (Ritchie and Johnson 2009). The accidental or intentional elimination of top predators from some food webs has led to increases in the abundance of mesopredators, and increased impacts to other species as a result (i.e. mesopredator release; Crooks and Soule 1999; Prugh et al. 2009). Thus, research describing the consequences of sharing a top predator or mesopredator and the mechanisms driving those direct and indirect pathways may lend insight into a wide variety of ecosystems.

The consequences of resource pulse induced changes to food web dynamics on the population trends of alternative prey are often difficult to predict because of the large spatial scale and complexity of potential interactions involved. In contrast, island food webs can be more tractable systems for studies of predator-prey dynamics (Terborgh and Estes 2010). Oceanic islands have inspired critical insights and ideas in ecology and evolution (Darwin 1859; MacArthur and Wilson 1963), and these insights may also have direct conservation implications since islands contain disproportionately more rare and endemic species compared to continents (Whittaker and Fernández-Palacios 2007).

Furthermore, islands can receive resource pulses from both terrestrial and marine derived sources (Polis and Hurd 1996, Stapp and Polis 2003). For example, rainfall pulses can boost terrestrial resources (Stapp et al. 1999; Russell and Ruffino 2012), while marine sources of a pulsed resource can be as varied as seaweed deposition (Piovia-Scott et al. 2011), animal carcasses (Rose and Polis 1998), or from populations of breeding seabirds (Anderson and Polis 1999). These linkages between marine and terrestrial food webs may provide rare insight into shifting trophic controls (e.g. top-down versus bottom-up) in food webs, as well as evidence for positive indirect effects between species (Giroux et al. 2012).

The Channel Islands are a group of eight islands off the coast of southern California, each with its own unique species and history (Figure 1), but like other islands may be influenced by either terrestrial or marine resource pulses. For instance, the climate in this region is semi-arid, and the years with unusually higher than normal rainfall are often linked with El Niño / Southern Oscillation (ENSO) events (Schoner and Nicholson 1989; Black et al. 2014), which therefore can periodically lead to a resource pulse. For example, in arid and semi-arid ecosystems with Mediterranean climates, years with heavy rainfall can result in remarkable increases in terrestrial productivity, including increases in the abundance of small mammal populations and their predators (Jaksic et al. 1997; Lima et al. 2002; Deguines et al. 2017). This region is also considered to be a climate change 'hotspot' (Diffenbaugh et al. 2008), and California has recently experienced record-breaking drought (Griffin and Anchukaitis 2014) followed by extreme rain, which may be part of a trend of increasing variance in rainfall over the last few decades (He and Gautam 2016). Therefore, understanding how climate influences island community dynamics has important implications for how species may be impacted by climate change and variability via species interactions. In particular, the bottom-up changes of rainfall on increased productivity have been well documented, but very little attention has been paid to potential subsequent top-down effects and whether this could extend across ecosystem boundaries to impact marine species.

On Santa Barbara Island, one of the smallest Channel Islands (Figure 1 and 2), the only mammal is a native endemic subspecies of deer mouse (*Peromyscus maniculatus elusus*), which is the primary prey for Barn Owls (*Tyto alba*). Both mice and owls can reach very high densities, among the highest documented, following the years with increased rainfall (Drost and Fellers 1991). Superimposed on this irregularly occurring event, is the annual arrival of crevice-nesting nocturnal seabirds, such as the Scripps's Murrelet (*Synthliboramphus scrippsi*; hereafter "murrelets"). Scripps's Murrelets are small (~165g) pursuit diving alcids that have a worldwide breeding distribution of just 10 island groups off the coast of Southern California and Mexico (Drost and Lewis 1995; Birt et al. 2012). The arrival of murrelets can therefore represent a seasonally abundant and allochthonous alternative prey source for island predators. Accordingly, murrelet eggs are consumed by deer mice and adults are preyed upon by Barn Owls (Drost and Lewis 1995; Drost and Fellers 1991). Since owls are predators of mice that consume murrelet eggs, this represents an exceptional system for studying the effects of resource pulses on predator-prey interactions. Additionally, some evidence suggests that murrelets have declined in abundance over the last few decades (Burkett et al. 2003, Whitworth et al. 2005), and it has been suggested that the primary reason for the observed decline on this island is the impact of their predators. Here, I assessed the role of these native predators on the population dynamics of murrelets. I had four main objectives:

Research objectives

1) To evaluate the role of climate-driven terrestrial resource pulses and subsequent cascading indirect interactions that determines Barn Owl predation on murrelets

First, I investigated the population dynamics and diet of Barn Owls on this island in response to varying densities of their primary prey, the deer mouse, and the seasonal influx of nesting seabirds.

2) To determine whether there are positive indirect effects of owls on murrelets

Next, I examined how owls have positive indirect effects on murrelet nest success through their impact on deer mice foraging behavior. I hypothesized 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.

3) To evaluate the relative roles of marine productivity and climate-driven terrestrial resource pulses and subsequent cascading indirect interactions in determining overall murrelet nest success

I also evaluated the relative roles of both terrestrial food web dynamics and marine productivity in ultimately determining murrelet nest success. Seabird breeding parameters are typically strongly influenced by food availability and ocean climate regimes (Piatt et al. 2007). Murrelets are also likely to be influenced by the marine environment, but egg predation by mice can vary each year between 8-70% of all murrelet eggs laid and is the main cause of reduced nest success (Drost and Lewis 1995). Therefore, I examined murrelet nest success over a span of 21 years (1993-2013) along with several indicators of terrestrial and marine productivity to determine how both ecosystems influence this key demographic parameter.

4) To determine whether owl management would benefit murrelets

Finally, I developed a mathematical model of island community dynamics to assess whether owl management might benefit murrelets given projected changes to rainfall patterns in this region.

Figure 1-1 Map of California showing the location of the Channel Islands and Santa Barbara Island in particular (highlighted in red). Scale bar in inset map is in kilometers.

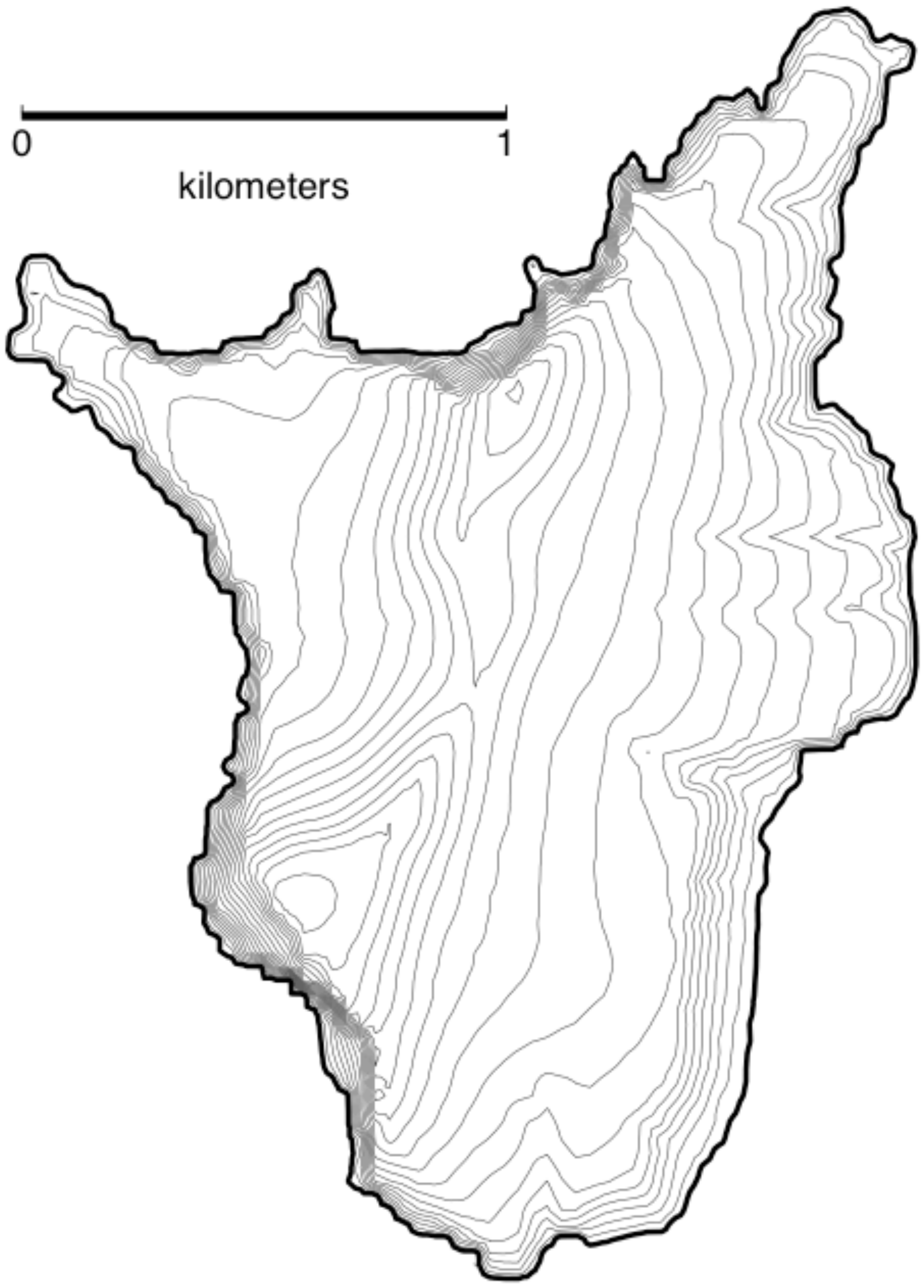


Figure 1-2 Shoreline and elevation of Santa Barbara Island. Lines are 10m contour lines of elevation created from LIDAR.

References

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332.

Bascompte, J., and C. J. Melián. 2005. Simple Trophic Modules for Complex Food Webs. Ecology 86:2868–2873.

Birt, T. P., H. R. Carter, D. L. Whitworth, A. McDonald, S. H. Newman, F. Gress, E. Palacios, J. S. Koepke, and V. L. Friesen. 2012. Rangewide population genetic structure of Xantus's Murrelet (*Synthliboramphus hypoleucus*). The Auk 129:44–55.

Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. García-Reyes, R. R. Rykaczewski, S. J. Bograd, and W. T. Peterson. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. Science 345:1498–1502.

Burkett, E. E., N. A. Rojek, A. E. Henry, M. J. Flu- Harty, L. Comrack, P. R. Kelly, A. C. Mahaney, AND K. M. Fien. 2003. Report to the California Fish and Game Commission: status review of Scripps's Murrelet (*Synthliboramphus hypoleucus*) in California. California Department of Fish and Game, Habitat Conservation Planning Branch Status Report 2003–01.

Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154:493–503.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology 69:154–164.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Darwin, C. (1859). The Origin of the Species by Means of Natural Selection. Murray, London.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Deguines, N., J. S. Brashares, and L. R. Prugh. 2016. Precipitation alters interactions in a grassland ecological community. Journal of Animal Ecology.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences 112:3931–3936.

Drost, C. A., and G. M. Fellers. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. Oikos:351–364.

Drost, C. A., and D. B. Lewis. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). The Birds of North America Online.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic Downgrading of Planet Earth. Science 333:301–306.

Giroux, M.-A., D. Berteaux, N. Lecomte, G. Gauthier, G. Szor, and J. Bêty. 2012. Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. Journal of Animal Ecology 81:533–542.

Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? Geophysical Research Letters 41:9017–9023.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R. D., and B. P. Kotler. 1987. Short-Term Apparent Competition. The American Naturalist 130:412–430.

Holt, R. D., and G. A. Polis. 1997. A Theoretical Framework for Intraguild Predation. The American Naturalist 149:745–764.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez. 1997. A Long-Term Study of Vertebrate Predator Responses to an El Niño (ENSO) Disturbance in Western South America. Oikos 78:341–354.

Kristan, W. B., and W. I. Boarman. 2003. Spatial Pattern of Risk of Common Raven Predation on Desert Tortoises. Ecology 84:2432–2443.

Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecology Letters 5:273–284.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15:232–237.

MacArthur, R.H. and Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. Evolution 17:373–387.

Peacor, S. D., and E. E. Werner. 1997. Trait-Mediated Indirect Interactions in a Simple Aquatic Food Web. Ecology 78:1146–1156.

Piatt, J. F., W. J. Sydeman, and F. Wiese. 2007. Introduction:: a modern role for seabirds as indicators. Marine Ecology Progress Series 352:199–204.

Piovia-Scott, J., D. A. Spiller, and T. W. Schoener. 2011. Effects of Experimental Seaweed Deposition on Lizard and Ant Predation in an Island Food Web. Science 331:461–463.

Polis, G. A., and S. D. Hurd. 1996. Linking Marine and Terrestrial Food Webs: Allochthonous Input from the Ocean Supports High Secondary Productivity on Small Islands and Coastal Land Communities. The American Naturalist 147:396–423.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to Death? The Effects of Intimidation and Consumption in Predator–Prey Interactions. Ecology 86:501–509.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343:1241484.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a Trophic Cascade? Trends in Ecology & Evolution 31:842–849.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. Proceedings of the National Academy of Sciences 99:791–796.

Rose, M. D., and G. A. Polis. 1998. The Distribution and Abundance of Coyotes: The Effects of Allochthonous Food Subsidies from the Sea. Ecology 79:998–1007.

Russell, J. C., and L. Ruffino. 2012. The influence of spatio-temporal resource fluctuations on insular rat population dynamics. Proceedings of the Royal Society of London B: Biological Sciences 279:767–774.

Schmidt, K. A., and R. S. Ostfeld. 2008. Numerical and Behavioral Effects Within a Pulse-Driven System: Consequences for Shared Prey. Ecology 89:635–646.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153–163.

Schonher, T., and S. E. Nicholson. 1989. The Relationship between California Rainfall and ENSO Events. Journal of Climate 2:1258–1269.

Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Stapp, P., G. A. Polis, and F. Sánchez Piñero. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. Nature 401:467–469.

Terborgh, J., and Estes, J. A. (Eds.). (2010). Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press.

Terborgh, J., L. Lopez, and J. Tello S. 1997. Bird Communities in Transition: The Lago Guri Islands. Ecology 78:1494–1501.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological Meltdown in Predator-Free Forest Fragments. Science 294:1923–1926.

Werner, E. E., and S. D. Peacor. 2003. A Review of Trait-Mediated Indirect Interactions in Ecological Communities. Ecology 84:1083–1100.

Whittaker RJ, and Fernández-Palacios JM. 2007. Island Biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford, UK, 2nd Ed.

Whitworth, D.L., H.R. Carter, J.S. Koepke, F. Gress, and S. Fangman. 2005. Population assessments and monitoring for Xantus's Murrelets at breeding colonies in the Southern California Bight in 2004. Unpublished report, California Institute of Environmental Studies, Davis, California (prepared for California Department of Fish and Game, Habitat Conservation Planning Branch, Sacramento, California). 47 pp.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What Can We Learn from Resource Pulses. Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Chapter 2. Evaluating the role of climate-driven terrestrial resource pulses and subsequent cascading indirect interactions determining Barn Owl predation on murrelets

Abstract

Most approaches for assessing species vulnerability to climate change have focused on direct impacts via abiotic changes rather than indirect impacts mediated by changes in species interactions. Changes in rainfall regimes may influence species interactions from the bottom-up by increasing primary productivity in arid environments, but subsequently lead to less predictable top-down effects. Our study demonstrates how the effects of an ENSO-driven rainfall pulse ricochets along a chain of interactions between marine and terrestrial food webs, leading to hyperpredation of a vulnerable marine predator on its island breeding grounds. On Santa Barbara Island, Barn Owls (*Tyto alba*) are the main predator of an endemic deer mouse, as well as a declining population of nocturnal seabirds, the Scripps's Murrelet (*Synthliboramphus scrippsi*). We followed the links between an ENSO-driven rainfall pulse, changes in NDVI, and the subsequent increase and then sharp decline in mouse and owl numbers on the island from 2010 to 2013. Although mouse and owl abundances both peaked relatively close in time after the ENSO event, the mouse population declined in winter 2012 before the owl population did, which coincided with a nearly 15-fold increase in the number of murrelets killed by owls. We then simulated these community dynamics with a mathematical model and demonstrate that bottom-up resource pulses can lead to subsequent declines in the murrelet population. Our study therefore highlights the need for understanding how species interactions will change with shifting rainfall patterns through the effects of ENSO under global change, and we suggest that such lagged top-down effects of ENSO associated rainfall are possibly more widespread in diverse systems.

Introduction

Climate variability can influence species interactions, and through these perturbations we can gain insight into shifting trophic controls in food webs and a greater understanding as to how climate change may interact with other conservation threats (Stenseth et al. 2002; Bellard et al. 2012; Blois et al. 2013; Gudmundson et al. 2015; Vazquez et al. 2015). The El Niño / Southern Oscillation (ENSO) is the most prominent of the global climate fluctuations, occurring at 2-7 year intervals and impacting productivity in both marine and terrestrial environments via physical forcing that affects the base of both food webs (McPhaden et al. 2006). For example, ENSO causes weakening trade winds and increased sea surface temperature that drives primary production in the ocean (McPhaden et al. 2006), while also inducing drought or extreme rainfall in different parts of the globe that influences primary productivity of plants (Holmgren et al. 2001). These bottom-up changes have effects that end up propagating throughout food webs, often through complex interactions (Holmgren et al. 2001; Auer and Martin 2013), that can possibly circle back in ways that connect both marine and terrestrial food webs (Stapp et al. 1999).

Islands are part of the global coastal ecotone where terrestrial and marine food webs connect (Polis et al. 2004) and this connection means island communities may respond to ENSO events driven by changes to either food web. For example, islands with seabirds can experience high nutrient input from the marine environment via guano deposition (Anderson and Polis 1999). These subsidies can then be disrupted during ENSO events when seabirds fail to return to the colony when foraging conditions are poor (Cubaynes et al. 2011), which subsequently impacts island vegetation (Stapp et al. 1999; Molina-Montenegro et al. 2013). Islands can also be affected by ENSO-associated rainfall, and these impacts are particularly spectacular on islands that are arid or semi-arid, because rainfall limits primary productivity in these areas (Noy-Meir 1973). After years with heavy rainfall, the vegetation flourishes, and arthropod and small mammal populations can all increase dramatically (Jaksic et al. 1997; Lima et al. 2002; Stapp and Polis 2003; Russell and Ruffino 2012). In both cases, the effects of ENSO are well described in terms of bottom-up changes and nutrient flows, but very little attention has been paid to potential subsequent top-down effects.

These top-down effects may be particularly strong on islands, as they often have relatively simple systems across which cascades can easily transmit (Schoener and Spiller 2010). For example, rodents are a key mesopredator species on many islands, and increases in their abundance can trigger increases in top predator populations, which can lead to indirect interactions that could impact alternative prey species (Holt 1977; Yang et al. 2010; Ringler et al. 2015). Once the resource pulse subsides and primary prey densities decline, prey switching by generalist predators can lead to a further increase in predation on alternative prey (Holt and Kotler 1987; Yang et al. 2008). If the decline is severe enough, models predict that such enhanced predation on alternative endangered prey could lead to extinction through hyperpredation (Courchamp et al. 2000).

Here, we describe a chain of interactions triggered by an ENSO-associated rainfall pulse and the resulting top-down cascade on an oceanic island in Southern California. In this semi-arid region, winters with increased rainfall are strongly correlated with ENSO events (Schoner and Nicholson 1989), which is a pattern that has persisted for hundreds of years (Black et al. 2014; Hart et al. 2015). On Santa Barbara Island, there is an endemic subspecies of deer mouse (*Peromyscus maniculatus elusus*) and a native population of Barn Owls (*Tyto alba*) that are known to reach extremely high densities that are associated with rainfall patterns (Drost and Fellers 1991). Barn Owls are generalist predators (Marti et al. 2005; Meek et al. 2012), and there is increasing concern about the impact they have on a declining population of nocturnal seabirds, the Scripps's Murrelet (*Synthliboramphus scrippsi;* Burkett et al. 2003). Therefore, we hypothesized that owl predation on murrelets would depend on the density of mice, which would in turn be influenced by variations in rainfall and food availability. To test this, first, we confirmed the links between an ENSO-driven rainfall pulse, terrestrial productivity, and the subsequent increase and then sharp decline in mouse and owl numbers on the island. Next, we evaluated evidence for prey switching in Barn Owls and demonstrate that an ENSO-driven resource pulse mediated the top-down cascade on this threatened seabird. Finally, we simulated these dynamics with a mathematical model and demonstrate that bottom-up resource pulses can lead to subsequent declines in the murrelet population.

Material and Methods

Study location and system

Santa Barbara Island (33º 29’ N, 119º 02 W) is the smallest of the California Channel Islands and is managed by the Channel Islands National Park. This 2.6 km^2 island is located about 63 km off-shore and is 39 km and 45 km from its closest neighbors, Santa Catalina Island and San Nicolas Island, respectively. The island receives an estimated average 21.76 cm of rainfall annually (Orrock et al. 2011). Steep cliffs rise abruptly up from the sea on nearly all sides of the island, above which is a gently sloping terrace covered mostly by non-native grassland (e.g. *Avena* spp, *Bromus* spp, etc) and patches of low growing native shrubs and cacti *(Leptosyne gigantea, Eriogonum giganteum* var. *compactum*, and *Opuntia* spp.; Junak et al. 1993). The two tallest peaks are 193 m and 171 m high and five small canyons are cut into the south and east sides of the island.

Scripps’s Murrelets are small (~165g) pursuit diving alcids that have a worldwide breeding distribution of approximately 10 island groups off the coast of Southern California and Mexico (Drost and Lewis 1995; Burkett et al. 2003; Birt et al. 2012). Murrelets are IUCN listed as Vulnerable and believed to be declining (BirdLife International 2016). The breeding season of this seabird typically extends from March-July on Santa Barbara Island (Drost and Lewis 1995). Murrelets and Barn Owls nest primarily along the coastal areas of the island within crevices in the rocky cliffs, in sea caves, and to a smaller extent underneath shrubs, while mice are found throughout all the island’s habitats. The island also has a population of Island Night Lizards (*Xantusia riversiana*), as well as several species of breeding and migrant landbirds. Barn Owls on Santa Barbara Island are demographically isolated from the mainland (Huang et al. 2016). Evidence of owl breeding activity could be found during all months of the year, at least in some years, and up to eight eggs were found in nests (Thomsen, unpub. data).

Temporal trends

NDVI and Rainfall

Rainfall in this region occurs primarily during the winter months (November-March; Yoho et al. 1999), so we summed the daily precipitation amounts (mm) from a weather station on nearby Santa Catalina Island (Avalon Airport, 33°24'18.0"N 118°24'57.6"W) into rainfall year totals beginning on April 1 each year from 2005 - 2013. Next, to quantify differences in spring primary productivity from 2006-2013, we calculated the Normalized Difference Vegetation Index (NDVI) for the island with 30m resolution Landsat satellite images (NASA LP DAAC, 2014). Values of NDVI are correlated with primary productivity (Pettorelli et al. 2005), and arthropod abundance (Sweet et al. 2015) and it can be used to predict mouse densities (*Peromyscus* spp.) at approximately one-year time lags (Cao et al. 2011). We selected cloud-free images captured during March (mean julian date= 73; range: 59-90), which coincided with mark-recapture studies of deer mice. We used ArcGIS 10.1 (ESRI 2011) to calculate the NDVI values from the satellite images and then determined an average island-wide value for each year.

Deer mouse monitoring

We used the deer mouse densities calculated by Stanley (2012) based on mark-recapture data collected annually by the National Park Service on two plots during the month of March as well as once during September-December from 2007-2013. We focus on this more recent time period because of greater completeness and consistency in the timing of capture sessions in March. The mouse monitoring protocol is described in detail in Fellers et al. (1988). Briefly, each plot has 100 permanent trap stations that are arranged in a 10 X 10 pattern spaced 7m apart, at which one small Sherman live-trap is placed during trapping sessions that are conducted over three consecutive nights. Abundance was estimated using Huggins (1991) closed population capture-recapture models that were implemented in program MARK by Stanley (2012). Density was derived by dividing abundance by the estimated area trapped described by Parmenter et al. (2003). Mouse captures in 2013 were far too low to reliably estimate density, so we excluded that year from statistical calculations but display the minimum number known alive (MNKA) in Figure 1.

We also established additional sites where we used track tubes to obtain a relative index of mouse density from 2011-2013 within murrelet nesting areas (Thomsen and Green 2016). Each of five sites in murrelet habitat consisted of nine track tubes that were placed in a 3x3 grid formation with 7m spacing. Track tubes were deployed before nightfall during the new moon phase twice during the murrelet breeding season (April and May), and the following day, we recorded the proportion of track tubes that had the presence of mouse tracks in each grid. The proportions for each grid were then averaged for the two months to create a metric for mouse density during each murrelet breeding season.

Barn Owl abundance

We monitored the relative abundance of Barn Owls on the island from 2010 – 2013 by repeating the trail transect survey methods developed by Drost (1989) twice each year in mid-winter (January/February) and late summer (July/August). Surveys began approximately one hour after sunset, when two observers walked the island trails with high intensity flashlights (72 lumens) and recorded the times and locations of all observations of Barn Owls. The total of all detections from all observers were added together to obtain a total count. All surveys had similar conditions of winds <15 knots, and no precipitation or fog.

Barn owls on the island have small and extensively overlapping home ranges and tended to concentrate their activity by their roost sites (Thomsen et al. 2014). Therefore, to quantify differences in owl abundance across the island, we also monitored the number and locations of owl nests and roost sites from 2010-2013. Surveys were conducted in mid-winter (Dec-Feb) and summer (June-Sept) within the canyons as well as shoreline cliff habitat accessible by non-technical climbing from the top of the island. Sites were determined to be active if there was the presence of an owl, signs of breeding activity, or if pellets were observed. There was also one annual visit in April/May to one roosting site located within a sea cave, Barn Owl Cave, during all four years. No mid-winter visits were conducted to collect pellets in 2011 in order to avoid potentially fatal disturbance to nesting Brown Pelicans (*Pelecanus occidentalis*), so these sites were monitored for the presence of owls from a distance and were later confirmed by collecting pellets from these sites during the summer.

Barn Owl Diet

We assessed the diet of Barn Owls from 2010-2013 using two complementary methods. First, we looked at annual changes in owl dietary breadth by identifying faunal remains in regurgitated pellets collected from owl nest and roost sites during surveys for these sites. Secondly, we also collected avian prey remains from areas surrounding owl nest and roost sites as well as from murrelet nesting habitat and counted the number of individual seabirds in those remains. These areas included the murrelet nest monitoring plots and along the island's hiking trails, both of which were checked 1-2 times per week from March to July each year (see Harvey et al. 2013; Harvey et al. 2014; Howard et al. 2014 for locations and dates). Although not all areas of the island were searched with the same intensity within a year, our methods were consistent across years, which allows us to make comparisons between years. We used a handheld GPS (Global Positioning System) unit to record the location of the remains, so that we could link patterns in the number of carcasses collected in different areas to local mouse and owl abundance.

After collection, pellets were disaggregated in the lab and all bones were identified to species. The number of individual pellets collected varied each year due to changes in owl abundance on the island, but we were able to analyze a minimum of 100 owl pellets per year for diet composition. When the remains of more than one individual from a species were present in each pellet, the number of skulls and/or lower mandibles was used to determine the number of prey items (Minimum Number of Individuals; MNI) of each species per pellet. Seabird prey remains were identified to species and collected when found. All other land bird remains were identified and deposited at the Santa Barbara Museum of Natural History, Santa Barbara, CA.

Data analyses

All statistical analyses were performed in R 3.2.1 (R Core Team, 2014). First, we evaluated whether there were temporal relationships between regional annual rainfall, NDVI and mouse density. To do so, we used linear regressions of annual rainfall and island-wide NDVI in March, and then NDVI in March of year t-1 and mouse density (log density in March of year t in two long-term monitoring plots; mouse data from Stanley, 2012 and NPS unpubl. data). We then compared the counts of prey types (mice, island night lizards, and all seabird species combined) within owl pellets among years with a contingency table chi-square test of differences. Rare prey items like arthropods and land bird species were not included in order to meet the assumptions of this test. We also did correlation analyses between the total number of carcasses found each year and the proportions of seabirds found in owl pellets for each year to confirm these metrics of owl diet were related.

Next, we used piecewise structural equation modeling (with the R package 'piecewiseSEM') to conduct a confirmatory path analysis of the effects of the ENSO-associated rainfall pulse on owl predation of murrelets in spatially replicated plots. Piecewise SEM has advantages over traditional path analysis because it uses localized estimators and also allows the use of hierarchical models (Lefcheck 2015). To be sure we had spatially linked data for this analysis, we created 250m spatial buffers with ArcGIS around each mouse track tube grid located in murrelet nesting habitat. We used the estimated maximum number of active owl roosts observed within the 250m buffer distance during the mid-winter period preceding each murrelet breeding season 2010-2013 as a proxy for localized owl abundance. We then summed the number of murrelets remains found within that distance for each year by using the GPS locations of the remains of murrelets killed by owls. We fit linear mixed effects models for each hypothesized pathway. We included site (n=5) as a random effect as well as a temporal correlation term with the function CAR1 from the package 'nlme' in all models (Pinheiro et al. 2013). Our *a priori* path model included: 1) NDVI from the year *t* -1 influences the number of owl roost sites in the mid-winter period as well as log mouse density in April-May of year *t*, 2) the number of owl roost sites in the mid-winter period influences log mouse density in April-May of year *t*, and 3) both mice and owls influence the log number of murrelets killed during their breeding season of year *t*. Piecewise SEM cannot include recursive effects, that is, the effect pathways must only go in one direction and not both directions at once (Lefcheck 2015). We therefore also considered an alternative model where the effect between owls and mice was flipped (i.e. bottom-up from mice to owls), but the model with the top-down effect of owls had an improved AICc (>∆2), which indicated it was a better fit. Hence, the model includes the lagged direct and indirect effects of NDVI on mice and owl abundance the following year, capturing the bottom-up processes that in turn drives the top-down effects of owls on mice and murrelets. The *d*-

separation test was conducted to determine if the *a priori* overall model was a good fit, which is indicated by a non-significant p-value (Shipley 2009), and path beta coefficients were used to compare effect sizes and directions.

Mathematical Model

Relatively few studies that examine the ecological effects of extreme climatic events have been able to include more than one event (Bailey and van de Pol 2016), therefore the simulation of these climate-driven predator-prey interactions is necessary to understand the potential impacts of ENSO-associated rainfall under global change. To test whether climate could influence murrelet population trends via hyperpredation, we developed a mathematical model consisting of a set of ordinary differential equations (ODE) modified for our system from the classic hyperpredation model (Courchamp et al. 1999). Details of this model have been covered elsewhere (Courchamp et al. 2000) and parameters were based on empirical or derived sources for our system (Appendix A; Table 1). Differential equations were solved numerically with the R package 'deSolve' (Soetaert et al. 2010). Briefly, all three species are characterized by intrinsic growth rates, carrying capacities, and mortality rates. The carrying capacities of mice and owls are linked by their respective predation rates on their terrestrial prey, which is itself influenced by climate variability. Murrelets are consumed by owls at a rate that is proportional relative to the availability of mice, and we demonstrate how murrelet population change (Nt+1/Nt) is driven by the strength of climate forcing of the previous year. To do so, we extracted a time series of the past 120 years of annual rainfall from a 4-km gridded surface (PRISM; Daly et al. 2008) and examined how variation in climate-driven resources influenced community dynamics in the model (see Appendix A for details).

Results

Annual rainfall totals and NDVI in March between 2007 and 2013 varied considerably among years and were tightly linked (r^2=0.56, p=0.03). Rainfall amounts ranged from as low as 17.8 cm to over twice that at 48.1 cm. NDVI in March between 2007 and 2012 predicted mouse densities in both monitoring plots one year later (Figure

1; β = 12.9±1.5, r^2=0.85 p<0.001) after controlling for differences between plots (β = 0.27±0.37, p=0.48). Just 20 individual mice were captured in March 2010, but their density increased substantially by March 2011, peaking in October 2011 at 467.55/ha before steadily declining to 21% of the peak by March 2012 and <0.1% by March 2013 (Figure 2a; mean density of the two plots relative to peak mean density). The numbers of owl detections on the trail surveys followed a similar pattern and were low in early 2010 at just 3 individuals seen, and peaked in August 2011 at 32 owls, before a steep decline by January 2013 (Figure 2a). Although mouse and owl abundances both peaked relatively close in time, the mouse population declined in 2012 before the owl population did, which coincided with major changes in owl diet.

A total of 3,281 vertebrate prey items were identified to species in the owl pellets. Deer mice dominated the diet of Barn Owls with 71% of the total prey items (n=2,331). However, there were significant differences in the proportions of different prey types in owl pellets collected each year (Table 1; χ^2 = 1075.5, p<0.001). When mice were super abundant in 2011, deer mice were the main dietary item, comprising 98% of all prey items. In other years, this percentage varied from a low of 40.7% in 2013 to 78.5% and 88.2% in 2010 and 2012, respectively. Of the seabirds, murrelets were the most common prey (86 of 95 seabird remains in pellets). Murrelets were identified in 3.3% of prey items in 2010, but comprised only 0.1% of owl prey items in 2011. The following year, after the mouse population had crashed, owl diet changed substantially. Murrelets were far more common prey items in 2012, peaking at 6% of prey items before dropping in 2013 to 1.5%. The number of murrelets found killed by owls followed a similar pattern as the pellets (r=0.89), with island-wide annual totals of 53, 11, 172, and 80 individuals represented in the prey remains, respectively, over the 4 years (Figure 2b).

The results from the piecewise SEM (Figure 3; Fisher's C= 2.44 p= 0.296) indicated that the pathway from NDVI to owls was positive (β = 0.33; p=0.008), and with greater owl abundance, the log number of murrelets killed also increased (β = 0.50; p=0.02). The magnitude of this indirect effect is obtained by multiplying the two coefficients along the path model, 0.165, indicating a moderately strong effect. However, log mouse density was negatively correlated with the log number of murrelets killed (β = -0.45; p=0.04). Hence, the ENSO-associated increase in rainfall indirectly increased owl predation of murrelets, but this was also mediated, in large part, by mouse density.

Finally, the bottom-up influence of NDVI on mice was positive but not significant (β = 0.38; p=0.08), but there was a strong top down negative effect of owls on log mouse density (β = -0.67; p=0.02).

Finally, the mathematical model demonstrated that the climate perturbations led to marked variability in the population trends for all three species over time (Figure A1 in Appendix A). Specifically, our model predicts outbreaks in both the mouse and owl populations as well as subsequent sharp declines in the murrelet population as a result of increased predation by owls after the mouse population declines (Figure 4; Figure A2 in Appendix A).

Figures and Table

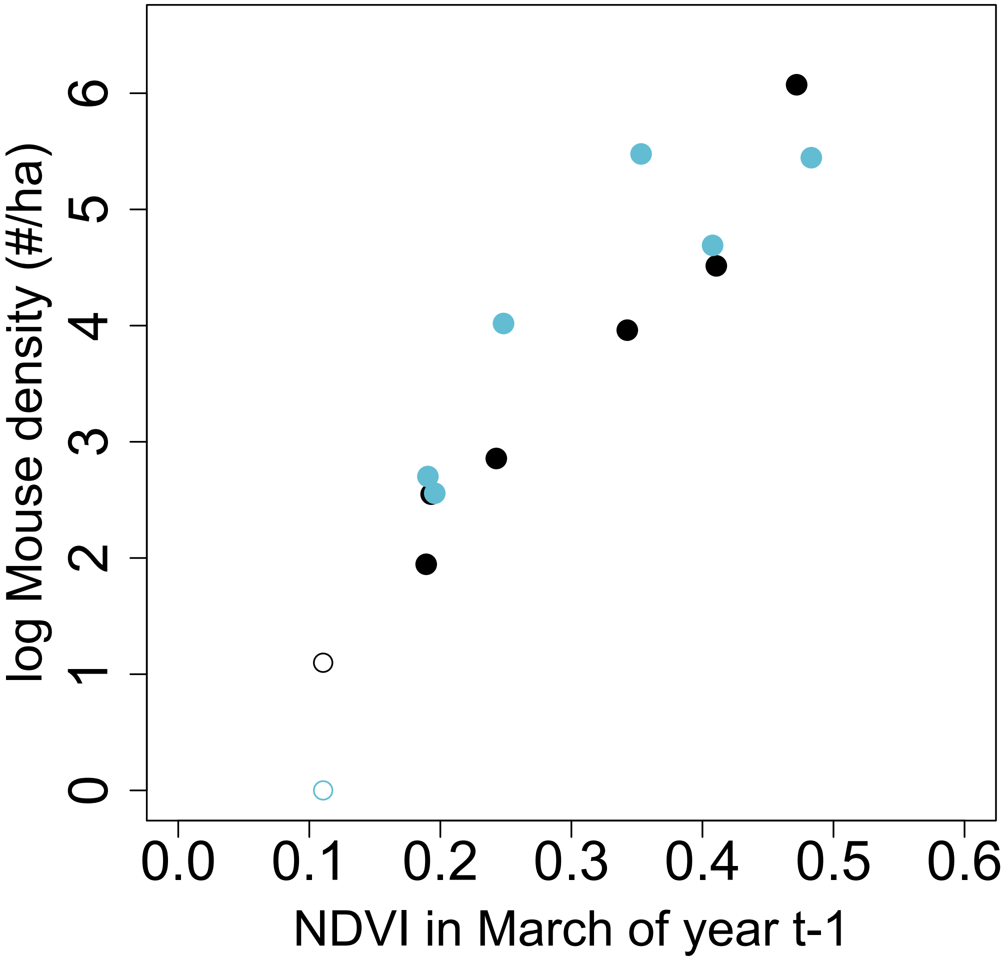


Figure 2-1 Density of mice on Santa Barbara Island in March 2007-2013 as predicted by Landsat derived NDVI values from the previous March (*t*-1). Points are jittered slightly and colors represent the identity of the two long-term monitoring plots. Two data points were excluded from the regression analysis when mouse density was too low to be reliably calculated and are represented by the colored hollow points.

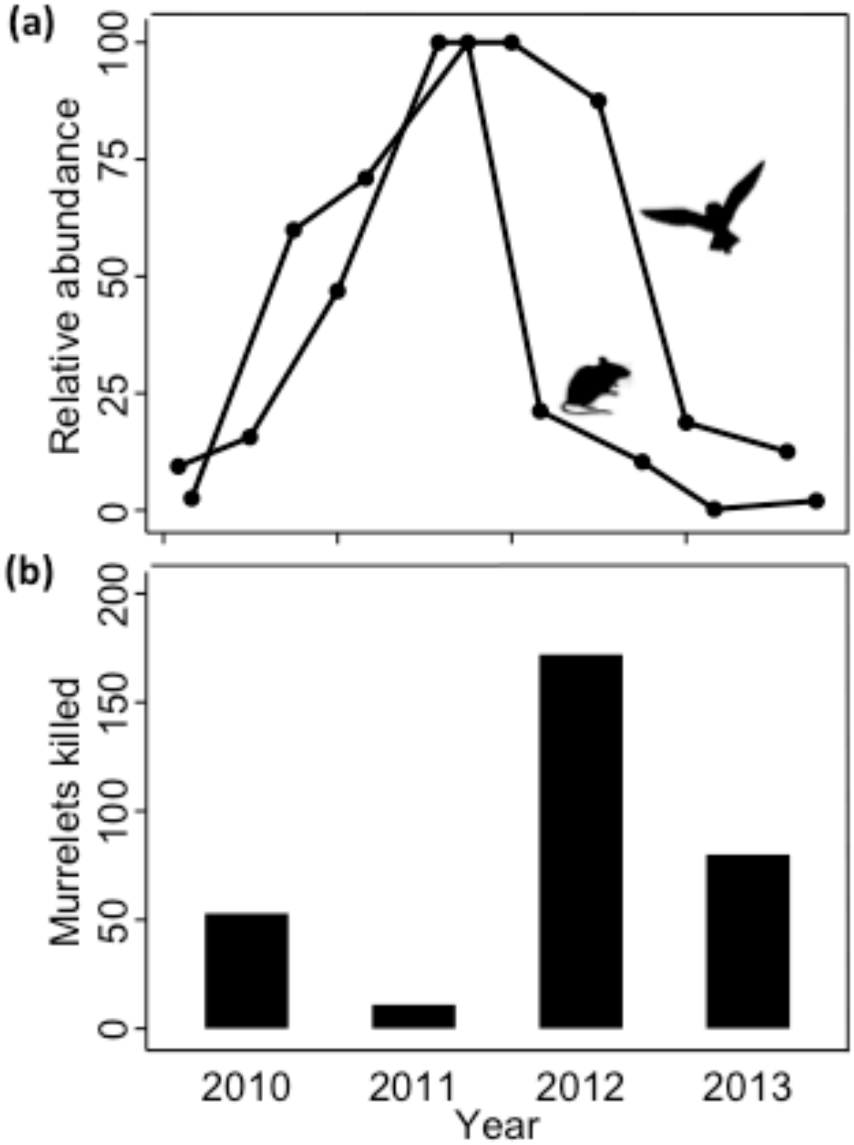


Figure 2-2 **a)** Trends in abundance of deer mice and Barn Owls relative to their respective peaks in density from 2010 – 2013. Lines connect irregularly spaced monthly surveys representing trends relative to maximum peaks observed in mouse density (mean density of two monitoring plots) and owl abundance (maximum number of owl detections on trail transect surveys). **b)** Total number of murrelets found killed by owls each year.

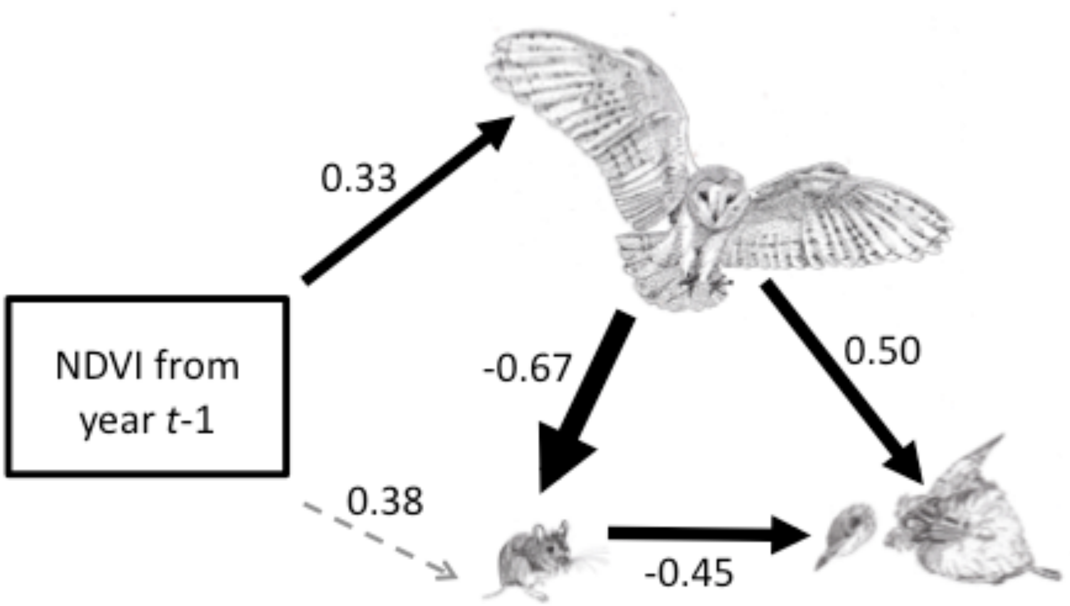


Figure 2-3 All arrows represent hypothesized pathways included in the *a priori* piecewise structural equation (SEM) model. Arrows indicate the direction of the relationship and the numbers shown are the standardized coefficients. Solid arrows indicate significant pathways ($p<0.05$) and the dashed arrow indicates the one non-significant pathway ($p=0.08$). Values of NDVI in March from the year *t*-1 were positively related to the number of owl roosts in mid-winter of year *t*, which negatively impacted mouse density in April and May (as measured with track tubes) in the year *t*. Mouse density was negatively related to the number of murrelet carcasses collected in year *t* in each site, which in turn was positively related to the number of owl roosts.

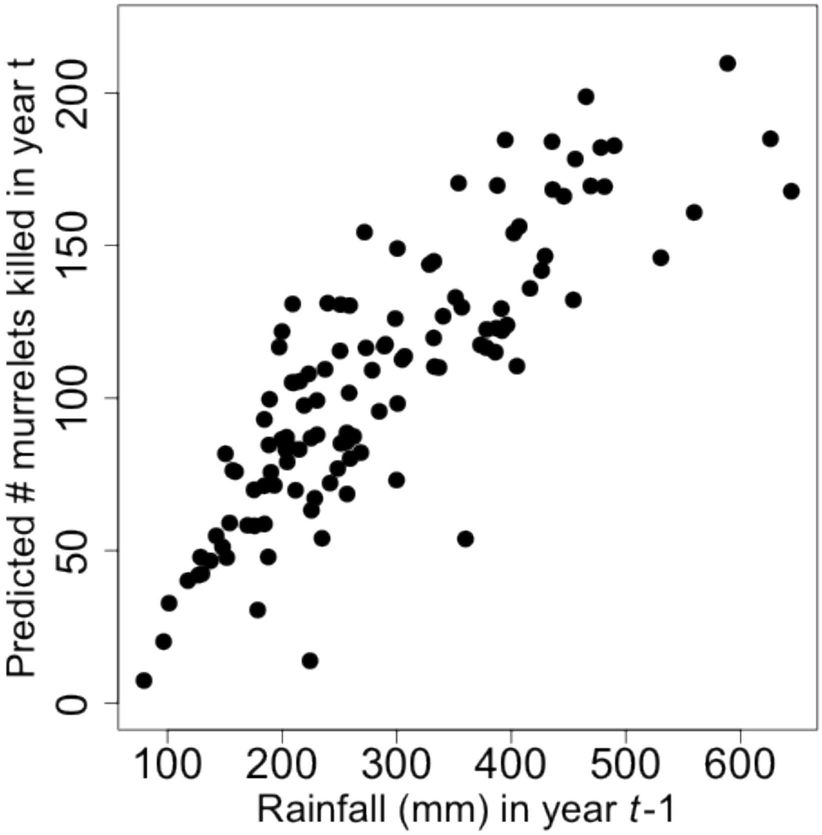


Figure 2-4 Changes in the number of murrelets killed by owls each year as a result of rainfall driven climate forcing from the year *t*-1 as simulated by a mathematical model of community dynamics over 120 years (details in Appendix A). Each point represents the expected number of murrelets killed by owls as calculated from the model given the effects of estimated rainfall on mice and owl abundance. Only 7.5% of observations were ≥ the number of murrelets found killed in 2012 (172), and most (66%) of those instances occurred since 1980.

Table 2-1 Proportions of prey types identified in owl pellets collected each year from Santa Barbara Island. Numbers in parentheses are individuals identified in the pellets.

Prey type	Year			
	2010	2011	2012	2013
Deer mice	88.2% (405)	98% (776)	78.5% (681)	40.7% (474)
Scripps's Murrelets	3.3% (15)	0.1% (1)	6% (52)	1.5% (18)
Night lizards	6.3% (29)	1.8% (14)	14.1% (122)	57.2% (666)
Landbirds	1.1% (5)	0.1% (1)	0.9% (8)	0.4% (5)
All seabirds	4.4% (20)	0.1% (1)	6.5% (56)	1.5% (18)

Discussion

Seabird survival and breeding parameters in many systems are typically strongly influenced by food availability and ocean climate regimes including ENSO events (Piatt et al. 2007), i.e. bottom-up processes. Here, our results demonstrate the consequences of an El Niño event on breeding seabirds that propagated through the terrestrial island food web where they nest. Specifically, our results suggest that owl predation of murrelets was mediated by prey switching triggered by climate-driven changes in the density of mice and owls (Figure 2). Other island systems in this region and elsewhere may be similarly affected. For example, deer mice are already known to increase by over 400% after El Niño years on islands in the Gulf of California (Stapp and Polis 2003), and rodent population outbreaks following increased rainfall are also commonly observed elsewhere (Singleton et al. 2010). Barn Owls are also distributed widely around the world (Marti et al. 2005), and are known to disperse and readily establish on oceanic islands (Lees and Gilroy 2014). However, other predators may respond similarly. Similar effects of lagged hyperpredation by introduced cats and foxes on native mammals following rainfall from the La Niña phase of ENSO have been observed even in a much more complex terrestrial food web in Australia (Letnic and Dickman 2006). These lagged top-down effects of ENSO could therefore easily be more widespread in diverse systems, particularly on islands in both the Pacific and Atlantic Oceans that receive increased rainfall associated with either phase of ENSO events (Dai and Wrigley 2000; Holmgren et al. 2001).

We observed an unprecedented level of predation by owls on murrelets two years after the ENSO associated rainfall pulse. Our high count of 172 murrelets killed during the 2012 breeding season potentially represents ~15% of the estimated breeding population on the island (475-650 breeding pairs, D. Whitworth, pers. comm.). This is unlikely to be an isolated case, as we note that previous Barn Owl population peaks on the island occurred at a 1-2 year lag from an ENSO event (Drost and Fellers 1991; NPS unpubl. data), and the highest numbers of murrelet carcasses have been found in the years after an ENSO event (Drost 1989; NPS unpubl. data). Moreover, the mathematical model with climate forcing also predicts such dynamics (Figure 4). Our results are therefore among the few empirical demonstrations of hyperpredation (Taylor 1979, Courchamp et al. 2000; Roemer et al. 2002; Ruscoe et al. 2006) where impacts to secondary prey are accelerated by high predator abundance following the sharp decline of the primary prey species (Holt and Kotler 1987; Serrouya et al. 2015). Here, we observed the mouse population plummet to 21% of the previous peak in just 6 months while the owl population had scarcely declined until after the 2012 murrelet breeding season. This timing was likely responsible for the increased predation on murrelets seen in 2012, as well as other island species such as the night lizards (Table 1). For a long-lived seabird with a low reproductive effort, high mortality events such as this could have lasting consequences on population dynamics (Frederiksen et al. 2008).

During the 2009-2010 ENSO event, the increased rainfall triggered a cascading bottom-up indirect effect leading to increased numbers of both mice and owls. During the time that mice were increasing to their peak abundance in 2011, owls consumed almost exclusively mice. Very few murrelets were found killed that year, despite the island having one of the highest known densities of Barn Owls documented in the literature (Taylor 2004). Barn Owls can double-brood and do not defend foraging ranges which means they can rapidly increase in abundance (Marti et al. 2005). Small seabirds like murrelets are highly vulnerable to avian predators while on land due to high wing-loading and reduced maneuverability (Spear and Ainley 1997), so these interludes of relaxed predation pressure could be very important. In several other systems, there is evidence that the temporary extreme abundance of a rodent can substantially benefit the nesting success or survival of birds by distracting predators (Ackerman, 2002; White and King 2006; Ims et al. 2013; Zárybnická et al. 2015). For example, in the arctic, during peak lemming years, predators like foxes largely ignore geese (Giroux et al. 2012), gull nests (Gauthier et al. 2015), shorebird nests (McKinnon et al. 2014), and eider nests (Iles et al. 2013). For some geese, the loss of these buffer years due to dampening lemming cycles is even suspected to be a contributing factor in declining population trends (Nolet et al. 2013).

These two particular years, 2011 and 2012, had highly contrasting impacts on murrelets. This pattern of boom and bust years resulting from ENSO events has important long-term implications for population viability of murrelets and possibly other predator-prey interactions similarly affected by ENSO. However, ENSO patterns are currently shifting in ways that may already be changing the impact on murrelets. Much of southern California in particular had been in a severe, record-breaking drought for most of the last decade except for the 2009-2010 ENSO (Diffenbaugh et al. 2015; Jones 2015), which is part of an ongoing recent trend of greater extremes in rainfall and drought cycles in this region due to climate change (Diffenbaugh et al. 2015; Yoon et al. 2015; He and Gautam 2016). Both the frequency of occurrence and extremity of ENSO events in relation to rainfall patterns are potentially important components describing the overall impact on murrelets, as variance in environmental conditions can have different effects than changes in the mean (Lawson et al. 2015). Our model, which demonstrates a connection between climate and murrelet population changes, also underscores this link.

Finally, the SEM results confirmed that the magnitude of owl predation on murrelets also strongly depended on the density of mice (Figure 2 and 3). This type of indirect interaction, where an endangered prey shares a predator with a more common prey, is a dynamic that increasingly threatens many species (DeCesare et al. 2009). To protect threatened species, conservation strategies have largely focused on reducing predator abundance through culling (Wittmer et al. 2012). However, in this situation, there are positive indirect effects of owls on murrelets that must also be considered. Mice themselves have a detrimental effect on murrelet nesting success and consume between 8-70% of murrelet eggs each year (Drost and Lewis 1995), and high owl abundance also reduces egg predation through fear-mediated changes in mouse foraging (Thomsen and Green 2016). This means that both nest success and survival of adult murrelets are influenced by climate-driven indirect interactions with predators, at times both positively and negatively. Given these complexities, adaptive management strategies that strive to maintain positive indirect effects while minimizing negative direct and indirect effects may be the most effective conservation approach.

Our study demonstrates how the effects of an ENSO associated rainfall pulse ricochets along a chain of interactions between the marine and terrestrial food webs, leading to hyperpredation of a vulnerable marine predator on its terrestrial breeding grounds. The latest ENSO event began in 2015 and was possibly one of the strongest events on record (see http://www.esrl.noaa.gov/psd/enso/mei/rank.html), and although advances have been made in predicting its occurrence and strength, it can still surprise us (McPhaden 2015). Most approaches for assessing species vulnerability to climate change have focused on direct impacts via abiotic changes and less so on species interactions (Pacifici et al. 2015), even though the latter tends to result in stronger impacts on species than the direct abiotic effects (Ockendon et al. 2014). Our study therefore highlights the urgent need for understanding how species interactions will change with shifting rainfall patterns through the effects of ENSO under global change, and we suggest that such lagged top-down effects of ENSO associated rainfall are possibly more widespread in systems with similar predator-prey relationships.

References

Ackerman, J. T. 2002. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. Oikos 99:469–480.

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332.

Auer, S. K., and T. E. Martin. 2013. Climate change has indirect effects on resource use and overlap among coexisting bird species with negative consequences for their reproductive success. Global Change Biology 19:411–419.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

BirdLife International (online). 2016. IUCN Red List for birds. <http://www.birdlife.org> (January 3, 2016).

Birt, T. P., H. R. Carter, D. L. Whitworth, A. McDonald, S. H. Newman, F. Gress, E. Palacios, J. S. Koepke, and V. L. Friesen. 2012. Rangewide population genetic structure of Xantus's Murrelet (*Synthliboramphus hypoleucus*). The Auk 129:44–55.

Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. García-Reyes, R. R. Rykaczewski, S. J. Bograd, and W. T. Peterson. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. Science 345:1498–1502.

Burkett, E.E., Rojek, N.A., Henry, A.E., Fluharty, M.J., Comrack, L., Kelly, P.R., et al. 2003. Report to the California Fish and Game Commission: status review of Xantus's Murrelet (*Synthliboramphus hypoleucus*) in California. California Department of Fish and Game, Habitat Conservation Planning Branch Status Report, 1, 96

Cao, L., T. J. Cova, P. E. Dennison, and M. D. Dearing. 2011. Using MODIS satellite imagery to predict hantavirus risk. Global Ecology and Biogeography 20:620–629.

Courchamp, F., M. Langlais, and G. Sugihara. 1999. Control of rabbits to protect island birds from cat predation. Biological Conservation 89:219–225.

Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology 69:154–164.

Cubaynes, S., P. F. Doherty, E. A. Schreiber, and O. Gimenez. 2011. To breed or not to breed: a seabird9s response to extreme climatic events. Biology Letters 7:303–306.

Dai, A., and T. M. L. Wigley. 2000. Global patterns of ENSO-induced precipitation. Geophysical Research Letters 27:1283–1286.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences 112:3931–3936.

Drost C.A. 1989. Predation and population cycles on a southern California island. Master's thesis. University of California–Davis.

Drost, C. A., and G. M. Fellers. 1991. Density Cycles in an Island Population of Deer Mice, *Peromyscus maniculatus*. Oikos 60:351–364.

Drost, C. A., and D. B. Lewis. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). The Birds of North America Online.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, CA.

Fellers, G.M., Drost, C.A., and Arnold, B.W. (1988). Terrestrial Vertebrates Monitoring Handbook, Channel Islands National Park, California. National Park Service, Channel Islands National Park, Ventura, CA, 17 pp. + appendices.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020–1029.

Gauthier, G., P. Legagneux, M.-A. Valiquette, M.-C. Cadieux, and J.-F. Therrien. 2015. Diet and reproductive success of an Arctic generalist predator: Interplay between variations in prey abundance, nest site location, and intraguild predation. The Auk 132:735–747.

Giroux, M.-A., D. Berteaux, N. Lecomte, G. Gauthier, G. Szor, and J. Bêty. 2012. Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. Journal of Animal Ecology 81:533–542.

Gudmundson, S., A. Eklöf, and U. Wennergren. 2015. Environmental variability uncovers disruptive effects of species9 interactions on population dynamics. Proc. R. Soc. B 282:20151126.

Hart, I. A., J. M. Broughton, and R. Gruhn. 2015. El Niño controls Holocene rabbit and hare populations in Baja California. Quaternary Research 84:46–56.

Harvey, A.L., Auer, S.A., Barnes, K.W., Mazurkiewicz, D.M., Carter, C.A., Jacques, M.E., et al. (2013). Scripps's Murrelet, Cassin's Auklet, and Ashy Storm-Petrel colony monitoring and restoration activities on Santa Barbara Island, California in 2010-2011. Unpublished report, California Institute of Environmental Studies. 81 pages.

Harvey, A.L., Howard, J.A., Robison, R.R., Mazurkiewicz, D.M. , Jacques, M.E., Auer, S.A. et al. (2014). Scripps's Murrelet, Cassin's Auklet, and Ashy Storm-Petrel reproductive monitoring and restoration activities on Santa Barbara Island, California in 2012. Unpublished report, California Institute of Environmental Studies. 38 pages.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutiérrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology & Evolution 16:89–94.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R. D., and B. P. Kotler. 1987. Short-Term Apparent Competition. The American Naturalist 130:412–430.

Howard, J.A., Harvey, A.L., Kim, S.J., Robison, R.E., Mazurkiewicz, D.M.,Yamagiwa, A.A et al. (2014). Scripps's Murrelet and Cassin's Auklet Reproductive Monitoring and Restoration Activities on Santa Barbara Island, California in 2013. Unpublished report. California Institute of Environmental Studies.

Huang, A. C., J. E. Elliott, K. M. Cheng, K. Ritland, C. E. Ritland, S. K. Thomsen, S. Hindmarch, and K. Martin. 2016. Barn owls (*Tyto alba*) in western North America: phylogeographic structure, connectivity, and genetic diversity. Conservation Genetics 17:357–367.

Huggins, R. M. 1991. Some Practical Aspects of a Conditional Likelihood Approach to Capture Experiments. Biometrics 47:725–732.

Iles, D. T., R. F. Rockwell, P. Matulonis, G. J. Robertson, K. F. Abraham, J. C. Davies, and D. N. Koons. 2013. Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. Journal of Animal Ecology 82:683–693.

Ims, R. A., J.-A. Henden, A. V. Thingnes, and S. T. Killengreen. 2013. Indirect food web interactions mediated by predator–rodent dynamics: relative roles of lemmings and voles. Biology Letters 9:20130802.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez. 1997. A Long-Term Study of Vertebrate Predator Responses to an El Niño (ENSO) Disturbance in Western South America. Oikos 78:341–354.

Jones, J. 2015. California's Most Significant Droughts: Comparing Historical and Recent Conditions.

Junak, S. 1995. A revised flora of Santa Barbara Island: An annotated catalog of the ferns and flowering plants and a brief history of botanical exploration. Santa Barbara Botanic Garden.

Lawson, C. R., Y. Vindenes, L. Bailey, and M. van de Pol. 2015. Environmental variation and population responses to global change. Ecology Letters 18:724–736.

Lees, A. C., and J. J. Gilroy. 2014. Vagrancy fails to predict colonization of oceanic islands. Global Ecology and Biogeography 23:405–413.

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Letnic, M., and C. R. Dickman. 2006. Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. Biodiversity & Conservation 15:3847–3880.

Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecology Letters 5:273–284.

Marti, C. D., A. F. Poole, and L. R. Bevier. 2005. Barn Owl (*Tyto alba*). The Birds of North America Online.

McKinnon, L., D. Berteaux, and J. Bêty. 2014. Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. The Auk 131:619–628.

McPhaden, M. J. 2015. Playing hide and seek with El Nino. Nature Climate Change 5:791–795.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2006. ENSO as an Integrating Concept in Earth Science. Science 314:1740–1745.

Meek, W. R., P. J. Burman, T. H. Sparks, M. Nowakowski, and N. J. Burman. 2012. The use of Barn Owl *Tyto alba* pellets to assess population change in small mammals. Bird Study 59:166–174.

Molina-Montenegro, M. A., C. Torres-Díaz, J. Gallardo-Cerda, M. Leppe, and E. Gianoli. 2013. Seabirds modify El Niño effects on tree growth in a southern Pacific island. Ecology 94:2415–2425.

NASA Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov).

Nolet, B. A., S. Bauer, N. Feige, Y. I. Kokorev, I. Y. Popov, and B. S. Ebbinge. 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. Journal of Animal Ecology 82:804–813.

Noy-Meir, I. 1973. Desert Ecosystems: Environment and Producers. Annual Review of Ecology and Systematics 4:25–51.

Ockendon, N., D. J. Baker, J. A. Carr, E. C. White, R. E. A. Almond, T. Amano, E. Bertram, R. B. Bradbury, C. Bradley, S. H. M. Butchart, N. Doswald, W. Foden, D. J. C. Gill, R. E. Green, W. J. Sutherland, E. V. J. Tanner, and J. W. Pearce-Higgins. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20:2221–2229.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers, D. G. Hole, T. G. Martin, H. R. Akçakaya, R. T. Corlett, B. Huntley, D. Bickford, J. A. Carr, A. A. Hoffmann, G. F. Midgley, P. Pearce-Kelly, R. G. Pearson, S. E. Williams, S. G. Willis, B. Young, and C. Rondinini. 2015. Assessing species vulnerability to climate change. Nature Climate Change 5:215–224.

Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C. White. 2003. Small-Mammal Density Estimation: A Field Comparison of Grid-Based Vs. Web-Based Density Estimators. Ecological Monographs 73:1–26.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Piatt, J. F., W. J. Sydeman, and F. Wiese. 2007. Introduction:: a modern role for seabirds as indicators. Marine Ecology Progress Series 352:199–204.

Polis, G.A., Sánchez-Piñero, F., Stapp, P.T., Anderson, W.B., and Rose, M.D. (2004). Trophic flows from water to land: marine input affects food webs of islands and coastal ecosystems worldwide. In Food webs at the landscape level. (eds Polis, G.A., Power, M.E., Huxel, G.R.). University of Chicago Press, Chicago, Illinois, USA. pp. 200-216.

Ringler, D., J. C. Russell, and M. Le Corre. 2015. Trophic roles of black rats and seabird impacts on tropical islands: Mesopredator release or hyperpredation? Biological Conservation 185:75–84.

Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. Proceedings of the National Academy of Sciences 99:791–796.

Ruscoe, W. A., G. Norbury, and D. Choquenot. 2006. Trophic Interactions Among Native and Introduced Animal Species. Pages 247–263 *in* D. R. B. Allen and D. W. G. Lee, editors. Biological Invasions in New Zealand. Springer Berlin Heidelberg.

Russell, J. C., V. Lecomte, Y. Dumont, and M. Le Corre. 2009. Intraguild predation and mesopredator release effect on long-lived prey. Ecological Modelling 220:1098–1104.

Russell, J. C., and L. Ruffino. 2012. The influence of spatio-temporal resource fluctuations on insular rat population dynamics. Proceedings of the Royal Society of London B: Biological Sciences 279:767–774.

Schoener, T.W., Spiller, D.A. (2010). Trophic cascades on islands. In Trophic cascades: predators, prey, and the changing dynamics of nature. (eds Terborgh, J., Estes, J.A.). Island Press, Washington, DC, USA. pp. 179-202.

Schonher, T., and S. E. Nicholson. 1989. The Relationship between California Rainfall and ENSO Events. Journal of Climate 2:1258–1269.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition. The American Naturalist 185:665–679.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Singleton, G.R., Belmain, S.R., and Brown, P.R. 2010. Rodent outbreaks: an age-old issue with an modern appraisal. In Rodent Outbreaks: ecology and impacts. (eds Singleton, G.R., Belmain, S.R., Brown, P.R., Hardy, B). Los Banos (Phillipines): International Rice Research Institute. 289 p.

Spear, L. B., and D. G. Ainley. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. Ibis 139:221–233.

Stanley TR. 2012. Analysis of deer mouse capture-recapture data from Anacapa, Santa Barbara, and San Miguel Islands. Unpublished draft report, Channel Islands National Park. 39 pp.

Stapp, P., and G. A. Polis. 2003a. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134:496–504.

Stapp, P., and G. A. Polis. 2003b. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Stapp, P., G. A. Polis, and F. Sánchez Piñero. 1999. Stable isotopes reveal strong marine and El Niño effects on island food webs. Nature 401:467–469.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological Effects of Climate Fluctuations. Science 297:1292–1296.

Sweet, S. K., A. Asmus, M. E. Rich, J. Wingfield, L. Gough, and N. T. Boelman. 2015. NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. Ecological Applications 25:779–790.

Taylor, I. 2004. Barn owls: predator-prey relationships and conservation. Cambridge University Press, UK.

Thomsen, S. K., and D. J. Green. 2016. Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island. Ecology 97:3530–3537.

Thomsen, S. K., C. E. Kroeger, P. H. Bloom, and A. L. Harvey. 2014. Space Use and Home-Range Size of Barn Owls on Santa Barbara Island. Monographs of the Western North American Naturalist 7:339–347.

Vázquez, D. P., E. Gianoli, W. F. Morris, and F. Bozinovic. 2017. Ecological and evolutionary impacts of changing climatic variability. Biological Reviews 92:22–42.

White, P. C. L., and C. M. King. 2006. Predation on native birds in New Zealand beech forests: the role of functional relationships between Stoats Mustela erminea and rodents. Ibis 148:765–771.

Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation Strategies for Species Affected by Apparent Competition. Conservation Biology 27:254–260.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What Can We Learn from Resource Pulses. Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Yoho, D., T. Boyle, and E. McIntire. 1999. The climate of the Channel Islands, California. Pages 81–88 Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Yoon, J.-H., S.-Y. S. Wang, R. R. Gillies, B. Kravitz, L. Hipps, and P. J. Rasch. 2015. Increasing water cycle extremes in California and in relation to ENSO cycle under global warming. Nature Communications 6:ncomms9657.

Zárybnická, M., J. Riegert, and M. Kouba. 2015. Indirect food web interactions affect predation of Tengmalm's Owls Aegolius funereus nests by Pine Martens Martes martes according to the alternative prey hypothesis. Ibis 157:459–467.

Chapter 3. Are there positive indirect effects of owls on murrelets? Evidence for a behaviorally mediated trophic cascade

A version of this chapter was published as Thomsen, S. K., and D. J. Green. 2016. Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island. Ecology 97:3530–3537.

Abstract

Apex predators can suppress the foraging activity of mesopredators, which may have 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 three 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.

Introduction

Widespread declines in top predator populations across many different ecosystems have 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, 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 (Towns 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 non-consumptive 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 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 (~165g) 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 at al. 2016), and their population rises and falls (from ~3-30+ 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 (33º 29' N, 119º 02 W) is located about 63 km from the nearest mainland location, and at 2.6 km^2 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, pers. comm). In addition to Barn Owls, other nocturnal raptors include the wintering Burrowing Owl (*Athene cunicularia*). 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 m and 171 m from the ocean below.

Owl abundance

To quantify owl abundance in different areas across the island, we set up 200m 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 two 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 ten sites where we used track tubes to obtain a relative index of mouse abundance from 2011-2013 (see Appendix B 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 3x3 grid formation with 7m 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 et al. (2012) in the NPS sites ($r=0.64$, $n=13$ site nights, $p=0.02$; see Appendix B).

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 2.4L round plastic containers (15 cm height x 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 300m 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 30m 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 2m 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 1L sifted dried sand and 7.5ml 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 ≤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 to 2013) using data collected by the National Park Service (NPS unpub. data). Murrelet nests were monitored using a standard protocol in two plots, Cat Canyon and Landing Cove, which are separated by ~2km (Lewis et al. 1988, Howard et al. 2013). 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 unpub. 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 days 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 B), 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 2 eggs in a clutch, the first of which is then left unattended by both adults for about 8 days (Murray 1983; Drost and Lewis 1995). Most instances of egg depredation happen during this initial neglect period (Murray 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. 2013), while the generalized linear mixed model (GLMM) of egg fate was fit with the package "lme4" (Bates et al. 2014).

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 to 4.33), after increasing from 2011 (mean=0.24±1.01, range: 0 to 1.33) and subsequently dropping in 2013 (mean=0.09±0.18, range: 0 to 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 ($\beta = 0.4 \pm 0.17$; $F_{1,98} = 5.59$; $p = 0.02$; Figure 1a), and was greater during the full moon compared to the new moon ($\beta = -0.76 \pm 0.16$; $F_{1,98} = 20.47$; $p < 0.001$; Figure 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 ($\beta = 1.03 \pm 0.23$; $F_{1,110} = 20.02$, $p < 0.001$).

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, $\chi2 = 32.06$, $p<0.001$; Figure 2) after controlling for the differences between nest monitoring plots (log odds=2.67; Wald CI: 0.58, 4.76, $\chi2 = 11.50$, $p<0.001$). 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 (Figure 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 ($\chi2 = 0.15$, $p=0.70$). 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, $p=0.048$; Figure 3).

Figures

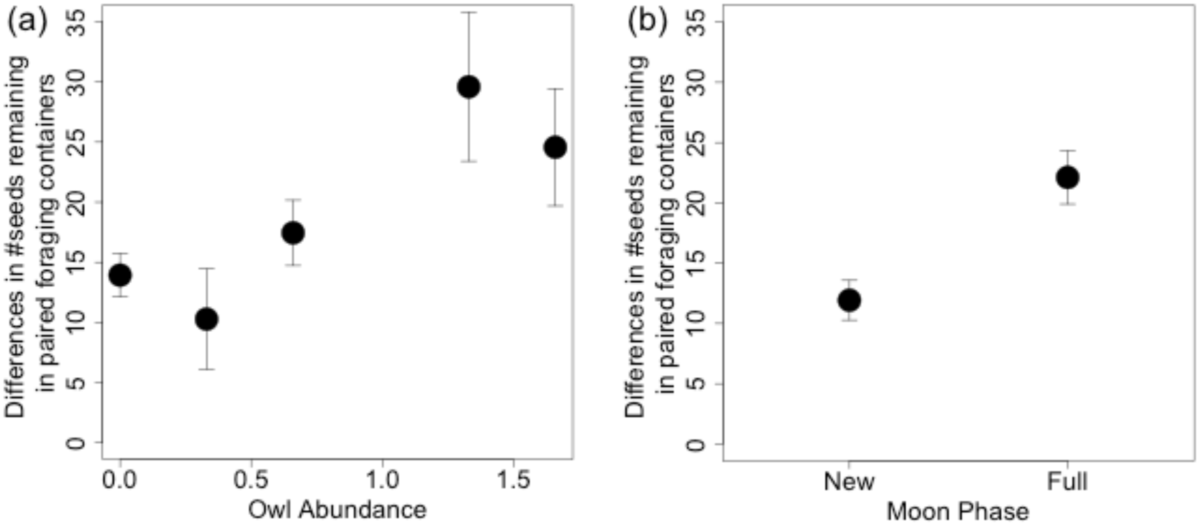


Figure 3-1 Impacts of owl abundance **a)** and moon phase **b)** on perceived predation risk by deer mice on Santa Barbara Island. Data presented are the mean differences in foraging amounts (GUDexposed-GUDsheltered) between the paired foraging containers (mean±SE). Greater differences reflect increasing perceived predation risk.

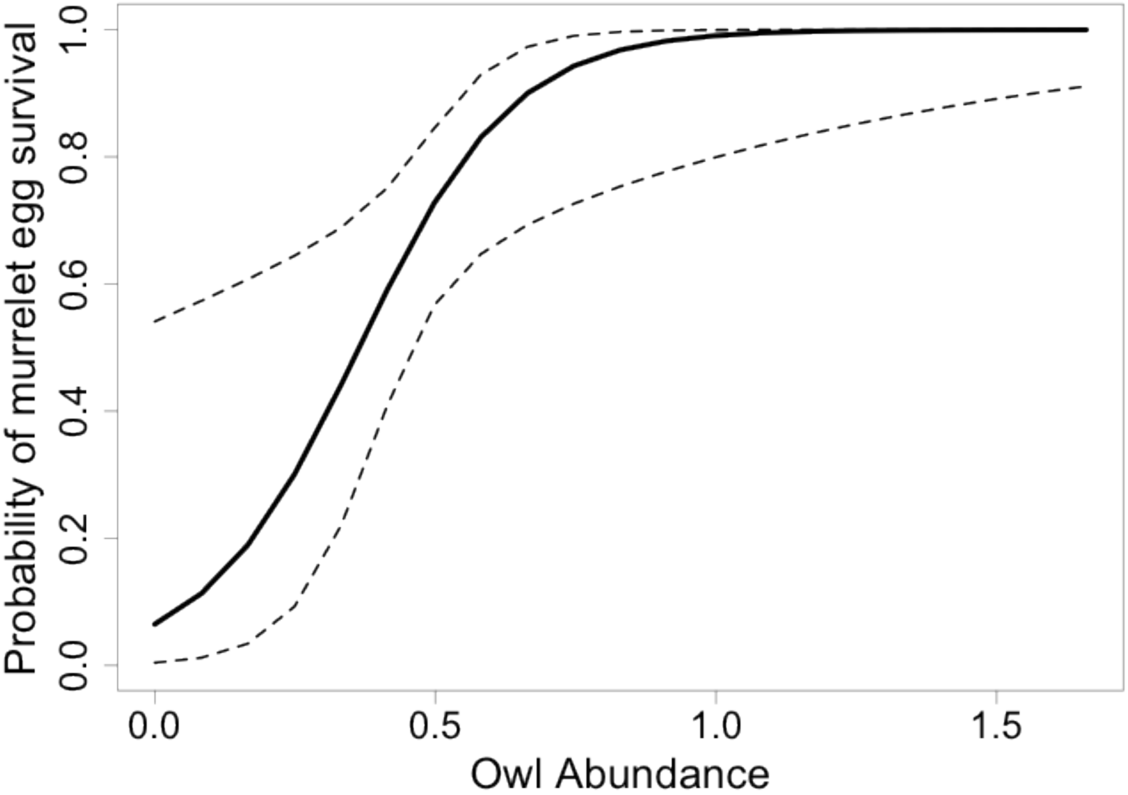


Figure 3-2 Predicted probability of murrelet egg survival (probability and CI) and owl abundance (mean count from line transect surveys) after controlling for differences in survival between two murrelet monitoring plots.

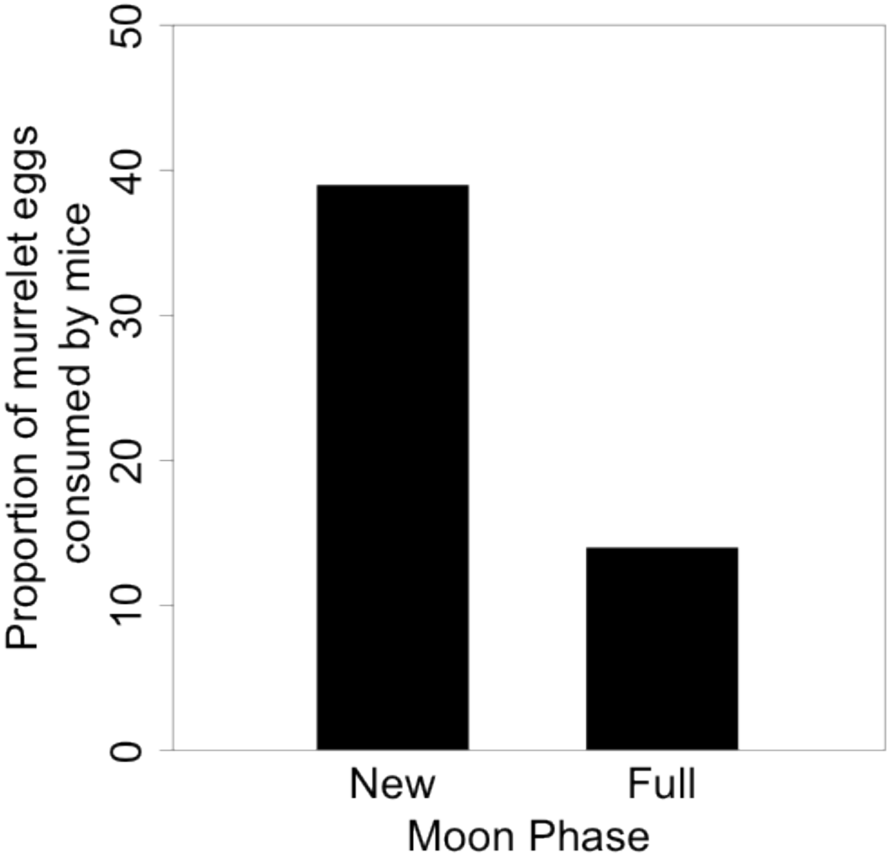


Figure 3-3 Murrelet egg predation by deer mice during the new and full moon phases on Santa Barbara Island.

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 (Figure 1). Murrelet egg predation was consequently lower with increasing owl abundance, and lower during the full moon compared to the new moon (Figure 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; Carthy 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-year period was unrelated to inter-annual 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 (Figure 1a,1b), 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 (Figure 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 (Chapter 2). The magnitude of murrelet predation by owls appears to be strongly related to differences in mouse density (Chapter 2), which suggests that murrelets are among those species of conservation concern that are impacted by apparent competition (DeCesare et al. 2009). 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.

References

Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. Ecology 74:726-733.

Angel, A., R. M. Wanless and J. Cooper. 2009. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats?. Biological Invasions 11:1743-1754.

Ashley, M., and C. Wills. 1987. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. Evolution 41:854-863.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Sciences 94:10735-10738.

Bergstrom, D. M., A. Lucieer, K. Kiefer, J. Wasley, L. Belbin, T. K. Pedersen, and S. L.Chown. 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46:73-81.

BirdLife International (online). 2016. IUCN Red List for birds. <http://www.birdlife.org> (January 3, 2016).

Bode, M., C.M. Baker, and M. Plein. 2015. Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. Journal of Applied Ecology 52:571-579.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37-47.

Brodier, S., B. Pisanu, A. Villers, E. Pettex, M. Lioret, J.L. Chapuis, and V. Bretagnolle. 2011. Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. Animal Conservation 14: 459–465.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999-1014.

Carthey, A. J. R., and P. B. Banks. 2016. Naiveté is not forever: responses of a vulnerable native rodent to its long term alien predators. Oikos 125:918–926.

Clotfelter, E. D., A. B., Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154:493-503.

Collins, P. W., and P. D. H. L. Jones. 2015. A Checklist of Birds of the California Channel Islands. Santa Barbara Museum of Natural History.

Collins, P. W., J. Storrer and K. Rindlaub. 1979. Vertebrate zoology: the biology of the deer mouse - In: Power, D. M., Natural resources study of the Channel Islands National Monument, California. Santa Barbara Museum of Natural History, Chapter 11.

Courchamp, F., M. Langlais, and G. Sugihara. 1999. Cats protecting birds: modelling the mesopredator release effect. Journal of Animal Ecology 68:282-292.

Crawley, M. J. 2014. Statistics: an introduction using R. John Wiley & Sons, 2014.

Davidson, D.L. and D.W. and Morris. 2001. Density-dependent foraging effort of Deer Mice (*Peromyscus maniculatus*). Functional Ecology, 15:575-583.

DeCesare N.J., M. Hebblewhite, H.S. Robinson, M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Drost C.A. and G. M. Fellers. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. Oikos 60:351-364.

Drost, C. A. and D. B. Lewis. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). in: The Birds of North America (A. Poole and F. Gill, eds) The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C

ESRI, R. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, CA.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346-349.

Fellers, Gary M., C.A. Drost, and B.W. Arnold. 1988. Terrestrial Vertebrates Monitoring

Handbook. Channel Islands National Park, California. National Park Service, Channel Islands National Park, Ventura, CA.

Glen, A.S., R. Atkinson, K.J. Campbell, E. Hagen, N.D. Holmes, B.S. Keitt, J.P Parkes, A. Saunders, J. Sawyer, and H. Torres. 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration?. Biological invasions, 15:2589-2603.

Greeney, H. F., M. R. Meneses, C. E. Hamilton, E. Lichter-Marck, R. W. Mannan, N. Snyder, H. Snyder, S. M. Wethington, and L. A Dyer. 2015. Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds. Science Advances 1:e1500310.

Hone, J., and R. M. Sibly. 2002. Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1171–1177.

Howard, J. A., A. L. Harvey, S. J. Kim, R. E. Robison, D. M. Mazurkiewicz, A. A. Yamagiwa, C. A. Carter, E. F. W. Wynd. 2014. Scripps's Murrelet and Cassin's Auklet Reproductive Monitoring and Restoration Activities on Santa Barbara Island, California in 2013.Unpublished report. California Institute of Environmental Studies.

Huang, A., J. E. Elliott, K. M. Cheng, K. Ritland, S. K. Thomsen, S. Hindmarch, and K. Martin. 2015. Barn owls (*Tyto alba*) in Western North America: Phylogeographic structure, connectivity, and genetic diversity. Conservation Genetics. Advance online publication: doi: 10.1007/s10592-015-0787-0

Jones, M. G. W., and P.G. Ryan. 2010. Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. Antarctic Science 22:39-42.

Jones, H.P., N.D. Holmes, S.H. Butchart, B.R Tershy, P.J. Kappes, I. Corkery, A. Aguirre-Muñoz, D.P. Armstrong, E. Bonnaud, A.A. Burbidge, and K. Campbell. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033-4038.

Junak, S., R. Philbrick and C. Drost. 1993. A Revised Flora of Santa Barbara Island. Santa Barbara Botanic Garden, Santa Barbara, CA, 112 pp.

Kotler, B. P., J. Brown, S. Mukherjee, O. Berger-Tal, and A. Bouskila. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proceedings of the Royal Society B: Biological Sciences 277:1469-1474.

Lewis, D. B., F. Gress, T. Ingram, G. L. Hunt Jr. and D. Anderson. 1988. Seabird Monitoring Handbook, Channel Islands National Park.National Park Service, Channel Islands National Park, Ventura, CA, 33 pp.

Li, B., A. Belasen, P. Pafilis, P. Bednekoff, and J. Foufopoulos. 2014. Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: insights from an ancient introduction. Proceedings of the Royal Society B: Biological Sciences 281:20140339–20140339.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Medina, F. M., E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. Josh Donlan, , B. S. Keitt, M. Le Corre, S. V. Horwath, and M. Nogales. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17:3503–3510.

Millus, S. A., Stapp, P., and P. Martin. 2007. Experimental control of a native predator may improve breeding success of a threatened seabird in the California Channel Islands. Biological Conservation 138:484-492.

Morris, D. W., and D. L. Davidson. 2000. Optimally foraging mice match patch use with habitat differences in fitness. Ecology 81:2061-2066.

Mougeot, F., and V. Bretagnolle. 2003. Predation risk and moonlight avoidance in nocturnal seabirds. Journal of Avian Biology 31:376-386.

Murray, K.G., K. Winnett-Murray, Z. A. Eppley, G. L. Hunt Jr., and D. B. Schwartz. 1983. Breeding Biology of the Xantus's Murrelet. Condor 85:12–21.

Nishijima, S., G. Takimoto and T. Miyashita. 2014. Roles of alternative prey for mesopredators on trophic cascades in intraguild predation systems: a theoretical perspective. The American Naturalist 183:625-637.

Nur, N., A. L. Harvey, S. K. Thomsen, R. Bradley, and J. Jahncke. 2013. Modeling the Population level Impacts of Barn Owls on Scripps's Murrelet Population Trends on Santa Barbara Island. Unpublished report prepared for: National Fish and Wildlife Foundation. Point Blue Conservation Science, Petaluma, California. PRBO contribution Number 1969.

Orrock, J. L., and R. J. Fletcher. 2014. An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. Proceedings of the Royal Society B: Biological Sciences 281:20140391.

Pinheiro, J., Bates, D., DebRoy, S., and R. Sarkar. 2014. nlme: Linear and Nonlinear Mixed Effects Models. R package version, 3, 118.

Preisser, E. L., Bolnick, D. I., and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., and Brashares, J. S. 2009. The rise of the mesopredator. Bioscience 59:779-791.

Prugh, L. R., and S. M. Arthur. 2015. Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release. Oikos 124: 1241–1250

Prugh, L. R., and C. D. Golden 2014. Does moonlight increase predation risk? Meta‐analysis reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal Ecology 83:504-514.

Rayner, M. J., Hauber, M. E., Imber, M. J., Stamp, R. K., and Clout, M. N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. Proceedings of the National Academy of Sciences 104:20862-20865.

Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138:514–519.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, and O.J. Schmitz. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ritchie, E. G., and Johnson, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982-998.

Sabo, J. L. 2008. Population viability and species interactions: life outside the single-species vacuum. Biological Conservation 141:276-286.

Salo, P., E. Korpimaki, P. B. Banks, M. Nordstrom, and C. R. Dickman. 2007. Alien predators are more dangerous than native predators to prey populations. Proceedings of the Royal Society B-Biological Sciences 274:1237-1243.

Schmidt, K. A., Goheen, J. R., and R. Naumann. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. Ecology 82: 2937-2947.

Schmidt, K. A., and Ostfeld, R. S. 2003. Mice in space: space use predicts the interaction between mice and songbirds. Ecology 84:3276-3283.

Schmidt, K. A. 2006. Non-additivity among multiple cues of predation risk: a behaviorally-driven trophic cascade between owls and songbirds. Oikos 113:82-90.

Schmitz O.J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153–163.

Shoji, A., K. H. Elliott, S. Aris-Brosou, D. Crump, and A.J. Gaston. 2011. Incubation patterns in a central-place forager affect lifetime reproductive success: scaling of patterns from a foraging bout to a lifetime. PloS one 6:e17760.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75-92.

Stanley, T. R. 2012. Analysis of deer mouse capture-recapture data from Anacapa, Santa Barbara, and San Miguel Islands. Unpublished draft report to Channel Islands National Park. 39 pp.

St. Juliana, J. R. S., B. P. Kotler, J. S. Brown, S. Mukherjee, and A. Bouskila. 2011. The foraging response of gerbils to a gradient of owl numbers. Evolutionary Ecology Research 13:869-878.

Stapp, P., and G.A Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134:496–504

Suraci, J. P., M. Clinchy, L. Y. Zanette, C. M. Currie, and L. M. Dill. 2014. Mammalian mesopredators on islands directly impact both terrestrial and marine communities. Oecologia 176:1087-1100.

Sutherland, W.J., R. Aveling, T.M. Brooks, M. Clout, L. V. Dicks, L. Fellman, E. Fleishman, D.W. Gibbons, B. Keim, F. Lickorish, and K.A. Monk. 2014. A horizon scan of global conservation issues for 2014. Trends in Ecology & Evolution 29:15-22.

Sydeman, W. J., N. Nur, and P. Martin. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-Petrel (*Oceanodroma homochroa*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*). Final report to the United States Geological Survey, Biological Resources Division, Species at Risk Program. Stinson Beach, CA: PRBO Conservation Science. 74 pp

Schoener, T. W., and D.A Spiller. 2010. Trophic cascades on islands. *In:* Terborgh, J., and J. A. Estes. (Eds.). Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, DC.

Terborgh, J., L. Lopez, and José Tello S. 1997. Bird communities in transition: the Lago Guri Islands. Ecology 78:1494–1501.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923-1926.

Thomsen, S. K, C. E Kroeger, P. H. Bloom and A. L. Harvey. 2014. Space use and home range size of Barn Owls on Santa Barbara Island. Monographs of the Western North American Naturalist. 7:339–347.

Towns, D. R., Atkinson, I. A., and Daugherty, C. H. 2006. Have the harmful effects of introduced rats on islands been exaggerated?. Biological Invasions 8:863-891.

US Navy (online). 2013. U.S. Naval Observatory astronomical applications: data services. <www.http://aa.usno.navy.mil/data/docs/MoonFraction.php> (November 16, 2013)

Wanless, R. M., A. Angel, R. J. Cuthbert, G. M. Hilton, and P.G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3:241-244.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

Zavaleta, E. S., R. J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454-459.

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

Chapter 4. Evaluating the relative roles of marine productivity and climate-driven terrestrial resource pulses and subsequent cascading indirect interactions in determining murrelet nest success

Abstract

Despite the profound impacts of drought on terrestrial productivity in coastal arid ecosystems, only a few studies have addressed how drought can influence ecological cascades across ecosystem boundaries. In this study, we examine the consequences of ENSO-driven rainfall pulses and drought that subsequently impact the breeding success of a small nocturnal seabird, the Scripps's Murrelet (*Synthliboramphus scrippsi*). On an island off the coast of southern California, the main cause of reduced nest success for one of their largest breeding colonies is egg predation by an endemic deer mouse. Mice on the island have an opportunistic diet of primarily seeds and insects, but drastic declines in terrestrial productivity from drought might be expected to increase their reliance on marine resources, including murrelet eggs. We compiled data on indicators of terrestrial and marine productivity between 1993-2013 to determine how conditions in these ecosystems affect murrelet nest success. We found that the severity of drought had the strongest influence on murrelet nest success. Nest success was much higher under normal or high rainfall conditions, depending on whether oceanic conditions were favorable to murrelets. We calculated that the reduction in fecundity during drought years were substantial enough to produce a declining population growth rate. Therefore, increased variability in precipitation regimes and more frequent drought resulting from global climate change could exacerbate this affect, and thus be detrimental to murrelets on this island.

Introduction

Increased variability and changes to precipitation regimes are predicted as a consequence of global climate change, and which have already been shifting around the globe in some regions (Milly et al. 2005, Power et al. 2013). Droughts are of particular concern as they are predicted to become more extreme, last longer, and increase in frequency (Dai 2013). Droughts are already relatively common in the arid and semi-arid ecosystems of the world, which cover ~41% of the earth's land, in part because these areas are characterized both by low mean annual precipitation but also high inter-annual variability (Maestre et al. 2012). During an extreme drought, the intense unmet need for water can cause increased plant die-off (Breshears et al. 2005; Miriti et al. 2007) as well as reduced survival and reproduction in animals (Grant and Grant 2002; Sperry and Weatherhead 2008; Rymer et al. 2016). The amount of annual rainfall is therefore a crucial input in arid and semi-arid areas, as it can directly limit plant primary productivity (De la Maza et al. 2009), which subsequently has direct effects on higher trophic levels (Jaksic et al. 1997; Deguines et al. 2017). However, only a few studies have addressed how drought and rainfall variability influences indirect interactions in food webs (e.g. Beier et al. 2012; Barton and Ives 2014). Given climate change projections, there remains an urgent need to understand how changes to precipitation patterns will influence ecological interactions, particularly if effects extend across ecosystems.

Ecosystem boundaries, such as those between the marine and terrestrial environments, are actually permeable to the flow of resources between the adjacent food webs (Loreau et al. 2003). If these resource flows are altered, such as by extreme drought, it could potentially lead to cascading effects across ecosystem boundaries (Knight et al. 2005). For example, after a sudden high rainfall year on arid islands, mice can consume predominantly terrestrial resources that then become extremely abundant, whereas in drier years they rely on marine resources to a much greater extent (Stapp and Polis 2003). Some marine resources, such as the eggs of nesting seabirds, can therefore represent a seasonally abundant and allochthonous alternative prey source for island rodents and other generalist predators (Russell and Ruffino 2012). But the extent to which rodents utilize this seasonal prey source then could depend on the effects of fluctuating terrestrial resources (Ruffino et al. 2013). Similarly, nest success of birds in a variety of environments can be strongly influenced by the availability of other prey types for predators (Ostfeld and Keesing 2000; Schmidt and Ostfeld 2008). Thus, depending on how strongly changes to rainfall patterns propagate in a food chain, this could increasingly affect some marine species through prey switching by terrestrial predators.

In this study, we examine whether rainfall patterns that influence terrestrial productivity have cascading effects that extend across ecosystem boundaries and influence the breeding success of a seabird on a semi-arid oceanic island. Santa Barbara Island is the smallest island in the Channel Islands National Park in California and is part of a region that has been identified as a climate change ‘hotspot’ (Diffenbaugh et al. 2008), where the risk of future unprecedented drought conditions are projected by some models (Cook et al. 2015). On this island, ~21% of the global population of a small nocturnal seabird, the Scripps’s Murrelet (*Synthliboramphus scrippsi*), arrives to breed each spring (Whitworth et al, in prep). Unlike most other seabirds, ocean productivity apparently only has a weak influence on murrelet nest success (Roth et al. 2005), largely because egg predation by an endemic subspecies of deer mice is the main cause of reduced nest success for murrelets on this island (8% to 70% of all eggs laid are lost to mice annually; Drost and Lewis 1995). However, inter-annual differences in reproductive success have not been conclusively linked to variations in mouse density alone either (Murray 1980, Schwemm and Martin 2005, Nur et al. 2013). Instead, murrelet nest success might be influenced by changes in mouse foraging behavior regardless of density (Thomsen and Green 2016), such that reduced food availability for mice during extreme drought could result in higher rates of egg predation compared to years with more abundant rainfall and vegetation. To investigate this, we examined murrelet nest success over a span of 21 years (1993-2013) and evaluated the relative importance of several indicators of terrestrial and marine productivity. We also assessed the impact of changes in nest success and how they influence the resulting population growth rates with a matrix population model.

Materials and Methods

Study area and system

Santa Barbara Island (33º 29’ N, 119º 02 W) is 2.6 km^2 in size and located ~63 km offshore within the Southern California Bight at the southern end of the California Current Large Marine Ecosystem in the northeast Pacific Ocean. The island is the location of one of the largest colonies of Scripps’s Murrelets in the US, a small (~165g) pursuit diving alcid that is endemic to this region and considered by the IUCN to be Vulnerable (Birdlife International 2016). This region of southern California is semi-arid, with the island only receiving an estimated average 21.8 cm of rainfall per year (Orrock et al. 2011). The vegetation of the island consists of mostly non-native grasses (*Avena* spp., *Bromus* spp., and *Hordeum* spp.) in the gently rolling slopes of the interior, while the perimeter has greater cover of native shrubs (e.g. *Leptosyne gigantea, Eriogonum giganteum var. compactum*) and cacti (*Opuntia* spp.; Halvorsen et al. 1988, Junak et al. 1993) that grow on the steep rocky cliffs that tower up to 193 m above the ocean.

Murrelet nest monitoring

The National Park Service and collaborators have been monitoring the nest success of Scripps’s Murrelets on the island annually since the early 1980s, with the exception of the year 2006 (NPS unpub. data). However, here we focus on one of the largest monitoring areas (Cat Canyon) during the time period spanning 1993-2013 because of the consistent data collection that overlaps with other important time series data. Murrelets lay only 1-2 eggs inside shallow rocky crevices or on the ground underneath the dense low-growing shrubs along the island’s sea cliffs (Drost and Lewis 1995). The first egg laid is neglected for ~8 days before the clutch is completed and incubation commences (Murray et al. 1983). Both parents incubate in shifts of ~3 days, until the eggs hatch about 34 days later, at which time the family unit departs the island as a group within 1-2 days (Drost and Lewis 1995). Nest sites in Cat Canyon were checked for contents and status once or twice weekly beginning in early-mid March and the fate of each egg can be reliably determined based on eggshell evidence (Lewis et al. 1988). The main cause of egg loss (~80%) is due to depredation by mice, which usually happens during the initial egg neglect period (Murray et al. 1983; Millus et al. 2007).

Recently obtained video footage of mice consuming murrelet eggs corroborates other evidence, such as teethmarks left on eggshells, that depredation is by mice (NPS unpub. data). Otherwise, eggs sometimes fail due to either abandonment or inviability (Millus et al. 2007). Each year, data from all monitored nests (n= 42-150 eggs) were summarized into mean nest success (total number of eggs hatched / total number of nest attempts) and mean hatching success (total number of eggs hatched / total number of eggs laid).

Marine environment

We obtained several key indices of marine environmental conditions during 1993-2013 that could potentially predict murrelet nest success. This included data for large-scale patterns such as the Pacific Decadal Oscillation (PDO; http://research.jisao.washington.edu/pdo/), the North Pacific Gyre Oscillation (NPGO; http://www.o3d.org/npgo/npgo.php), and the Multivariate ENSO Index (MEI; http://www.esrl.noaa.gov/psd/enso/mei/table.html). We also obtained data for conditions near the island such as sea surface temperature (Station 46025; 33°44'58" N 119°3'10" W, http://www.ndbc.noaa.gov/), Bakun's upwelling index (33°N 119°W; http://orpheus.pfeg.noaa.gov/products/PFELData/upwell/monthly/upindex.mon), and mesozooplankton abundance. Although murrelet diet is not well characterized, the abundance of mesozooplankton was previously identified as potentially being important to murrelet breeding parameters (Roth et al. 2005) and possibly correlates with the availability of other prey types (Koehn et al. 2016). Therefore, following Roth et al. (2005), we compiled mesozooplankton data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI; http://calcofi.org/new.data/index.php/zooplankton), which conducts standardized net tows at long term monitoring stations located in potential murrelet foraging habitat. All marine indices were averaged across March-May to represent breeding season conditions.

Terrestrial environment

Terrestrial productivity

We obtained the Palmer Drought Severity Index (PDSI) for the South Coast climate division in California (available from ftp://ftp.ncdc.noaa.gov/pub/data/cirs/climdiv/), in order to examine inter-annual variation in terrestrial productivity on the island. The PDSI is a widely used metric of meteorological drought that accounts for both precipitation inputs and evaporative loss (mainly via temperature), with negative values indicating the severity of dry spells and positive values indicating the extent of wet spells (Dai 2011). Therefore, the monthly index reflects the accumulation of both current and long-term lagged effects of climate that contribute to soil moisture anomalies compared to normal conditions (Dai 2011), and potentially represents water availability on the semi-arid island better than current rain year precipitation amounts alone. We selected the PDSI value in April of each year to represent conditions that influenced food availability for mice during each murrelet breeding season.

Rainfall data has not been consistently collected on the island over the entire study period so it could not be included in our analyses. However, the impact of variation in rainfall on terrestrial productivity can be observed with satellite-derived measures of greenness such as the Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2011). Variation in NDVI and rainfall has been found to correlate with the abundance of seeds and insects (Batzli and Pitelka 1970; St. Clair et al. 2009; Sofaer et al., 2012; Sweet et al. 2015), which contributes most of the diet of deer mice (Collins et al. 1979; Millus and Stapp 2008). NDVI thus represents an integrated measure of terrestrial conditions so it was important to verify that PDSI and NDVI were related. To do so, we compared the PDSI values with the NDVI value calculated from Landsat TM satellite images of the island captured during March 1993-2011 (mean ordinal date= 77; range: 60-90; NASA LP DAAC, 2014). The NDVI and PDSI values were positively correlated (n=15, rho = 0.6, p =0.02) in the subset of years where NDVI could be calculated.

Deer mouse densities

The National Park Service has also conducted long-term mark-recapture studies of deer mice on the island, and we used the deer mouse densities calculated by Stanley (2012) on the plot nearest to the murrelet monitoring area (~1 km away). Trapping occurred during the month of either March or April from 1993-2013, except for 1994 and 2006 when no data collection occurred. The plot has 100 permanent trap stations, at which one small Sherman live-trap is set over three consecutive nights during trapping sessions (Fellers et al. 1988). In two years when mouse abundance was very low, this level of capture effort was too low to reliably estimate density. In those cases, we used the Minimum Number Known Alive (MNKA) in our models. Otherwise, abundance was calculated in program MARK by Stanley (2012) by using Huggins (1991) closed population capture-recapture models, from which density was derived by dividing abundance by the estimated area trapped as described in Parmenter et al. (2003).

Data analysis

We used R 3.2.1 ("World Famous Astronaut" R Core Team, 2014) to conduct all statistical analyses. We screened all explanatory variables for collinearity and did not include variables together in multiple regression if the correlation was $|r| > 0.5$ (Zuur et al. 2010). Many of the marine variables were highly correlated so we used principal components analysis (PCA) to reduce the number of variables prior to analysis in the candidate model set. The first principal component (PC1) explained a total of 64% of the variability of the six marine environmental variables (NPGO, PDO, MEI, upwelling, SST, and log mesozooplankton volume; Table 1). Log mesozooplankton volume, the NPGO index, and upwelling were positively and moderately loaded on PC1 (0.43, 0.37, and 0.42, respectively), while MEI, local SST, and PDO were all loaded negatively on PC1 (-0.39, -0.42, and -0.4, respectively; Table 1). PC1 thus represents a range of conditions that correspond with colder waters, increased upwelling and higher ocean productivity including higher mesozooplankton amounts. The remaining principal components each explained ≤ 12% of the variation therefore only PC1 was retained for the subsequent linear regression analysis of nest success.

We examined the relationships between murrelet nest success (i.e. the mean number of eggs hatched per nest each year) and the marine and terrestrial environments with linear regression models, weighted by the total number of eggs monitored each year. We used an information-theoretic approach to assess support for alternative mechanisms driving murrelet nest success by comparing models with Akaike's information criterion, adjusted for small sample sizes (AICc; Burnham and Anderson 2002). The candidate model set included eight combinations of marine and/or terrestrial variables that represent different *a priori* hypotheses and a null model (Table 2). Mouse density was log transformed, and all input variables were standardized (mean = 0 and sd= 1) prior to running models so that the magnitudes of the coefficients were comparable (Schielzeth 2010). We also tested for the presence of linear trends in all covariates over time, and repeated the same model selection procedures with the detrended variables with residual regression to confirm whether changes in hatching success were not due to spurious correlations with co-occurring long-term trends (Grosbois et al. 2008). We also conducted a complementary regression tree analysis with the R package '*rpart*' (Therneau et al. 2015) to further explore relationships among all of the marine and terrestrial explanatory variables and to identify the most influential variables on murrelet nest success. All six marine and the three terrestrial variables (PDSI, NDVI, and mouse density) were included and left untransformed for this analysis, as the method is flexible and can handle different types of predictors as well as accommodate missing values (De'Ath and Fabricius 2000). Trees were grown with 10-fold cross validation and with a minimum bucket size of four to prevent overfitting so that only the most relevant variables are retained in the final model (Therneau et al. 2015).

Finally, to examine the potential impacts of observed variation in reproductive success on population growth rates, we created a deterministic matrix population model parameterized with fecundity rates from the 1993-2013 nest success data. We used a stage-structured model that contains juvenile, subadult, and adult stages (Lefkovitch 1965, Caswell 2001). Adult annual survival was set at 0.8305 based on a previously published regression equation relating adult body mass with adult survival in twelve other alcid species (Beissinger and Peery 2007). Juvenile and sub-adult survival rates were then set at 70% and 89% of the adult value, respectively (Sydeman et al. 1998), while sub-adult fecundity rates were set at half of adult rates to account for the delay in the age of first breeding to around the third or fourth year (Gaston 1990, Drost and Lewis 1995) following Beissinger and Peery (2007). Based on the node splits identified by the regression tree analysis, we then created a set of matrices with different mean fecundity rates and compared the resulting asymptotic population growth rates, λ, and stochastic log growth rates (Tuljapukar's approximation λs) calculated with the R package '*popbio*' (Stubben and Milligan 2007). Values of $\lambda > 1$ indicate the rate of population growth while values of $\lambda < 1$ indicate population declines.

Results

A total of 930 murrelet nest attempts were monitored during the years 1993 to 2013 in the Cat Canyon area (range: 30-91 nests per year). Mean nest success over this time period of 19 years was 0.79±0.26 chicks hatched per nest (range: 0.37 - 1.18) while mean hatching success was 49.9±15.1% sd (range 22.1 - 74.7%). Nest productivity and hatching success varied between years but reached its lowest level in 2009 when hatching success was only 22.1% (Figure 1a).

The best-ranked models explaining variation in murrelet nest success included the effects of PDSI and ocean conditions (marine PC1 scores; Table 2). Only the marine PC1 scores demonstrated a significant trend over the study period, indicating an increase in more favorable ocean conditions for murrelets ($F_{1,17}$ =8.518, $p<0.01$, r^2 = 0.29). When this trend was removed, the model rankings remained completely unchanged (Table 2), suggesting that nest success was influenced by these same variables independent of co-occurring long term trends. The top model with detrended data had a slightly improved AICc compared to the non-detrended model (∆AICc = 0.6), therefore, hereafter we focus on the parameter estimates from the top model in the detrended data analysis. Murrelet nest success was positively related to the PDSI (β = 0.19, 95%CI[0.09, 0.29]) indicating that the extremity of drought conditions was associated with increased eggs lost to predation (Figure 2a). Nest success was also positively related to marine PC1 scores (β = 0.06; 95%CI[-0.006, 0.12]; Figure 2b), indicating that colder ocean temperatures and higher ocean productivity was associated with increased nest success. However, despite relatively higher ocean productivity during more recent years, murrelet nest success was extremely low during recent drought years (Figure 1a; Figure 1c). There was no support for a negative relationship between mouse density and murrelet nest success (Table 2, Figure 1d), suggesting that the intensity of egg predation is driven by other factors that influence mouse foraging.

The regression tree analysis produced similar results, where the most important variable determining murrelet nest success was the occurrence of a moderate to extreme drought (< -2.2 on the PDSI scale; Figure 3). Mean nest success for those drought years (0.525 eggs hatched per nest attempt) produced a sharply declining population growth rate (λ = 0.93) when this value was input as the fecundity rate in the matrix population model (Table 3). During closer to normal rainfall conditions or during wet spells (PDSI > -2.2), murrelet nest success was much higher, but how much higher depended on whether there was a positive NPGO index (>1.1; Figure 3). A positive NPGO index signifies higher salinity, nutrients and chlorophyll-*a* in the ocean (Di Lorenzo et al. 2008). When this index was < 1.1, murrelet nest success was moderate (0.85 eggs hatched per nest attempt), and the resulting population growth rate was closer to stability but still declining (λ = 0.98). Murrelets had the highest nest success (1.05 eggs hatched per nest attempt) when the NPGO index was >1.1 and the PDSI was >-2.2, which would be sufficient to produce a stable population growth rate (λ = 1.001; Table 3). However, the mean population growth rate for the entire study period suggested there would be an overall decline (λ = 0.97; Table 3).

Figures and Tables

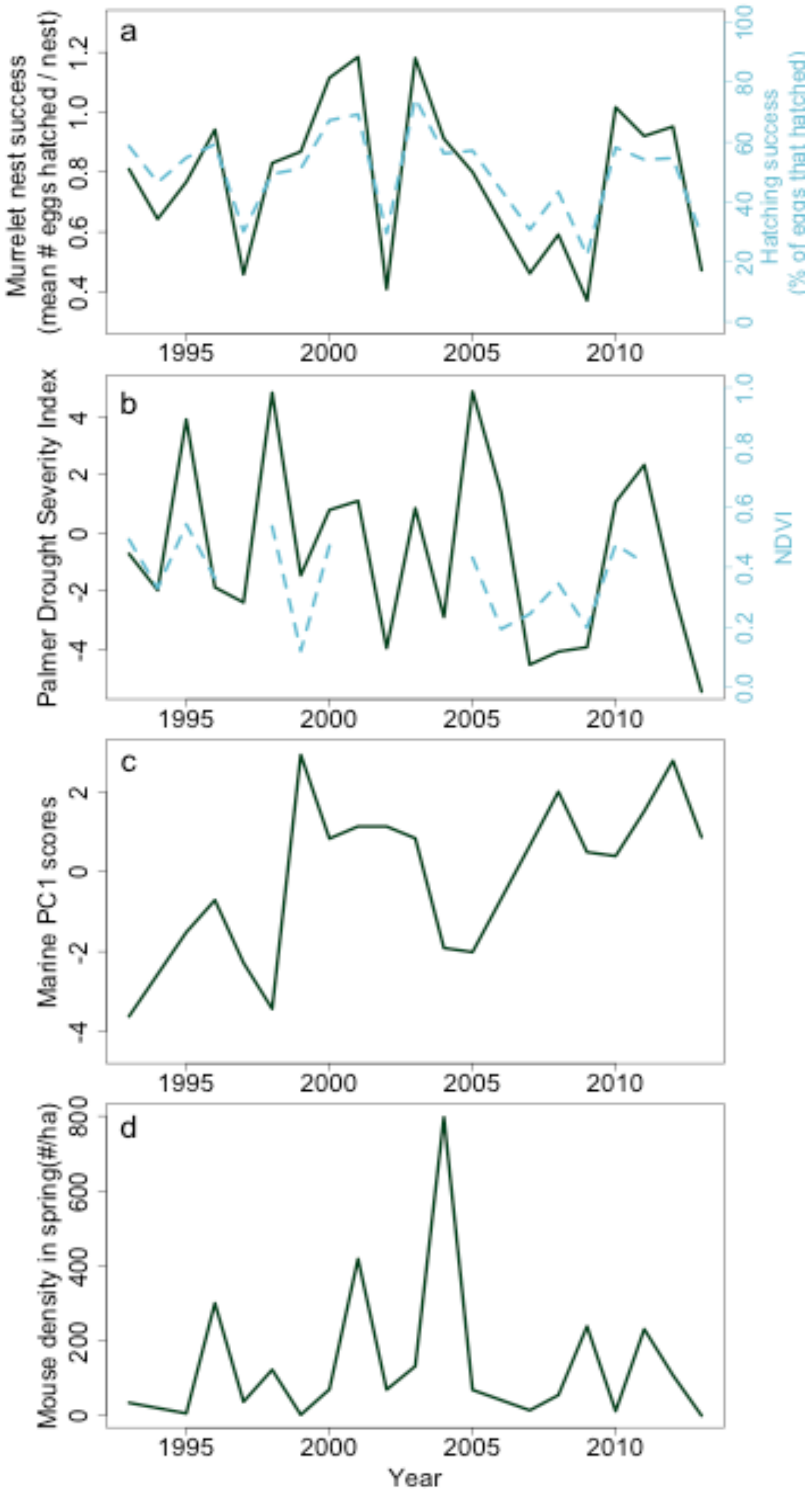
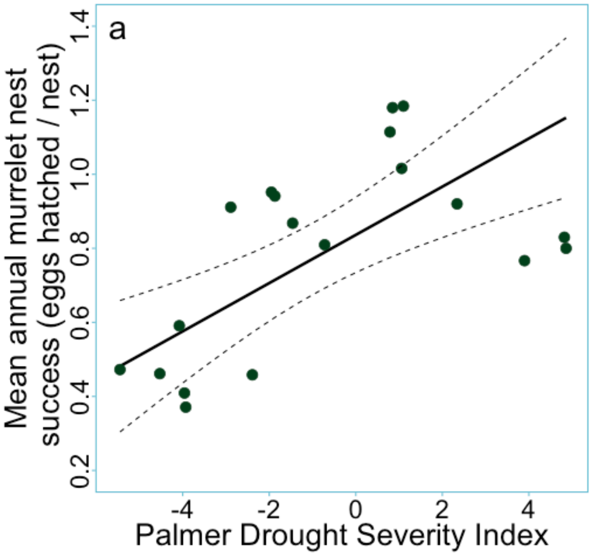


Figure 4-1 Observations from 1993-2013 of **a)** Murrelet nest success, displayed as both the mean # eggs hatched per nest and the proportion of total eggs laid that hatched each year **b)** Terrestrial productivity as measured by Palmer Drought Severity Index (PDSI) where negative number denote the increasing severity of drought, and the Normalized Difference Vegetation Index (NDVI) where higher numbers indicate higher terrestrial productivity **c)** Marine PC1 scores increase over time, with higher scores indicating more favorable conditions for murrelets and **d)** Mouse density during the murrelet breeding season



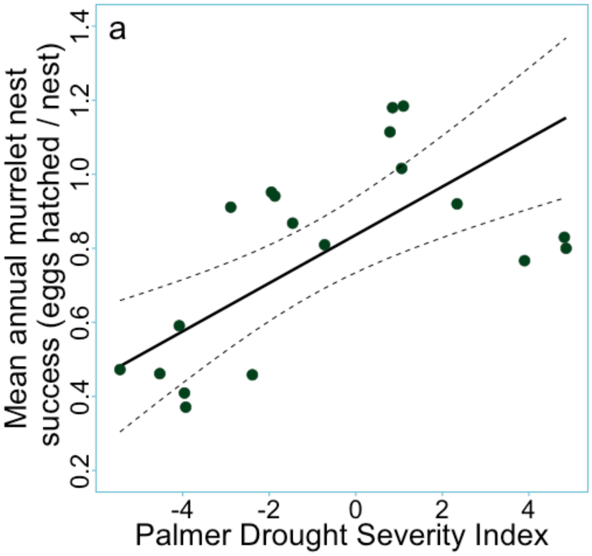


Figure 4-2 **a)** Murrelet nest success and PDSI values in April. Negative values indicate severity of drought; -4 or less = Extreme drought, -3 to -4 = Severe drought, -2 to -3 = Moderate drought. Values above 0 similarly indicate severity of wet spells. **b)** Murrelet nest success and marine PC1 scores. Positive scores indicate more favorable marine environmental conditions for murrelets. Points display the raw data while the solid and dashed lines display the predicted relationship and confidence intervals from the top model.

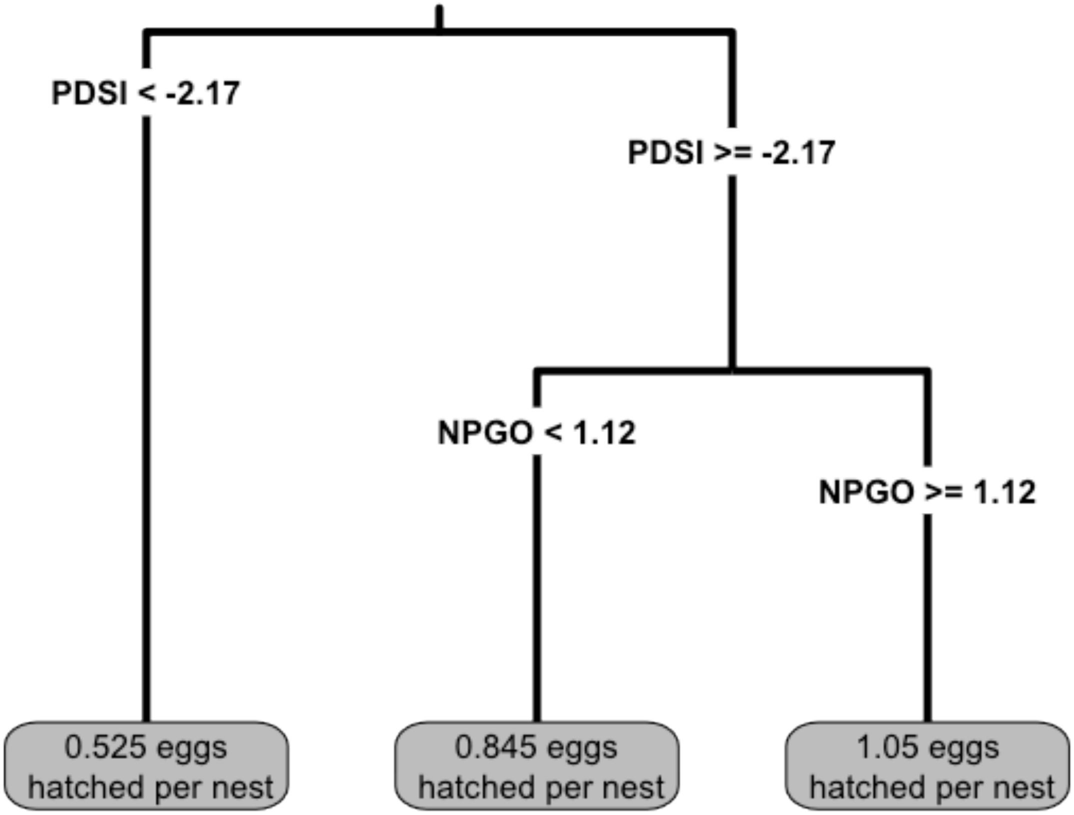


Figure 4-3 Dendrogram of regression tree analysis of murrelet nest success. Very poor nest success occurred during moderate to extreme droughts (PDSI <-2.2), while the greatest nest success occurred when drought was minimal and the NPGO index was positive (>1.12).

Table 4-1 **Loadings of the first three principle components of six marine environmental variables in spring/early summer (March-May) including NPGO (North Pacific Gyre Oscillation), log mesozooplankton volume from CalCOFI (California Cooperative Oceanic Fisheries Investigations) surveys, Bakun's upwelling index, MEI (Multivariate ENSO Index), local SST (sea surface temperature), and the PDO (Pacific Decadal Oscillation).**

Variable	Factor loading		
	PC1	PC2	PC3
NPGO	0.377	-0.670	-0.095
Log mesozooplankton volume	0.434	0.264	-0.482
Upwelling	0.423	0.203	0.232
MEI	-0.395	-0.569	-0.288
Local SST	-0.417	0.100	0.505
PDO	-0.401	0.327	-0.607
Eigenvalue	1.95	0.84	0.78
% Variance	63.6%	11.6%	10.3%

Table 4-2 Model selection results for murrelet hatching success 1993-2013 with detrended and non-detrended environmental variables.

	Murrelet hatching success and detrended environmental variables							Murrelet hatching success and environmental variables (non-detrended)						
Model	ΔAICc	AICc	rank	W_i	k	β	r^2	ΔAICc	AICc	rank	W_i	k	β	r^2
PDSI + Marine PC1	0	0.07	1	0.489	4	0.189 0.061	0.481	0	0.69	1	0.429	4	0.208 0.099	0.464
PDSI	1.36	1.44	2	0.247	3	0.173	0.377	0.74	1.44	3	0.296	3	0.173	0.377
Mice + PDSI + Marine PC1	2.39	2.47	3	0.148	5	0.046 0.174 0.063	0.485	2.17	2.87	2	0.145	5	0.050 0.193 0.105	0.474
Mice + PDSI	3.76	3.84	4	0.074	4	0.041 0.159	0.367	3.14	3.84	4	0.089	4	0.041 0.159	0.367
Mice + PDSI + Mice:PDSI + Marine PC1	6.33	6.41	5	0.021	6	0.064 0.179 0.028 0.067	0.461	6.54	7.23	5	0.016	6	0.054 0.194 0.006 0.105	0.437
Mice + PDSI + Mice:PDSI	7.51	7.58	6	0.011	5	0.045 0.160 0.006	0.326	6.89	7.58	6	0.014	5	0.045 0.160 0.006	0.326
Null (intercept only)	8.6	8.67	7	0.007	2	-	-	7.98	8.67	7	0.008	2	-	-
Marine PC1	10.3	10.3	8	0.003	3	0.042	0.005	10.7	11.4	8	0.002	3	0.023	-0.051

Table 4-3 Comparison of population growth rates based on the regression tree node splits versus the overall mean. Both the asymptotic population growth rate (λ) and the stochastic log growth rate (λs) estimated by Tuljapukar's approximation are shown.

Environmental conditions	Population growth rate (λ)	Stochastic log growth rate (λs)
Overall mean	0.969	-0.031 (n=19)
PDSI < -2.2	0.932	-0.070 (n=7)
PDSI > -2.2 & NPGO <1.1	0.977	-0.024 (n=6)
PDSI > -2.2 & NPGO >1.1	1.001	0.002 (n=6)

Discussion

Seabirds are often heralded as sentinels of ocean climate variability and change, as is demonstrated with other long-term monitoring studies of their reproductive success on islands (e.g. Ainley 1990; Wanless et al. 2007; Divoky et al. 2015). In this study, however, we found that murrelet nest success since the 1990s was instead mainly associated with a different hallmark of climate variability, the severity of drought (Figure 2 and 3). Specifically, our results support the hypothesis that climate driven changes in terrestrial productivity primarily drove murrelet nest success via a cross-ecosystem cascade of indirect interactions with mice. Furthermore, our study demonstrates that the effect of drought on this key vital rate is also potentially substantial enough to trigger population declines in a threatened nocturnal seabird (Table 3). In 2009 and 2013, only 22.1- 28.6% of eggs successfully hatched (Figure 1a) as a result of very high egg predation rates by mice (Harvey et al. 2012, Howard et al. 2014). Likewise, other breeding land birds in this region lose more nests to rodents during drought years, but unlike murrelets, they are primarily directly affected by limited terrestrial food availability themselves (Morrison and Bolger 2002; Chase et al. 2005, Preston and Rotenberry 2006, Borgman and Wolf 2016). Therefore, the observed increases in mouse predation of murrelet eggs are consistent with the effects of drastic declines in terrestrial resources for mice as a result of drought.

Given the context of fluctuating resources on the island, there are compelling reasons why drought would be a strong indicator of island conditions that lead to increased egg predation. During a drought, common island plants such as *Avena* spp.

produce fewer seeds and have reduced biomass (Ewing and Menke 1983). Notably, the NDVI in some drought years indicated there was almost no green vegetation in April (Figure 1b; Pettorelli et al. 2011). Secondly, eggs themselves might be an important source of nutrients and water to mice during droughts, which could also increase egg predation as rodents seek needed moisture to survive (Norman 1975). This is supported by stable isotope analysis, where there is an apparent shift in the diet of mice towards more succulent C_4 plants during drought years (Thomsen, unpub. data). Finally, the availability of food resources can influence the risks that prey, such as mice, might be willing to take while foraging (Brown and Kotler 2004; Laundre et al. 2014; Riginos 2015). Persistent severe drought would lead to declines in the abundance of mice (Spevak 1983, Morton et al. 1995), but also their main predators, Barn Owls (*Tyto alba*; Drost and Fellers 1991, Cruz-McDonnell and Wolf 2016). Mice on the island drastically reduced their foraging activity when owls were more abundant (Thomsen and Green 2016), therefore, drought stressed mice likely consume more eggs when there are fewer risks from predators, but also greater need, to do so.

Despite the relatively large influence of the terrestrial environment on murrelet nest success, results from the regression tree analysis suggest that ocean climate conditions were still important in determining whether there was higher than average murrelet nest success (Figure 3). Higher PC1 scores and a positive (>1.1) NPGO index were associated with increased breeding success, and these favorable conditions likely contribute to breeding parameters such as slight increases in mean clutch size (Roth et al. 2005; Thomsen, in prep), as well as a reduction in days of egg neglect (Murray 1980). Poor foraging conditions can increase the extent of egg neglect in other alcids during incubation (Blight et al. 2010), which can leave eggs much more vulnerable to predation by rodents (Ronconi and Hipfner 2009). Interestingly, the NPGO index has also been identified as an important variable explaining seabird reproductive success on other islands in California during roughly the same time period, in contrast to the historically predominant influence of the El Nino (Schmidt at el. 2014). However, without detailed studies linking foraging effort, marine habitat use and diet with murrelet breeding success, we cannot yet say for certain which mechanisms are most important. Future studies should address this crucial data gap, as the ocean is changing in ways that are increasingly negative for seabirds and other marine predators (Croxall et al. 2012). Arguably, the loss of highly successful breeding seasons as a result of higher ocean productivity coincident with non-drought years could be just as detrimental to long-term persistence as would an increase in very poor breeding seasons due to more frequent severe drought.

For long-lived seabirds with a low reproductive rate, including murrelets, adult survival is the most sensitive demographic parameter determining population trajectories and as such conservation efforts tend to prioritize protection of adults over other vital rates (Saether and Bakke 2000). However, despite this, if the mean reproductive rate is low enough, the population will still decline. Results from our matrix model suggest this key vital rate for murrelets has been mostly below replacement and would lead to an expected average ~3% annual decline over the study period (Table 3), which is similar in magnitude to the estimated population trend on Santa Barbara Island (Burkett et al. 2002, Nur et al. 2013). Although nest success has tended to be higher in other parts of the island, the overall mean is still fairly low (0.813 eggs hatched/pair; Sydeman et al. 1998, Nur et al. 2013). Thus, if we assume that the estimate of adult survival is representative of murrelets on the island, poor reproductive success could alone be largely responsible for an observed decline, as has been noted previously (Sydeman 1998). Furthermore, predicted increases in the occurrence of severe droughts could mean murrelets are more likely to have years of drastically low nest productivity. However, the matrix model assumes a known and constant adult survival rate, which in reality can vary substantially between years from predators, such as Barn Owls and Peregrine Falcons (*Falco peregrinus*) that consume adults (Chapter 2; Drost and Lewis 1995). Therefore, the optimal strategy for conservation of murrelets on Santa Barbara Island will likely need to address both life stages.

Ultimately, overall murrelet nest success appears to be influenced by a combination of factors from both the marine and terrestrial environments. However, in southern California both of these are coupled via the influence of the ocean on regional precipitation patterns and may mediate murrelet nest success in opposing ways. For example, under poor ocean conditions, the resulting slight increase in one-egg clutches, as well as an increase in egg neglect after incubation begins (Murray 1980), would leave murrelets more vulnerable to the terrestrial factors influencing egg predation or survival to hatching. However, oftentimes, increased SST and the resulting poor foraging conditions for murrelets are the same conditions that usually lead to increased rainfall in this region (Schoner and Nicholson 1989; Black et al. 2014). This suggests the possibility that the negative effects of poor ocean conditions on breeding success can be partially offset in some years, if eggs are more likely to survive when terrestrial productivity is higher. Conversely, cool-phase PDO and La Nina conditions tend to be associated with drought conditions in this region (McCabe-Glynn et al. 2013). However, even with relatively better ocean conditions, first laid egg is always at least neglected for the first ~8 days (Drost and Lewis 1995), and is most vulnerable to predation by mice during this time and especially so during drought conditions. It remains to be seen how under global climate change whether these connections between SST and winter precipitation in southern California will remain stable or become more variable (Kam and Sheffield 2016).

It is well known that climate change will affect ecological processes (Parmesan 2006), but uncertainty remains around the effects of increasing drought or how often species interactions could even accelerate the effects of drought (He et al. 2017). In this study, we found that the severity of drought on an oceanic island was associated with negative impacts on the breeding success of a seabird via a cross-ecosystem cascade. In 2013, much of California was in an exceptional drought of a magnitude that had not been experienced for over ~1200 years (Griffin and Anchukaitis 2014). As the PDSI is projected to remain negative for much of the twenty-first century (Gutzler and Robbins 2011), this has potentially worrisome implications for murrelets breeding on Santa Barbara Island. The results of our long-term study therefore have wider implications about the profound impact of drought on species interactions in arid environments and we suggest that other island species affected by rodent predation might be similarly affected.

References

Ainley, D. G. 1990. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford University Press.

Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, B. D. Wardlow, C. H. Flather, P. D. Culbert, and V. C. Radeloff. 2010. Combined effects of heat waves and droughts on avian communities across the conterminous United States. Ecosphere 1:UNSP 12.

Barton, B. T., and A. R. Ives. 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. Ecology 95:486–494.

Beier, C., C. Beierkuhnlein, T. Wohlgemuth, J. Penuelas, B. Emmett, C. Koerner, H. J. de Boeck, J. H. Christensen, S. Leuzinger, I. A. Janssens, and K. Hansen. 2012. Precipitation manipulation experiments - challenges and recommendations for the future. Ecology Letters 15:899–911.

Beissinger, S. R., and M. Zachariah Peery. 2007. Reconstructing the historic demography of an endangered seabird. Ecology 88:296–305.

Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. Garcia-Reyes, R. R. Rykaczewski, S. J. Bograd, and W. T. Peterson. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. Science 345:1498–1502.

Blight, L. K., D. F. Bertram, T. D. Williams, and L. Cowen. 2010. Interannual variation in egg neglect and incubation routine of rhinoceros auklets Cerorhinca monocerata during the 1998-1999 El Niño/La Niña events. Marine Ornithology 38:11–15.

Borgman, C. C., and B. O. Wolf. 2016. The indirect effects of climate variability on the reproductive dynamics and productivity of an avian predator in the arid Southwest. Oecologia 180:279–291.

Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. J. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America 102:15144–15148.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Burnham, K. P., and D. R. Anderson, editors. 2004. Model Selection and Multimodel Inference. Springer New York, New York, NY.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates.

Catenazzi, A., and M. A. Donnelly. 2007. The Ulva connection: marine algae subsidize terrestrial predators in coastal Peru. Oikos 116:75–86.

Chase, M. K., N. Nur, and G. R. Geupel. 2005. Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: A long-term study. Auk 122:571–592.

Climate Impacts in the U.S. Islands | Climate Change Impacts | US EPA. (n.d.). . https://www.epa.gov/climate-impacts/climate-impacts-us-islands.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:e1400082.

Croxall, J. P., S. H. M. Butchart, B. Lascelles, A. J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22:1–34.

Cruz-McDonnell, K. K., and B. O. Wolf. 2016. Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. Global Change Biology 22:237–253.

Dai, A. 2011. Drought under global warming: a review. Wiley Interdisciplinary Reviews-Climate Change 2:45–65.

Dai, A. 2013. Increasing drought under global warming in observations and models. Nature Climate Change 3:52–58.

De La Maza, M., M. Lima, P. L. Meserve, J. R. Gutierrez, and F. M. Jaksic. 2009. Primary production dynamics and climate variability: ecological consequences in semiarid Chile. Global Change Biology 15:1116–1126.

De’ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

Deguines, N., J. S. Brashares, and L. R. Prugh. 2016. Precipitation alters interactions in a grassland ecological community. Journal of Animal Ecology.

Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Riviere. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35:L08607.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences 112:3931–3936.

Divoky, G. J., P. M. Lukacs, and M. L. Druckenmiller. 2015. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. Progress in Oceanography 136:151–161.

Drost, C., and G. Fellers. 1991. Density Cycles in an Island Population of Deer Mice, *Peromyscus-Maniculatus*. Oikos 60:351–364.

Ewing, A. L., and J. W. Menke. 1983. Reproductive potential of *Bromus mollis* and *Avena barbata* under drought conditions. Madrono:159–167.

Gaston, A. 1990. Population Parameters of the Ancient Murrelet. Condor 92:998–1011.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin’s finches. Science 296:707–711.

Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? Geophysical Research Letters 41:9017–9023.

Grosbois, V., O. Gimenez, J.-M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Moller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357–399.

Gutzler, D. S., and T. O. Robbins. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics 37:835–849.

Halvorson, W., D. Fenn, and W. Allardice. 1988. Soils and Vegetation of Santa-Barbara Island, Channel-Islands-National-Park, California, Usa. Environmental Management 12:109–118.

He, Q., B. R. Silliman, Z. Liu, and B. Cui. 2017. Natural enemies govern ecosystem resilience in the face of extreme droughts. Ecology Letters 20:194–201.

Huang, A. C., J. E. Elliott, K. M. Cheng, K. Ritland, C. E. Ritland, S. K. Thomsen, S. Hindmarch, and K. Martin. 2016. Barn owls (*Tyto alba*) in western North America: phylogeographic structure, connectivity, and genetic diversity. Conservation Genetics 17:357–367.

Huggins, R. 1991. Some Practical Aspects of a Conditional Likelihood Approach to Capture Experiments. Biometrics 47:725–732.

Junak, S., C. A. Drost, R. N. Philbrick, M. Daily, and others. 1993. A revised flora of Santa Barbara Island.

Kam, J., and J. Sheffield. 2016. Increased Drought and Pluvial Risk over California due to Changing Oceanic Conditions. Journal of Climate 29:8269–8279.

Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880–883.

Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. Ecological Modelling 335:87–100.

Laundre, J. W., L. Hernandez, P. Lopez Medina, A. Campanella, J. Lopez-Portillo, A. Gonzalez-Romero, K. M. Grajales-Tam, A. M. Burke, P. Gronemeyer, and D. M. Browning. 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology 95:1141–1152.

Lefkovitch, L. P. 1965. Study of Population Growth in Organisms Grouped by Stages. Biometrics 21:1–18.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecology Letters 6:673–679.

McCabe-Glynn, S., K. R. Johnson, C. Strong, M. Berkelhammer, A. Sinha, H. Cheng, and R. L. Edwards. 2013. Variable North Pacific influence on drought in southwestern North America since AD 854. Nature Geoscience 6:617–621.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: desertification synthesis.

Millus, S. A., and P. Stapp. 2008. Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California. Canadian Journal of Zoology 86:1031–1041.

Millus, S. A., P. Stapp, and P. Martin. 2007. Experimental control of a native predator may improve breeding success of a threatened seabird in the California Channel Islands. Biological Conservation 138:484–492.

Milly, P. C. D., K. A. Dunne, and A. V. Vecchia. 2005. Global pattern of trends in streamflow and water availability in a changing climate. Nature 438:347–350.

Miriti, M. N., S. Rodriguez-Buritica, S. J. Wright, and H. F. Howe. 2007. Episodic death across species of desert shrubs. Ecology 88:32–36.

Morrison, S. A., and D. T. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133:315–324.

Morton, M., M. Morrison, L. Hall, and M. Pereyra. 1995. Life-History Parameters in Mice Exposed to a Prolonged Drought. Southwestern Naturalist 40:18–28.

Murray, K. G. 1980. Predation by deer mice on Xantus' Murrelet eggs on Santa Barbara Island, California. M.Sc. thesis. California State Univ., Northridge.

Murray, K. G., K. Winnett-Murray, and G. L. Hunt. 1980. Egg neglect in Xantus' murrelet. Pages 186–195 Proceedings of the Colonial Waterbird Group. JSTOR.

Murray, K., K. Winnettmurray, Z. Eppley, G. Hunt, and D. Schwartz. 1983. Breeding Biology of the Xantus-Murrelet. Condor 85:12–21.

Norman, F. I. 1975. The murine rodents Rattus rattus, exulans and norvegicus as avian predators. Atoll Research Bulletin 182:1–13.

Nurse, L. A., R. F. Mclean, J. Agard, L. P. Briguglio, V. Duvat-Magnan, N. Pelesikoti, E. Tompkins, and A. Webb. 2014. Small islands. Cambridge University Press.

Orrock, J. L., B. F. Allan, and C. A. Drost. 2011. Biogeographic and Ecological Regulation of Disease: Prevalence of Sin Nombre Virus in Island Mice Is Related to Island Area, Precipitation, and Predator Richness. American Naturalist 177:691–697.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15:232–237.

Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. M. Shenk, T. R. Stanley, and G. C. White. 2003. Small-mammal density estimation: A field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73:1–26.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in ecology & evolution 20:503–510.

Power, S., F. Delage, C. Chung, G. Kociuba, and K. Keay. 2013. Robust twenty-first-century projections of El Nino and related precipitation variability. Nature 502:541–545.

Preston, K. L., and J. T. Rotenberry. 2006. Independent effects of food and predator-mediated processes on annual fecundity in a songbird. Ecology 87:160–168.

Riginos, C. 2015. Climate and the landscape of fear in an African savanna. Journal of Animal Ecology 84:124–133.

Ronconi, R. A., and J. M. Hipfner. 2009. Egg neglect under risk of predation in Cassin's Auklet (Ptychoramphus aleuticus). Canadian Journal of Zoology 87:415–421.

Roth, J. E., W. J. Sydeman, and P. L. Martin. 2005. Xantus's Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. Marine Ornithology 33:115–121.

Ruffino, L., J. Russell, and E. Vidal. 2013a. Anthropogenic subsidies mitigate environmental variability for insular rodents. Oecologia 172:737–749.

Ruffino, L., J. Russell, and E. Vidal. 2013b. Anthropogenic subsidies mitigate environmental variability for insular rodents. Oecologia 172:737–749.

Russell, J. C., and L. Ruffino. 2012. The influence of spatio-temporal resource fluctuations on insular rat population dynamics. Proceedings of the Royal Society B-Biological Sciences 279:767–774.

Rymer, T. L., N. Pillay, and C. Schradin. 2016. Resilience to Droughts in Mammals: A Conceptual Framework for Estimating Vulnerability of a Single Species. Quarterly Review of Biology 91:133–176.

Saether, B. E., and O. Bakke. 2000a. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Saether, B. E., and O. Bakke. 2000b. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schmidt, A. E., L. W. Botsford, J. M. Eadie, R. W. Bradley, E. Di Lorenzo, and J. Jahncke. 2014. Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. Marine Ecology Progress Series 499:249-U501.

Schmidt, K. A., and R. S. Ostfeld. 2008a. Numerical and behavioral effects within a pulse-driven system: Consequences for shared prey. Ecology 89:635–646.

Schmidt, K. A., and R. S. Ostfeld. 2008b. Numerical and behavioral effects within a pulse-driven system: Consequences for shared prey. Ecology 89:635–646.

Schonher, T., and S. Nicholson. 1989. The Relationship Between California Rainfall and Enso Events. Journal of Climate 2:1258–1269.

Seager, R., and G. A. Vecchi. 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. Proceedings of the National Academy of Sciences of the United States of America 107:21277–21282.

Sofaer, H. R., T. S. Sillett, S. I. Peluc, S. A. Morrison, and C. K. Ghalambor. 2013. Differential effects of food availability and nest predation risk on avian reproductive strategies. Behavioral Ecology 24:698–707.

Sperry, J. H., and P. J. Weatherhead. 2008. Prey-Mediated Effects of Drought on Condition and Survival of a Terrestrial Snake. Ecology 89:2770–2776.

Spevak, T. 1983. Population-Changes in a Mediterranean Scrub Rodent Assembly During Drought. Southwestern Naturalist 28:47–52.

St Clair, S. B., E. A. Sudderth, C. Castanha, M. S. Torn, and D. D. Ackerly. 2009. Plant responsiveness to variation in precipitation and nitrogen is consistent across the compositional diversity of a California annual grassland. Journal of Vegetation Science 20:860–870.

Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Stubben, C., B. Milligan, and others. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1–23.

Sweet, S. K., A. Asmus, M. E. Rich, J. Wingfield, L. Gough, and N. T. Boelman. 2015. NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. Ecological Applications 25:779–790.

Sydeman, W. J., N. Nur, and P. Martin. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-Petrel (*Oceanodroma homochroa*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*). Final report to the United States Geological Survey, Biological Resources Division, Species at Risk Program. Stinson Beach, CA: PRBO Conservation Science. 74 pp

Therneau, T. M., and E. J. Atkinson. 2015. An introduction to recursive partitioning using the RPART routines. Rochester: Mayo Foundation.

Thomsen, S. K., and D. J. Green. 2016. Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island. Ecology 97:3530–3537.

Thornton, P. K., P. J. Ericksen, M. Herrero, and A. J. Challinor. 2014. Climate variability and vulnerability to climate change: a review. Global Change Biology 20:3313–3328.

Wanless, S., M. Frederiksen, F. Daunt, B. E. Scott, and M. P. Harris. 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. Progress in Oceanography 72:30–38.

Whitworth, D. L., H. R. Carter, and F. Gress. 2013. Recovery of a threatened seabird after eradication of an introduced predator: Eight years of progress for Scripps's murrelet at Anacapa Island, California. Biological Conservation 162:52–59.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Chapter 5. Could the effects of resources pulses on shared predation explain murrelet population declines?

Abstract

Predator management can sometimes reverse population declines in threatened species, but if mesopredator release occurs, management may provide little of the anticipated benefits. On one of the smallest islands in the Channel Islands National Park in California, breeding Scripps's Murrelets (*Synthliboramphus scrippsi*), a rare nocturnal seabird, are killed in large numbers by Barn Owls (*Tyto alba*) in some years. Here, we assess the potential outcomes for murrelets if owl management is undertaken to reduce these hyperpredation events, given the potential for mesopredator release of an endemic deer mouse that is the primary prey for owls. Mice can depredate well over half of all murrelet eggs laid in a given year, and this proportion declines as owl abundance increases through a behaviorally mediated cascade. Variations in rainfall influence terrestrial productivity on this semi-arid island, and outbreaks in the endemic deer mouse population drive peaks in owl abundance. When the mouse population subsequently crashes, this leads to peaks in murrelet predation by owls. Climate-driven indirect interactions with predators therefore influence both survival and nest success of adult murrelets, at times both positively and negatively. We assessed the potential outcomes for murrelets if owls are removed completely or kept at a low abundance, compared to no management interventions, with a mathematical model of island community dynamics that includes negative direct effects and positive indirect effect of owls on murrelets. We incorporated climatic variation by using projected rainfall variations for the years 2020-2050 from downscaled CMIP5 climate models. We found that neither owl management scenario resulted in substantial increases in murrelet population abundance. This appeared to be entirely due to the loss or weakening of the positive indirect effects of

owls on egg survival. Our study highlights the importance of considering both direct and indirect effects of predators when evaluating potential conservation strategies.

Introduction

Predator-prey dynamics have been increasingly recognized for their potential role in contributing to species declines (e.g. DeCesare et al. 2010; Serrouya et al. 2015). In such cases, management of predators is commonly undertaken and can sometimes lead to unequivocal successes in reversing population declines in species at risk (Wittmer et al. 2013; Whitworth et al. 2014; Jones et al. 2016). For example, on oceanic islands the complete eradication of feral cats has led to remarkable recoveries for rare island endemics (Nogales et al. 2004; Brooke et al. 2017). However, in other cases, predator control may lead to unexpected outcomes or provide little of the anticipated benefits for the species at risk (Coté and Sutherland 1997; Prugh and Arthur 2015). Unintended consequences may happen when elimination or reduction in the abundance of top predators leads to increases in predation by smaller mesopredators that impact the prey at risk (i.e. mesopredator release; Crooks and Soule 1999; Rayner et al. 2007). That is, top predators can have positive indirect effects on prey by suppressing the abundance of the mesopredator, or even by simply altering the mesopredator's foraging behavior (Thomsen and Green 2016). Therefore, it is important to consider both direct and indirect effects to determine optimal predator management schemes (Zavaleta et al. 2001).

The Barn Owl (*Tyto alba*) is one of the most widely distributed avian predator species in the world, and has a flexible generalist diet that is usually predominantly rodents (Taylor 2004). Barn owls naturally occur on many oceanic islands, and have actually been introduced intentionally for rodent control on other islands (CABI 2017). However, introduced Barn Owls have often failed at controlling rodents while also contributing to additional mortality of native species (CABI 2017). On Santa Barbara Island in southern California, where the owls occur naturally (Collins and Jones 2015, Huang et al. 2015), management of the owl population has been considered to reduce predation on a rare species of nocturnal seabird, the Scripps's Murrelet (*Synthliboramphus scrippsi*: Burkett et al. 2003; Nur et al. 2013). Owls on this 2.6 km^2

semi-arid island mostly consume an endemic deer mouse (*Peromyscus maniculatus elusus*), but murrelets provide an alternative prey when mouse abundance is low (Chapter 2). These mice can also reach extremely high densities as a consequence of heavy winter rainfall that is associated with ENSO events (Drost and Fellers 1991; Chapter 2). This rainfall leads to increases in terrestrial productivity including the primary food sources for mice (seeds and insects; Collins et al. 1979). Irruptions in the mouse population drive peaks in owl abundance, which precedes peaks in murrelet predation when the mouse population subsequently crashes (i.e. hyperpredation, Chapter 2). In some years, owl predation of murrelets can be up to ~15% of the estimated breeding population on the island (172 murrelets; Chapter 2). Murrelets are relatively long-lived seabirds (Drost and Lewis 1995), so such extreme mortality events would be expected to be detrimental to long-term population growth (Frederiksen et al. 2008).

However, Barn Owls on Santa Barbara Island also have positive indirect effects on murrelets through their influence on mice (Thomsen and Green 2016). Mice can depredate up to 70% of all murrelet eggs laid in a given year (Drost and Lewis 1995; Nur et al. 2013). This proportion declines as owl abundance increases through a behaviorally mediated cascade, where mice eat fewer eggs as predation risk by owls increases (Thomsen and Green 2016). At the same time, the magnitude of egg predation can also vary with the availability of primary resources for mice (seeds and insects; Murray 1980; Chapter 4). This means that both survival and nest success of adult murrelets are influenced by climate-driven indirect interactions with predators, at times both negatively and positively (Figure 1). An enormous challenge, then, is to determine if owl management would be beneficial to murrelets despite the potential for mesopredator release. A previously developed matrix population model of murrelet population growth did find that decreasing adult mortality from owls would be beneficial, but, if egg predation also increased in response, the increased survival may not be enough to reverse murrelet population decline (Nur et al. 2013). However, although matrix models are frequently used in conservation biology as decision support tools (e.g. Crouse et al. 1987; Hunter et al. 2010; Wootton and Bell 2014), those models rarely incorporate any potential feedback loops of predator removal on other species' direct and indirect effects on the species at risk (Sabo 2008).

Here, we evaluate the potential effectiveness of owl management for increasing the breeding population of Scripps's Murrelets on Santa Barbara Island. To do so, we develop a mathematical model of island community dynamics that incorporates the direct and indirect effects of mice and owls empirically demonstrated to be important for murrelets. We consider the potential outcomes for murrelets if owl management is not implemented, compared to two different owl management strategies, given projected rainfall variations from climate models. Precipitation in this region is predicted to be either more variable (Berg and Hall 2015; Yoon et al. 2015), or lead to more extreme or frequent drought (Cook et al. 2015), either of which could impact murrelets more severely than in the past regardless of management. The first management option we consider is the complete elimination of the owl population, and the second is an management scheme that keeps the owl population at low abundance in order to maintain some positive indirect effects while eliminating the high peaks in owl abundance that lead to enhanced predation on murrelet adults.

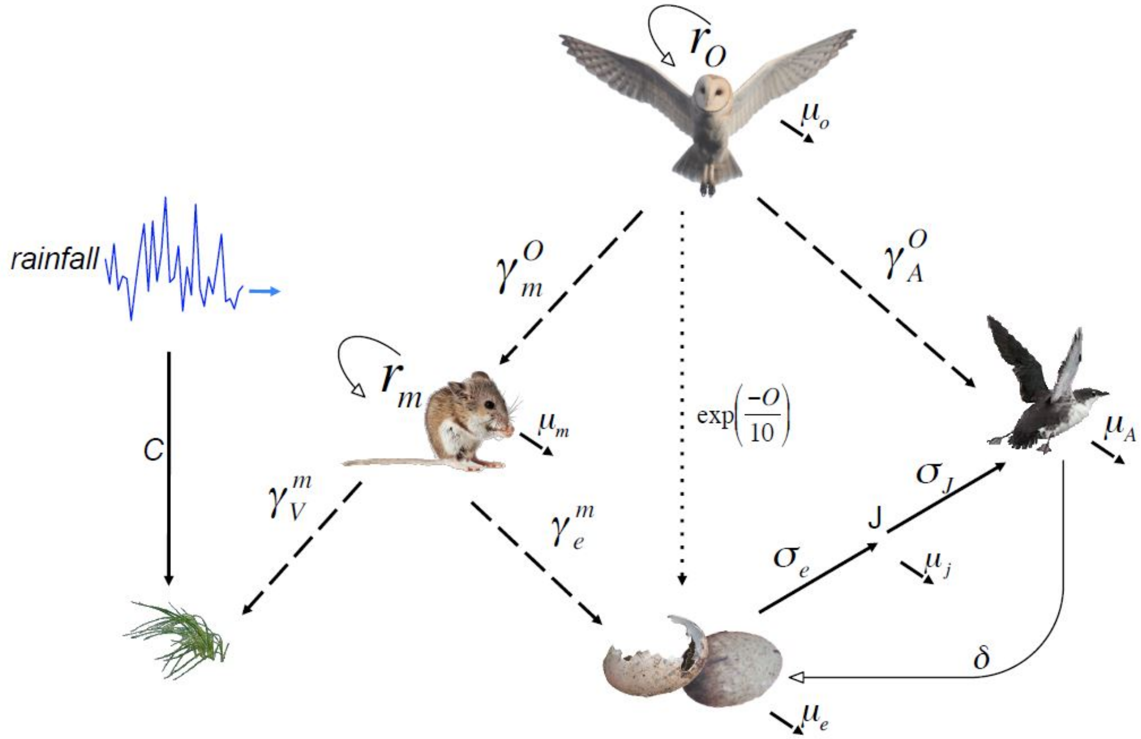


Figure 5-1 Conceptual model of the relationships between climate (C), vegetation (V), mice (m), owls (O) and murrelet eggs (E), juveniles/subadults (J), and adults (A). Changes in rainfall drives annual variation in the carrying capacities of mice and owls, both of which have annual growth (*r*), mortality (μ) and predation rates (γ) on primary (seeds/insects and mice, respectively) and alternative prey (murrelet eggs and adults, respectively). The murrelet population grows at a rate determined by the number of breeding pairs that lay eggs (δ), and transition to a juvenile / subadult phase (σ) that then become breeding adults. See methods and Appendix C for further details.

Materials and Methods

Our model consists of a set of coupled nonlinear ordinary differential equations (ODE) that are parameterized with empirical data for this system and described in detail in Appendix C. Here, we will only describe the key components of the model (Figure 1). Briefly, murrelets are represented by three stages in the model, eggs, juveniles/subadults, and adults. The murrelet population grows at a rate determined by the number of eggs laid each year per breeding pair, which corresponds to an average clutch size and the number of pairs of breeding adults modified by a fixed carrying capacity. Eggs are then subject to some mortality due to reasons other than mouse predation, while being mainly influenced by the predation rate of mice on eggs. This predation rate is relative to climate driven changes in vegetation, which is the primary source of food for mice. In addition, egg predation is also influenced by a positive indirect effect of owls, which was modeled as a decelerating function of increasing owl abundance. Surviving eggs transition to a juvenile/subadult stage where murrelets are entirely at sea and therefore neither breeding nor vulnerable to predation by owls. Finally, murrelets transition from the juvenile/subadult stage to adults, which are then subject to predation by owls in addition to other sources of mortality. This predation rate of owls on murrelets is relative to the more abundant mice as an alternative prey for owls.

Mice and owls are each characterized by their intrinsic growth rates modified by their carrying capacities, and natural mortality rates. Mice are also subject to additional mortality from predation by owls, which is inversely proportional to the abundance of adult murrelets. Carrying capacities of mice and owls are determined by their predation rates on their main respective prey, which is then modified proportionally by variability in rainfall. To generate the time series vectors representing rainfall driven changes in carrying capacities, we obtained precipitation data for 28 of the Coupled Model Intercomparison Project Phase 5 (CMIP5) climate projections that have recently been statistically downscaled for California for the years 2007-2100 (Pierce et al. 2014, data accessed from: http://cida.usgs.gov/thredds/dodsC/loca_future). We used the [representative concentration pathway] RCP8.5 climate scenarios, which assume ‘business as usual’ carbon emissions rates (Riahi et al. 2011). Daily projected precipitation amounts from each model were then summed into rain year totals beginning in April, because most rainfall in this region occurs from November to March (Yoho et al. 1999). This time series was then rescaled into proportional changes in annual carrying capacity of mice and owls, which produces realistic values in population sizes and predation levels (see Appendix A and C).

Data Analysis

All models and analyses were performed in R 3.2.1 (‘World Famous Astronaut’ R Core Team, 2014). Differential equations were solved numerically with the R package ‘deSolve’ (Soetaert et al. 2010; Appendix C). For each scenario, we compared the overall mean abundance of adult murrelets and mean murrelet population change *r* =log(Nt+1/Nt), for each of the 28 CMIP5 climate models in the near future (2020 to 2050). We also compared the mean numbers of murrelets killed by owls and the mean percentage of eggs lost to predation by mice to determine how these two key parameters were influenced by owl management. For scenario A, we considered what would happen if owls were removed completely from the island. Secondly, we compared the outcome if owls were managed so that their abundance was controlled to never reach above ~25% of the peak abundance of individuals (scenario B). This threshold was selected because this was the model estimated abundance of owls when there was no climatic variation (see Appendix C for details). Finally, we used correlation analyses (spearman’s rho) to compare the relationships between egg predation and both mouse and owl abundance for each model run to determine if there was a loss of positive indirect effects as a consequence of owl management. We report effect sizes but not p-values because their use is generally considered uninformative with simulation model outcomes (White et al. 2013). Finally, we conducted a global sensitivity analysis by simulating the model with a range of parameter values, followed by examining relative variable importance with a random forest analysis (details in Appendix C).

Results

Predation and population dynamics simulated by the model were similar to those observed on the island over the last three decades (Appendix C). For each of the 28 CMIP5 climate scenarios, the mean murrelet population varied substantially between years, from as few as 868 to as many as 1123 adults (overall mean ± sd; 971±47; Figure 2a). Annual predation rates by owls also varied, from as few as 2 to as many as 266 murrelets killed by owls per year, depending on the climate scenario (89±42; Figure 2c). Overall, climate models that predicted higher mean rainfall amounts tended to be correlated with higher mean numbers of murrelets killed by owls (rho=0.91, n=28). This was primarily due to the lagged effect of a heavy rainfall year increasing the mouse and owl populations, followed by declines which results in hyperpredation in some years (Chapter 2). Despite this interannual variation, overall population trends (mean r) during the entire 30 year period tended to be slightly increasing (0.0004±0.002; Figure 2b).

Annual rates of egg predation also varied between <0.01% and 65% of all eggs laid eaten by mice across all climate scenarios (38±16%; Figure 2d). Egg predation was negatively correlated with owl abundance in each climate scenario (rho= -0.69 to -0.94; Figure 3a), indicating that egg survival increased as owl abundance increased. In addition, egg predation also was negatively correlated with mouse abundance (rho= -0.01 to -0.59; Figure 3b). This suggests that the extent of egg predation in the models decreased as mouse abundance increased, which is similar to observed dynamics where murrelet nest success appears to be slightly positively related to mouse abundance, despite egg predation by mice being the main cause of reduced nest success (Chapters 2 and 3). Egg predation tended to be higher with the climate models that predicted less average rain overall (rho=-0.93, n=28), which is consistent with drought-mediated effects that increase egg predation by mice (Chapter 4). In addition, climate scenarios with lower mean rainfall amounts were also associated with lower predicted mean murrelet population sizes (rho = 0.82, n=28).

Next, under the first management scenario (A) where owls were removed completely, adult predation by owls was predictably reduced to zero. However, this did not lead to substantial increases in the murrelet population. Across all climate scenarios, the murrelet population ranged from 813 to only 947 breeding adults (867±28) while overall growth (mean r) tended to be slightly declining (-0.003±0.0006; Figure 2a and 2b). Conversely, egg predation increased overall to 52-64% of all eggs laid each year (overall mean 59±2%), which was substantial enough to prevent overall increases in murrelet abundance (Figure 2d). Under the second management scenario (B), adult predation was substantially reduced compared to no owl management, from as few as one to a maximum of 53 killed by owls per year across all climate scenarios (mean 25± 10; Figure 2c). However, the murrelet population was only slightly affected overall. The murrelet population ranged from 840 to 948 breeding adults (885±19) while overall growth (mean r) was slightly decreasing (-0.001±0.0008; Figure 2a and 2b). This was again likely due to a dramatic increase in egg predation, which rose to 49-64% of all eggs laid each year (56±2%; Figure 2d). In the second management scenario of owl management (B), egg predation was no longer as strongly negatively correlated with owl abundance (rho = -0.62 to 0.11), indicating the loss or weakening of the positive indirect effects of owls on murrelet nest success (Figure 3a). Instead, egg predation became positively correlated with abundance of mice in both management scenarios (A: rho =

0.18 – 0.65; B: rho = 0.18 – 0.58), suggesting the occurrence of mesopredator release (Figure 3b).

Figures

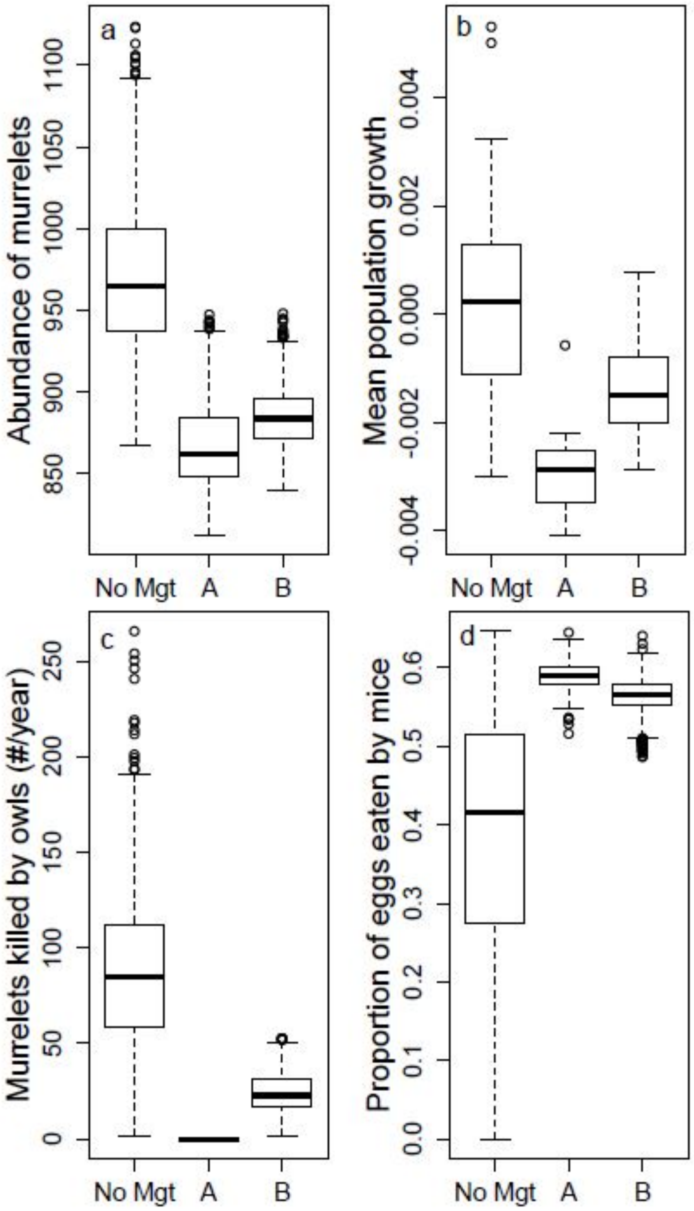


Figure 5-2 Comparison of simulation model results for no management, owl removal (A), and targeted control to prevent spikes in owl population (B) given projected rainfall estimates from 28 CMIP5 climate models (see Appendix C) for **a)** mean abundance of murrelets **b)** mean murrelet population growth (r=log(Nt+1/Nt)) **c)** mean number of murrelets killed by owls each year and **d)** the proportion of eggs eaten by mice each year from 2020-2050.

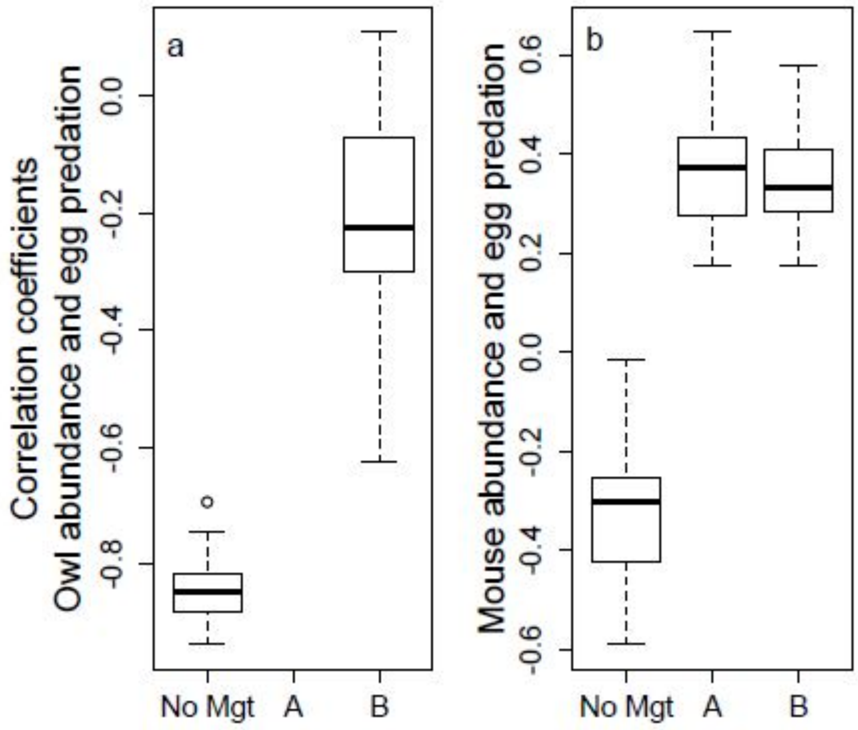


Figure 5-3 Direction and strength of correlation coefficients (spearman's rho) between **a)** owls and egg predation and **b)** mouse abundance and egg predation before and after owl management is applied. When owls are removed (scenario A), or are kept at a low abundance (<8; scenario B), egg predation increases as mouse abundance increases suggesting the occurrence of mesopredator release.

Discussion

Positive indirect effects via mesopredator suppression are oftentimes downplayed in recommendations to managers for predator management on islands (Russell et al. 2009, Bode et al. 2015). We found, contrary to our expectation, that neither owl management scenario resulted in substantial increases in murrelet population abundance. In fact, the complete or partial removal of owls usually resulted in net negative outcomes, where the murrelet population was actually lower on average compared to no management interventions at all (Figure 2a). This outcome appeared to be entirely due to the loss or weakening of the positive indirect effects of owls on egg survival. Indeed, without owl management interventions, we found a high correlation between owl abundance and egg survival as well as a counterintuitive and generally positive relationship between mouse abundance and egg survival (Figure 3a). When owl management was applied and owls were removed or kept at a low abundance, these correlations became reversed and egg predation tended to increase with mouse abundance (Figure 3b). Our model therefore demonstrates that this behaviorally mediated cascade can be strong enough to compensate for the negative direct effects of predation on adults.

We incorporated both direct and indirect effects of owls on murrelets in our model, and found that despite periodic rainfall pulses leading to subsequent dramatic increases in the number of murrelets killed (Chapter 2), these hyperpredation events do not appear to threaten the murrelet population in the long-term. While this may seem unexpected, other evidence also suggests that murrelets can coexist with their native predators on this island. For example, when murrelet population growth was modeled with a conventional PVA approach that included a positive indirect effect of owls, even a 50% reduction in owl caused mortality paired with a 50% increase in egg predation resulted in no net gains in population growth (Nur et al. 2013). Our modeling approach also demonstrates that when terrestrial productivity varies substantially between years, the temporary escapes from egg predation by mice that are mediated by high owl abundance could be very important for murrelets. Without these positive indirect effects from high owl abundance, the elimination of the wave of juveniles from highly successful breeding years that would otherwise recruit into the breeding population appears to dampen population growth (Figure 2b). Furthermore, archeological evidence of Barn Owl predation of seabirds on Santa Barbara Island has recently been determined to have occurred as far back as ~2000 years ago (Collins, pers comm.). This suggests that murrelet coexistence with owls and mice has persisted for a very long time over a wide range of climate scenarios.

Large fluctuations in rodent populations and their predators are a well-documented occurrence in semi-arid ecosystems due to variability in rainfall that drives terrestrial productivity (Holmgren et al. 2006). However, it is not clear whether the exotic plants (e.g. *Avena* spp. grasses and iceplant *Mesembryanthemum crystallinum*) or non-native arthropods (e.g. earwigs *Forficula auricularia*) could influence these dynamics on Santa Barbara Island. It has long been suspected that exotic plants are the reason for such high densities of mice or that that exotic plants contribute to greater fluctuations in the mouse population (Murray 1983; Burkett et al. 2003). If so, possibly the non-native plants would ultimately be responsible for increasing predation on murrelets (Harvey and Barnes 2009). Certainly, it is possible that these invasive species may provide anthropogenic resource subsidies to the mouse population that increases their mean density (Ruffino et al. 2012), which could influence the magnitude of predation (Norbury et al. 2013; Nishijima et al. 2014). Conversely, fluctuations in primary prey are not always detrimental to alternative prey populations (Abrams et al. 1998; Ruel and Ayres 1999; Barraquand et al. 2015; Serrouya et al. 2015). Further studies are needed to determine whether these introduced species influence predation on murrelets and how those effects compare to climate driven fluctuations in terrestrial productivity. However, our model shows that, even in the presence of non-native food resources for mice, murrelets can still be relatively resilient to these fluctuations.

It is important to evaluate potential impacts of predator management in the context of anticipated changes in climate, especially because the southwestern U.S. is considered a climate change ‘hotspot’ (Diffenbaugh et al. 2008). We found that of these 28 climate models, those that predicted less average rainfall overall were correlated with lower average murrelet populations over the 30-year period. Some climate projections for the southwestern U.S. include increased risk of very extreme drought conditions (Cook et al. 2015), which could therefore negatively impact murrelets. Murrelet nest success can be substantially reduced during drought years as a result of increased predation by mice (Chapter 4), and in our model, egg predation also tended to be higher with the climate models that predicted less average rain overall. Notably, we also found owls were the most sensitive species in the model to low rainfall, reaching just 2 individuals or less in ~5% of cases of our simulations because of drought caused declines in the mouse population (Appendix C). Such low densities would increase the risk of extirpation of owls from the island, in which case would result in cascading impacts to murrelets from increased egg predation by mice in response. The risk of such an ecological spiral is consistent with evidence that higher trophic levels tend to be relatively more sensitive to changes in climate, often from biotic effects like declines in food availability (Blois et al. 2013; Ockenden et al. 2014), which also has cascading effects within food webs (Zarnetske et al. 2012; Nolet et al. 2013; Post 2013)

Predator control continues to be planned and implemented on islands worldwide (Glen et al. 2013, Sutherland et al. 2014), and can be a successful conservation strategy (Whitworth at al. 2014). However, we conclude there is not strong evidence that owl management would enhance the murrelet population at Santa Barbara Island at this time. Our study demonstrates that it is important to consider potential unintended outcomes that can happen when indirect interactions in the food web change as a result of predator control, as well as the importance of evaluating impacts given the context of climate variability and change.

References

Abrams, P. A., R. D. Holt, and J. D. Roth. 1998. Apparent Competition or Apparent Mutualism? Shared Predation When Populations Cycle. Ecology 79:201–212.

Barraquand, F., L. F. New, S. Redpath, and J. Matthiopoulos. 2015. Indirect effects of primary prey population dynamics on alternative prey. Theoretical Population Biology 103:44–59.

Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. Trends in Ecology & Evolution 22:185–191.

Berg, N., and A. Hall. 2015. Increased Interannual Precipitation Extremes over California under Climate Change. Journal of Climate 28:6324–6334.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. Science 341:499–504.

Bode, M., C. M. Baker, and M. Plein. 2015. Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. Journal of Applied Ecology 52:571–579.

Burkett, E. E., N. A. Rojek, A. E. Henry, M. J. Fluharty, L. Comrack, P. R. Kelly, A. C. Mahaney, and K. M. Fien. 2003. Report to the California Fish and Game Commission: status review of Xantus's Murrelet (*Synthliboramphus hypoleucus*) in California. California Department of Fish and Game, Habitat Conservation Planning Branch Status Report 1:96.

CABI. 2017. *Tyto alba* (Barn owl) [original text by C. Leopold]. Page Invasive Species Compendium. Wallingford, UK: CAB International.

Carter, H. R., D. L. Whitworth, J. Y. Takekawa, T. W. Keeney, P. R. Kelly, and D. Browne. 2000. At-sea threats to Xantus' murrelets (*Synthliboramphus hypoleucus*) in the Southern California Bight. Pages 435–447 Proceedings of the fifth California Islands symposium.

Collins, P. W., and P. D. H. L. Jones. 2015. A Checklist of Birds of the California Channel Islands. Santa Barbara Museum of Natural History.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:e1400082.

Côté, I. M., and W. J. Sutherland. 1997. The Effectiveness of Removing Predators to Protect Bird Populations. Conservation Biology 11:395–405.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. Ecology 68:1412–1423.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Drost, C. A., and G. M. Fellers. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. Oikos:351–364.

Drost, C. A., and D. B. Lewis. 1995. Xantus' Murrelet: *Synthliboramphus Hypoleucus*. American Ornithologists' Union.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020–1029.

Glen, A. S., R. Atkinson, K. J. Campbell, E. Hagen, N. D. Holmes, B. S. Keitt, J. P. Parkes, A. Saunders, J. Sawyer, and H. Torres. 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biological Invasions 15:2589–2603.

Holmgren, M., P. Stapp, C. R. Dickman, C. Gracia, S. Graham, J. R. Gutiérrez, C. Hice, F. Jaksic, D. A. Kelt, M. Letnic, M. Lima, B. C. López, P. L. Meserve, W. B. Milstead, G. A. Polis, M. A. Previtali, M. Richter, S. Sabaté, and F. A. Squeo. 2006a. Extreme Climatic Events Shape Arid and Semiarid Ecosystems. Frontiers in Ecology and the Environment 4:87–95.

Holmgren, M., P. Stapp, C. R. Dickman, C. Gracia, S. Graham, J. R. Gutiérrez, C. Hice, F. Jaksic, D. A. Kelt, M. Letnic, M. Lima, B. C. López, P. L. Meserve, W. B. Milstead, G. A. Polis, M. A. Previtali, M. Richter, S. Sabaté, and F. A. Squeo. 2006b. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environment 4:87–95.

Huang, A. C., J. E. Elliott, K. M. Cheng, K. Ritland, C. E. Ritland, S. K. Thomsen, S. Hindmarch, and K. Martin. 2016. Barn owls (*Tyto alba*) in western North America: phylogeographic structure, connectivity, and genetic diversity. Conservation Genetics 17:357–367.

Hunter, C. M., H. Caswell, M. C. Runge, E. V. Regehr, S. C. Amstrup, and I. Stirling. 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. Ecology 91:2883–2897.

Jones, H. P., N. D. Holmes, S. H. M. Butchart, B. R. Tershy, P. J. Kappes, I. Corkery, A. Aguirre-Muñoz, D. P. Armstrong, E. Bonnaud, A. A. Burbidge, K. Campbell, F. Courchamp, P. E. Cowan, R. J. Cuthbert, S. Ebbert, P. Genovesi, G. R. Howald, B. S. Keitt, S. W. Kress, C. M. Miskelly, S. Oppel, S. Poncet, M. J. Rauzon, G. Rocamora, J. C. Russell, A. Samaniego-Herrera, P. J. Seddon, D. R. Spatz, D. R. Towns, and D. A. Croll. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038.

Lawson, C. R., Y. Vindenes, L. Bailey, and M. Pol. 2015. Environmental variation and population responses to global change. Ecology letters 18:724–736.

Murray, K. G. 1980. Predation by deer mice on Xantus' Murrelet eggs on Santa Barbara Island, California. M.Sc. thesis. California State Univ., Northridge.

Nishijima, S., G. Takimoto, and T. Miyashita. 2014. Roles of Alternative Prey for Mesopredators on Trophic Cascades in Intraguild Predation Systems: A Theoretical Perspective. The American Naturalist 183:625–637.

Nogales, M., A. Martín, B. R. Tershy, C. J. Donlan, D. Veitch, N. Puerta, B. Wood, and J. Alonso. 2004. A Review of Feral Cat Eradication on Islands. Conservation Biology 18:310–319.

Nolet, B. A., S. Bauer, N. Feige, Y. I. Kokorev, I. Y. Popov, and B. S. Ebbinge. 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. Journal of Animal Ecology 82:804–813.

Norbury, G., A. Byrom, R. Pech, J. Smith, D. Clarke, D. Anderson, and G. Forrester. 2013. Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. Ecological Applications 23:1707–1721.

Nur, N., A. L. Harvey, S. K. Thomsen, R. W. Bradley, and J. Jahncke. 2013. Modeling the Population level Impacts of Barn Owls on Scripps's Murrelet Population Trends on Santa Barbara Island. Unpublished report prepared for: National Fish and Wildlife Foundation. Point Blue Conservation Science, Petaluma, California. PRBO contribution Number 1969.

Ockendon, N., D. J. Baker, J. A. Carr, E. C. White, R. E. A. Almond, T. Amano, E. Bertram, R. B. Bradbury, C. Bradley, S. H. M. Butchart, N. Doswald, W. Foden, D. J. C. Gill, R. E. Green, W. J. Sutherland, E. V. J. Tanner, and J. W. Pearce-Higgins. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20:2221–2229.

Pierce, D. W., D. R. Cayan, and B. L. Thrasher. 2014. Statistical Downscaling Using Localized Constructed Analogs (LOCA). Journal of Hydrometeorology 15:2558–2585.

Post, E. 2013. Erosion of community diversity and stability by herbivore removal under warming. Proceedings of the Royal Society of London B: Biological Sciences 280:20122722.

Prugh, L. R., and S. M. Arthur. 2015. Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release. Oikos 124:1241–1250.

Rayner, M. J., M. E. Hauber, M. J. Imber, R. K. Stamp, and M. N. Clout. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. Proceedings of the National Academy of Sciences 104:20862–20865.

Riahi, K., S. Rao, V. Krey, C. Cho, V. Chirkov, G. Fischer, G. Kindermann, N. Nakicenovic, and P. Rafaj. 2011a. RCP 8.5—A scenario of comparatively high greenhouse gas emissions. Climatic Change 109:33.

Riahi, K., S. Rao, V. Krey, C. Cho, V. Chirkov, G. Fischer, G. Kindermann, N. Nakicenovic, and P. Rafaj. 2011b. RCP 8.5—A scenario of comparatively high greenhouse gas emissions. Climatic Change 109:33.

Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology & Evolution 14:361–366.

Ruffino, L., J. Russell, and E. Vidal. 2013. Anthropogenic subsidies mitigate environmental variability for insular rodents. Oecologia 172:737–749.

Russell, J. C., V. Lecomte, Y. Dumont, and M. Le Corre. 2009. Intraguild predation and mesopredator release effect on long-lived prey. Ecological Modelling 220:1098–1104.

Russell, J. C., and L. Ruffino. 2012. The influence of spatio-temporal resource fluctuations on insular rat population dynamics. Proceedings of the Royal Society of London B: Biological Sciences 279:767–774.

Sabo, J. L. 2008. Population viability and species interactions: Life outside the single-species vacuum. Biological Conservation 141:276–286.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015a. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. The American Naturalist 185:665–679.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015b. Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition. The American Naturalist 185:665–679.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015c. Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition. The American Naturalist.

Soetaert, K., T. Petzoldt, and R. Setzer. 2010. Solving Differential Equations in R: Package deSolve. Journal of Statistical Software. American Statistical Association, Alexandria, VA 33:1–25.

Sutherland, W. J., R. Aveling, T. M. Brooks, M. Clout, L. V. Dicks, L. Fellman, E. Fleishman, D. W. Gibbons, B. Keim, F. Lickorish, K. A. Monk, D. Mortimer, L. S. Peck, J. Pretty, J. Rockström, J. P. Rodríguez, R. K. Smith, M. D. Spalding, F. H. Tonneijck, and A. R. Watkinson. 2014. A horizon scan of global conservation issues for 2014. Trends in Ecology & Evolution 29:15–22.

Taylor, I. 2004. Barn Owls: Predator-Prey Relationships and Conservation. Cambridge University Press.

Thomsen, S. K., and D. J. Green. 2016. Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island. Ecology 97:3530–3537.

USFWS, U. S. F. and W. S. 2016. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the Scripps's Murrelet as threatened or endangered. Notice of 12-month petition finding. Federal Register 81:64843–64857.

White, J. W., A. Rassweiler, J. F. Samhouri, A. C. Stier, and C. White. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123:385–388.

Whitworth, D. L., H. R. Carter, and F. Gress. 2013. Recovery of a threatened seabird after eradication of an introduced predator: Eight years of progress for Scripps's murrelet at Anacapa Island, California. Biological Conservation 162:52–59.

Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013a. Conservation Strategies for Species Affected by Apparent Competition. Conservation Biology 27:254–260.

Wittmer, H. U., R. Serrouya, L. ELBROCH, and A. J. Marshall. 2013b. Conservation strategies for species affected by apparent competition. Conservation Biology 27:254–260.

Wootton, J. T., and D. A. Bell. 2014. Assessing predictions of population viability analysis: Peregrine Falcon populations in California. Ecological Applications 24:1251–1257.

Yoho, D., T. Boyle, and E. McIntire. 1999. The climate of the Channel Islands, California. Pages 81–88 Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Yoon, J.-H., S. S. Wang, R. R. Gillies, B. Kravitz, L. Hipps, and P. J. Rasch. 2015. Increasing water cycle extremes in California and in relation to ENSO cycle under global warming. Nature communications 6.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic Multipliers of Climate Change. Science 336:1516–1518.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454–459.

Chapter 6. General Conclusions

The ENSO cycle drives fluctuations in climate around the globe (McPhaden et al. 2006), and in southern California, the El Niño phase usually leads to increased rainfall (Black et al. 2014). The sudden increase in rainfall on Santa Barbara Island sets off a chain of reactions that can quickly progress from the flourishing of vegetation up to peaks in the abundance of deer mice and Barn Owls (Chapter 2). Once drought returns, however, the mouse and owl populations decline, and murrelets face increased predation on adults and their nests from owls and deer mice, respectively (Chapters 2,3, and 4). Other regional oceanographic indices are also linked to patterns of drought in this area (McCabe-Glynn et al. 2013), so along with ENSO, this means that this looping ecological cascade ultimately begins in the ocean and ends up circling back onto the marine food web via murrelets.

In this thesis, I have demonstrated the potential mechanisms and consequences of this cascade on Scripps's Murrelets on Santa Barbara Island. Specifically, my research suggests that owl predation of murrelets is mediated by prey switching that is triggered by climate-driven changes in the density of mice and owls, and that murrelet nest success is influenced by both the marine environment and cascading indirect interactions with mice and owls (Chapters 2,3, and 4). A key result was evidence for positive indirect effects of owls on murrelets (Chapter 3). I found that mouse foraging was strongly suppressed as the abundance of owls increased, and survival of murrelet eggs was also positively related to owl abundance. Overall, this means that both survival and nest success of adult murrelets are influenced by climate-driven indirect interactions with predators, at times both negatively and positively. The mathematical model of island community dynamics also demonstrates these interactions (Chapter 5, Appendix C). Therefore, it appears that despite short-term negative effects, over the long term, murrelets are capable of persisting with their native predators on this island. Moreover, the model demonstrates that murrelets would not benefit from management efforts targeted to only reduce adult mortality from owls.

However, these results must still be viewed in the context of a wide variety of other conservation threats that currently exist for murrelets (e.g. non-native predators on other islands, potential for catastrophic oil spills, gill netting, pollution, coastal development, changes in food availability and marine environmental conditions; Roth et al. 2005; Carter et al. in prep). If the population was already declining for these other reasons, this could make them more vulnerable to predation (Sydeman 1998). For example, the consequences of a sudden adverse event that resulted in a sharp decline of breeding murrelets on the island, such as from an oil spill, combined with a subsequent hyperpredation event, could be particularly disastrous. However, if predator management was considered in the future, owl management would still be highly controversial (Doherty and Richie 2016), and unlikely to succeed without also managing the mouse population to compensate for lost positive indirect effects. To do so, options could include temporary supplemental feeding of mice (Vander Lee et al. 1999) during drought years, enhancement of the perception of predation risk for mice by playback of owl vocalizations (Hendrie et al. 1998; Suraci et al. 2016) during low owl abundance, conditioned taste aversion for mice (Baylis et al. 2012), or even genetic engineering to reduce breeding success of mice (Backus and Gross 2016).

These interventions might help in a crisis situation, but at the same time, it is important to remember that several life history traits and behaviors of *Synthliborampus* murrelets can be viewed as potential anti-predator adaptations (Gaston 1992). First, many colonial seabirds, even if nocturnal, are highly social on the surface of their breeding colonies (Schreiber and Burger 2010), while Scripps's Murrelets are not. Instead, they congregate on the water surrounding breeding islands and vocalize extensively throughout the dark hours where they are out of reach of foraging owls (Drost and Lewis 1995). Secondly, their incubation shifts are about three days long and shared evenly between parents (Murray 1983), which minimizes the number of trips to switch incubation duties. Chicks are also precocial, leaving the island with the family group within days of hatching, which further limits the overall time on or near the island (Murray 1980). These life history and behavioral traits can be viewed as strategies that minimize risk, when compared with other nocturnal seabirds. For example, another similarly sized nocturnal alcid on Santa Barbara Island, the Cassin's Auklet, is much more active and vocal on breeding islands at night (Manuwal and Thoresen 2011). Auklets also have much shorter incubation shifts (24 hours), and they continue to feed their chick on the island until fledging (Manuwal and Thoresen 2011), which means they are exposed to owls much more frequently and over a longer period of time. Accordingly, auklets do experience a higher per capita predation by owls than murrelets (Drost 1989; Thomsen and Plumb 2014), which offers some support to this idea that murrelets minimize these potentially risky behaviors.

Understanding how murrelets can coexist with their predators also has important implications for many other species of seabirds in a diversity of systems that are increasingly affected by growing raptor populations (Hipfner et al. 2012). In addition, non-native invasive mammals on islands continue to be a significant threat to biodiversity, not just seabirds, and the pace of extinctions continues to increase globally (Jones et al. 2016; McCreeless et al. 2016). Predator management or eradication campaigns on islands are therefore necessary, but despite a growing understanding of the need to address multiple species at the same time (Roemer et al. 2002; Glen et al. 2013), there are recent recommendations that still downplay the potential for indirect effects (e.g. Bode et al. 2015). My results suggest that positive indirect effects from predators should not be underestimated. In particular, the lack of density-dependent predation rates, similar to the counterintuitive relationship between mouse density and murrelet egg predation on Santa Barbara Island (Chapters 3 and 4), should perhaps lead to more careful assessment about the risk of mesopredator release. Results of this work are therefore important in an applied conservation context as well as potentially having broader implications for understanding community dynamics in ecology.

References

Backus, G. A., and K. Gross. 2016. Genetic engineering to eradicate invasive mice on islands: modeling the efficiency and ecological impacts. Ecosphere 7:n/a-n/a.

Baylis, S. M., P. Cassey, and M. E. Hauber. 2012. Capsaicin as a Deterrent Against Introduced Mammalian Nest Predators. The Wilson Journal of Ornithology 124:518–524.

Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. García-Reyes, R. R. Rykaczewski, S. J. Bograd, and W. T. Peterson. 2014. Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. Science 345:1498–1502.

Bode, M., C. M. Baker, and M. Plein. 2015. Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. Journal of Applied Ecology 52:571–579.

Doherty, T. S., and E. G. Ritchie. 2017. Stop Jumping the Gun: A Call for Evidence-Based Invasive Predator Management. Conservation Letters 10:15–22.

Drost C.A. 1989. Predation and population cycles on a southern California island. Master's thesis. University of California–Davis.

Drost, C. A., and D. B. Lewis. 1995. Xantus's Murrelet (*Synthliboramphus hypoleucus*). The Birds of North America Online.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic Downgrading of Planet Earth. Science 333:301–306.

Gaston, A. 1992. The Ancient Murrelet a Natural History in the Queen Charlotte Islands

Glen, A. S., R. Atkinson, K. J. Campbell, E. Hagen, N. D. Holmes, B. S. Keitt, J. P. Parkes, A. Saunders, J. Sawyer, and H. Torres. 2013. Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biological Invasions 15:2589–2603.

Hendrie, C. A., S. M. Weiss, and D. Eilam. 1998. Behavioural response of wild rodents to the calls of an owl: a comparative study. Journal of Zoology 245:439–446.

Hipfner, M. J., L. K. Blight, R. W. Lowe, S. I. Wilhelm, G. J. Robertson, R. Barrett, T. Anker-Nilssen, and T. P. Good. 2012. Unintended consequences: how the recovery of sea eagle Haliaeetus spp. populations in the northern hemisphere is affecting seabirds.

Jones, H. P., N. D. Holmes, S. H. M. Butchart, B. R. Tershy, P. J. Kappes, I. Corkery, A. Aguirre-Muñoz, D. P. Armstrong, E. Bonnaud, A. A. Burbidge, K. Campbell, F. Courchamp, P. E. Cowan, R. J. Cuthbert, S. Ebbert, P. Genovesi, G. R. Howald, B. S. Keitt, S. W. Kress, C. M. Miskelly, S. Oppel, S. Poncet, M. J. Rauzon, G. Rocamora, J. C. Russell, A. Samaniego-Herrera, P. J. Seddon, D. R. Spatz, D. R. Towns, and D. A. Croll. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038.

Manuwal, D. A., and A. C. Thoresen. 1993. Cassin's Auklet (Ptychoramphus aleuticus). The Birds of North America Online.

McCabe-Glynn, S., K. R. Johnson, C. Strong, M. Berkelhammer, A. Sinha, H. Cheng, and R. L. Edwards. 2013. Variable North Pacific influence on drought in southwestern North America since AD 854. Nature Geoscience 6:617–621.

McCreless, E. E., D. D. Huff, D. A. Croll, B. R. Tershy, D. R. Spatz, N. D. Holmes, S. H. M. Butchart, and C. Wilcox. 2016. Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. Nature Communications 7:12488.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2006. ENSO as an Integrating Concept in Earth Science. Science 314:1740–1745.

Murray, K., K. Winnettmurray, Z. Eppley, G. Hunt, and D. Schwartz. 1983. Breeding Biology of the Xantus-Murrelet. Condor 85:12–21.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World’s Largest Carnivores. Science 343:1241484.

Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. Proceedings of the National Academy of Sciences 99:791–796.

Roth, J. E., W. J. Sydeman, and P. L. Martin. 2005. Xantus’s Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. Marine Ornithology 33:115–121.

Russell, J. C., H. P. Jones, D. P. Armstrong, F. Courchamp, P. J. Kappes, P. J. Seddon, S. Oppel, M. J. Rauzon, P. E. Cowan, G. Rocamora, P. Genovesi, E. Bonnaud, B. S. Keitt, N. D. Holmes, and B. R. Tershy. 2016. Importance of lethal control of invasive predators for island conservation. Conservation Biology 30:670–672.

Schreiber, E. A., and J. Burger. 2001. Biology of Marine Birds. CRC Press.

Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. Nature Communications 7:10698.

Sydeman, W. J., N. Nur, and P. Martin. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-Petrel (*Oceanodroma homochroa*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*). Final report to the United States Geological Survey, Biological Resources Division, Species at Risk Program. Stinson Beach, CA: PRBO Conservation Science. 74 pp

Thomsen, S.K. and S.T. Plumb. 2014. Factors influencing depredation of Scripps's Murrelets by Barn Owls on Santa Barbara Island: Summary results from the 2012 field season. Unpublished report prepared for: Montrose Settlements Restoration Program. 15 pp.

VanderLee, B. A., R. S. Lutz, L. A. Hansen, and N. E. Mathews. 1999. Effects of Supplemental Prey, Vegetation, and Time on Success of Artificial Nests. The Journal of Wildlife Management 63:1299–1305.

Appendix A.

Details of mathematical model for Chapter 2

The relationships between murrelets, mice, and owls are described with a set of ordinary differential equations (ODE). These equations are based on the classic hyperpredation model (Courchamp et al. 1999), and fit with empirical or derived parameters for our system (Table A1). For the mice (M) and owls (O), both are characterized by their intrinsic growth rate (r_i), carrying capacity (K_i), and mortality rates (μ_i). The mice are also subject to mortality from predation by owls (γ), relative to adult murrelets (S). Their populations then thus can be represented by:

$$\frac{dM}{dt} = r_m M\left(1 - \frac{M}{K_m}\right) - \mu_m M - \frac{M}{M + A}\gamma_m^O O \qquad \text{(eqn. 1)}$$

$$\frac{dO}{dt} = r_o O\left(1 - \frac{O}{K_o}\right) - \mu_o O \qquad \text{(eqn. 2)}$$

The carrying capacities of mice and owls are linked by their respective predation rates on their respective main prey (γ_i^i), which results in realistic population sizes for the island. The carrying capacity of mice and owls then varies over time through the action of the climate forcing variable (C).

$$K_m = \left(\frac{V}{\gamma_V^m}\right)C \qquad \text{(eqn. 3)}$$

$$K_o = \left(\frac{M}{\gamma_m^o}\right)C \qquad \text{(eqn. 4)}$$

We extracted monthly estimates of precipitation from the PRISM 4-km gridded surface and compiled them into rainfall year totals for the island during 1897-2015 (PRISM; Daly et al. 2008). This time series of estimated historical precipitation was then rescaled into a range of proportional values (minimum =0.03, maximum = 3.5) with the R package 'scales' to create the vector representing variable climate driven resources (C) that directly influences carrying capacities of mice and owls in the model.

Seabird adults (S) are represented by an intrinsic growth rate (r_S) and the number of breeding seabird adults (S), modified by a fixed carrying capacity (K_S). Adult murrelet population change is then subject to mortality from reasons other than predation (μ_S), as well as a predation rate of owls (O) on murrelets relative to mice as an alternative prey for owls (γ).

$$\frac{dS}{dt} = r_s S\left(1 - \frac{S}{K_s}\right) - \mu_s S - \frac{S}{M + S}\gamma_s^O SO \qquad \text{(eqn. 5)}$$

All analyses were done in R 3.2.1 ('World Famous Astronaut' R Core Team, 2014). Differential equations were solved numerically with the function *ode* with the R package 'deSolve' (Soetaert et al. 2010). Initial population sizes were set to: S=1125, M=1600, and O=3. Maximum intrinsic rates of growth (r_i) were estimated based on the Cole's (1954) equation with empirical parameters for each species. The model was run with climate forcing (Figure A1, A2) and also without climate forcing (C=1) to 120 time steps (years) to determine whether stable equilibrium values could be reached under constant conditions (Figure A3). Finally, we also confirmed the robustness of the model results to parameter values by changing the parameters by ±10% following Russell et al. (2010) and verified that output values and dynamics remained similar.

Table A1. Summary of parameter values used in the model

Parameter	Value	Reference(s)
Deer mouse growth rate (r)	12.4	Collins 1979
Mouse predation on vegetation (γ)	0.05	fixed
Vegetation (V)	1000	fixed
Deer mouse mortality rate (μ)	0.22	Ozer et al. 2011
Owl predation on mice (γ)	2130	Thomsen and Plumb 2014
Barn owl growth rate (r)	2.2	this study; Taylor 2004
Barn owl mortality (μ)	0.25	Taylor 2004
Murrelet growth rate (r)	0.38	NPS unpub. data; Nur et al. 2013
Murrelet carrying capacity (K)	3500	fixed
Murrelet adult mortality (μ)	0.16	Nur et al. 2013
Owl predation on murrelets (γ)	0.18	this study

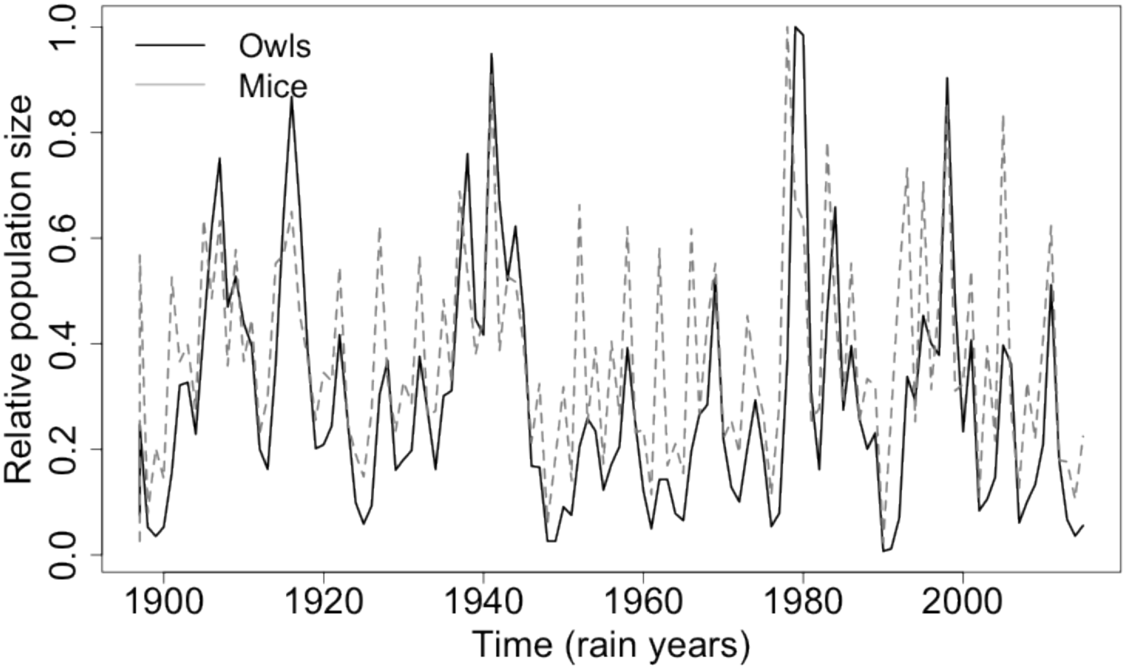


Figure A1. Simulated population changes in mice and owls over 120 years based on estimated historical rainfall. Values were rescaled for this figure relative to their maximum abundances predicted by the model (peak abundance for mice = 61840; peak abundance for owls = 40).

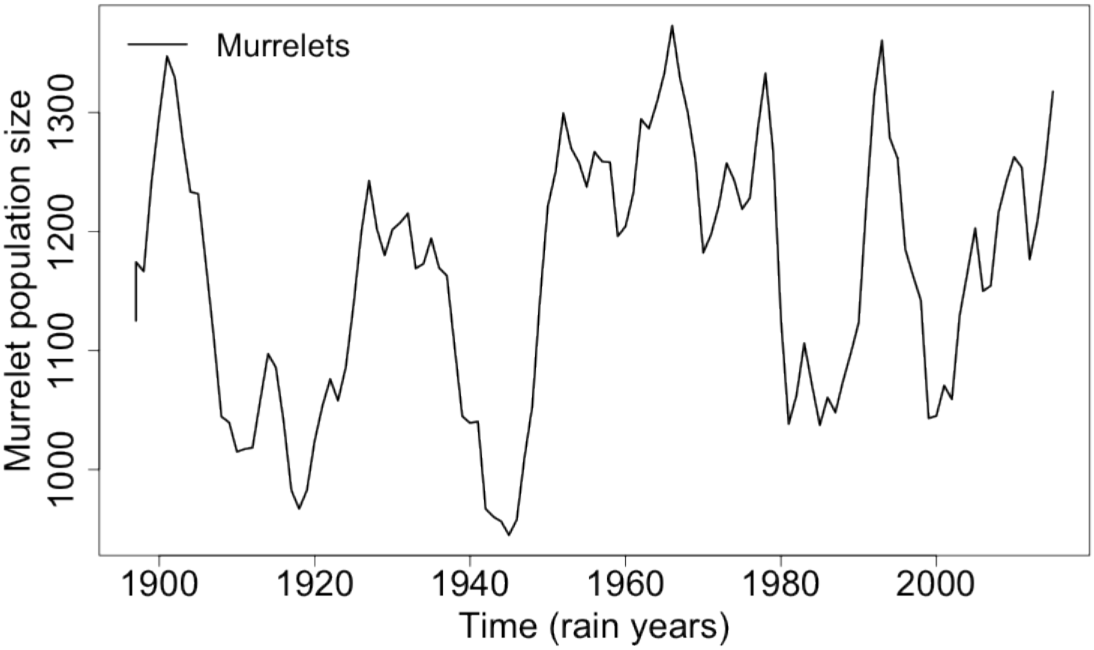


Figure A2. Simulated population changes in murrelets over 120 years

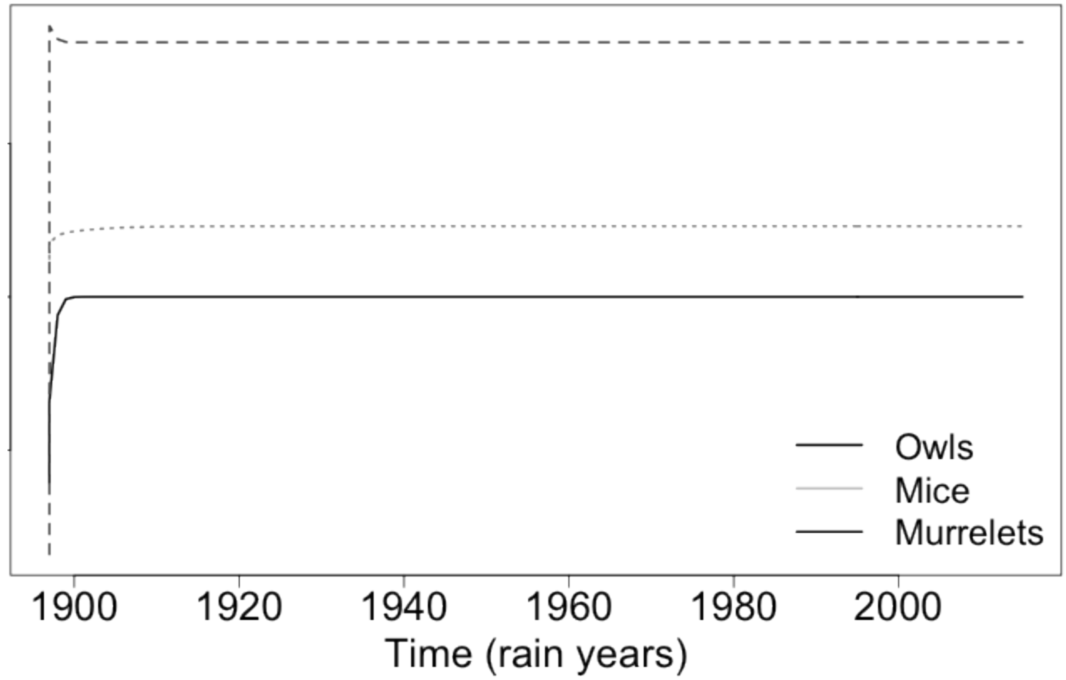


Figure A3. Simulated population dynamics with no climate forcing (C=1) over 120 years to demonstrate stable equilibrium is reached after a short transient period. Y-axis values in figure are arbitrary.

References

L. C. Cole. (1954). The population consequences of life history phenomena. Q. Rev. Biol. 29, 103 doi:10.1086/400074 pmid:13177850

Collins, P. W., J. Storrer and K. Rindlaub. (1979). Vertebrate zoology: the biology of the deer mouse - In: Power, D. M., Natural resources study of the Channel Islands National Monument, California. Santa Barbara Museum of Natural History, Chapter 11.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Nur, N., A. L. Harvey, S. K. Thomsen, R. Bradley, and J. Jahncke. (2013). Modeling the Population level Impacts of Barn Owls on Scripps's Murrelet Population Trends on Santa Barbara Island. Unpublished report prepared for: National Fish and Wildlife Foundation. Point Blue Conservation Science, Petaluma, California. PRBO contribution Number 1969.

Ozer, F., Gellerman, H., and Ashley, M. V. (2011). Genetic impacts of Anacapa deer mice reintroductions following rat eradication. Molecular ecology 20:3525-3539.

Taylor, I. 2003. Barn owls: Predator-prey relationships and conservation. Cambridge University Press, Cambridge.

Courchamp, F., M. Langlais, and G. Sugihara. 1999. Control of rabbits to protect island birds from cat predation. Biological Conservation 89:219–225.

Soetaert, K., T. Petzoldt, and R. Setzer. 2010. Solving Differential Equations in R: Package deSolve. Journal of Statistical Software. American Statistical Association, Alexandria, VA 33:1–25.

Thomsen, S.K. and S.T. Plumb. 2014. Factors influencing depredation of Scripps's Murrelets by Barn Owls on Santa Barbara Island: Summary results from the 2012 field season. Unpublished report prepared for: Montrose Settlements Restoration Program. 15 pp.

Appendix B.

Track Tube Methods and Validation Study

Track tube sites (n=10) were selected in 5 locations by randomly selecting a murrelet nest that had been monitored in 2010. The other 5 locations were selected randomly with ArcGIS 10.0 (ESRI 2011). We made modifications to the track tube designs of Connors et al. (2005) and Drennan et al. (1998) to make them smaller, lightweight, and yet still covered from the elements. Track tubes were constructed with white corrugated plastic sheets that were cut and folded into triangular tubes (30cm length by ~5.2cm maximum height). The tracking surface consisted of an acetate sheet cut to fit the inside bottom of the tube (6cm x 28cm) and painted with a suspension made of ethyl alcohol, graphite, and mineral oil (Connors et al. 2005). Mouse tracks were clearly visible when mice travel across the track sheet and remove the graphite layer from the acetate sheet in the shape of their feet. We did not use bait to attract mice to the tubes.

Each site consisted of nine track tubes placed in a 3x3 grid formation with 7m spacing. In 2011-2013, they were deployed in April, May, July and August, except for July 2013. Track tubes were set out within 3 nights of the new moon when lunar illumination is typically ≤3% (US Navy 2013) so that comparisons across time and space were not confounded with changes in moonlight. Track tubes were deployed in formation before nightfall. On the following day, we recorded the number of track tubes in each grid that had the presence of mouse tracks.

A validation study was also conducted in 2011 and 2012 by deploying the track tubes within the two plots used for deer mouse mark-recapture studies by the Channel Islands National Park (Fellers et al. 1988). Each plot has 100 permanent trap stations that are arranged in a 10 X 10 pattern spaced 7m apart. Track tubes were deployed with the same arrangement as those used in the other grids (7m spacing and 3x3 array). First, shortly after the live-trapping was completed in March 2011, track tubes were replaced daily for three consecutive nights in both grids to determine variation between nights. The number of track tubes with mouse tracks for each plot varied only slightly between nights (mean=3, sd=1 and mean = 7.66 sd= 0.57). Thereafter, track tubes were placed in both grids for one night around the time of the subsequent mouse mark-recapture studies in October 2011, and March and September 2012. We then used the mouse densities (mice/ha) calculated by Stanley et al. (2012) using the data collected by the National Park Service and found a significant positive correlation between those values and our track tube index (r=0.64, n=13 site nights, p=0.02). Our track tube index performed well for predicting mouse density that ranged from 16 mice/ha to 619 mice/ha (Stanley et al, 2012; NPS unpub. data).

References

Connors, Matthew J., Eric M. Schauber, Andrew Forbes, Clive G. Jones, Brett J. Goodwin and Richard S. Ostfeld. 2005. Use of track plates to quantify predation risk at small spatial scales. Journal of Mammalogy 86:5, 991-996

Drennan, J. E., P. Beier, and N. L. Dodd. 1998. Use of track stations to index abundance of sciurids. Journal of Mammalogy 79:352–359.

Fellers, G.M., Drost, C.A., and Arnold, B.W. (1988). Terrestrial Vertebrates Monitoring Handbook, Channel Islands National Park, California. National Park Service, Channel Islands National Park, Ventura, CA, 17 pp. + appendices.

Stanley, T. R. 2012. Analysis of deer mouse capture-recapture data from Anacapa, Santa Barbara, and San Miguel Islands. Unpublished draft report to Channel Islands National Park. 39 pp.

US Navy (online). 2013. U.S. Naval Observatory astronomical applications: data services. <www.http://aa.usno.navy.mil/data/docs/MoonFraction.php> (November 16, 2013)

Appendix C.

Details of mathematical model and sensitivity analyses for Chapter 5

Model Equations

The basic model from Chapter 2, described in detail in Appendix A, is expanded here to include an egg and juvenile/subadult stage for murrelets, with additional parameters that were fit with empirical or derived parameters for our system (Table C1).

Mice (M) and owls (O) are both characterized by their intrinsic growth rates (r_i), carrying capacities (K_i), and mortality rates (μ_i). Maximum intrinsic rates of growth (r_i) were estimated based on the Cole's (1954) equation with empirical parameters for mice and owls. The mice are also subject to mortality from predation by owls (γ_i^j), relative to adult murrelets (A). Their populations then thus can be represented by:

$$\frac{dM}{dt} = r_m M\left(1 - \frac{M}{K_m}\right) - \mu_m M - \frac{M}{M+A}\gamma_m^O O$$

(eqn.1)

$$\frac{dO}{dt} = r_o O\left(1 - \frac{O}{K_o}\right) - \mu_o O$$

(eqn. 2)

The carrying capacities of mice and owls are linked by their respective predation rates on their respective main prey (γ_i^j), which results in realistic population sizes for the island (Figure C1 and C2). The carrying capacity of mice and owls then varies over time through the action of the climate forcing variable (C).

$$K_m = \left(\frac{V}{\gamma_V^m}\right)C$$

(eqn. 3)

$$K_o = \left(\frac{M}{\gamma_m^o}\right)C \qquad \text{(eqn. 4)}$$

The number of murrelet eggs (E) laid each year corresponds to an average clutch size (δ) and the number of pairs of breeding adults (A), modified by a fixed carrying capacity (K). Eggs are then subject to some mortality due to reasons other than mice predation (μ), while being subject to a predation rate of mice (M) on eggs relative to climate (C) driven changes in vegetation (V) as an alternative source of food for mice. In addition, egg predation is also influenced by a positive indirect effect of owls, which was modeled as a decelerating function of increasing owl abundance. This parameter [exp(-Owls/10)] is based off the coefficient value determined from a non-linear regression of owl abundance from line transects and the proportion of first eggs that were depredated by mice in two plots over a 3 year period (8.301±1.232; Chapter 3). For the model, we used a more conservative estimate of this positive indirect effect, and we address this and other uncertainties further in a sensitivity analysis below. Murrelet eggs also transition to juveniles/subadults (J) at a rate (σ) that is inverse to mortality following Russell et al. (2009). This juvenile/subadult stage is included to represent the period where murrelets are neither vulnerable to predation by owls or mice, and for simplicity we only include this one transition stage. The change in the juvenile/subadult population is modeled as the survival rate of eggs (σ), and subtracting by the mortality rate of the juvenile/ subadult stage (μ) and the transition rate from the juvenile/ subadult stage to adults. Finally, adult murrelet population change is modeled as a function of the survival of juveniles/subadults (σ), subject to a mortality rate for reasons other than predation (μ), as well as a predation rate of owls (γ) on murrelets relative to mice as an alternative prey for owls. For all transition and survival rates, we similar estimates to those estimated by others (Sydeman et al. 1998; Nur et al. 2013).

Altogether, these three stages of the murrelet population are represented by the following equations:

$$\frac{dE}{dt} = \delta A\left(1 - \frac{A}{K_A}\right) - \mu_E E - \sigma_E E - \left(\frac{E}{E + (VC)}\gamma_e^m ME\right) * \exp\left(\frac{-O}{10}\right)$$ (eqn. 5)

$$\frac{dJ}{dt} = \sigma_E E - \mu_j J - \sigma_j J$$ (eqn. 6)

$$\frac{dA}{dt} = \sigma_j J - \mu_A A - \frac{A}{M + A}\gamma_A^O OA$$ (eqn. 7)

Table C1. Summary of parameter values used in the model

Parameter	Default Value	Sensitivity range (min, max)	Reference(s)
Deer mouse growth rate (r)	12.4	11, 14	Collins 1979
Mouse predation on V (γ)	0.05	0.045, 0.055	fixed
Vegetation (V)	1000	900, 1100	fixed
Climate (C)	varies	0.001, 6.2	
Deer mouse mortality rate (μ)	0.22	0.2, 0.24	Ozer et al. 2011
Owl predation on mice (γ)	2130	1917, 2343	Thomsen and Plumb 2014
Barn owl growth rate (r)	2.2	2, 2.4	this study; Taylor 2003
Barn owl mortality (μ)	0.25	0.22, 0.27	Taylor 2004
Murrelet growth rate (δ)	0.875	0.5, 1	eggs laid per pair: Murray 1983
Murrelet carrying capacity (K)	3500	3150, 3850	fixed
Murrelet adult mortality (μ)	0.16	0.145, 0.175	Nur et al. 2013
Owl predation on murrelets (γ)	0.18	0.16, 0.2	Chapter 2
Indirect effect owls on eggs	exp(-Owls/10)	7, 12	data from Chapter 4
Mouse predation on eggs (γ)	0.0005	0.00045, 0.00055	fixed
Murrelet egg mortality (μ)	0.12	0.05 , 0.30	Murray 1983; Millus et al. 2007
Juvenile/subadult mortality (μ)	0.26	0.23, 0.28	Sydeman et al. 1998
Initial population sizes:			
Eggs	300		
Juvenile/subadults	200		
Adults	1125		Whitworth pers. comm.
Mice	1662		
Owls	7		

Climate and Management Scenarios

Previously, for Chapter 2, we extracted monthly historical estimates of precipitation from the PRISM 4-km gridded surface and compiled them into rainfall year totals for the island during 1897-2015 (PRISM; Daly et al. 2008). Here, we also obtained daily precipitation data from 28 of the Coupled Model Intercomparison Project Phase 5 (CMIP5) climate models that have recently been statistically downscaled for California for the years 2007-2100 (Pierce et al. 2014, data accessed from: http://cida.usgs.gov/thredds/dodsC/loca_future; Table C2). Daily projected precipitation amounts from each model were then summed into rain year totals beginning in April. These time series of estimated future annual precipitation amounts were then rescaled into a range of proportional values (minimum =0.001, maximum = 6.2), relative to the historical estimates (min =0.01, maximum = 3.5), with the R package 'scales'. From this, we then had time series vectors for each of the 28 climate models that represent a range of potential rainfall changes (C) that directly influences carrying capacities of mice and owls in the model. Models were run using the full time series of 94 years, but we focus on results from the near-future (2020-2050) as this time frame would be most relevant to any policy decisions (Hunter et al. 2010).

For owl management scenario A, the owl population was reduced to zero in the model (Figure 1), which also eliminated predation on both mice and murrelets. For owl management scenario B, we set a threshold of 8 owls, representing ~25% of the current known maximum density (Chapter 2), that would immediately trigger management action that reduced the population to 2 individuals by the following year. Differential equations were solved numerically with the function *ode* with the R package 'deSolve' (Soetaert et al. 2010), with R 3.2.1 ('World Famous Astronaut' R Core Team, 2014).

Table C2: List of CMIP5 climate models used for this assessment

CMIP5 Model name
HadGEM2-CC_r1i1p1
HadGEM2-ES_r1i1p1
IPSL-CM5A-LR_r1i1p1
IPSL-CM5A-MR_r1i1p1
MIROC-ESM-CHEM_r1i1p1
MIROC-ESM_r1i1p1
MIROC5_r1i1p1
CESM1-BGC_r1i1p1
MPI-ESM-LR_r1i1p1
MPI-ESM-MR_r1i1p1
MRI-CGCM3_r1i1p1
NorESM1-M_r1i1p1
bcc-csm1-1-m_r1i1p1
CESM1-CAM5_r1i1p1
CMCC-CMS_r1i1p1
CMCC-CM_r1i1p1
CNRM-CM5_r1i1p1
CSIRO-Mk3-6-0_r1i1p1
CanESM2_r1i1p1
EC-EARTH_r2i1p1
FGOALS-g2_r1i1p1
GFDL-CM3_r1i1p1
GFDL-ESM2G_r1i1p1
GFDL-ESM2M_r1i1p1
CCSM4_r6i1p1
GISS-E2-H_r2i1p1
GISS-E2-R_r2i1p1
HadGEM2-AO_r1i1p1

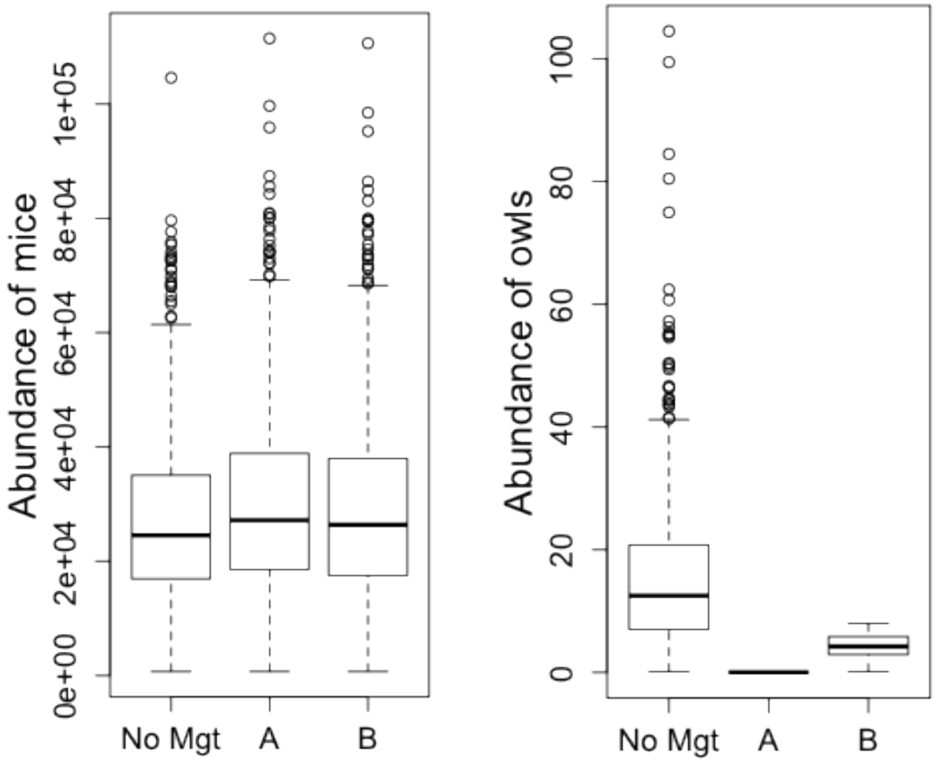


Figure C1 and C2. Model predictions of the abundance of mice and owls

Sensitivity Analyses and Parameter Uncertainty

We conducted a global sensitivity analysis by simulating the model 1000 times with a range of parameter values generated with Latin hypercube sampling (Table C1), followed by analyzing the output with a random forest algorithm to determine the relative importance of each of the 18 parameters on predicting murrelet abundance (Harper et al. 2011). The model output was subset to match the same 30-year period used in our model runs, which produced 31000 samples, from which 1000 trees were built with the R package ‘randomForest’ (Breiman and Cutler 2011). From this, we determined the top four parameters that murrelet abundance was the most sensitive to included the climatic effects on the carrying capacity of mice and owls, the number of eggs laid per breeding pair, predation rates of owls on adult murrelets, and predation rates of mice on murrelet eggs (Figure C3). Fortunately, the mean and range of these particular parameters are fairly well established from empirical data so we can conclude that our results are robust and not unduly influenced by parameters that are far less certain.

We also conducted a local sensitivity analysis to assess the specific influence of parameter uncertainty of adult annual survival rates on our conclusions regarding the potential benefits of owl management. Murrelets are relatively long-lived species with low reproductive rates, and population growth rates would therefore be expected to be highly sensitive to adult annual survival rates (Saether and Bakke 2000). Unfortunately, there have been no successful mark-recaptures studies conducted on Santa Barbara Island to determine murrelet annual survival rates. Instead, we have estimated this rate to be 84% based on other studies for murrelets on this island (80% - Sydeman et al. 1998; 84.44% Nur et al. 2013; 83.05% Chapter 4). The closely related Ancient Murrelet (*Synthliboramphus antiquus*) has an estimated annual survival rate of ~76% (Gaston 1992), which suggests that Scripps's Murrelets may also be towards the lower end of this range. While these estimates are relatively similar, even small changes could have a large effect. Therefore, the model was run again with the only change in the parameters being either a higher (85.5%) or lower (82.5%) annual murrelet survival rate. We still found that neither owl management scenarios resulted in substantially higher murrelet abundance between 2020-2050 for any of the climate scenarios (Figure C4 and C5). Our results were therefore still qualitatively similar, which confirms that our main conclusions are robust to these differences.

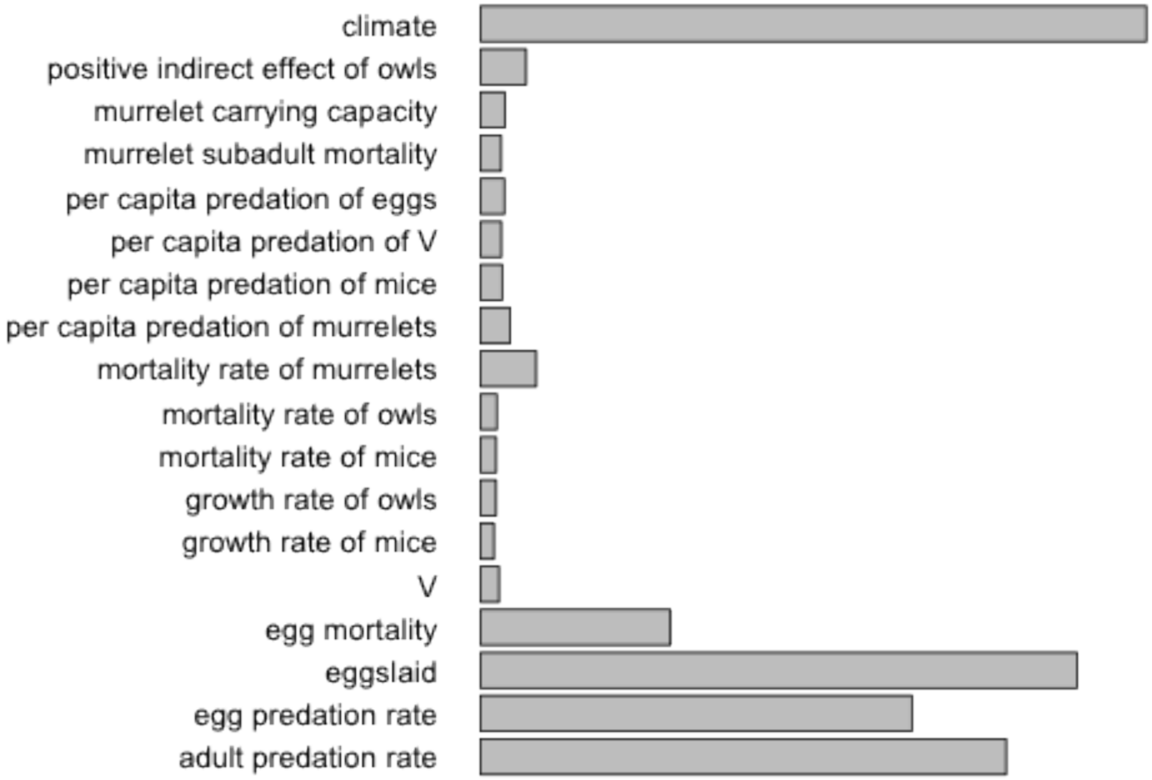


Figure C3. Relative importance of parameters in the model determined with a random forest analysis. Larger values (% mean square error) indicate that the murrelet abundance has greater sensitivity to those parameters.

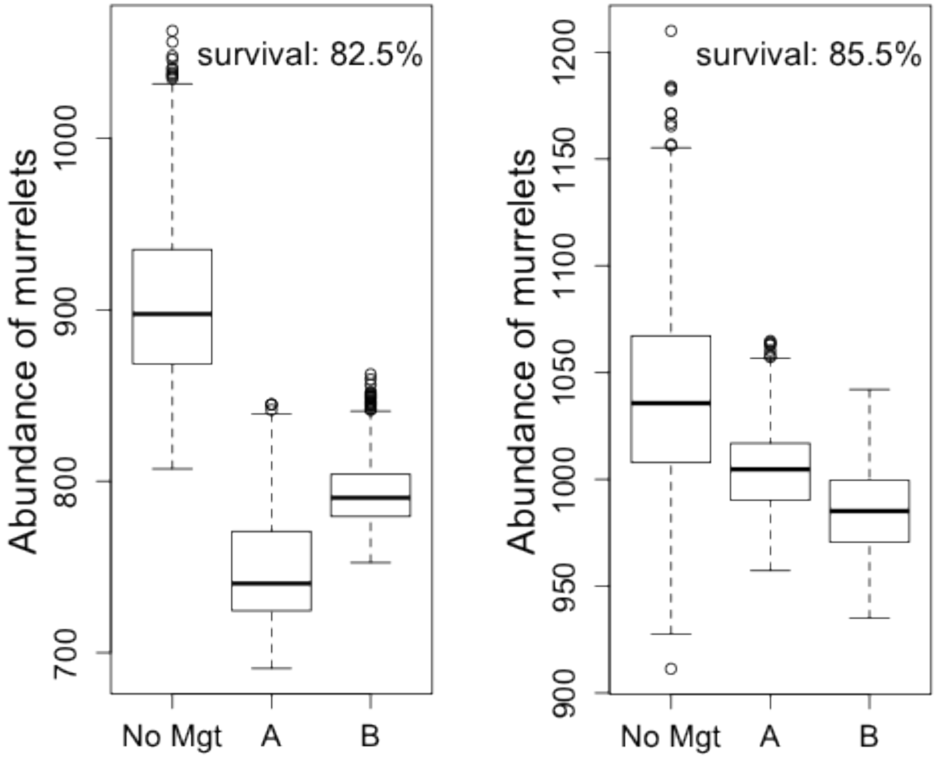


Figure C4 and C5. Management outcomes given changes in annual murrelet survival compared to the default value (84%).

References

Breiman, T., and A. Cutler. 2011. Package ramdomForest. http://cran.r-project.org/web/packages/randomForest/randomForest.pdf

Cole. L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29, 103 doi:10.1086/400074 pmid:13177850

Collins, P. W., J. Storrer and K. Rindlaub. (1979). Vertebrate zoology: the biology of the deer mouse - In: Power, D. M., Natural resources study of the Channel Islands National Monument, California. Santa Barbara Museum of Natural History, Chapter 11.

Courchamp, F., M. Langlais, and G. Sugihara. 1999. Control of rabbits to protect island birds from cat predation. Biological Conservation 89:219–225.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

Gaston, A. 1992. The Ancient Murrelet a Natural History in the Queen Charlotte Islands

Millus, S. A., Stapp, P., and P. Martin. 2007. Experimental control of a native predator may improve breeding success of a threatened seabird in the California Channel Islands. Biological Conservation 138:484-492.

Murray, K.G., K. Winnett-Murray, Z. A. Eppley, G. L. Hunt Jr., and D. B. Schwartz. 1983. Breeding Biology of the Xantus's Murrelet. Condor 85:12–21.

Nur, N., A. L. Harvey, S. K. Thomsen, R. Bradley, and J. Jahncke. (2013). Modeling the Population level Impacts of Barn Owls on Scripps's Murrelet Population Trends on Santa Barbara Island. Unpublished report prepared for: National Fish and Wildlife Foundation. Point Blue Conservation Science, Petaluma, California. PRBO contribution Number 1969.

Ozer, F., Gellerman, H., and Ashley, M. V. (2011). Genetic impacts of Anacapa deer mice reintroductions following rat eradication. Molecular ecology 20:3525-3539.

Saether, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Soetaert, K., T. Petzoldt, and R. Setzer. 2010. Solving Differential Equations in R: Package deSolve. Journal of Statistical Software. American Statistical Association, Alexandria, VA 33:1–25.

Sydeman, W. J., N. Nur, and P. Martin. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-Petrel (*Oceanodroma homochroa*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*). Final report to the United States Geological Survey, Biological Resources Division, Species at Risk Program. Stinson Beach, CA: PRBO Conservation Science. 74 pp

Taylor, I. 2003. Barn owls: Predator-prey relationships and conservation. Cambridge University Press, Cambridge.

Thomsen, S.K. and S.T. Plumb. 2014. Factors influencing depredation of Scripps's Murrelets by Barn Owls on Santa Barbara Island: Summary results from the 2012 field season. Unpublished report prepared for: Montrose Settlements Restoration Program. 15 pp.