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EGG ORDER AND OCEANOGRAPHIC FACTORS DRIVE EGG SIZE DIFFERENCES IN SCRIPPS’S MURRELETS *SYNTHLIBORAMPHUS SCRIPPSI* AT SANTA BARBARA ISLAND, CALIFORNIA, USA

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ABSTRACT

TODD ZARAGOZA, M.I., DUVALL, A.J., MAZURKIEWICZ, D.M., HOWARD, J.A., & CONVERSE, S.J. 2021. Egg order and oceanographic factors drive egg size differences in Scripps’s Murrelets *Synthliboramphus scrippsi* at Santa Barbara Island, California, USA. *Marine Ornithology* 49:

Egg size is an important avian life history parameter, with larger eggs indicating a greater investment of resources in the chick. Oceanic conditions are known to affect a variety of life history parameters in seabirds, but the degree to which egg size responds to environmental conditions has been studied only rarely. We investigated the effects of oceanographic conditions and egg order on Scripps’s Murrelet *Synthliboramphus scrippsi* egg size at Santa Barbara Island, California, USA, using data from 2009-2017. Environmental covariates that characterize the marine environment were evaluated for their effect on egg size. We evaluated large-scale oceanographic indices, including the Pacific Decadal Oscillation (PDO) index, the Oceanic Niño Index (ONI), and the North Pacific Gyre Oscillation (NPGO) index. Larval anchovy catch-per-unit-effort (ANCHL) indices and the Biologically Effective Upwelling Transport Index (BEUTI) were used as region-wide indices, and sea surface temperature (SST) was used as a local covariate.. We tested the effect of oceanographic conditions during the breeding and non-breeding season and lagged effects using initial model selection. We also accounted for egg order (egg 1 or egg 2) as a fixed effect and plot as a random effect. The top two best-fitting models provided support for negative relationships between egg size and both BEUTI and NPGO and a positive relationship between egg size and both ONI and egg order. The resources available to an avian embryo have the potential to influence the survival of the embryo and of the chick post-hatching. Our results point towards another mechanism through which changing oceanographic conditions may impact seabird populations.

# Key words:alcid, egg size, egg order, index, ocean productivity, monitoring

# **INTRODUCTION**

Seabirds have been identified as reliable indicators of marine ecosystem conditions (Mallory *et al*. 2010; Cairns 1988; Velarde *et al*. 2019). Fluctuating marine conditions that affect prey availability can impact the demography of seabirds due to their dependence on marine ecosystems for foraging. For example, Cassin’s Auklets *Ptychoramphus aleuticus* at Triangle Island (British Columbia, Canada), have shown reduced offspring survival and fledgling mass in years of warm sea surface temperatures (SSTs) due to limited prey availability (Hipfner 2008). Changes in marine conditions have also been linked to declines in growth rate and fledging success of Tufted Puffins *Fratercula cirrhata* off the coast of British Columbia (Gjerdrum 2003) as well as changes in clutch size of Scripps’s Murrelets *Synthliboramphus scrippsi* off the coast of California, USA(Roth *et al*. 2005).

Interannual and interdecadal oceanographic variation also plays an important role in determining the egg size of some seabird species, though this relationship has been only rarely investigated. In general, egg size varies with the amount of energy invested in egg production, and the energy available to invest can be a function of environmental conditions (Williams 2005). In Norway, Atlantic Puffin *Fratercula arctica* populations at two separate colonies (1980-2011) showed parallel declines in population size and egg volume (Barrett *et al*. 2012). Investigators found relationships between egg volume and various prey? population indices (mixed relationships), the North Atlantic Oscillation (positive relationship), and SST (negative relationship), and concluded that low food availability led to lower egg size. In contrast, Hipfner (2012) found that egg size increased with SST for Glaucous-winged Gulls *Larus glaucescen*s at Triangle Island, but the effect was small and limited to one and three-egg clutches.

The Scripps’s Murrelet (hereafter referred to as “murrelets”) is a small seabird in the Alcidae family that breeds along the west coast of southern California, United States and Baja California, Mexico. Investigation of the relationships between marine conditions and murrelet breeding success have been limited to an analysis of the effects of ocean productivity on murrelet clutch initiation timing and clutch size (Roth *et al*. 2005). That analysis revealed that higher ocean productivity leads to earlier clutch initiation dates and larger clutch sizes. However, there has not been any analysis of the relationship between oceanographic conditions and egg size. Murrelet eggs represent, on average, 23.7% of the female body mass, making them one of the largest eggs relative to body weight in the Alcidae family (Sealy 1975). Females typically lay two eggs, with the second egg laid ~8 days after the first (Murray *et al*. 1983). Murrelet chicks are precocial, departing the nest ~1-2 days after hatching. This precociality requires large eggs and females must forage several days before laying each egg to obtain the necessary nutrients (Murray *et al*. 1983).

The largest US-based breeding colony of murrelets occurs at Santa Barbara Island (SBI), the smallest island in Channel Islands National Park, California (Carter *et al*. 1992; Figure 1). SBI is in the Southern California Bight, which is highly dynamic and experiences interannual fluctuations in ocean productivity (Checkley & Barth 2009) and therefore provides an opportunity to investigate the ways in which marine productivity may influence murrelet egg size.

We hypothesized that greater marine productivity would lead to greater investment in eggs by females, and therefore predicted that we would see a positive relationship between egg size and environmental indices that are indicative of cool, nutrient-rich marine conditions and higher ocean productivity. We evaluated environmental indicators at multiple scales. At the largest scale, we considered the Oceanic Niño Index (ONI; lower values indicate higher productivity), the North Pacific Gyre Oscillation (NPGO; higher values indicate higher productivity), and the Pacific Decadal Oscillation (PDO; lower values indicate higher productivity). At the regional scale, we considered the Biologically Effective Upwelling Transport Index (BEUTI; higher values indicate higher productivity) and larval anchovy catch-per-unit-effort (ANCHL; higher values are directly indicative of greater resource availability). Finally, at the local scale, we considered sea surface temperatures (SST; lower values indicate higher productivity).

We predicted that oceanographic conditions during the breeding and non-breeding season may impact individual fitness, and thus egg size, so we tested the inclusion of oceanographic covariates at two temporal scales, during the breeding season only and during the breeding and non-breeding season. In addition, we predicted the impact of oceanographic conditions on individual fitness may not manifest immediately, so we tested the inclusion of a lag effect on covariates. We also predicted that there would be inherent differences between size of the first and second eggs laid in each clutch.

# **METHODS**

## ***Data Collection***

Santa Barbara Island (33.4756°N, 119.0373°W) is the smallest (2.6 km2) of the eight California Channel Islands and it hosts the largest breeding colony of murrelets in the region. The data used for this analysis were part of a larger project funded primarily by the Montrose Settlements Restoration Program at Channel Islands National Park. Data were collected from 2009-2017 during the breeding season, which lasts from March to June and peaks in April (Murray *et al*. 1983). To obtain egg measurements, accessible eggs were removed from the nest and measured using Vernier calipers. Eggs were considered accessible if they were within safe reach of the observer and no adult bird was present at the nest. Egg length and width (at the widest point) were measured to the nearest millimeter. After measurement, the egg was returned to its original position and orientation. Eggs were only measured once at each nest. If both eggs were present upon first encounter, egg order was indeterminable, but if the nest was encountered between the laying of the first and second eggs, eggs were labeled with a marker to indicate egg order. We only included eggs in this analysis for which egg order was known. Egg size data were obtained from eight monitoring plots on Santa Barbara Island for this analysis: Arch Point North Cliffs (APNC), Bunkhouse (BH), Boxthorn (BT), Cat Canyon (CC), Dock (DO), Elephant Seal Cove (ESC), Landing Cove (LC), and West Cliffs (WC) (Figure 2).

## ***Covariates***

Edatathat we considered PDO, at the large scale, ANCHL and at the regional scale, and at the local scaleBEUTI estimates vertical nitrate flux, which is the amount of nitrate upwelled/downwelled, near the U.S. West Coast at a latitude of 39°N (Jacox *et al*. 2018).

We averaged covariate data that were reported at a monthly scale to create input covariates at two temporal scales (except for ANCHL, for which only an annual index, collected in spring, was available). We created a 12-month covariate (covariate values averaged from July in year *t*-1to June in year *t* to model egg size observed in year *t*) and a 6-month covariate (from January in year *t* to June in year *t*). We included values through June to encompass the murrelet breeding season, which peaks in April (Murray *et al*. 1983) but extends for several months into the summer. The ANCHL covariate collected in spring of year *t* wasused to model egg size observed in year *t.* We also considered analogous covariates with a 1-year lag, where values from either July in year *t*-2 (12-month lagged covariate) or January of year *t*-1 (6-month lagged covariate) through June in year *t*-1 were used to model egg size in year *t*. An ANCHL lagged covariate was considered as well, i.e., ANCHL collected in spring of year *t*-1 used to model eggs observed in year *t*. All covariates were Z-scored before modeling.

## ***Model Formulation and Selection***

We developed a set of models to investigate the relationship between environmental covariates and egg size, calculated as egg size = egg length\*egg width. Egg size was modeled using a linear mixed model with normal errors and random processes. We initially considered two random effects. The first of these was a plot random effect, which we included to account for potential variability in egg size by plot that could arise due to characteristics of plots (e.g., different microclimates) and the birds using plots (e.g., different feeding areas). The second was an observer random effect, to account for potential differences in how different observers measured eggs in the field. Our general model was:

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where is the size of egg *i,*  is the intercept*, k* is the number of predictors in a given model, are model coefficients for covariates (including egg order), is the random effect of plot with variance , is the random effect of observer with variance , and is the residual error for egg *i* with model variance .

We began by evaluating the appropriate temporal scale for each covariate. We built four single-variable models without random effects (using lme4 in R; R Core Team 2021), i.e., 6-month, 12-month, 6-month lagged, and 12-month lagged for all covariates except ANCHL, for each we built two single-variable models, unlagged and lagged. The single-variable models for each covariate were compared using AIC. We used the form of the covariate that appeared in the top-ranked model in all subsequent analyses.

Next, we evaluated support for inclusion of random effects of plot and observer. We performed bootstrapped likelihood ratio tests (exactLRT and exactRLRT functions in the RLRsim package; Scheipl 2008) in R (R Core Team 2021). When calculating these tests, we used the “global” form for the fixed effects portion of the model. Because of correlations between covariates (see below), the number of fixed effect covariates in our global model was five (three environmental covariates, egg order, and intercept) rather than eight. Based on these tests, we decided to drop the observer random effect and retain the plot random effect.

Once we identified the form of the input covariates and the random effects structure, we considered all possible combinations of covariates in a series of models, except that covariates with a correlation coefficient that had an absolute value ≥ 0.65 were not included in the same model. These correlated covariate pairs included ANCHL/NPGO, ANCHL/ONI, ANCHL/PDO, BEUTI/ONI, BEUTI/PDO, NPGO/PDO, NPGO/SST, and ONI/PDO. Egg order was also included to determine whether and how egg size differs between the first and second eggs in a clutch. The models were compared using Akaike’s Information Criterion (AIC) = , where is the maximum value of the likelihood function for the model and *k* is the number of fixed effect parameters in the model. Models were fit using function lmer in the lme4 package (Bates 2015) in R (R Core Team 2021).

Model diagnostics were performed on the five-parameter model with the plot random effect to determine whether model assumptions were reasonably met. Diagnostics included Q-Q plots to evaluate the normality of residuals, autocorrelation function plots to evaluate the independence of residuals, and residual plots along with Levene’s test to evaluate whether residuals had equal variance.

***Ethics Statement***

*\*insert\**

## **RESULTS**

For records where egg order was known, there were 7 records for 2009, 135 for 2010, 90 for 2011, 123 for 2012, 92 for 2013, 101 for 2014, 121 for 2015, 135 for 2016, and 70 for 2017. There were 695 values for first egg in the clutch and 177 values for second egg (*n* = 872 total samples). There were eight different plots with egg measurements, with the number of eggs per plot varying between 1 and 275. There were 27 different observers who measured eggs, with the number of eggs per observer varying between 1 and 192. Model diagnostics were generally acceptable, but did alert us to two outliers for which egg size was notably small (>6 SD smaller than the mean egg size with these two eggs excluded). These eggs were in the same nest but were measured by different observers on different dates, indicating that both eggs in the clutch were physiologically abnormal rather than that a measurement error was made. All results reported here are based on analyses from which these two eggs were excluded.

Covariate forms selected included the 12-month lagged covariate form for ONI, 6-month lagged for PDO (January to June average), 6-month unlagged for NPGO, unlagged for ANCHL, 12-month lagged for BEUTI, and 6-month unlagged for SST (Table 1).

Likelihood ratio tests showed moderate support for inclusion of a plot random effect (*p* = 0.0598) but did not support inclusion of an observer random effect (*p* = 0.1836). Thus, all mixed models included only plot as a random effect. The plot random effect had a variance of = 161.8 while the residual variance was = 10701.0.

Using combinations of the seven potential fixed effects (six environmental covariates and egg order) without large correlations between predictors, and the plot random effect, we fit 30 models (full results in supplementary materials). The four top-ranked models provided accounted for 98% of the total model weight, and all models with an Akaike weight > 0.05 (Table 2). Each of the covariates we considered appeared in one or more of these four top-ranked models. Parameter estimates for the fixed effects in these four models are shown in Table 3.















**DISCUSSION**

Understanding the relationship between environmental drivers and physiological responses in seabirds is crucial to a fuller understanding of how seabirds are responding to changing ocean conditions. Our analysis revealed that large-scale and region-wide oceanographic processes as well as egg order drive egg size differences in murrelets. However, the relationships that were found were opposite to what was expected.

As indicated by the first competitive model, I found a negative relationship between one-year lagged BEUTI values and egg size (Table 3). As BEUTI aims to capture the bottom-up dynamics of productivity, a positive value indicates the drawing of nutrient-rich water toward the surface, and a negative value the opposite effect through downwelling (Jacox *et al* 2016). Additional driving forces could be impacting the direct relationship between upwelling and biological responses, which are not being captured solely by BEUTI. These could include variable light levels and availability of nutrients other than nitrate that are driving productivity and therefore foraging opportunities for murrelets (Jacox *et al* 2018).

The relationship indicated by the second-best model, between a one-year lagged ONI and egg size, indicates that eggs tend to be larger when ONI is positive (Table 3). A negative value indicates a cool phase along the California coast with colder and more nutrient-rich waters. Positive values are therefore indicating warmer waters, which are not ideal conditions for prey, particularly anchovy, which are the main prey for murrelets. During positive phases of the oscillation, juvenile and adult anchovy abundances have been shown to decline in areas off Southern California (Fiedler *et al* 1986). Given this relationship between the effects of ONI and the main prey for murrelets, it is surprising to observe larger egg sizes in relation to positive ONI values, although notably I was not able to document a relationship between egg size and anchovy themselves.

The finding that negative NPGO values lead to larger egg size is contrary to what has been found for murrelet nest success, although it has not been characterized directly for egg size. Thomsen and Green (2019) found that when the NPGO is positive, murrelet nest success is high, resulting in stable population growth. A high state of NPGO, in which the gyre is expanded, has also been found to be an important driver of reproductive success for Laysan albatrosses *Phoebastria immutabilis* and Black-footed albatrosses *Phoebastria nigripes* breeding in the Northwest Hawaiian Islands (Thorne *et al* 2015). However, the relationship between NPGO and egg size has not been directly defined. When the NPGO is positive, changes in wind forcing create upwelling-favorable conditions in the California Current region (Lorenzo *et al* 2008), particularly creating a more productive planktonic ecosystem throughout the spring and summer (Chenillat *et al* 2012). As NPGO operates on a decadal time scale, it is possible that the effect it is having on egg size is not completely being captured by the timeframe of this study.

As indicated by its inclusion in the two competitive models, I found that the second egg was substantially larger than the first egg. Murray *et al* (1983) found that, on average, the second egg of the clutch was ~1 g heavier than the first. This indicates that murrelets are allocating more resources towards the second egg, which is consistent with the life history of this species. Murrelet females abandon the nest for eight days after laying the first egg to procure additional resources for themselves (Murray *et al* 1980). This extended period of inter-egg foraging allows murrelets to produce a larger second egg. The natural history of SBI could explain the reason why murrelets allocate more energy towards the second egg. Deer mice *Peromyscus* were introduced to SBI following the arrival of Native Americans ~4 000 years ago (Durst 2014). As native predators to murrelets, deer mice have been documented to predate on murrelet eggs when they abandon the nest during the incubation period, with especially high predation during drought years when vegetation is sparse (Murray *et al* 1980; Thomsen & Green 2019). Given this high predation, murrelets could have developed an evolutionary adaptation by investing more energy in the second egg as a form of investment. Thus, as murrelets invest more in that second egg, they are ensuring that if the first egg gets predated on, the chances of having one egg in the clutch hatch are higher.

I found support for the inclusion of a plot random effect, indicating micro-scale variation in egg size. Adaptations that occur at very fine spatial scales can lead to microgeographic adaptive divergence that can explain fine scale differences in fitness (Richardson *et al*. 2014). Habitat selection can be a possible mechanism driving these microgeographic adaptations, such that areas offering higher fitness through proximity to better foraging opportunities could be driving physiological differences in murrelets. Given that murrelets show high site fidelity, future studies could investigate differences in foraging habitat used by birds in different plots to assess whether foraging habitat differences might explain egg size variation across plots.

The southern California Current System (CCS) is a resilient ecosystem with upwelling mediated by equatorial wind-stress (Brady *et al* 2017). Like other eastern boundary upwelling systems (EBUS), it can quickly recover from disturbance and maintain high ecosystem function and productivity (Bakun *et al 2015*). For example, the 1997-1998 El Niño event that caused large changes in community composition and limited biological yield was sharply followed by a rebound of primary and secondary productivity (Bograd & Lynn 2001). Climate models varying in resolution concur that upwelling will become more intense in the spring and less intense in the summer due to changes in alongshore winds (Brady *et al* 2017). Furthermore, simulations also predict changes in stratification (Bakun *et al* 2015), hypoxia, and acidification, all of which can affect pelagic seabirds (Pozo Buil *et al* 2021). Under a high emission climate scenario, Brady *et al* (2017), found that internal variability will remain the dominant factor in determining trends in the CCS. Thus, it will not be possible to discern between anthropogenic forcing and natural variability in this system until the second half of the century. Uncertainty regarding the extent to which climate change will impact oceanographic processes calls for a better understanding of the current mechanisms in which murrelets are responding to their surrounding environment. Ensuring this understanding will warrant better management in the future.

***Management Implications***

Egg measurements have been collected at Santa Barbara Island since the 1990s without any indication of its relative importance for various research and conservation priorities of murrelets. My analysis has revealed that there is value in collecting this data and that we can begin to understand the physical processes that are driving egg size differences. Given the large relative size of eggs produced by murrelets, necessary to support precociality, investment in egg production requires a large amount of nutrient and energy requirements (Robins 1981; Williams 2005; Nager 2006). As murrelets rely on their dynamic marine environment to gain the necessary resources, fluctuations in the marine conditions most likely reflect fluctuations in egg size. Egg size can have influences on offspring fitness and survival, making it an important avenue for future population monitoring (Krist 2011; Lee *et al*. 2012). Continued monitoring and measurement collection is important. An area of research that might be prioritized in future investigations is the relationship between egg size and hatching success or chick survival.

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TABLE 1. The form of six environmental covariates selected for modeling Scripp’s Murrelet egg size at Santa Barbara Island, California. For each covariate except ANCHL, four covariate forms were considered: 12-month lagged, 6-month lagged, 12-month unlagged, and 6-month unlagged. For ANCHL, which was a single value each year collected in spring, only lagged and unlagged forms were considered. Single variable models containing the candidate forms were fit and the final selection was based on Akaike’s Information Criterion (AIC).

|  |  |  |
| --- | --- | --- |
| **Covariate** | **Covariate form** | **Monthly values averaged to model eggs observed in year *t*** |
| Pacific Decadal Oscillation (PDO) index | 6-month lagged | January through June, year *t*-1 |
| Oceanic Niño Index (ONI) | 6-month lagged | January through June, year *t*-1 |
| North Pacific Gyre Oscillation (NPGO) index | 6-month unlagged | January through June, year *t* |
| Larval anchovy catch-per-unit-effort (ANCHL) | Unlagged | Spring metric, year *t* |
| Biologically Effective Upwelling Transport Index (BEUTI) | 12-month lagged | July year *t*-2 through June year *t*-1 |
| Sea surface temperature (SST) | 6-month unlagged | January through June, year *t* |

**TABLE 2. Top six models fitted to the data……. The form of the covariate (i.e., months included) is given in Table 1.**

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed effects** | **AIC** | **ΔAIC** | **AICw** |
| Egg order, BEUTI, NPGO | 10 558.27 | 0.00 | 0.58 |
| Egg order, NPGO, ONI, | 10 559.64 | 1.37 | 0.29 |
| Egg order, ANCHL, BEUTI, SST | 10 562.81 | 4.54 | 0.06 |
| Egg order, PDO, SST | 10 563.05 | 4.78 | 0.05 |
| Egg order, PDO | 10 566.19 | 7.92 | 0.01 |
| Egg order, BEUTI, SST | 10 566.81 | 8.54 | 0.008 |

**TABLE 3. Parameter estimates of the fixed effects of the two best-fitting models.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Model** | **Parameter** | **Estimate** | **Standard Error** | **95% Confidence Interval** |
| Egg order, NPGO, BEUTI | Egg order | 36.18 | 8.71 |  |
|  | NPGO0 | -15.61 | 3.52 |  |
|  | BEUTI1 | -13.34 | 4.71 |  |
|  |  |  |  |  |
| Egg order, NPGO, ONI | Egg order | 36.54 | 8.72 |  |
|  | NPGO0 | -13.43 | 3.85 |  |
|  | ONI1 | 12.40 | 4.86 |  |
| Egg order, ANCHL, BEUTI, SST | Egg order |  |  |  |
|  | ANCHL |  |  |  |
|  | BEUTI |  |  |  |
|  | SST |  |  |  |
| Egg order, PDO, SST | Egg order |  |  |  |
|  | PDO |  |  |  |
|  | SST |  |  |  |

**FIGURES**

**Figure 1**. The Channel Islands, California, USA.

**Figure 2**. Santa Barbara Island monitoring plots used in this analysis.



