

# Predator-mediated effects of severe drought associated with poor reproductive success of a seabird in a cross-ecosystem cascade

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## 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 rainfall pulses and drought that subsequently impact the breeding success of a threatened 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 (*Peromyscus maniculatus elusus*). Mice on the island have an opportunistic diet of primarily terrestrial sources, 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 terrestrial and marine productivity between 1983 and 2013 to determine how conditions in these ecosystems influence murrelet nest success. We found that the severity of drought had the strongest negative impact on murrelet nest success. We calculated that the reduction in fecundity during drought years due to increased egg predation by mice was substantial enough to produce a declining population growth rate. Nest success was much higher under normal or high rainfall conditions, depending on whether oceanic conditions were favorable to murrelets. Therefore, the more frequent and severe drought that is projected for this region could lead to an increased risk of murrelet population decline on this island. Our study highlights the need for understanding how species interactions will change through the effects of increasing drought and altered rainfall regimes under global change.

## KEYWORDS

cross-ecosystem cascade, drought, indirect effects, predation, rainfall, seabirds

## 1 | INTRODUCTION

Global climate change is expected to result in increased variability and changes to precipitation regimes across many regions of the world (Milly, Dunne, & Vecchia, 2005; Power, Delage, Chung, Kociuba, & Keay, 2013). In particular, droughts are predicted to become more

extreme, last longer, and increase in frequency (Dai, 2013). During an extreme drought, the intense unmet need for water can cause plant die-off (Breshears et al., 2005; Miriti, Rodriguez-Buritica, Wright, & Howe, 2007), as well as reduced survival and reproduction in animals (Grant & Grant, 2002; Rymer, Pillay, & Schradin, 2016; Sperry & Weatherhead, 2008). The amount of rainfall is particularly

crucial for the arid and semi-arid ecosystems of the world, which already receive low annual precipitation (Maestre, Salguero-Gómez, & Quero, 2012), as it can strongly limit plant primary productivity (De la Maza, Lima, Meserve, Gutierrez, & Jaksic, 2009). This limitation is vividly illustrated by the landscape green-up that occurs after drought-breaking rainfall, which subsequently has direct effects on higher trophic levels (Deguines, Brashares, & Prugh, 2017; Jaksic, Silva, Meserve, Gutiérrez, & Gutierrez, 1997). Although these characteristics of drylands are shared by ~41% of the earth's land (Maestre et al., 2012), there remains much uncertainty around how drought and rainfall variability influence indirect interactions in food webs (e.g., Barton & Ives, 2014; Beier et al., 2012). Given climate change projections, there remains an urgent need to understand how changes to precipitation patterns will influence ecological interactions (McCluney et al., 2012), particularly if effects extend across ecosystems.

Ecosystem boundaries, such as those between the marine and terrestrial environments, can be permeable to the flow of resources between the adjacent food webs (Gende, Edwards, Willson, & Wipfli, 2002; Loreau, Mouquet, & Holt, 2003; Piovato-Scott, Spiller, & Schoener, 2011). If these resource flows are altered, such as by extreme drought, it could potentially lead to cascading effects across ecosystem boundaries (Knight, McCoy, Chase, McCoy, & Holt, 2005; Larsen, Muehlbauer, & Marti, 2016). For example, after a 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 & 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 & Ruffino, 2012). But the extent to which rodents utilize this seasonal prey source then could depend on the effects of fluctuating terrestrial resources (Ruffino, Russell, & Vidal, 2013). Similarly, nest success of birds in a variety of environments can be strongly influenced by the availability of other prey types for predators (Ims, Henden, Thingnes, & Killengreen, 2013; Johnston, 2016; Ostfeld & Keesing, 2000; Schmidt & Ostfeld, 2008). Thus, depending on how strongly changes to rainfall patterns propagate in a food chain, these changes 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, Giorgi, & Pal, 2008), where the risk of future unprecedented drought conditions are projected by some models (Cook, Ault, & Smerdon, 2015). On this island, ~21% of the global population of a threatened nocturnal seabird, the Scripps's Murrelet (*Synthliboramphus scrippsi*; Whitworth, personal communication, 2018), arrives to breed each spring. Unlike most other seabirds (Weimerskirch, 2002), ocean productivity apparently only

has a weak influence on Scripps's Murrelet nest success on Santa Barbara Island (Roth, Sydeman, & Martin, 2005), largely because egg predation by an endemic subspecies of deer mouse (*Peromyscus maniculatus elusus*) is the main cause of reduced nest success for murrelets there (up to 70% of all eggs laid are lost to mice annually; Drost & Lewis, 1995). However, interannual differences in reproductive success have not been conclusively linked to variations in mouse density alone (Murray, 1980; Nur, Harvey, Thomsen, Bradley, & Jahncke, 2013; Schwemm & Martin, 2005). Instead, murrelet nest success might be influenced by changes in mouse foraging behavior regardless of mouse abundance (Thomsen & 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 hypothesis, we examined murrelet nest success over a span of 31 years (1983–2013) and evaluated the relative importance of several indicators of terrestrial and marine productivity. We also assessed how changes in murrelet nest success might influence the resulting population growth rates with a matrix population model.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and system

Santa Barbara Island (33°29'N, 119°02'W) is 2.6 sq km 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 (~475–650 breeding pairs; Whitworth, personal communication, 2018), a small (~165 g) pursuit diving alcid that is endemic to this region and considered by the IUCN to be Vulnerable (Birdlife International, 2017) and state-listed as Threatened. This region of southern California is semi-arid, with the island only receiving an estimated average 21.8 cm of rainfall per year (Orrock, Allan, & Drost, 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.; Halvorson, Fenn, & Allardice, 1988; Junak, Drost, & Philbrick, 1993) that grow on the steep rocky cliffs that tower up to 193 m above the ocean.

### 2.2 | Murrelet nest monitoring

The U.S. National Park Service and collaborators have been monitoring the nest success of Scripps's Murrelets on the island since the early 1980s (Lewis, Gress, Ingram, Hunt, & Anderson, 1988; Millus, Stapp, & Martin, 2007; Sydeman, Nur, & Martin, 1998 and references therein; <http://www.montroserestoration.noaa.gov/multimedia/publications/>). Here, we focus on one of the largest monitoring areas on the island (Cat Canyon) that has been consistently studied annually throughout this time period except for the year 2006. 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 & Lewis, 1995). The first egg laid is left unattended for ~8 days before the clutch is completed and incubation commences (Murray, Winnettmurray, Eppley, Hunt, & Schwartz, 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 & 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% of cases) is due to depredation by mice, which usually happens during the initial egg neglect period (Millus et al., 2007; Murray et al., 1983). Video footage of mice consuming murrelet eggs corroborates other evidence, such as teethmarks left on eggshells, that depredation is only 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 were summarized into mean nest success (total number of eggs hatched/total number of nest attempts).

## 2.3 | Marine environment

Ocean productivity in the California Current is highly dynamic and influenced by both interannual and interdecadal climatic variations. Periods of high marine productivity are characterized by wind-driven upwelling of cold, nutrient-laden water, which subsequently influences higher trophic levels including increased seabird reproductive success (e.g., Ainley, 1990). We therefore obtained several key indices of marine environmental conditions during 1983–2013 that could potentially predict murrelet nest success. We included three indices of physical processes that describe large-scale patterns in the Northeast Pacific Ocean 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>). For example, when El Niño conditions occur every ~2–7 years, they cause increases in sea surface temperature and a reduction in upwelling (McPhaden, Zebiak, & Glantz, 2006). The PDO also describes shifts in ocean temperature but operates on decadal time scales (Mantua & Hare, 2002). In addition, the NPGO describes the second dominant mode of sea surface height variability and is associated with additional fluctuations of ocean temperature and upwelling (Di Lorenzo et al., 2008).

We also obtained data for local to regional-scale conditions near the island such as sea surface temperature (SST; Station 46025 buoy; 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. Murrelets are generalist predators (Hamilton, Carter, & Golightly, 2004), and the abundance of mesozooplankton was previously identified as potentially being important to murrelet breeding parameters (Roth et al., 2005). Mesozooplankton abundance

also 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. Marine indices were averaged across March–May to match and represent breeding season conditions for each year.

## 2.4 | Terrestrial environment

### 2.4.1 | 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 interannual 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.

Data on rainfall amounts were not consistently collected on the island over the entire study period so this variable 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 & Pitelka, 1970; Sofaer, Sillett, Peluc, Morrison, & Ghalambor, 2013; St. Clair, Sudderth, Castanha, Torn, & Ackerly, 2009; Sweet et al., 2015), which contributes most of the diet of deer mice (Collins, Storrer, & Rindlaub, 1979; Millus & Stapp, 2008). NDVI thus represents an integrated measure of terrestrial conditions so it was important to verify that the regional PDSI and NDVI on the island were related. To check this, we compared the PDSI values with the NDVI value calculated from Landsat satellite images of the island captured during March 1985–2013 (median ordinal date = 78; range: 52–92; NASA LP DAAC, 2014). The PDSI and NDVI values were positively correlated ( $n = 26$ ,  $\rho = 0.82$ ,  $p < 0.001$ ) in the subset of years where NDVI could be calculated.

### 2.4.2 | Deer mouse abundance

The National Park Service has also conducted long-term mark-recapture studies of deer mouse abundance on the island, and we used the

abundance index (number of unique individuals captured) on the plot nearest to the murrelet monitoring area (~1 km away) from published reports (Coonan, 2013, 2016; Schwemm, 2009) for our analyses. This abundance index correlates strongly with other more complex mark-recapture models of population size of mice on the island (Schwemm, Drost, Orrock, Coonan, & Stanley, 2018). Trapping occurred during the spring (March–May) from 1993 to 2013, except for 1994 and 2006 when no data collection occurred in spring. The mouse plot has 100 permanent trap stations, at which one small Sherman live trap is set over three consecutive nights during trapping sessions (Fellers, Drost, & Arnold, 1988). Traps are checked the following morning, and captured mice are weighed, sexed, and given an individually numbered ear tag before being released unharmed (Coonan, 2016).

## 2.5 | Data analysis

We used R 3.2.1 (R Core Team, 2014) to conduct all statistical analyses. First, 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. For this analysis, we limited it to the time period 1993–2013 because of the consistent data collection of all time series resulting in few missing observations. 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 & 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 S2). Mouse abundance was log transformed, and all input variables were standardized ( $\mu = 0$  and  $\sigma^2 = 1$ ) 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 screened all explanatory variables for collinearity and did not include variables together in multiple regression if the correlation was  $|r| > 0.5$  (Zuur, Ieno, & Elphick, 2010). As expected, many of the marine variables were highly correlated so we used principal component analysis (PCA) to reduce the number of variables prior to analysis in the candidate model set. The first principal component ("marine 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 S1 and Figure S1). Log mesozooplankton volume, the NPGO index, and upwelling were positively loaded on marine PC1 (0.43, 0.37, and 0.42, respectively), while MEI, local SST, and PDO were all loaded negatively (−0.39, −0.42, and −0.4, respectively; Table S1). Marine PC1 thus represents a range of conditions that correspond with colder waters, increased upwelling and higher ocean productivity

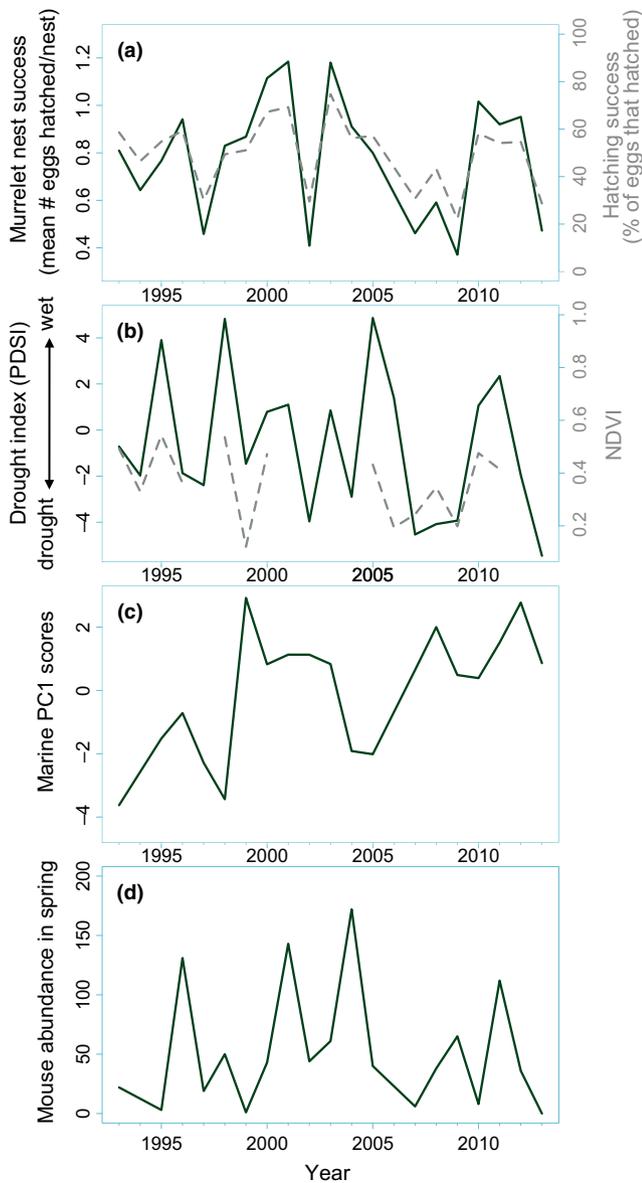
including higher mesozooplankton amounts. The remaining principal components each explained  $\leq 12\%$  of the variation therefore only marine PC1 was retained for the subsequent linear regression analysis of nest success.

Next, we conducted a complementary regression tree analysis with the R package "rpart" (Therneau & Atkinson, 2015) to further explore the relationships among all of the marine and terrestrial explanatory variables and to identify the most influential individual variables on murrelet nest success for the entire 1983–2013 time period. All six marine and two terrestrial variables (PDSI and NDVI) 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 and correlations between variables (De'ath & 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 were retained in the final model (Therneau & Atkinson, 2015).

Finally, we developed a deterministic matrix population model parameterized with fecundity rates from the 1983 to 2013 nest success data to examine environmental impacts on population growth rates. To do so, we used a stage-structured model that contains juvenile, subadult, and adult stages (Caswell, 2001; Lefkovich, 1965). Adult annual survival was set at 0.8305 based on a previously published regression equation relating adult body mass with adult survival in 12 other alcid species (Beissinger & Peery, 2007). Juvenile and subadult survival rates were then set at 70% and 89% of the adult value, respectively (Sydeman et al., 1998), while subadult 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 (Drost & Lewis, 1995; Gaston, 1990) following Beissinger and Peery (2007). We then calculated the resulting stochastic population growth rates ( $\lambda_s$ ) with the function "stoch.growth.rate" from the R package "popbio" (Stubben & Milligan, 2007). We could then assess whether the murrelet population would be more likely to increase ( $\log \lambda_s > 0$ ) or decline ( $\log \lambda_s < 0$ ) in response to different environmental conditions that were identified by the regression tree analysis as important. Lastly, we used the same function to simulate how the population growth rate would change in response to projected increases in drought years by increasing the probability of selection of annual matrices that occurred during severe drought years.

## 3 | RESULTS

A total of 1,368 murrelet nest attempts were monitored during the years 1983 to 2013 in the Cat Canyon area (approximately  $45 \pm 12$  nests per year; range 29–91). Mean nest success over this time period of 30 years was  $0.77 \pm 0.25$  eggs hatched per nest (range: 0.37–1.18). Egg predation by mice was the main cause of egg loss leading to reduced nest success in all years. Nest success varied, but despite reaching its lowest levels more often in recent years (1990, 1997, 2002, 2007, 2009 and 2013; Figures 1a; 3), there was no evidence of a linear trend over time ( $p > 0.88$ ).



**FIGURE 1** Observations from 1993 to 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 numbers denote the increasing severity of drought, and the Normalized Difference Vegetation Index (NDVI) where higher numbers indicate higher terrestrial productivity (c) Marine PC1 scores increased over time, with higher scores indicating more favorable conditions for murrelets (see also supplemental Figure S1) and (d) Mouse abundance (number of unique individuals captured; as reported in Coonan, 2013, 2016; Schwemm, 2009) during the murrelet breeding season

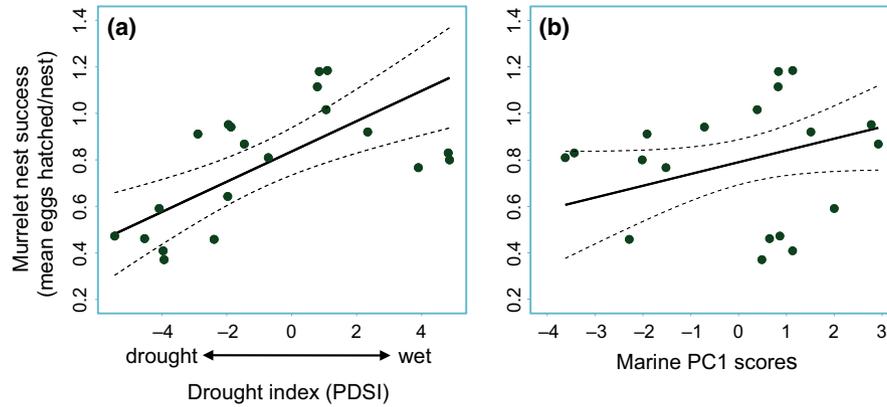
The best-ranked models explaining variation in murrelet nest success included the effects of PDSI and ocean conditions (marine PC1 scores; Table S2). Only the marine PC1 scores demonstrated a significant upward trend between 1993 and 2013, indicating an increase in more favorable ocean conditions for murrelets over time ( $F_{1,17} = 8.518$ ,  $p < 0.01$ ,  $r^2 = 0.29$ ; Figure 1c). When this trend was

removed, the model rankings remained completely unchanged (Table S2), suggesting that nest success was influenced by these same variables independent of co-occurring long-term trends (Grosbois et al., 2008). The top model with detrended data had a slightly improved AICc compared to the non-detrended model ( $\Delta AIC_c = 0.6$ ), therefore, hereafter we focus on the parameter estimates from the top model in the detrended data analysis which had a  $r^2$  of 0.48 (Table S2). Murrelet nest success was positively related to the PDSI ( $\beta = 0.19$ , 95% CI [0.09, 0.29]) indicating that the severity of drought conditions was associated with low nest success due to increased eggs lost to predation (Figure 2a). Nest success was also positively related to marine PC1 scores ( $\beta = 0.06$ ; 95% CI [-0.006, 0.12]; Figure 2b), indicating that colder ocean temperatures and higher ocean productivity were also associated with increased nest success. There was no support for a relationship between increased mouse abundance leading to low murrelet nest success (Table S2; Figure 1d). This suggests that the intensity of egg predation is driven by other factors that influence mouse foraging independent of mouse abundance.

The regression tree analysis for the longer time series 1983–2013 produced similar results, where the most important variable determining poor murrelet nest success was the occurrence of a severe to extreme drought ( $< -2.9$  on the PDSI scale; Figure 3). Mean nest success for those drought years (0.48 eggs hatched per nest attempt;  $n = 8$ ) produced a sharply declining population growth rate ( $\lambda_s = -0.08$ ) when this value was input as the fecundity rate in the matrix population model (Figure 3). During closer to normal rainfall conditions or during wet spells (PDSI  $> -2.9$ ), murrelet nest success was much higher, but how much higher depended on whether ocean temperatures were colder (SST  $< 15.7^\circ\text{C}$ ) and the NPGO index was positive ( $> 1.1$ ; 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  $< 1.1$  but SST was colder ( $< 15.7^\circ\text{C}$ ), murrelet nest success was still moderate (0.93 eggs hatched per nest attempt), and the resulting population growth rate was closer to stability but still declining ( $\lambda_s = -0.01$ ;  $n = 6$ ). Murrelets had the highest nest success over the 30 years of this study (1.05 eggs hatched per nest attempt) when the SST was  $< 15.7^\circ\text{C}$ , the NPGO index was  $> 1.1$ , and without drought conditions, which would be sufficient to produce a stable population growth rate ( $\lambda_s = 0.002$ ;  $n = 6$ ; Figure 3). However, the mean population growth rate for the entire study period suggested there would be an overall decline ( $\lambda_s = -0.03$ ). Moreover, as the frequency of severe drought years was increased, the murrelet population on the island would be expected to experience even more drastic declines (Figure 4).

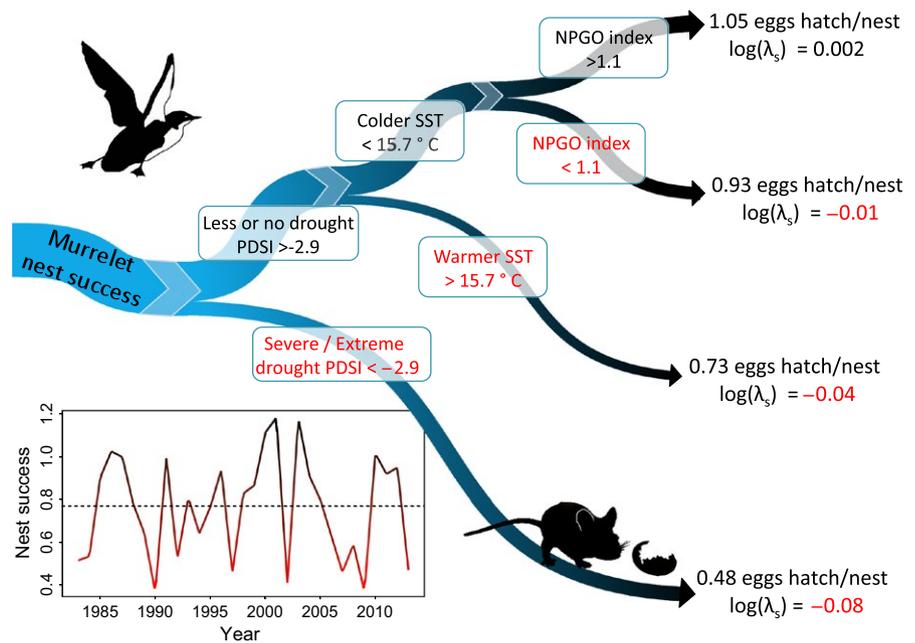
## 4 | DISCUSSION

Seabirds are often heralded as sentinels of ocean climate variability and change, as is demonstrated by many long-term monitoring studies of seabird reproductive success (e.g., Ainley, 1990; Divoky, Lukacs, & Druckenmiller, 2015; Wanless, Frederiksen, Daunt, Scott, & Harris, 2007). In this study, however, we found that murrelet nest success since the 1980s was mainly associated with a



**FIGURE 2** (a) Murrelet nest success and PDSI values in April for the years 1993–2013. 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 (see Table S1 and Figure S1). Solid and dashed lines indicate the regression fit and standard errors from the top model (see Table S2)

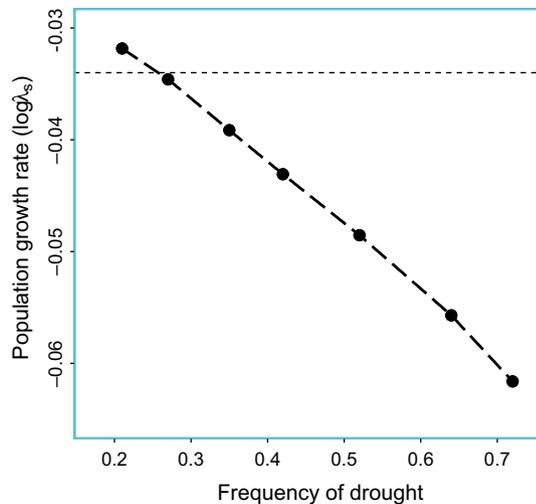
**FIGURE 3** Dendrogram of regression tree analysis of murrelet nest success over 30 years (1983–2013). Horizontal dashed line on inset figure indicates the overall mean. Very poor nest success occurred during severe to extreme droughts (PDSI  $< -2.9$ ) when egg predation by mice was highest, resulting in a declining population growth rate ( $\log \lambda_s$ ). Higher than average nest success occurred when drought was minimal, the ocean temperature (SST) was cooler and the NPGO index was positive ( $> 1.1$ ), resulting in a stable population growth rate ( $\log \lambda_s$ )



different hallmark of climate variability, the severity of drought (Figures 2,3). Specifically, our results support the hypothesis that climate-driven changes in terrestrial productivity drives murrelet nest success via a cross-ecosystem cascade of indirect interactions with terrestrial productivity. Furthermore, our study demonstrates that the effect of drought on reproductive success, a key vital rate, could be substantial enough to trigger population declines in this seabird (Figures 3,4). 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, Hand, & Auer, 2012; Howard et al., 2014). Likewise, other breeding land birds in this region lose more nests to predators during drought years, but unlike murrelets, they can be primarily directly affected by limited terrestrial food availability themselves (Chase, Nur, & Geupel, 2005; Cruz-McDonnell & Wolf, 2016; Morrison & Bolger, 2002; Preston & Rotenberry, 2006). 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.

There are compelling reasons why drought would be the major driver of increased egg predation and not mouse abundance. None of the top models included mouse abundance ( $\Delta AIC_c < 2$ ; Table S2). This is likely because the conditions during severe drought would also lead to declines in the abundance of mice compared to wetter years with more abundant resources (Morton, Morrison, Hall, & Pereyra, 1995; Spevak, 1983). For example, during a drought, common island plants such as *Avena* spp. have reduced biomass and produce fewer seeds (Ewing & Menke, 1983). Notably, the NDVI in some drought years indicated there was almost no green vegetation in March (Figure 1b; Pettorelli et al., 2005). Additionally, eggs themselves might be an important source of both nutrients and water to mice during droughts, which could also increase egg predation as rodents seek needed moisture to survive (Morton et al.,



**FIGURE 4** Decline in the stochastic population growth rate ( $\log \lambda_s$ ) for murrelets in response to increasing the probability of severe drought (PDSI  $< -2.9$ ), similar to what is projected for this region. Horizontal dashed line indicates overall  $\log \lambda_s$  under the frequency of severe drought occurrence between 1983 and 2013 (i.e., 8 of 30 years), which suggests the population on the island could already be declining

1995; Norman, 1975). Finally, the availability of food resources can influence the risks that mice might be willing to take while foraging in the presence of predators (Brown & Kotler, 2004; Laundre et al. 2014; Riginos, 2015). Mice on the island drastically increased their foraging activity when owls were least abundant (Thomsen & Green, 2016), which coincided with a severe drought year (Thomsen, Mazurkiewicz, Stanley, & Green, 2018). 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, our results suggest that ocean climate conditions were still critically important in determining murrelet nest success. Higher marine PC1 scores and specifically colder ocean temperatures (SST) and a positive NPGO index ( $>1.1$ ) were associated with higher than average breeding success (Figures 2b, 3). These favorable conditions likely mean better foraging conditions and increased prey availability for murrelets similar to how it benefits other seabirds in the California Current ecosystem (Ainley, 1990; Jones et al., 2018). Only when the NPGO was positive, in the absence of drought conditions, was murrelet nest success high enough to produce a stable or increasing population growth rate (Figure 3). This finding is also consistent with the rising influence of the NPGO for both seabirds and salmon elsewhere in the California Current (Kilduff, Lorenzo, Botsford, & Teo, 2015; Schmidt et al., 2014; Sydeman, Santora, Thompson, Marinovic, & Lorenzo, 2013). Our study therefore corroborates other research that suggests the ocean is changing in ways that are potentially increasingly negative for seabirds and other marine predators (Croxall et al., 2012). However, additional comparative studies of murrelet breeding success on other islands, particularly

those islands where egg predation by mice is less of an issue (Whitworth, Carter, & Gress, 2013), are needed to further clarify how ocean climate change will impact murrelets.

Ultimately, overall murrelet nest success on Santa Barbara Island appears to be influenced by a combination of factors from both the marine and terrestrial environments. However, in southern California, both of these ecosystems are coupled via the influence of the ocean on regional precipitation patterns (Black et al., 2014), and could mitigate impacts to maintain murrelet nest success despite a highly variable environment. For example, oftentimes, warmer ocean temperatures (SST) and the resulting poor foraging conditions for murrelets are the same conditions that usually lead to increased rainfall in this region (Black et al., 2014). Under such poor ocean conditions, the resulting slight increase in one-egg clutches (Roth et al., 2005), as well as an increase in egg neglect after incubation begins (Blight, Bertram, Williams, & Cowen, 2010; Murray et al., 1980), would leave murrelet eggs much more vulnerable to predation by rodents (Ronconi & Hipfner, 2009). However, because this increased vulnerability generally occurs when terrestrial productivity is higher and egg predation rates are lower, this suggests the possibility that the negative effects of poor ocean conditions on breeding success can be partially offset in some years. However, it remains to be seen whether these connections between SST and winter precipitation in southern California will remain stable or become more variable under global climate change (Kam & Sheffield, 2016).

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 & 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  $\sim 3\%$  annual decline over the study period, which is similar in magnitude to the estimated population trend on Santa Barbara Island (Burkett et al., 2003; 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 et al., 1998). Furthermore, predicted increases in the occurrence of severe droughts could mean murrelets are more likely to have years of drastically low nest productivity (Figure 4). 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 (*Tyto alba*) and Peregrine Falcons (*Falco peregrinus*) that consume adults (Drost & Lewis, 1995; Thomsen et al., 2018). Therefore, the optimal strategy for conservation of murrelets on Santa Barbara Island will likely need to address both life stages. We strongly suggest that further studies use individually marked birds in a mark-recapture design study to estimate adult survival and breeding probability to better assess which conservation actions may be the most effective.

It is well established that climate can influence community dynamics in both terrestrial (Hansen et al., 2013; Post & Forchhammer, 2002) and marine ecosystems (Poloczanska et al., 2013). In this study, we found that the severity of drought on a semi-arid oceanic island was associated with negative impacts on the breeding success of a seabird via a cross-ecosystem cascade. Drought conditions in this area are also linked to regional oceanographic indices (McCabe-Glynn et al., 2013), so this long ecological cascade ultimately begins with ocean-atmosphere interactions and ends up looping back onto the marine food web via murrelets. Similar synchronous effects between marine and terrestrial ecosystems have been increasingly recognized through the effects of rainfall (Black et al., 2018; Ong et al., 2016; Thomsen et al., 2018), but our study is unique for the California Current system in that long-term data revealed a stronger connection between terrestrial productivity and the reproductive dynamics of a marine predator. In 2013, much of California was in an exceptional drought of a magnitude that had not been experienced for perhaps over ~1,200 years (Griffin & Anchukaitis, 2014; Diffenbaugh, Swain, & Touma, 2015). As the PDSI is projected to become more frequently negative for much of the 21st century (Gutzler & Robbins, 2011), this has potentially worrisome implications for murrelets breeding on Santa Barbara Island. Our study therefore has wider implications about the profound impacts of drought and highlights the need for understanding how species interactions will change through the effects of altered rainfall regimes under global change.

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## REFERENCES

- Ainley, D. G. (1990). *Seabirds of the Farallon Islands: Ecology, dynamics, and structure of an upwelling-system community*. Palo Alto, CA: Stanford University Press.
- Barton, B. T., & Ives, A. R. (2014). Species interactions and a chain of indirect effects driven by reduced precipitation. *Ecology*, *95*(2), 486–494. <https://doi.org/10.1890/13-0044.1>
- Batzli, G. O., & Pitelka, F. A. (1970). Influence of meadow mouse populations on California grassland. *Ecology*, *51*(6), 1027–1039. <https://doi.org/10.2307/1933629>
- Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., ... Hansen, K. (2012). Precipitation manipulation experiments – Challenges and recommendations for the future. *Ecology Letters*, *15*(8), 899–911. <https://doi.org/10.1111/j.1461-0248.2012.01793.x>
- Beissinger, S. R., & Peery, M. Z. (2007). Reconstructing the historic demography of an endangered seabird. *Ecology*, *88*(2), 296–305. <https://doi.org/10.1890/06-0869>
- Birdlife International. (2017). *Synthliboramphus scrippsi* (Scripps's Murrelet). Retrieved from <http://www.iucnredlist.org/details/62101249/0>
- Black, B. A., Sydeman, W. J., Frank, D. C., Griffin, D., Stahle, D. W., Garcia-Reyes, M., ... Peterson, W. T. (2014). Six centuries of variability and extremes in a coupled marine-terrestrial ecosystem. *Science*, *345*(6203), 1498–1502. <https://doi.org/10.1126/science.1253209>
- Black, B. A., van der Sleen, P., Di Lorenzo, E., Griffin, D., Sydeman, W. J., Dunham, J. B., ... Bograd, S. J. (2018). Rising synchrony controls western North American ecosystems. *Global Change Biology*, *24*(6), 2305–2314. <https://doi.org/10.1111/gcb.14128>
- Blight, L. K., Bertram, D. F., Williams, T. D., & Cowen, L. (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.
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Meyer, C. W. (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*(42), 15144–15148. <https://doi.org/10.1073/pnas.0505734102>
- Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999–1014. <https://doi.org/10.1111/j.1461-0248.2004.00661.x>
- Burkett, E. E., Rojek, N. A., Henry, A. E., Fluharty, M. J., Comrack, L., Kelly, P. R., ... Fien, K. M. (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.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference* (2nd ed.). New York, NY: Springer.
- Caswell, H. (2001). *Matrix population models: Construction analysis and interpretation* (2nd ed.). Sunderland, MA: Sinauer Associates.
- Chase, M. K., Nur, N., & Geupel, G. R. (2005). Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: A long-term study. *The Auk*, *122*(2), 571–592. [https://doi.org/10.1642/0004-8038\(2005\)122\[0571:EOWAPD\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2005)122[0571:EOWAPD]2.0.CO;2)
- Collins, P. W., Storrer, J., & Rindlaub, K. (1979). Vertebrate zoology: The biology of the deer mouse, Chapter 11. In D. M. Power (Eds.), *Natural resources study of the Channel Islands National Monument*. Santa Barbara, CA: Santa Barbara Museum of Natural History.
- Cook, B. I., Ault, T. R., & Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, *1*(1), e1400082. <https://doi.org/10.1126/sciadv.1400082>
- Coonan, T. J. (2013). *2012 Deer mouse monitoring annual report: Channel Islands National Park*. Natural Resource Data Series NPS/MEDN/NRDS—2013/571. Fort Collins, CO: National Park Service.
- Coonan, T. J. (2016). *2013–2015 deer mouse monitoring annual report: Channel Islands National Park*. Natural Resource Data Series NPS/MEDN/NRDS—2016/1070. Fort Collins, CO: National Park Service.

- Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, 22(1), 1–34. <https://doi.org/10.1017/S0959270912000020>
- Cruz-McDonnell, K. K., & Wolf, B. O. (2016). Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. *Global Change Biology*, 22(1), 237–253. <https://doi.org/10.1111/gcb.13092>
- Dai, A. (2011). Drought under global warming: A review. *Wiley Interdisciplinary Reviews-Climate Change*, 2(1), 45–65. <https://doi.org/10.1002/wcc.81>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3(1), 52–58. <https://doi.org/10.1038/NCLIMATE1633>
- De La Maza, M., Lima, M., Meserve, P. L., Gutierrez, J. R., & Jaksic, F. M. (2009). Primary production dynamics and climate variability: Ecological consequences in semi-arid Chile. *Global Change Biology*, 15(5), 1116–1126. <https://doi.org/10.1111/j.1365-2486.2008.01796.x>
- De'ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, 81(11), 3178–3192. [https://doi.org/10.1890/0012-9658\(2000\)081\[3178:CARTAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2)
- Deguines, N., Brashares, J. S., & Prugh, L. R. (2017). Precipitation alters interactions in a grassland ecological community. *Journal of Animal Ecology*, 86(2), 262–272. <https://doi.org/10.1111/1365-2656.12614>
- Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., ... Rivière, P. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, 35(8), L08607. <https://doi.org/10.1029/2007GL032838>
- Diffenbaugh, N. S., Giorgi, F., & Pal, J. S. (2008). Climate change hot spots in the United States. *Geophysical Research Letters*, 35, L16709.
- Diffenbaugh, N. S., Swain, D. L., & Touma, D. (2015). Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences of the United States of America*, 112(13), 3931–3936. <https://doi.org/10.1073/pnas.1422385112>
- Divoky, G. J., Lukacs, P. M., & Druckenmiller, M. L. (2015). Effects of recent decreases in arctic sea ice on an ice-associated marine bird. *Progress in Oceanography*, 136, 151–161. <https://doi.org/10.1016/j.pocean.2015.05.010>
- Drost, C. A., & Lewis, D. B. (1995). Xantus's Murrelet (*Synthliboramphus hypoleucus*). *The Birds of North America Online*. <https://doi.org/10.2173/bna.164>
- Ewing, A. L., & Menke, J. W. (1983). Reproductive potential of *Bromus mollis* and *Avena barbata* under drought conditions. *Madrono*, 30, 159–167.
- Fellers, G. M., Drost, C. A., & Arnold, B. W. (1988). *Terrestrial vertebrates monitoring handbook, Channel Islands National Park, California*. Ventura, CA: National Park Service, Channel Islands National Park.
- Gaston, A. (1990). Population parameters of the Ancient Murrelet. *Condor*, 92(4), 998–1011. <https://doi.org/10.2307/1368736>
- Gende, S. M., Edwards, R. T., Willson, M. F., & Wipfli, M. S. (2002). Pacific Salmon in aquatic and terrestrial ecosystems. *BioScience*, 52(10), 917–928. [https://doi.org/10.1641/0006-3568\(2002\)052\[0917:PSIAAT\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2)
- Grant, P. R., & Grant, B. R. (2002). Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, 296(5568), 707–711. <https://doi.org/10.1126/science.1070315>
- Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, 41(24), 9017–9023. <https://doi.org/10.1002/2014GL02433>
- Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., ... Weimerskirch, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, 83(3), 357–399. <https://doi.org/10.1111/j.1469-185X.2008.00047.x>
- Gutzler, D. S., & Robbins, T. O. (2011). Climate variability and projected change in the western United States: Regional downscaling and drought statistics. *Climate Dynamics*, 37(5–6), 835–849. <https://doi.org/10.1007/s00382-010-0838-7>
- Halvorson, W., Fenn, D., & Allardice, W. (1988). Soils and vegetation of Santa-Barbara Island, Channel-Islands-National-Park, California, USA. *Environmental Management*, 12(1), 109–118. <https://doi.org/10.1007/BF01867382>
- Hamilton, C. D., Carter, H. R., & Golightly, R. T. (2004). Diet of Xantus's Murrelets in the Southern California Bight. *The Wilson Bulletin*, 116(2), 152–157. <https://doi.org/10.1676/03-114>
- Hansen, B. B., Grotan, V., Aanes, R., Saether, B.-E., Stien, A., Fuglei, E., ... Pedersen, A. O. (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. *Science*, 339(6117), 313–315. <https://doi.org/10.1126/science.1226766>
- Harvey, A. L., Hand, C. E., & Auer, S. A. (2012). Scripps's Murrelet reproductive performance on Santa Barbara Island, California in 2008–2009. Montrose Settlements Trustee Council. 20 pp. Retrieved from <http://www.montroserecovery.noaa.gov/multimedia/publications/>
- Howard, J. A., Harvey, A. L., Kim, S. J., Robison, R. E., Mazurkiewicz, D. M., Yamagiwa, A. A., ... Wynd, E. F. W. (2014). Scripps's Murrelet and Cassin's Auklet reproductive monitoring and restoration activities on Santa Barbara Island, California in 2013. California Institute of Environmental Studies. Retrieved from <http://www.montroserecovery.noaa.gov/multimedia/publications/>
- Ims, R. A., Henden, J.-A., Thingnes, A. V., & Killengreen, S. T. (2013). Indirect food web interactions mediated by predator–rodent dynamics: Relative roles of lemmings and voles. *Biology Letters*, 9(6), 20130802. <https://doi.org/10.1098/rsbl.2013.0802>
- Jaksic, F. M., Silva, S. I., Meserve, P. L., Gutiérrez, J. R., & Gutierrez, J. R. (1997). A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in Western South America. *Oikos*, 78(2), 341–354. <https://doi.org/10.2307/3546302>
- Johnston, G. R. (2016). Drought increases the impact of introduced European foxes on breeding Australian pelicans. *Wildlife Research*, 43(6), 507–514. <https://doi.org/10.1071/WR15207>
- Jones, T., Parrish, J. K., Peterson, W. T., Bjorkstedt, E. P., Bond, N. A., Ballance, L. T., ... Harvey, J. (2018). Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophysical Research Letters*, 45(7), 3193–3202. <https://doi.org/10.1002/2017GL076164>
- Junak, S., Drost, C. A., & Philbrick, R. N. (1993). *A revised flora of Santa Barbara Island* (112 pp). Santa Barbara, CA: Santa Barbara Botanic Garden.
- Kam, J., & Sheffield, J. (2016). Increased drought and pluvial risk over California due to changing oceanic conditions. *Journal of Climate*, 29(22), 8269–8279. <https://doi.org/10.1175/JCLI-D-15-0879.1>
- Kilduff, D. P., Lorenzo, E. D., Botsford, L. W., & Teo, S. L. H. (2015). Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences of the United States of America*, 112(35), 10962–10966. <https://doi.org/10.1073/pnas.1503190112>
- Knight, T. M., McCoy, M. W., Chase, J. M., McCoy, K. A., & Holt, R. D. (2005). Trophic cascades across ecosystems. *Nature*, 437(7060), 880–883. <https://doi.org/10.1038/nature03962>
- Koehn, L. E., Essington, T. E., Marshall, K. N., Kaplan, I. C., Sydeman, W. J., Szoboszlai, A. I., & Thayer, J. A. (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. <https://doi.org/10.1016/j.ecolmodel.2016.05.010>
- Larsen, S., Muehlbauer, J. D., & Marti, E. (2016). Resource subsidies between stream and terrestrial ecosystems under global change. *Global Change Biology*, 22(7), 2489–2504. <https://doi.org/10.1111/gcb.13182>
- Laundre, J. W., Hernandez, L., Lopez Medina, P., Campanella, A., Lopez-Portillo, J., Gonzalez-Romero, A., ... Browning, D. M. (2014). The

- landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, 95(5), 1141–1152. <https://doi.org/10.1890/13-1083.1>.
- Lefkovich, L. P. (1965). Study of population growth in organisms grouped by stages. *Biometrics*, 21(1), 1–18. <https://doi.org/10.2307/2528348>
- Lewis, D. B., Gress, F., Ingram, T., Hunt, G. L. Jr, & Anderson, D. (1988). *Seabird monitoring handbook, Channel Islands National Park* (33 pp). Ventura, CA: National Park Service, Channel Islands National Park.
- Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, 6(8), 673–679. <https://doi.org/10.1046/j.1461-0248.2003.00483.x>
- Maestre, F. T., Salguero-Gómez, R., & Quero, J. L. (2012). It is getting hotter in here: Determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1606), 3062–3075. <https://doi.org/10.1098/rstb.2011.0323>
- Mantua, N. J., & Hare, S. R. (2002). The pacific decadal oscillation. *Journal of Oceanography*, 58(1), 35–44. <https://doi.org/10.1023/A:1015820616384>
- McCabe-Glynn, S., Johnson, K. R., Strong, C., Berkelhammer, M., Sinha, A., Cheng, H., & Edwards, R. L. (2013). Variable North Pacific influence on drought in southwestern North America since AD 854. *Nature Geoscience*, 6(8), 617–621. <https://doi.org/10.1038/NCEO1862>
- McCluney, K. E., Belnap, J., Collins, S. L., González, A. L., Hagen, E. M., Nathaniel Holland, J., ... Wolf, B. O. (2012). Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews*, 87(3), 563–582. <https://doi.org/10.1111/j.1469-185X.2011.00209.x>
- McPhaden, M. J., Zebiak, S. E., & Glantz, M. H. (2006). ENSO as an integrating concept in earth science. *Science*, 314(5806), 1740–1745. <https://doi.org/10.1126/science.1132588>
- Millus, S. A., & Stapp, P. (2008). Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California. *Canadian Journal of Zoology*, 86(9), 1031–1041. <https://doi.org/10.1139/Z08-081>
- Millus, S. A., Stapp, P., & Martin, P. (2007). Experimental control of a native predator may improve breeding success of a threatened seabird in the California Channel Islands. *Biological Conservation*, 138(3–4), 484–492. <https://doi.org/10.1016/j.biocon.2007.05.017>
- Milly, P. C. D., Dunne, K. A., & Vecchia, A. V. (2005). Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, 438(7066), 347–350. <https://doi.org/10.1038/nature04312>
- Miriti, M. N., Rodriguez-Buritica, S., Wright, S. J., & Howe, H. F. (2007). Episodic death across species of desert shrubs. *Ecology*, 88(1), 32–36. [https://doi.org/10.1890/0012-9658\(2007\)88\[32:EDASOD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[32:EDASOD]2.0.CO;2)
- Morrison, S. A., & Bolger, D. T. (2002). Variation in a sparrow's reproductive success with rainfall: Food and predator-mediated processes. *Oecologia*, 133(3), 315–324. <https://doi.org/10.1007/s00442-002-1040-3>
- Morton, M., Morrison, M., Hall, L., & Pereyra, M. (1995). Life-history parameters in mice exposed to a prolonged drought. *Southwestern Naturalist*, 40(1), 18–28.
- Murray, K. G. (1980). *Predation by deer mice on Xantus' Murrelet eggs on Santa Barbara Island, California* (M.Sc. thesis). Northridge: California State University.
- Murray, K., Winnettmurray, K., Eppley, Z., Hunt, G., & Schwartz, D. (1983). Breeding Biology of the Xantus-Murrelet. *Condor*, 85(1), 12–21. <https://doi.org/10.2307/1367880>
- Murray, K. G., Winnett-Murray, K., & Hunt, G. L. (1980). Egg neglect in Xantus' Murrelet. *Proceedings of the Colonial Waterbird Group*, 3, 186–195.
- Norman, F. I. (1975). The murine rodents *Rattus rattus*, *exulans* and *norvegicus* as avian predators. *Atoll Research Bulletin*, 182, 1–13. <https://doi.org/10.5479/si.00775630.182.1>
- Nur, N., Harvey, A. L., Thomsen, S. K., Bradley, R., & Jahncke, J. (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*. Petaluma, California: Point Blue Conservation Science. PRBO Contribution Number 1969.
- Ong, J. J. L., Rountrey, A. N., Zinke, J., Meeuwig, J. J., Grierson, P. F., O'Donnell, A. J., ... Meekan, M. G. (2016). Evidence for climate-driven synchrony of marine and terrestrial ecosystems in north-west Australia. *Global Change Biology*, 22(8), 2776–2786. <https://doi.org/10.1111/gcb.13239>
- Orrock, J. L., Allan, B. F., & Drost, C. A. (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(5), 691–697. <https://doi.org/10.1086/659632>
- Ostfeld, R. S., & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15(6), 232–237. [https://doi.org/10.1016/S0169-5347\(00\)01862-0](https://doi.org/10.1016/S0169-5347(00)01862-0)
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, 46(1), 15–27. <https://doi.org/10.3354/cr00936>
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20(9), 503–510. <https://doi.org/10.1016/j.tree.2005.05.011>
- Piovia-Scott, J., Spiller, D. A., & Schoener, T. W. (2011). Effects of experimental seaweed deposition on lizard and ant predation in an island food web. *Science*, 331(6016), 461–463. <https://doi.org/10.1126/science.1200282>
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), 919–925. <https://doi.org/10.1038/nclimate1958>
- Post, E., & Forchhammer, M. C. (2002). Synchronization of animal population dynamics by large-scale climate. *Nature*, 420(6912), 168. <https://doi.org/10.1038/nature01064>
- Power, S., Delage, F., Chung, C., Kociuba, G., & Keay, K. (2013). Robust twenty-first-century projections of El Niño and related precipitation variability. *Nature*, 502(7472), 541–545. <https://doi.org/10.1038/nature12580>
- Preston, K. L., & Rotenberry, J. T. (2006). Independent effects of food and predator-mediated processes on annual fecundity in a songbird. *Ecology*, 87(1), 160–168. <https://doi.org/10.1890/05-0344>
- R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124–133. <https://doi.org/10.1111/1365-2656.12262>
- Ronconi, R. A., & Hipfner, J. M. (2009). Egg neglect under risk of predation in Cassin's Auklet (*Ptychoramphus aleuticus*). *Canadian Journal of Zoology*, 87(5), 415–421. <https://doi.org/10.1139/Z09-027>
- Roth, J. E., Sydeman, W. J., & Martin, P. L. (2005). Xantus's Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. *Marine Ornithology*, 33, 115–121.
- Ruffino, L., Russell, J., & Vidal, E. (2013). Anthropogenic subsidies mitigate environmental variability for insular rodents. *Oecologia*, 172(3), 737–749. <https://doi.org/10.1007/s00442-012-2545-z>
- Russell, J. C., & Ruffino, L. (2012). The influence of spatio-temporal resource fluctuations on insular rat population dynamics. *Proceedings of the Royal Society B-Biological Sciences*, 279(1729), 767–774. <https://doi.org/10.1098/rspb.2011.1121>

- Rymer, T. L., Pillay, N., & Schradin, C. (2016). Resilience to droughts in mammals: A conceptual framework for estimating vulnerability of a single species. *Quarterly Review of Biology*, 91(2), 133–176. <https://doi.org/10.1086/686810>
- Saether, B. E., & Bakke, O. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81(3), 642–653. <https://doi.org/10.2307/177366>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Schmidt, A. E., Botsford, L. W., Eadie, J. M., Bradley, R. W., Di Lorenzo, E., & Jahncke, J. (2014). Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. *Marine Ecology Progress Series*, 499, 249–258. <https://doi.org/10.3354/meps10629>
- Schmidt, K. A., & Ostfeld, R. S. (2008). Numerical and behavioral effects within a pulse-driven system: Consequences for shared prey. *Ecology*, 89(3), 635–646. <https://doi.org/10.1890/07-0199.1>
- Schwemm, C. (2009). Population monitoring of deer mice (*Peromyscus maniculatus*) on the California Channel Islands, 1989–2009: Summary Data and Metadata. United States Geological Survey.
- Schwemm, C. A., Drost, C. A., Orrock, J. L., Coonan, T. J., & Stanley, T. R. (2018). Comparison of estimators for monitoring long-term population trends in deer mice, *Peromyscus maniculatus*, on the California Channel Islands. *Western North American Naturalist*, 78(3), 14.
- Schwemm, C. A., & Martin, P. L. (2005). Response of nest success of Xantus's Murrelets (*Synthliboramphus hypoleucus*) to native predator abundance, Santa Barbara Island, California. Proceedings of the Sixth California Islands Symposium, Ventura, California.
- Sofaer, H. R., Sillett, T. S., Peluc, S. I., Morrison, S. A., & Ghaleb, C. K. (2013). Differential effects of food availability and nest predation risk on avian reproductive strategies. *Behavioral Ecology*, 24(3), 698–707. <https://doi.org/10.1093/beheco/ars212>
- Sperry, J. H., & Weatherhead, P. J. (2008). Prey-mediated effects of drought on condition and survival of a terrestrial snake. *Ecology*, 89(10), 2770–2776. <https://doi.org/10.1890/07-2017.1>
- Spevak, T. (1983). Population changes in a mediterranean scrub rodent assembly during drought. *Southwestern Naturalist*, 28(1), 47–52. <https://doi.org/10.2307/3670591>
- St. Clair, S. B., Sudderth, E. A., Castanha, C., Torn, M. S., & Ackerly, D. D. (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(5), 860–870. <https://doi.org/10.1111/j.1654-1103.2009.01089.x>
- Stapp, P., & Polis, G. A. (2003). Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos*, 102(1), 111–123. <https://doi.org/10.1034/j.1600-0706.2003.12445.x>
- Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, 22(11), 1–23.
- Sweet, S. K., Asmus, A., Rich, M. E., Wingfield, J., Gough, L., & Boelman, N. T. (2015). NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. *Ecological Applications*, 25(3), 779–790. <https://doi.org/10.1890/14-0632.1>
- Sydeman, W. J., Nur, N., & Martin, P. (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.
- Sydeman, W. J., Santora, J. A., Thompson, S. A., Marinovic, B., & Lorenzo, E. D. (2013). Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology*, 19(6), 1662–1675. <https://doi.org/10.1111/gcb.12165>
- Therneau, T. M., & Atkinson, E. J. (2015). An introduction to recursive partitioning using the RPART routines. Mayo Foundation. Retrieved from <https://cran.r-project.org/web/packages/rpart/vignettes/longintro.pdf>
- Thomsen, S. K., & Green, D. J. (2016). Cascading effects of predation risk determine how marine predators become terrestrial prey on an oceanic island. *Ecology*, 97(12), 3530–3537. <https://doi.org/10.1002/ecy.1614>
- Thomsen, S. K., Mazurkiewicz, D. M., Stanley, T. R., & Green, D. J. (2018). ENSO-driven rainfall pulse amplifies predation by owls on seabirds via apparent competition with mice. *Proceedings of the Royal Society B*, 285(1889), 20181161. <https://doi.org/10.1098/rspb.2018.1161>
- Wanless, S., Frederiksen, M., Daunt, F., Scott, B. E., & Harris, M. P. (2007). Black-legged kittiwakes as indicators of environmental change in the North Sea: Evidence from long-term studies. *Progress in Oceanography*, 72(1), 30–38. <https://doi.org/10.1016/j.pocean.2006.07.007>
- Weimerskirch, H. (2002). Seabird demography and its relationship with the marine environment. In E. A. Schreiber, & J. Burger (Eds.), *Biology of marine birds* (pp. 115–135). Boca Raton: CRC Press.
- Whitworth, D. L., Carter, H. R., & Gress, F. (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. <https://doi.org/10.1016/j.biocon.2013.03.026>
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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