# USING REMOTE VIDEO TECHNOLOGY TO STUDY ENVIRONMENTAL FACTORS INFLUENCING PRODUCTIVITY OF BLACK-LEGGED KITTIWAKES RISSA TRIDACTYLA

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# ABSTRACT

TANEDO, S.A., HOLLMÉN, T.E., MANISCALCO, J.M. & ULMAN, S.E.G. 2021. Using remote video technology to study environmental factors influencing productivity of Black-legged Kittiwakes *Rissa tridactyla*. *Marine Ornithology* 49: 293–299.

Monitoring seabirds and their responses to ecosystem change provides essential information for understanding the reasons behind any changes in productivity or populations. However, many species nest in remote locations, which poses logistical challenges for long-term studies. Remote cameras offer an opportunity to confront this issue. The Black-legged Kittiwake *Rissa tridactyla* (kittiwake) has been used as an indicator of changes in its environment and is a prime candidate for monitoring via remote cameras. To investigate the potential for camera application, we used a remote camera system to collect six years (2010–2015) of reproductive data from a sub-colony of kittiwakes in Resurrection Bay near Seward, Alaska, USA. Our objective was to identify factors influencing the reproductive success of kittiwakes at our study location by 1) establishing the reproductive phenology and estimates of productivity, 2) determining the effect of physical nest-site characteristics and locations on individual nest success, and 3) identifying the effect of seasonal weather patterns on nest, egg, and chick loss events. We found a significant positive correlation between nest success and both nest height from mean high tide level and nest location on island vs. mainland habitat. Nest loss was positively correlated with wind speed; egg loss was negatively correlated with wind speed; and chick loss was uncorrelated with measured weather conditions, including rainfall and air temperature. Remote camera technology proved to be a useful tool in monitoring and identifying factors influencing nesting parameters in this cliff-nesting seabird.

Key words: Rissa tridactyla, Black-legged Kittiwake, productivity, phenology, nest site, seasonal weather, remote cameras

## **INTRODUCTION**

Throughout the past few decades, monitoring climate change and how it affects species' natural history patterns and related ecosystem processes has become critically important toward understanding species' population dynamics. This is particularly true in northern marine environments, where change is evident (Harley et al. 2006, Piatt et al. 2007, Bluhm et al. 2011, Sydeman et al. 2012). Seabird species, such as the circumpolar Black-legged Kittiwake Rissa tridactyla (kittiwake), have long been considered as indicators of environmental change. Thus, their natural history patterns are a suitable subject for long-term monitoring, particularly with the intent to track changes in ecosystems (see also Springer et al. 1996, Dragoo et al. 2019). Establishing reliable, efficient techniques to monitor those patterns is paramount to detecting, tracking, and understanding change in the local environment. Kittiwakes, however, mostly occur in remote habitats and can be difficult to monitor consistently over long periods (Hatch et al. 2020, Piatt et al. 2007). Remote camera technology could offer the means to monitor birds in remote locations consistently enough to not only identify factors influencing reproductive ecology, but track changes over multiyear time periods (Tanedo & Hollmén 2020).

The structural characteristics and location of a nest site within a colony can affect individual nest success; colony density and location have been found to be positively correlated with individual nest success, owing to protection from predators (Regehr *et al.* 1998, Kildaw 1999, Massaro *et al.* 2001). Structural protection

such as overhangs or nest height above water can also provide shelter from both biological threats, such as larger gull species, and physical elements, such as heavy precipitation (Olsthoorn & Nelson 1990, Regehr & Montevecchi 1997, Regehr *et al.* 1998). Increases in air temperature could negatively affect the physiological health of breeding pairs, while a change precipitation rates can influence breeding success through nest loss (Sydeman *et al.* 2012, Hatch *et al.* 2020). Understanding the relationship between local environmental conditions and the reproductive health of breeding seabird populations is an essential component for determining whether change in reproductive health is caused by the local environment or by larger-scale factors.

The goal of our study was to test whether remote camera technology can sufficiently identify environmental factors that influence the reproductive ecology of a sub-colony of kittiwakes in Resurrection Bay, Gulf of Alaska, USA. To meet this goal, we chose three objectives targeting four factors that have been previously found to influence kittiwake reproductive ecology. Our first objective was to establish the reproductive phenology and estimates of productivity for kittiwakes at Cape Resurrection. Our second was to determine the effect of nest characteristics and location on individual nest success, or the total number of fledglings produced per individual nest site. We targeted individual nest success to identify how finescale differences between nest sites could influence the degree of success. Finally, our third objective was to determine whether loss events (nest, egg, and chick) were influenced by seasonal weather patterns and, if so, how.

## STUDY AREA AND METHODS

## Estimating productivity from monitoring data

Real-time remote video cameras equipped with pan-tilt-zoom functionality were used to monitor kittiwakes at a sub-colony located 1.5 km north of Cape Resurrection (59.8827°N, 149.2932°W), Resurrection Bay, in the state of Alaska, USA (Fig. 1, Maniscalco *et al.* 2006). Approximately 2000 breeding pairs of kittiwakes, or ~14% of the Cape Resurrection population, nest at this sub-colony (TEH unpubl. data). Cameras monitored 149 randomly chosen nest sites in 17 plots, which were divided between island (plots 1–9) and mainland locations (plots 10–17; Fig. 2). The original 149 randomly chosen nest sites were monitored for the entirety of the project. Plots were approximately 4 m × 3 m in area. Additional details are described in Tanedo & Hollmén (2020).

Video records of all plots were collected over a period of six years, 2010–2015. Sites were monitored once every 3–4 days for the breeding seasons (May–August) of 2010–2012. For 2013–2015, observation frequency was increased to twice daily (morning and afternoon), to the extent possible. Video analysis for reproductive phenology and estimates of productivity were conducted by the same observer for all years. Our target reproductive behaviors, such

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as presence of a nest, nest attempt, physical presence and number of adults/chicks, incubation behavior, and brooding behavior, were recorded and analyzed in R for estimates of productivity and reproductive phenology (R Core Team 2015; see also Tanedo & Hollmén 2020). Productivity was calculated from the total number of fledglings produced per nest attempt. A chick was considered a "fledgling" once it reached 40 days of age after the first detection of brooding. In the case of two-chick nests, the second chick's age was determined from the total number of days from first detection of brooding to the last day two chicks were observed on the nest. Research was conducted in compliance with the University of Alaska Fairbanks Institutional Animal Care and Use Committee (Observational Research Protocol#: 580845-1).

#### Effects of nest characteristics and location on nest success

The number of chicks produced per individual nest site per year was the response variable used to determine if nest characteristics influenced individual nest success. Physical parameters were analyzed using a combination of video observations and on-site images taken with a high-resolution Canon EOS Digital Rebel XSI DSLR camera (Canon USA, Lake Success, New York, USA). Images taken using the DSLR camera were paired with images taken from the remote cameras and analyzed in Adobe Photoshop CS3 for detailed nest characteristics. Target physical characteristics of each nest included nest height (m) above the water (high tide line), presence of an overhang, number of vertical walls adjacent to the nest, and nest location (island or mainland). A biological nest-site characteristic, the average number of visible nests (in the remote camera image, area  $\sim$ 4 m  $\times$  3 m), was also included in the analysis to represent local density. Nest height was calculated using a combination of a range finder on site, images taken using the DSLR camera



**Fig. 1.** Location of Cape Resurrection study site relative to the state of Alaska, USA.

Fig. 2. Map of island and mainland locations relative to the camera location.

from the camera location, and the ImageJ software program (Abràmoff *et al.* 2004). We calculated the nest height according to

$$h = \sqrt{d_1^2 - d_2^2}$$

where h is the vertical distance from the high tide line to the nest,  $d_1$  is the distance from the boat to the nest, and  $d_2$  is the distance from the boat to the high tide line directly below the nest (Pythagorean theorem). This height was used as a measurement scale in ImageJ to measure the height above the high tide line of all other nest sites monitored for reproductive behaviors. The presence of an overhang was classified as: Type 0 (no overhang), Type 1 (directly over the nest within two body lengths that shaded at least 80% of the nest), or Type 2 (more than two body lengths above the nest and covering multiple nests). Type 1 overhangs were hypothesized to provide protection from both predators and precipitation, while Type 2 could provide some shelter from rain, but less protection from predators. The number of vertical walls adjacent to the nest was determined by counting the number of walls immediately adjacent to a nest that were higher than an incubating bird. If the adjacent wall had a slope of less than 60° it was not considered to be a vertical wall. The degree of slope was calculated using the measuring tools in ImageJ. The average number of visible nests within the camera view was calculated by averaging the number of nests in videos recorded on three different days once nests have been established (first and second week of June). Island and mainland locations were approximately south-facing, and the island location was south of the mainland location (Fig. 2).

#### Effect of weather on loss events

Total loss per day per type of loss (nest, egg, and chick) in 2014-2015 was recorded to determine if loss events were influenced by seasonal variation in weather patterns. The Vantage Vue weather station collected several types of weather data but only target variables were used for this project, including air temperature (°C), wind speed  $(m \cdot s^{-1})$  and direction, and precipitation (mm). A Vantage Vue weather station and a WeatherLink USB data logger from Davis Instruments (Davis Instruments Corp., Hayward, California, USA) were installed at the study site on 29 April 2014. The weather station was programmed to record every hour and effort was made to download data every 2.5 months. This minimized researcher visits to the colony to collect data from the logger, while still recording frequent weather measurements at the colony. Data in May-August were included for the analysis during the breeding seasons of 2014 and 2015. Three different analyses were run for determining the effect of seasonal weather patterns on the three types of loss. All losses were included except for 1) nests lost after the nest was classified as successful and 2) if a chick was lost earlier and the nest was lost late in August.

#### Data analysis

#### Effects of nest characteristics and location on nest success

Nest success was modeled using a Poisson regression as a function of nest characteristics with the "lme4" package in R (Bates *et al.* 2015, R Core Team 2015). Overhang and island/mainland location were treated as categorical fixed effects; nest height, number of walls, and number of visible nests were treated as continuous fixed effects; and nest site was treated as a random effect. Model predictors were standardized to have a mean of zero and standard deviation (SD) of 0.5 using Gelman's approach (Gelman 2008, Grueber *et al.* 2011). Standardization of model predictors was done in preparation for model averaging using the "arm" package in R on the global model (Gelman 2008, Grueber *et al.* 2011, Gelman & Su 2015, R Core Team 2015). Using the "MuMIn" package, a full sub-model set was generated from the standardized global model (Bartoń 2015, R Core Team 2015). The top models were selected for averaging using an Akaike information criterion with a correction for small sample sizes (AIC<sub>c</sub>) cutoff value of 2.0 (Grueber *et al.* 2011).

#### Effect of weather on loss events

Given the single-subject repeated-measures design (i.e., repeated measures of loss at the same colony over time), the assumption of independence was expected to be violated and a high rate of zeros was anticipated. Our initial data exploration revealed potential lag in weather effects on loss (e.g., a weather event occurs on one date and loss occurs the following date). Losses and target weather variables were averaged over three-day periods to address the issue of independence and account for the lag in weather effects on loss. Averaged losses were normalized with a squareroot transformation; the large number of true zero observations warranted a negative binomial analysis (Warton 2005). Each type of loss was evaluated using a separate regression. Automated model selection was conducted using the "MuMIn" package (Bartoń 2015, R Core Team 2015). Top models were chosen based on a  $\Delta AIC_c$ value of less than 3.0. Model averaging was conducted using the model-averaging functions in the "MuMIn" package (Bartoń 2015, R Core Team 2015).

#### RESULTS

#### Estimating productivity from monitoring data

Reproductive metrics of kittiwakes at Cape Resurrection fluctuated throughout all six years (Fig. 3, Table 1). Total nesting attempts changed little, ranging from 134–156 attempts, while the total number of chicks varied from 36–128. Productivity ranged from



**Fig. 3.** Total nests, hatchlings, fledglings, and estimates of productivity for 2010–2015.

0.015–0.442, while the total number of fledglings ranged from 2–69. The most successful year was 2014, with the highest estimate of productivity and the greatest number of chicks (128) and fledglings (69). The mean dates of target reproductive behaviors such as the initiation of nest, incubation, hatch, and fledge initiation changed, on average, three days between chronological years and ranged between 6 and 10 days overall (Table 1). In 2013, we observed the earliest mean date for nest initiation (19 May), while 2015 had the earliest mean date for incubation initiation (02 June). The earliest observed mean dates for hatch was 05 July in both 2013 and 2015. Notably, the earliest observed mean fledge date (08 August) occurred during the year with the lowest estimate for productivity, 2012.

#### Effects of nest characteristics and location on nest success

Nest height, overhang, adjacent walls, and island/mainland location remained the same throughout all years of observation. Nest sites where a nest was not created in any year of observation were eliminated from our analysis. The number of visible nests within each plot changed little between years: 0.5–4.5 nests per nest site. Nest height ranged 0.96–17.71 m above the high tide line, with most nests occurring 5–12 m above the high tide line. Fourteen nest sites (10%) had a Type 1 overhang and seven nest sites (5%) had a Type 2 overhang. Thirty-three nest sites (22%) had more than one adjacent wall. Of these 33 nest sites, 29 had two walls and 4 had three walls. Nests were approximately evenly divided between island and mainland locations, with 71 on the mainland and 76 on the island.

 TABLE 1

 Mean dates of nest, incubation, hatch, and fledge initiation dates with standard deviation (SD) for 2010–2015

Year	Nest		Incubation		Hatch		Fledge	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2010	05/27	3.49	06/06	5.70	07/07	5.13	08/10	2.81
2011	05/29	4.11	06/11	5.80	07/11	5.23	08/15	3.33
2012	05/24	4.69	06/07	7.00	07/08	6.55	08/08	2.70
2013	05/19	6.21	06/03	4.73	07/05	4.80	08/15	4.00
2014	05/25	3.96	06/05	5.26	07/07	4.57	08/15	3.46
2015	05/24	4.89	06/02	5.03	07/05	4.50	08/14	3.39

The full model was ranked third best in the statistical modeling and indicated that island/mainland location (Poisson regression: z = 4.1, P < 0.001) and nest height (Poisson regression: z = 2.7, P = 0.008) had significant influences on the number of fledglings produced per nest. The full model and four additional models had  $\Delta AIC_c$  scores of < 2.0 and were averaged for parameter estimates. These averaged models indicated that island/mainland location and nest height above water were the most important predictors for success, with Type 1 overhangs having 85% relative importance to these two factors (Table 2). The importance of island/mainland location was a significant factor influencing nest success in all years, but nest height seemed to vary in importance (Fig. 4).

#### Effect of weather on loss events

The Vantage Vue weather station operated during 2014–2015, with only one technical failure resulting in loss of data over 24 days (27 May–19 June 2015). The average temperate for the study period (May–August) was 11.8 °C (SD = 2.7 °C) for 2014 and 13.3 °C (SD = 3.0 °C) for 2015. Average precipitation was 0.30 mm (SD = 0.91 mm) for 2014 and 0.25 mm (SD = 0.79 mm) for 2015. Average wind speeds were 1.27 m·s<sup>-1</sup> (SD = 1.21 m·s<sup>-1</sup>) for 2014 and 1.12 m·s<sup>-1</sup> (SD = 1.08 m·s<sup>-1</sup>) for 2015.

Average wind speed had significant but opposite effects on nest loss (negative binomial regression: P = 0.01) and egg loss (negative binomial regression: P = 0.03). The degree of nest loss generally increased with increasing wind speeds in 2014 (Fig. 5), whereas egg loss decreased with increasing wind speeds (Table 3). Average rainfall and temperature were of much lesser importance, but they did appear in models predicting nest and egg losses with a  $\Delta AIC_c$  value of < 3.0 (Table 3). It should be noted, however, that confidence intervals were relatively broad in most cases (Table 3). In contrast, the null intercept model for predicting chick losses best fit the data, indicating that weather effects provided no predictive power for chick losses.

#### DISCUSSION

## Estimating productivity from monitoring data

Remote video camera technology proved to be a useful tool for monitoring estimates of both productivity and reproductive phenology at the kittiwake study colony. The cause behind the poor reproductive success in 2011 was not investigated, but

TABLE 2

Model averaged parameter estimates of nest characteristics on nesting success based on the five best models from regression analysis

Parameter	Estimate	Unconditional standard error	Confidence interval	<b>Relative importance</b>
(Intercept)	-1.122	0.073	(-1.264, -0.980)	
c.MI <sup>a</sup>	0.562	0.137	(0.294, 0.830)	1.000
Overhang1 <sup>b</sup>	-0.361	0.280	(-0.909, 0.187)	0.850
Overhang2	-0.942	0.514	(-1.949, 0.065)	0.850
Nest height	0.390	0.147	(0.102, 0.678)	1.000
Visible nests	0.194	0.116	(-0.033, 0.420)	0.620
Walls	-0.110	0.137	(-0.379, 0.158)	0.290

<sup>a</sup> Island was the reference category

<sup>b</sup> No overhang (Type 0) was the reference category



Fig. 4. Total fledglings produced per year (2010–2015) with regard to nest height above the high tide line.



Fig. 5. Total nest loss and average wind speed  $(m \cdot s^{-1})$  per day throughout the breeding season of 2014.

the low success could indicate a temporary change in the local environment, such as reduced food resources or poor weather conditions surrounding Cape Resurrection (Roberts & Hatch 1993, Byrd 2008, Sydeman *et al.* 2012). Following 2012, estimates of productivity returned to > 0.3 fledglings produced per nest attempt. While seasonal weather effects were investigated, the equipment used for monitoring weather was not installed until 2014 and thus we could obtain only two years of data.

#### Effects of nest characteristics and location on nest success

Nest height above the water and location (island vs. mainland) were the most important factors to influence individual nest success. Overhangs directly over the nest that were within two body lengths of the nest were less important. Physical characteristics were thus more important than biological characteristics (e.g., nest density), contrary to some previous studies of this species in which nest

(b) egg loss, based on negative binomial regression models with $\Delta AIC_c$ values < 3.0								
Parameter	Estimate	Standard error	<b>Confidence interval</b>	Relative importance				
a)								
(Intercept)	-1.694	0.555	(-2.802, -0.585)					
AvgWind	2.010	0.793	(0.421, 3.599)	1.00				
AvgTemp	0.818	0.896	(-0.978, 2.614)	0.26				
AvgRain	0.405	0.618	(-0.832, 1.643)	0.21				
b)								
(Intercept)	0.357	0.631	(-0.930, 1.643)					
AvgWind	-3.623	1.586	(-6.855, -0.390)	1.00				
AvgTemp	-0.289	1.494	(-3.335, 2.758)	0.18				
AvgRain	0.045	1.317	(-2.640, 2.730)	0.18				

 TABLE 3

 Model averaged parameter estimates showing weather variable effects on (a) nest loss and

 (b) egg loss, based on negative binomial regression models with ΔAIC<sub>c</sub> values < 3.0</td>

density was more important (Kildaw 1999, Massaro *et al.* 2001). Nests located in high-density areas of a colony are less susceptible to predation (Massaro *et al.* 2001). Depredation of eggs or chicks was not observed in any video observations in all six years of this study, though predation may have occurred outside of the observation period (SAT unpubl. obs.).

A greater influence of physical nest characteristics indicates that weather patterns may be more important than predation. The importance of nest height may be linked to storm surge events, when the tide is high and wave action is intense (SAT unpubl. obs.). Entire plots have been lost during these storm surges, eradicating several lower-elevation nests that were preparing to fledge a chick. Despite consistent loss throughout all six years, birds returned to nest in these sites. It is important to note that, while nest height had a significant influence on individual nest success, it may be more important in some years than others and could depend on the timing and strength of weather patterns.

The significance of location (island vs. mainland) could be due to varying exposure to weather patterns. The island location consistently produced fewer chicks (except for 2012) and experienced greater losses each year than the mainland locations, despite both locations having a comparable number of monitored nests. The mainland location also contained the plot with the lowest elevation, which produced the most consistent failure rate for all six years due to wave action. Both island and mainland locations are oriented in the same south-facing direction, but the island location is south of the mainland, essentially acting as a protective barrier for the mainland against the open ocean. This configuration and the significance of island vs. mainland locations on individual nest success indicates that the mainland locations were buffered against adverse weather conditions.

## Effect of weather on loss events

The effect of weather changes on losses experienced by breeding kittiwakes varied among types of loss. As average wind speed increased, egg loss significantly decreased but nest loss increased. Nest loss at higher wind speeds was an anticipated result, considering that kittiwake nests are composed of mud and grass

material and are constructed on narrow ledges (Hatch *et al.* 2020). When a nest is lost, all contents within the nest bowl (i.e., eggs or chicks) are usually lost as well, indicating that chick and egg loss, when coupled with nest loss, were also significantly influenced by high average wind speed. Comparatively, egg loss alone was significantly less during periods of greater average wind speed, potentially due to adults restricting movement away from the nest during high wind events. This result could also indicate reduced impact from predation. Predation has been positively correlated with windy conditions by increasing the range of nests that can be attacked by of large gull species (Massaro *et al.* 2001). As mentioned previously, predation of eggs and chicks was not directly observed or investigated for this project and may have occurred outside observation periods.

Analysis of seasonal weather patterns on different types of loss indicated some interesting results that warrant further longterm investigation. Continued data collection may emphasize the importance of other weather factors and shape a better understanding of how this colony is influenced by seasonal weather patterns. Results of this analysis conclude that, for the breeding seasons of 2014 and 2015, average wind speeds had an important influence on nest and egg loss.

#### CONCLUSIONS

Our objective of identifying factors influencing kittiwake reproductive ecology in Resurrection Bay using remote video techniques was successful. We found remote camera technology to be a valuable tool for monitoring reproductive ecology of a cliff-nesting seabird over a multiyear time period. We recommend the use of this technology to study cliff-nesting seabirds in remote locations.

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## REFERENCES

- ABRÀMOFF, M.D., MAGALHAES, P.J. & RAM, S.J. 2004. Image Processing with ImageJ. *Biophotonics International* 11: 36–42.
- BARTON<sup>´</sup>, K. 2015. *MuMIn: Multi-Model Inference*. R package version 1.15.1.
- BATES D., MÄCHLER M., BOLKER B, & WALKER S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48. doi:10.18637/jss.v067.i01
- BLUHM, B.A., GEBRUK, A.V., GRADINGER, R. ET AL. 2011. Arctic marine biodiversity: An update of species richness and examples of biodiversity change. *Oceanography* 24: 232–248. doi:10.5670/oceanog.2011.75
- BYRD, G.V., SYDEMAN, W.J., RENNER, H.M. & MINOBE, S. 2008. Responses of piscivorous seabirds at the Pribilof Islands to ocean climate. *Deep-Sea Research Part II* 55: 1856–1867. doi:10.1016/j.dsr2.2008.04.015
- DRAGOO, D.E., RENNER, H.M. & KALER, R.S.A. 2019. Breeding status and population trends of seabirds in Alaska, 2018. US Fish and Wildlife Service Report AMNWR 2019/03. Homer, USA: Department of the Interior, US Fish and Wildlife Service.
- GELMAN, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27: 2865–2873.
- GELMAN, A. & SU, Y.-S. 2015. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.8-6.
- GRUEBER, C.E., NAKAGAWA, S., LAWS, R.J. & JAMIESON, I.G. 2011. Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711. doi:10.1111/j.1420-9101.2010.02210.x
- HARLEY, C.D.G., HUGHES, A.R., HULTGREN, K.M. ET AL. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9: 228–241. doi:10.1111/j.1461-0248.2005.00871.x

- HATCH, S.A., ROBERTSON, G.J. & BAIRD, P.H. 2020. Black-legged Kittiwake (*Rissa tridactyla*), version 1.0. In: BILLERMAN, S.M. (Ed.) *The Birds of North America*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.bklkit.01
- KILDAW, S.D. 1999. Competitive displacement? An experimental assessment of nest site preferences of cliff-nesting gulls. *Ecology* 80: 576–586.
- MANISCALCO, J.M., PARKER, P. & ATKINSON, S. 2006. Interseasonal and interannual measures of maternal care among individual Steller sea lions (*Eumetopias jubatus*). Journal of Mammalogy 87: 304–311. doi:10.1644/05-MAMM-A-163R2.1
- MASSARO, M., CHARDINE, J.W. & JONES, I.L. 2001. Relationships between Black-legged Kittiwake nest-site characteristics and susceptibility to predation by large gulls. *The Condor* 103: 793–801.
- OLSTHOORN, J.C.M. & NELSON, J.B. 1990. The availability of breeding sites for some British seabirds. *Bird Study* 37: 145–164. doi:10.1080/00063659009477052
- PIATT, J.F., SYDEMAN, W.J. & WIESE, F. 2007. Introduction: Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352: 199–204. doi:10.3354/meps07070
- R CORE TEAM 2015. *R: A language and environment for statistical computing.* Vienna, Austria: The R Foundation for Statistical Computing.
- REGEHR, H.M. & MONTEVECCHI, W.A. 1997. Interactive effects of food shortage and predation on breeding failure of Black-legged Kittiwakes: Indirect effects of fisheries activities and implications for indicator species. *Marine Ecology Progress Series* 155: 249–260. doi:10.3354/meps155249
- REGEHR, H.M., RODWAY, M.S. & MONTEVECCHI, W.A. 1998. Antipredator benefits of nest-site selection in Blacklegged Kittiwakes. *Canadian Journal of Zoology* 76: 910–915. doi:10.1139/cjz-76-5-910
- ROBERTS, B.D. & HATCH, S.A. 1993. Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. *The Condor* 95: 330–342.
- SPRINGER, A.M., PIATT, J.F. & VAN VLIET, G.B. 1996. Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc. *Fisheries Oceanography* 5: 45–55.
- SYDEMAN, W.J., THOMPSON, S.A. & KITAYSKY, A. 2012. Seabirds and climate change: Roadmap for the future. *Marine Ecology Progress Series* 454: 107–117. doi:10.3354/meps09806
- TANEDO, S.A. & HOLLMÉN, T.E. 2020. Refining remote observation techniques to estimate productivity of Black-legged Kittiwakes *Rissa tridactyla* in Resurrection Bay, Gulf of Alaska. *Marine Ornithology* 48: 61–69.
- WARTON, D.I. 2005. Many zeros does not mean zero inflation: Comparing goodness-of-fit of parametric models to multivariate abundance data. *Environmetrics* 16: 275–289. doi:10.1002/env.702