DESIGN- AND MODEL-BASED APPROACHES TO ESTIMATING BURROWING SEABIRD COLONY SIZE IN HAIDA GWAII, CANADA

SARAH E. GUTOWSKY[1]*, DAVID T. ILES[1], PETER SINKINS[2], JAKE BURTON[2], & LAURIE WILSON[3]

[1]*Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, Ontario, Canada *(sarahegutowsky@gmail.com)*
[2]*Parks Canada, Skidegate, British Columbia, Canada*
[3]*Canadian Wildlife Service, Environment and Climate Change Canada, Delta, British Columbia, Canada*

Received 21 November 2025, accepted 15 April 2026

ABSTRACT

Gutowsky, S. E., Iles, D. T., Sinkins, P., Burton, J., & Wilson, L. (2026). Design- and model-based approaches to estimating burrowing seabird colony size in Haida Gwaii, Canada. *Marine Ornithology*, *54*(2), 387–402. http://doi.org/10.5038/2074-1235.54.2.1716

Estimating colony size of burrow-nesting seabirds is critical yet challenging due to inaccessible nest sites, spatially variable distributions, and difficulties in defining colony boundaries. We combined design-based and model-based approaches to estimate colony size for Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* on Alder Island, Haida Gwaii, Canada. We repeated a 1985 systematic transect plot-based survey in 2023, using a design-based bootstrap approach to estimate total burrows and occupied burrows while accounting for sampling uncertainty. For 2023, we also developed Boosted Regression Tree Species Distribution Models that incorporated Light Detection and Ranging (LiDAR)-derived habitat covariates to predict fine-scale burrow density. Variation in observed occupancy rates was combined with predicted burrow densities to estimate island-wide numbers of occupied burrows and associated uncertainty. Ancient Murrelets occurred broadly across the island at lower densities, whereas Cassin's Auklets were concentrated near the island perimeter at higher densities. Model-based estimates of colony size for 2023 were slightly lower and less precise than design-based estimates but provided additional insight into spatial distribution and uncertainty. Compared with 1985, burrow density in 2023 was higher for both species. However, Ancient Murrelet occupancy was lower, resulting in fewer occupied burrows in 2023, while Cassin's Auklet occupancy remained similar, producing higher numbers of occupied burrows in 2023. Our results demonstrate that combining design-based and model-based approaches provides complementary perspectives on colony size and distribution, informing future monitoring, survey design, analytical approaches, and conservation planning for burrow-nesting seabirds.

Key words: boosted regression tree, colony monitoring, demography, population size, seabirds, species distribution modelling

INTRODUCTION

Seabirds are among the most threatened bird groups globally, with populations of over half of all species decreasing due to pressures such as invasive predators, habitat degradation, climate change, fisheries bycatch (Dias et al., 2019), and fish depletion (Paleczny et al., 2015). Monitoring seabird population abundance and trends is essential for conservation but remains difficult, particularly for burrow-nesting species like alcids and petrels, whose nests are often inaccessible and concealed. Standard methods, such as counting burrows and estimating occupancy within survey plots, are frequently used but can be logistically challenging and prone to bias, especially when habitat is complex or burrow density is spatially variable (Oppel et al., 2014; Pearson et al., 2013). These challenges are compounded by difficulties in defining colony boundaries and ensuring that surveyed plots are representative of the entire inhabited area (Buckland et al., 2001).

In Canada, the Canadian Wildlife Service (CWS) branch of Environment and Climate Change Canada (ECCC) is responsible for the stewardship, conservation, and management of migratory birds. On the Pacific coast, long-term monitoring of seabird populations is coordinated through the British Columbia (BC) Seabird Colony Monitoring Program. Intensive surveys conducted in the 1980s established baseline population estimates for colonies of most burrow-nesting seabirds in BC. However, because colonies are numerous (17 species at roughly 650 sites; ECCC, 2023), with many being quite large and located in remote areas, repeated full censuses are rarely feasible. Consequently, the BC Seabird Colony Monitoring Program focuses on a subset of priority colonies and species, for which permanent plots are surveyed on a rotating basis to detect population change over time. Complete censuses, from which total colony size can be extrapolated, are conducted opportunistically at both priority sites and other sites as resources permit.

Extrapolating seabird colony size from plot surveys can be approached using either a design-based or a model-based framework (e.g., Bird et al., 2022; Scott et al., 2009). Design-based approaches rely on probability sampling theory to estimate population totals directly from survey data without making explicit assumptions about underlying ecological processes. Within this framework, surveys are designed using systematic, stratified, or random plot selection, with estimators accounting for unequal survey weights and sampling variability, if necessary (e.g., Horvitz & Thompson, 1952). Design-based estimates are robust to model misspecification but may lack accuracy and precision when survey coverage is incomplete, environmental gradients are not captured, or sample sizes are limited. Furthermore, they cannot generate spatially continuous predictions, which can be useful for conservation planning and prioritization.

Model-based approaches, including species distribution models (SDMs), explicitly model the relationship between abundance and habitat covariates, enabling prediction across unsampled areas (e.g., Bird et al., 2022; Clark et al., 2019; Scott et al., 2009). These models can improve estimation where data are sparse or distributions are heterogeneous, but they require careful model specification, ecologically meaningful covariates, and validation to assess bias (Hedley & Buckland, 2004; Oppel et al., 2012). The strengths and limitations of each approach are complementary: design-based inference is reliable with well-designed surveys, whereas model-based approaches are flexible and powerful for spatial prediction when relevant covariates are available and representatively sampled.

We estimated population size for two burrow-nesting alcids breeding sympatrically at Alder Island, Haida Gwaii, Canada: Ancient Murrelet *Synthliboramphus antiquus* (herein, *ANMU*) and Cassin's Auklet *Ptychoramphus aleuticus* (herein, *CAAU*), using both design-based and model-based approaches. Alder Island is not part of the core set of priority colonies monitored repeatedly under the BC Seabird Colony Monitoring Program; instead, available data consist of a baseline census conducted in 1985 (Rodway et al., 1988) and a repeat census in 2023 using a comparable nonrandom, systematic transect-based design. Using the 2023 transect data combined with habitat covariates derived from Light Detection and Ranging technology (LiDAR), we developed Boosted Regression Tree (BRT) models to predict species distribution and abundance. In parallel, we estimated abundance in 2023 using a design-based approach, allowing us to compare precision and potential bias between model-based and design-based estimates. We also compared colony size between 1985 and 2023 using design-based estimates. This comparison is intended to quantify differences between survey periods rather than to infer population trends, as we have data from only two survey years nearly four decades apart.

Our objectives, therefore, were to (i) generate updated estimates of colony size for Alder Island, (ii) evaluate the performance of model-based and design-based approaches for estimating abundance in a heterogeneously distributed burrow-nesting seabird colony, and (iii) assess how these approaches may inform future survey design in systems where intensive plot monitoring or frequent, repeated full censuses are not feasible. Our results provide updated baseline information on colony size and spatial distribution and illustrate how alternative analytical approaches can support monitoring and conservation planning for burrow-nesting seabirds.

METHODS

Study Site

Haida Gwaii is the largest and most isolated island archipelago off the Northwest Pacific coast of BC (Fig. 1), consisting of roughly 350 islands. Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site (referred to hereafter as *Gwaii Haanas*) comprise the southern portion of Haida Gwaii and are managed cooperatively by the Haida Nation and the Government of Canada through the Archipelago Management Board (Government of Canada, 2018). The 4,940 km^2 protected area safeguards a diversity of marine, intertidal, and terrestrial ecosystems, from mountaintops to the seafloor, as well as a rich cultural history. Many smaller islands in Gwaii Haanas are isolated from land predators and are unique havens for ground-nesting seabirds. An estimated 1.5 million seabirds nest at over 200 islands encompassed by Gwaii Haanas, including at the study site on Alder Island (Fig. 1).

Alder Island (52.448°N, 131.321°W) is located to the east of Moresby Island, off the northern coast of Burnaby Island (Fig. 1). Over 90% of the island is a mixed Sitka spruce *Picea sitchensis*/western hemlock *Tsuga heterophylla* forest with a minor component of red alder *Alnus rubra* and red cedar *Thuja plicata* on moderate to steep slopes rising to a maximum elevation of about 100 m (Rodway et al., 1988). Much of the understorey is open moss or bare ground scattered with deadfall. The slopes on the east side of the island are more moderate, where the terrain alternates between small seepage valleys and drier ridges. The slopes on the west side tend to be steeper, with a particularly large, steep gully towards the northern end. The islet to the north of Alder (herein, the "northern islet") has steep, rocky sides, with the eastern half at a higher elevation than the western half. The vegetated areas tend to be open and mossy under a spruce forest, with a patch of young spruce in the interior of the western half. Other seabird species nesting on Alder Island include storm petrels (Fork-tailed Storm Petrel *Hydrobates furcatus* and Leach's Storm Petrel *Hydrobates leucorhous*) on the northern islet, as well as Black Oystercatchers *Haematopus bachmani*, potentially Pigeon Guillemots *Cepphus columba*, and Glaucous-winged Gulls *Larus glaucescens* on the main island.

Study Species

ANMU and CAAU have similar diets, both preying predominately on zooplankton but also on small fishes when available (Burger & Powell, 1989; Gaston et al., 1993; Sealy, 1975; Vermeer et al., 1985). Their at-sea breeding distributions differ: ANMU nesting in Haida Gwaii tend to target the shallower areas of Hecate Strait (Pattison et al., 2023), whereas CAAU tend to forage over or near the continental shelf (Domalik et al., 2018). For nesting, both species seek islands with suitable burrow habitat and little to no mammalian predator presence. Historically, on Alder Island, ANMU burrows were located across most of the island's drier, forested areas, under live and dead tree roots and old deadfall (Rodway et al., 1988). CAAU distribution was more limited to the perimeter of the island within 10–20 m of the edge of the vegetation, with burrows found under roots but also in rock crevices. Unlike most seabirds, ANMU chicks, typically two per nest, leave the nest one to three days after hatching and are raised entirely at sea. In contrast, CAAU provide prolonged parental care, with both parents incubating a single egg and feeding the chick for several weeks before fledging. Despite these differences in life history and fine-scale habitat preferences, both species nest in burrows on islands where eggs, chicks, and nesting adults are vulnerable to predation by introduced mammalian predators. In Canada, both species are listed as "Special Concern" under Schedule 1 of the Species at Risk Act (SARA). ANMU has held this designation since 2004 following significant population declines caused by introduced mammalian predators (ECCC, 2018). CAAU has held this designation since 2019, reflecting local decreases from both habitat degradation and predation by introduced species (Committee on the Status of Endangered Wildlife in Canada [COSEWIC, 2014]). According to the International Union for Conservation of Nature (IUCN) Red List, both species are currently assessed as decreasing globally, with ANMU classified as Least Concern and CAAU as Near Threatened (IUCN, 2025).

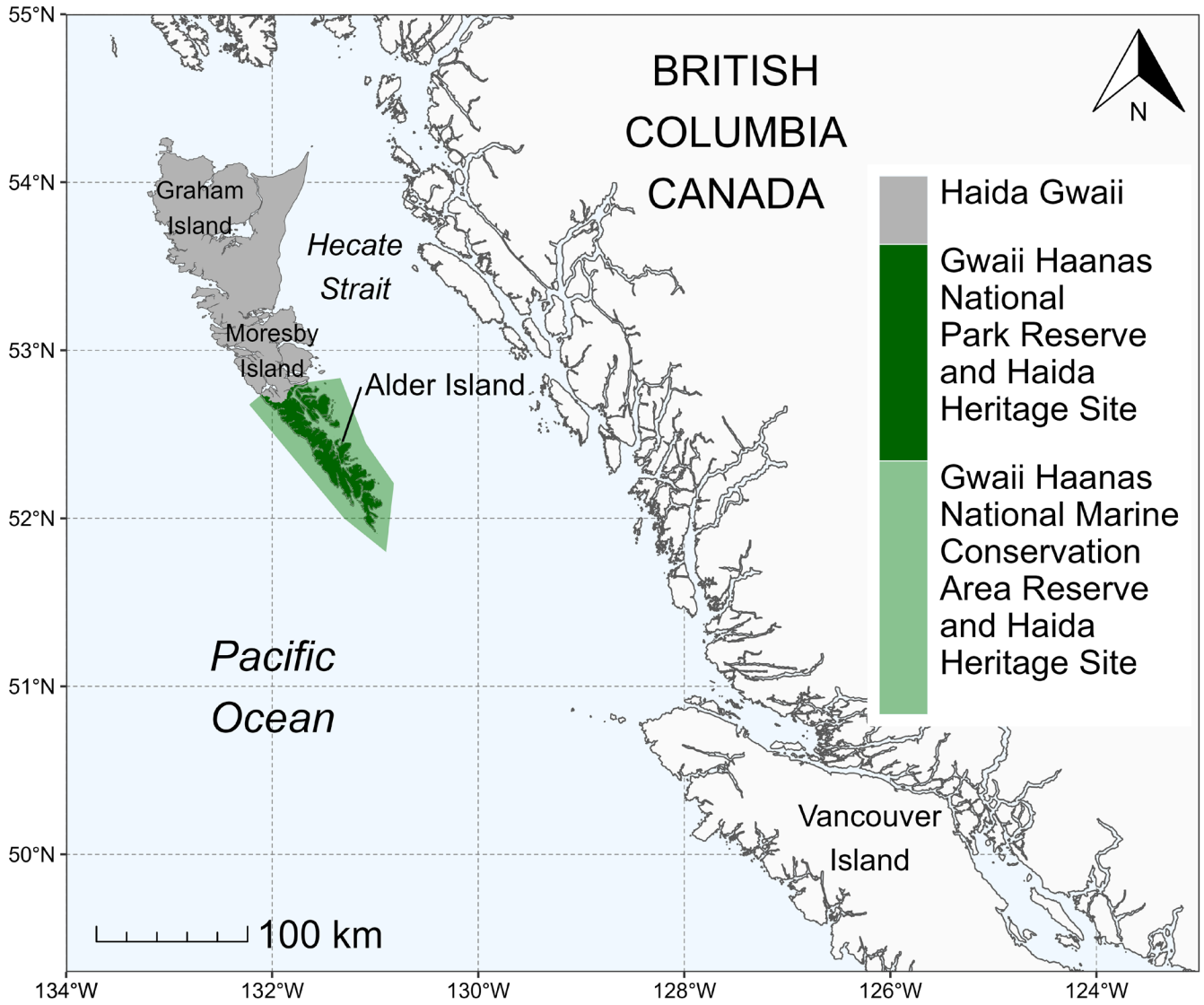


Fig. 1. Location of the study site, Alder Island (52.448°N, 131.321°W), within Haida Gwaii, British Columbia, Canada. Alder island is located within Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site.

Monitoring and conservation efforts for both species in Gwaii Haanas are guided by the Multi-Species Action Plan (Parks Canada Agency, 2016), which focuses on maintaining populations at sites that have never been affected by invasive species and increasing populations at sites that have. Programs to eradicate rats *Rattus* spp. on Langara Island, initiated in 1995, successfully facilitated the recovery of Ancient Murrelet colonies, with populations rebounding following rat eradication (Regehr et al., 2007). Similar initiatives in Gwaii Haanas, such as the "SG̲in X̲aana Sdiihltl'lx̲a: Night Birds Returning" initiative, have aimed to restore seabird habitats by removing invasive species (Parks Canada Agency, 2025). For Cassin's Auklet, ongoing conservation efforts include habitat protection, biosecurity measures to prevent the reintroduction of predators, and monitoring of populations in key breeding areas (COSEWIC, 2014). Alder Island is monitored year-round for the presence of invasive mammals using motion-triggered cameras. Although rats have never been detected, two short-lived incursions by raccoons have occurred since the 1990s.

Systematic Survey Design and Data Collection

Burrow Density

In 1985, from 18 to 22 April, species-specific burrow density was determined within 87 7 × 7 m (49 m^2) plots placed 30 m apart along parallel transects spaced 200 m apart on the main island, with an additional three 7 × 7 m plots on a transect across the west side of the northern islet (Fig. 2). Additionally, burrow density was determined within a larger plot (2,714 m^2) on the east side of the northern islet (Fig. 2). The details of these 1985 surveys are provided in a CWS technical report (Rodway et al., 1988). Briefly, all potentially inhabited burrow entrances were counted and assigned a likely species based on the following cues: finding an adult, chick, freshly hatched eggshell membrane, feathers, or eggshell fragment in the burrow; and for CAAU, the presence of regurgitated food or a latrine. This survey design was recreated in 2023 in a collaborative effort between CWS and Parks Canada, during 10 to 22 May, with the exception of the east side of the northern islet. At the latter,

burrow density was determined for the same localized region but delineated into four smaller irregularly shaped plots ranging from 196 to 1,401 m^2 (Fig. 2). Overall, approximately 2% of the island's area (including the northern islet) was surveyed for burrow density.

Burrow Occupancy Rate

Burrow occupancy is more challenging and time-consuming to ascertain for these species and was determined by thorough examination of a subset of burrows. Burrows were manually checked (i.e., "grubbed"), and a hatch was dug to reach the end if necessary. If an egg, chick, freshly hatched egg membrane, regurgitate, or latrine was found, with or without an attending adult, the burrow was considered occupied. Burrows were considered empty if all tunnel branches were explored and none of the above were found. Burrows with an adult but no other evidence of active breeding were not included in calculations of occupancy rate (OR). Thus, our OR does not include burrows occupied by possible prospecting or floating non-breeding adults. In 1985, burrow OR was determined on a single day (23 April) in an area located on the east side of the island (description of location only, coordinates unknown). Thus, only a single "plot" was sampled for occupancy rate in 1985, with 15 of 23 (OR = 0.65) ANMU burrows found to be occupied and 12 of 15 (OR = 0.80) CAAU burrows found occupied. It should be noted that 23 April is relatively early to estimate occupancy rate for ANMU because laying may still

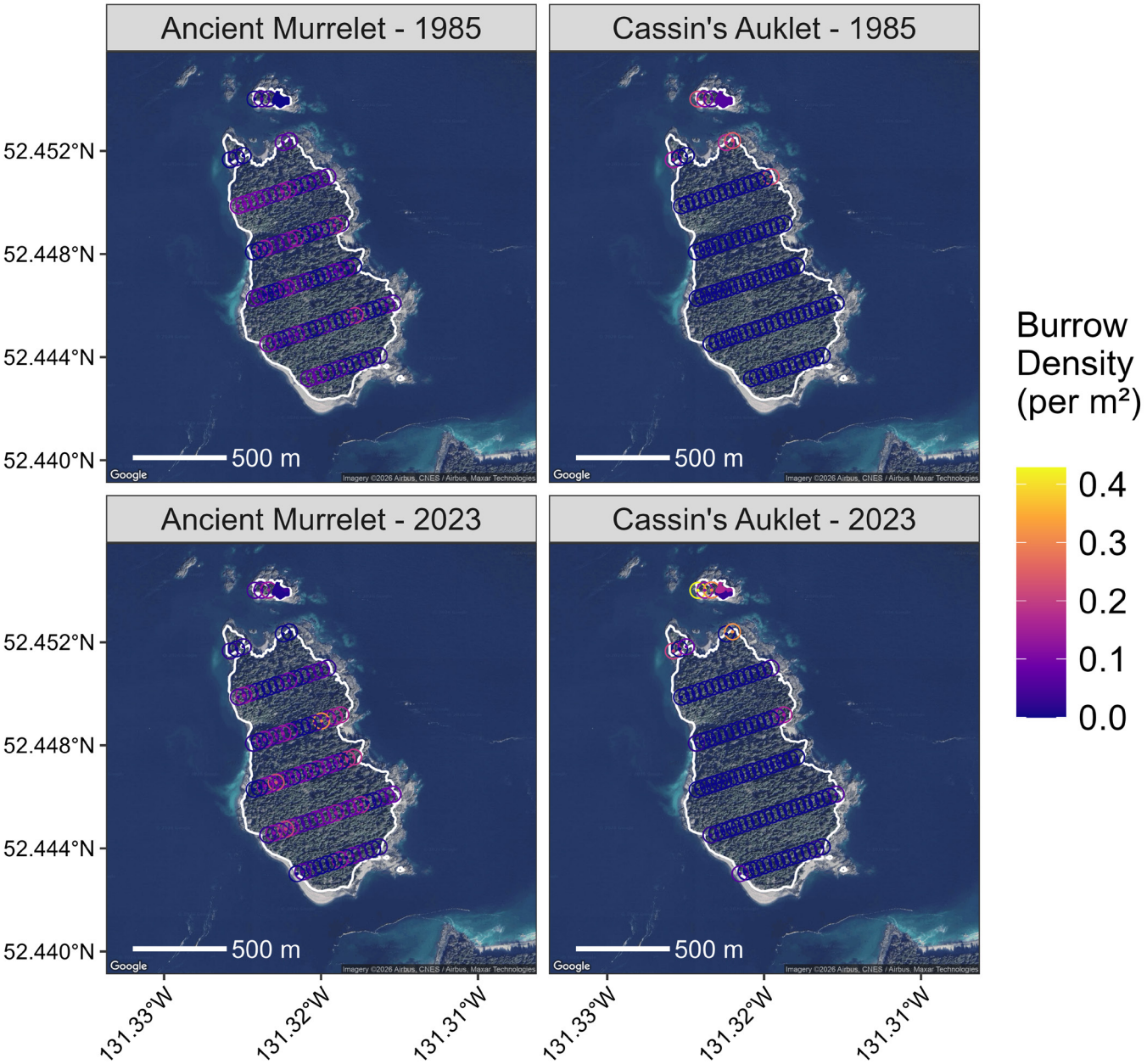


Fig. 2. Plots surveyed in 1985 and 2023 to estimate burrow densities of Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* on Alder Island, British Columbia, Canada. The areas delineated as "potentially habitable area" is also shown, demarcated by the white line. Transect plot locations are shown as points, represented as 20-m-diameter circles rather than the true 7 × 7 m square plots, with an additional larger ring surrounding each plot to aid visibility.

occur after that date if it was a particularly late breeding season. In 2023, burrow occupancy was determined in mid-May (10 to 23 May) when the majority of nesting attempts for both species would be underway with eggs or chicks in the burrows. Occupancy was assessed concurrently with burrow density sampling, during which accessible burrows within a subset of density plots were checked for occupancy (n = 15 plots for ANMU and n = 6 plots for CAAU; Fig. 3). Additionally, areas outside the plots were checked opportunistically, with n = 7 extra "plots" checked for ANMU and n = 4 extra "plots" checked for CAAU (Fig. 3). These additional plots were located in areas of suitable habitat; ANMU plots were situated on the upper sections of slopes and CAAU plots closer to shore, often on headlands. When assessing occupancy in these additional plots, the field crew moved systematically through the area, investigating the next burrow closest to the previously examined one to avoid selectively targeting only "promising" burrows. In total, 18 of 50 (OR = 0.36) ANMU burrows were found to be occupied and 26 of 34 (OR = 0.76) CAAU burrows were found to be occupied in 2023. In 2023, we also recorded the number of burrows for which occupancy could not be determined; many burrows were too deep or cavernous, or their tunnels extended under large roots or rocks, making it impossible to reach the end or dig a hatch for deeper access. Consequently, occupancy determination was attempted but not possible for 74% of ANMU burrows (144/194) and 68% of CAAU burrows (71/105) where occupancy checks were initiated. This highlights the effort required to estimate occupancy rates, as well as a potential bias, because we must assume that occupancy rates in accessible burrows are representative of those in inaccessible burrows.

Estimating Abundance and Distribution in 2023

First we used a BRT species distribution model approach to predict abundance and distribution of each species on the island in 2023 by combining fine-scale habitat spatial layers derived from LiDAR data with geo-referenced plot-level burrow density and occupancy data. We derived and selected habitat covariates for inclusion in species-specific SDMs of burrow density. The SDMs were used to generate 5,000 bootstrap predictions of burrow density for each cell of a 7 × 7 m grid covering the habitable portion of the island. We then evaluated plot-level variation in OR to predict occupancy across the island by again generating 5,000 bootstrap predictions of OR for each grid cell using an intercept-only model. We then multiplied grid-cell-level predictions of burrow density and occupancy to estimate the number of occupied burrows in each grid cell and associated uncertainty in those estimates.

Habitat Covariate Derivation and Selection

We acquired LiDAR data covering the extent of our study area from a larger dataset collected by Parks Canada as part of a fixed-wing LiDAR survey in 2018. From these LiDAR data, we used ArcGIS Pro version 3.2.0 to derive high-resolution rasters of nine habitat metrics potentially relevant to burrow site selection by one or both of our study species.

Using the "ground" classified LiDAR point returns, we created a digital elevation model (DEM) to represent the ground elevation across the study area on a raster grid with a spatial resolution of 0.5 m. Using this DEM, the "Spatial Analyst" toolbox was used in ArcGIS Pro version 3.2.0 to create slope and aspect surfaces on the same raster grid. For each pixel in this raster grid, the Euclidean distance was calculated from its centre to the nearest shoreline to represent the distance to shore. With the same DEM, the Semi-Automated Geoscientific Analysis (SAGA) version 7.8.2 was used to model wetness across the study area (Conrad et al., 2015). The Topographic Wetness Index (TWI) tool in SAGA incorporates the upslope area and topography to estimate the water accumulation likelihood at each grid cell as a proxy for potential soil moisture (Mattivi et al., 2019).

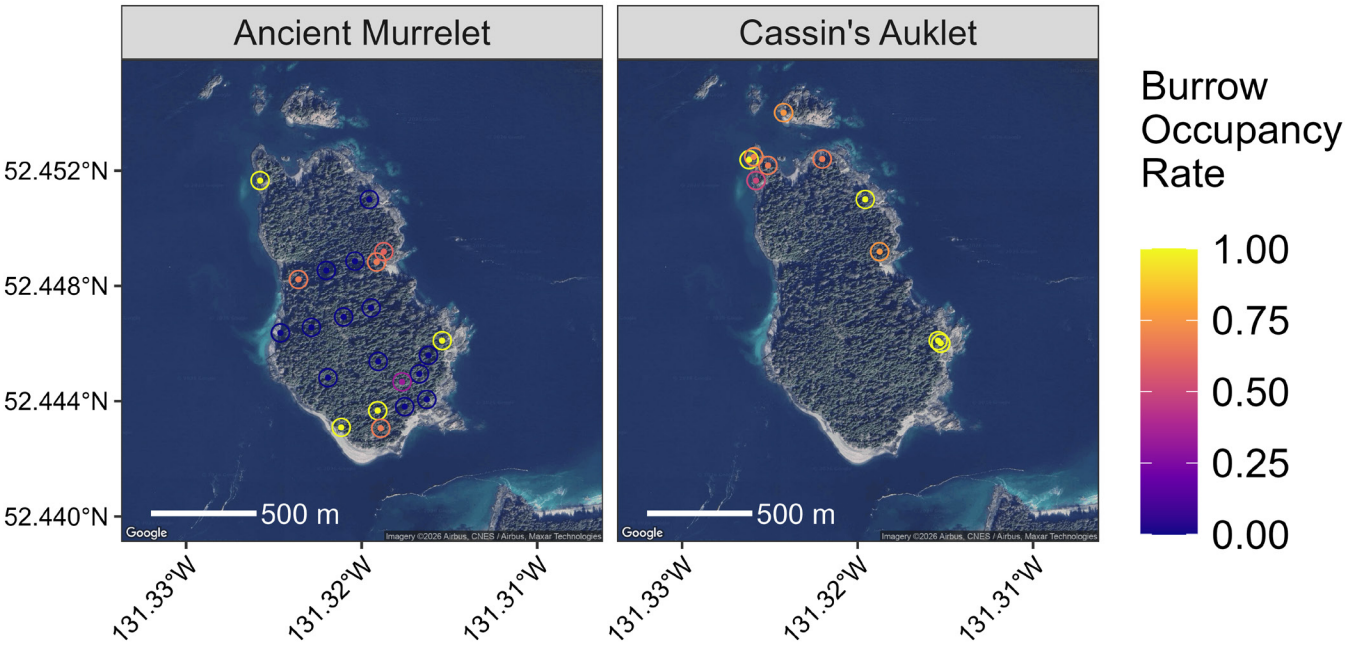


Fig. 3. Survey plot locations surveyed in 2023 for burrow occupancy of Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* on Alder Island, British Columbia, Canada. Plot locations are shown as points with an additional larger ring surrounding each plot to aid visibility.

Next, we derived three vegetation structure metrics from the LiDAR point cloud. Canopy height was calculated at a 0.5 m pixel resolution using the difference between the canopy top (first LiDAR return) and ground elevation values. Canopy density was calculated using the proportion of canopy points (first LiDAR return) to the total number of points in a 2-m grid cell. Shrub density was estimated using the number of LiDAR points in the 1–2 m height range relative to the total number of points within and below that range for a given grid cell. This method is intended to mitigate the effects of a dense overstorey canopy when estimating understorey forest metrics (Campbell et al., 2018).

Finally, we used the DEM to understand which areas of Alder Island and the northern islet are more visible to birds approaching from the sea. To do this, we combined the DEM of the surrounding area with a buffer containing simulated bird locations at a distance of 5 km from Alder Island. These birds were represented by x-y point locations and assigned a height of 5 m based on the typical height of a closely-related alcid (Rhinoceros Auklet *Cerorhinca monocerata*) flying at sea (Okado & Watanuki, 2023). Each point was assigned a viewshed area in relation to the DEM using the ArcGIS Pro Viewshed tool. The output viewsheds represented the visible area for each bird. Each bird's viewshed was aggregated into a grid and areas of Alder Island that were more visible to approaching birds were assigned higher values. Each output raster dataset was masked using a vector shoreline dataset to ensure a consistent processing extent. Negative values resulting from the input LiDAR point cloud extending slightly below 0 m were set to 0.

To match the spatial resolution of the habitat metrics to the survey data, we created a 7 × 7 m grid covering the habitable portion of the island (i.e., the maximum potential colony area). This area was manually delineated using satellite imagery and included all areas of the main island and the northern islet beyond the narrow strip of rocky coastline around the perimeter (Fig. 2). The total area of this potentially habitable region was 519,912 m^2. We then calculated the mean value of each habitat metric within a 10-m-diameter circular buffer centered on each grid cell (Fig. 4). The resulting grid contained 11,025 cells, each measuring 7 × 7 m. Similarly, we calculated the mean value of each habitat metric within a 10-m-diameter circle centered on each of the 91 burrow density survey plots, as well as the mean values within the four plots on the east side of the northern islet. A 10-m-diameter circular buffer was chosen to capture the corners of the square 7 × 7 m plots and grid cells, ensuring that local habitat conditions were adequately represented while allowing for slight uncertainty in the exact location of each plot. Comparisons of plotted density histograms of habitat conditions within surveyed plots relative to the gridded island-wide values suggested that the surveyed plots adequately captured the range of habitat variability across the island (Appendix, Fig. A1, available on the website).

To select habitat covariates to include in our BRT SDMs, we first calculated pairwise correlations among the nine measured habitat variables (Appendix, Fig. A2). Variables showing high correlation ($|r| > 0.7$) were considered for exclusion to avoid multicollinearity. Elevation was highly correlated with distance to shore ($r = 0.78$); elevation was excluded because both species are also known to nest on relatively flat islands, rendering elevation effects less generalizable. Distance to shore was retained because it more directly reflects nesting preferences, particularly for CAAU, whereas ANMU is less sensitive to this gradient. The three vegetation metrics (shrub cover, canopy density, and canopy height) were moderately correlated. Canopy density was retained because it was the most reliably derived metric from LiDAR data, whereas canopy height and shrub cover were excluded due to potential measurement biases and lower reliability in dense or regenerating forests.

Species-specific considerations guided further variable selection for the BRT SDMs. For ANMU, all six retained habitat variables (wetness, distance to shore, slope, aspect, viewshed, and canopy density) were included. For CAAU, we limited the set of habitat predictors to distance to shore and wetness. This decision was based on preliminary examination of the relationships between burrow density and habitat variables within the plots, which suggested that the other four predictors were less likely to explain variation in burrow occurrence for this species. Limiting the number of predictors was required to reduce model complexity and overfitting given the limited number of occupied plots for CAAU.

Species Distribution Models of Burrow Density

We developed BRT SDMs to predict burrow densities for each species across the island-wide 7 × 7 m grid. BRT models were implemented in R version 4.4.1 (R Core Team, 2024) using the "dismo" package (Hijmans et al., 2022), which interfaces with the "gbm" package (Ridgeway, 2020). Model complexity was specified using a tree complexity of two for ANMU and one for CAAU, reflecting differences in variable number and data richness. Learning rates were selected from species-specific candidate sets (ANMU: 0.01, 0.005, 0.001; CAAU: 0.002, 0.001, 0.0005) to balance predictive performance and computational efficiency, with optimal values determined via five-fold cross-validation. To account for sampling uncertainty associated with the systematic survey design, models were fitted using 5,000 bootstrap iterations. In each iteration, 7 × 7 m plots were resampled with replacement from the full dataset (i.e., not constrained by transect), and models were refitted to generate a distribution of predictions. Burrow counts from the large plots covering the east side of the northern islet were not included in the model data or the prediction grid. For each bootstrap iteration, we computed:

1. Cell-level burrow density predictions across the 7 × 7 m grid.
2. Total burrow counts across the island, calculated by summing the products of predicted density and cell area across all grid cells and adding the known burrow counts from the east side of the islet. This approach integrates empirical counts, where available, with model-based extrapolation to unsurveyed areas.
3. Model performance metrics, including cross-validation statistics (deviance explained and correlation between observed and predicted counts) and calibration statistics (mean residuals computed within five equal-frequency bins of predicted values to quantify bias across the prediction range.
4. Relative influence and partial dependence of habitat covariates, summarizing the marginal effect of each variable on predicted burrow density across bootstrap iterations.

We summarized predicted burrow counts at both grid-cell and island-wide levels by calculating the mean and 95% confidence intervals (CI) across the 5,000 bootstrap iterations. Model performance metrics and covariate effects were similarly summarized across bootstrap iterations.

Occupancy Modeling and Estimation of Total Occupied Burrows

To estimate the number of occupied burrows, we multiplied cell-level predicted burrow counts by estimated OR. Due to limited plot-level occupancy data, spatial variation in OR was not directly modeled. Instead, we fitted an intercept-only binomial Generalized Linear Model (GLM) to the available OR data. For each species, 5,000 parametric bootstrap draws of the intercept

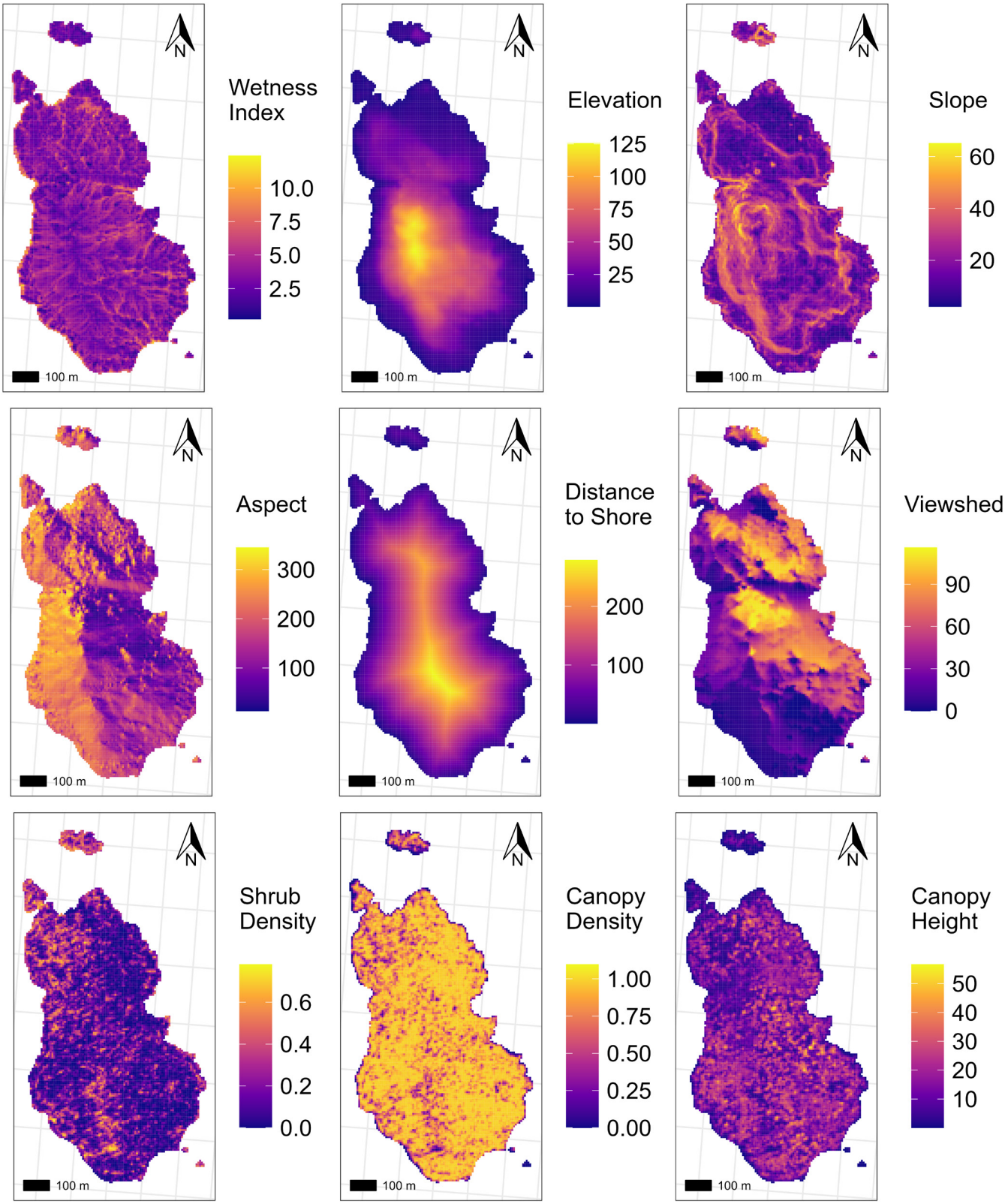


Fig. 4. Mean values of nine Light Detection and Ranging (LiDAR)-derived habitat metrics within a 10-m-wide circle centered on each cell of a 7 × 7 m grid covering the habitable area of Alder Island, British Columbia, Canada.

were generated using the "MASS" package (Venables & Ripley, 2002). These draws capture uncertainty in the intercept estimate given the sampled plots. To assign occupancy rates to grid cells while maintaining independence among cells, we generated 5,000 occupancy draws per grid cell by sampling from a normal distribution with mean equal to the fitted intercept and variance equal to the model variance. This approach ensures that the occupancy simulations incorporate both estimation uncertainty and spatial variation in occupancy across the island. For each bootstrap, we computed cell-level occupied burrows as the product of predicted burrow density and occupancy rate in each grid cell. We also calculated 5,000 estimates of occupied burrows in the plots on the east side of the islet by multiplying the known burrow counts by the 5,000 parametric draws of the occupancy rate intercept. Bootstrapped estimates of the total number of occupied burrows across the island were then computed as the sum of predicted occupied burrows on the grid plus the east side of the islet. The bootstrap distributions of island-wide occupied burrows were then summarized as mean and 95% CIs. This approach propagated uncertainty from both burrow density predictions and occupancy estimates, providing robust measures of confidence in both cell-level and island-wide estimates.

We also estimated island-wide totals of burrows and occupied burrows in 2023 using a direct design-based approach, in which the 5,000 bootstrap resamples of the plot-level burrow densities were scaled to the full island area without using the BRT models. For each bootstrap iteration, the total burrow count was computed as the sum of burrow counts in the sampled plots divided by the total area sampled and multiplied by the total island area, with the known counts from the east side of the northern islet added. Occupied burrows were then estimated by multiplying these design-based totals by 5,000 occupancy rate draws from the intercept-only binomial GLM described above. This approach provides a complementary estimate of island-wide burrow and occupied burrow totals that incorporates sampling uncertainty inherent in the plot-level survey design, independent of the SDM-based framework, and allows for comparison with model-based predictions.

Cross-Year Comparison of Abundance

To compare estimates of abundance (burrows and occupied burrows) between 1985 and 2023 in a consistent framework, we applied a similar design-based bootstrap procedure to the 1985 survey data. Plot-level burrow densities from 1985 were resampled with replacement 5,000 times, matching the same resampled plots in the 2023 bootstraps, to propagate sampling uncertainty associated with the original survey design. Total burrow counts across the island were then estimated for each bootstrap by scaling the resampled plot densities to the full island area. Because only a single OR was available from 1985, we multiplied each of the 5,000 bootstrapped burrow totals by this single OR to estimate total occupied burrows. To ensure comparability with 2023 estimates, we also derived 2023 occupied burrow totals using the design-based bootstrap approach described above but multiplied by the mean species-specific occupancy rates across the sampled plots rather than the 5,000 parametric draws. This ensured that estimates for both years reflected the same treatment of occupancy while retaining uncertainty from burrow sampling, allowing direct comparisons of design-based estimates of total and occupied burrows between 1985 and 2023.

RESULTS

Estimating Abundance and Distribution in 2023 with Model-Based and Design-Based Approaches

The BRT models showed good predictive performance for both species, calculated across 5,000 bootstrap iterations of the burrow density plots sampled with replacement. For ANMU, mean cross-validation deviance was 2.53 (95% CI: 1.61, 3.41), and the mean correlation between observed and predicted values was 0.57 (95% CI: 0.25, 0.81) (Appendix, Fig. A3). For CAAU, mean deviance was 1.55 (95% CI: 0.46, 3.10), and predictive correlation was higher at 0.77 (95% CI: 0.51, 0.95) (Appendix, Fig. A3). Because deviance scales with mean abundance, it is not a reliable basis for comparing performance between species; however, it provides an indication of predictive performance under resampling. Calibration statistics similarly summarized alignment between predicted and observed values across abundance bins for each resampled dataset, indicating that predicted burrow densities were generally well aligned with observed values across most abundance bins, with minor bias in the lowest bin for ANMU and greater variability in low-density bins for CAAU due to sparse observations (Appendix, Fig. A4). Taken together, the observed–predicted correlations, stable deviance under resampling, and generally good agreement between predicted and observed values across calibration bins indicate that both species' models had sufficient calibration and predictive performance for spatial prediction of burrow density across the island.

Spatial predictions suggested that ANMU had a broad but heterogeneous distribution across the island at lower densities, whereas CAAU were concentrated in a narrow band around the island perimeter at higher densities (Fig. 5). For ANMU, the most important predictors of burrow density were slope, canopy density, and wetness (19%–21% mean relative influence), whereas distance to coast, viewshed, and aspect were less important (13%–14.4% mean relative influence) (Appendix, Fig. A5). For CAAU, distance to shore was the dominant predictor (80.8% mean relative influence), but wetness was still important, with nearly 20% relative influence (Appendix, Fig. A6).

Model-based total burrow counts were 29,784 (95% CI: 22,986, 36,619) for ANMU and 8,966 (95% CI: 2,918, 15,428) for CAAU. These estimates were largely consistent with design-based estimates of total burrows (ANMU: 31,911 [95% CI: 24,980, 38,957], CAAU: 10,964 [95% CI: 4,646, 18,886]; Fig. 6). A comparison of pairwise bootstrap estimates from the two methods indicated a 78% probability that model-based estimates for both ANMU and CAAU were lower than the design-based estimates for both ANMU and CAAU (i.e., the difference between the model-based and design-based estimate was < 0). The model-based estimates were, on average, 6% lower for ANMU (−6%[−21%, 8%]) and 16% lower for CAAU (−16%[−50%, 29%]).

Burrow occupancy rates derived from 5,000 bootstrap draws across the prediction grid averaged 0.36 (95% CI: 0.24, 0.50) for ANMU and 0.76 (95% CI: 0.59, 0.88) for CAAU. Applying these occupancy rates to predicted burrow counts produced model-based estimates of occupied burrows of 10,802 (95% CI: 8,330, 13,266) for ANMU and 6,789 (95% CI: 2,212, 11,697) for CAAU. These model-based estimates were comparable to the design-based estimates (ANMU: 12,348 [95% CI: 9,666, 15,074], CAAU: 8,966 [95% CI: 3,799, 15,444]; Fig. 6), although they were slightly lower

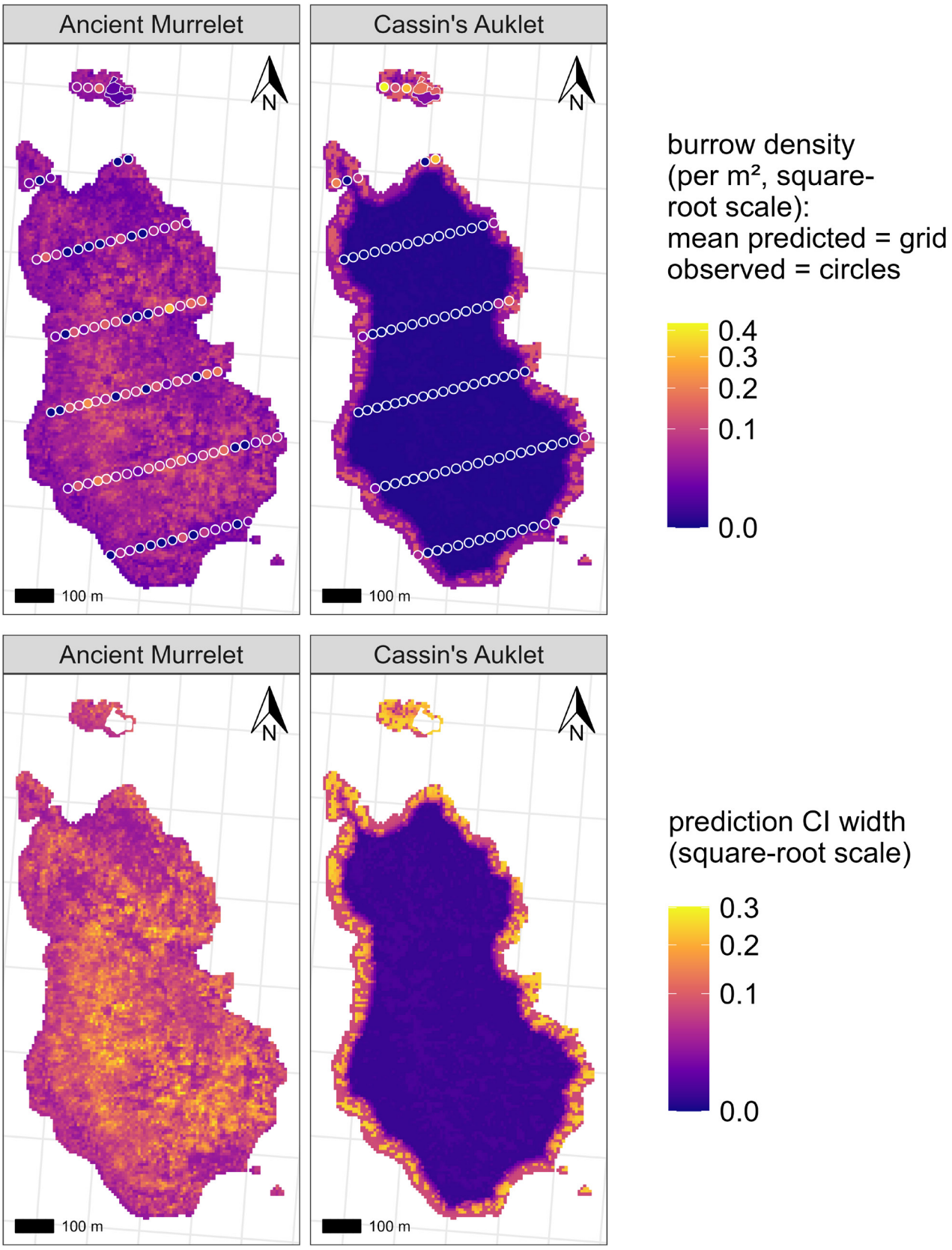


Fig. 5. Bootstrap predictions of burrow densities of Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* across the island-wide 7 × 7 m grid generated from the Boosted Regression Tree Species Distribution Models on Alder Island, British Columbia, Canada. Mean predicted burrow densities across 5,000 bootstrapped predictions are shown on a square-root color scale to enhance contrast between low- and high-density areas, along with the observed values within survey plots, including zero counts. Uncertainty in predicted values is represented as the 95% confidence interval (CI).

in both species. For ANMU, there was a 93% probability that the model-based estimates of occupied burrows were lower than the design-based estimates, differing by −12% (95% CI: −26%, 2%); for CAAU, there was 85% probability, differing by −22% (95% CI: −57%, 20%). The greater uncertainty in estimates of occupied burrows for CAAU reflects the smaller number of plots used to estimate occupancy (10 vs. 22 for ANMU) and the higher variance in observed occupancy rates among sampled plots. These sources of uncertainty propagated through the parametric bootstrap, producing broader confidence intervals for island-wide occupied burrows.

Overall, the model-based estimates aligned reasonably well with the design-based estimates. For ANMU, the precision of the estimates from the two methods was similar, with the 95% CIs for both total and occupied burrow estimates being 2% narrower for the design-based estimates than for the model-based estimates. The CIs represented 46% of the mean design-based estimate, compared with 44% for the model-based estimate (Fig. 6). In contrast, for CAAU, the design-based estimates were slightly more precise, with 95% CIs that were 10% narrower than the model-based estimates. However, the CIs were generally wide, at 130% of the mean design-based-based estimate (Fig. 6).

Estimating Abundance in 1985 and 2023 with a Design-Based Approach

Comparisons of burrow counts between 1985 and 2023 indicated differences between years. For ANMU, the mean burrow count in 2023 was 31,911 (95% CI: 24,980, 38,957), which lies above the upper 95% confidence limit of the 1985 estimate of 22,902 (95% CI: 18,063, 27,904) (Fig. 7). The mean percent change based on 5,000 paired bootstrap replicates was 41% (95% CI: 8%, 79%) with a 94% probability there were more burrows in 2023 than 1985 (i.e., the difference between burrow counts in 2023 and 1985 was > 0), indicating strong evidence that ANMU burrow counts were higher in 2023 relative to 1985. For CAAU, mean burrow counts were also higher in 2023 (1985: 7,105 [95% CI: 2,301, 12,949]; 2023: 10,964 [95% CI: 4,646, 18,886]; Fig. 7), with a mean percent change of 69% (95% CI: –6%, 180%) and an 87% probability that 2023 was greater than 1985. Although the CAAU burrow count means in 1985 overlap the 95% CIs in 2023 and vice versa, and the percent change 95% CI overlaps zero, the bootstrap distributions suggest that an increase in burrow numbers is plausible given the available data.

Estimated occupied burrows were based on a single occupancy rate per year (ANMU: 0.65 in 1985, 0.36 in 2023; CAAU: 0.80 in 1985, 0.76 in 2023). For ANMU, mean occupied burrows were lower in 2023 (11,488 [95% CI: 8,993, 14,024]) compared with 1985 (14,887 [95% CI: 11,741, 18,138]), with the 95% CI for 2023 not overlapping the 1985 mean (Fig. 7). The mean percent change was −22% (95% CI: −40%, −1%), with a 96% probability there were fewer occupied burrows in 2023 than 1985, providing strong support that the number of occupied ANMU burrows was lower in 2023 relative to 1985. For CAAU, mean occupied burrows were higher in 2023 (8,333 [3,531, 14,353]) than in 1985 (5,684 [1,841, 10,359]). However, as with the burrow count findings described above, the 95% confidence intervals and means overlapped substantially. The mean percent change was 61% (95% CI: −10%, 166%), with a 90% probability that there were more occupied burrows in 2023 than 1985. These results suggest that an increase in occupied burrows is plausible, but considerable uncertainty remains.

Overall, comparisons between 1985 and 2023 provide strong evidence that ANMU burrow counts were higher in 2023, but the number of occupied burrows was lower. For CAAU, there was moderate evidence that both burrow counts and occupied burrows were higher in 2023 than in 1985.

DISCUSSION

Our study updated colony size estimates for ANMU and CAAU breeding at Alder Island, comparing survey results nearly four decades apart while evaluating the strengths and limitations of two estimation frameworks: traditional direct, design-based inference and ecological habitat model-based approaches. These complementary methods yielded insights not only into potential shifts in colony size over time, but also into the spatial structure of burrow distribution and the importance of considering burrow occupancy dynamics in interpreting colony size estimates.

The model-based approach tended to yield lower estimates of abundance with marginally lower precision relative to the design-based approach, particularly for CAAU. This pattern is consistent with the cross-validation results, which showed lower predictive accuracy in the lowest density bins for both species. For ANMU, which nests across the island at generally low densities, underestimation was modest, and predictions were generally reliable across the higher-density areas. In contrast, for CAAU, which occurs in more discrete, high-density pockets around the island perimeter, the lowest density areas were more prone to underestimation. This was largely due to the patchy distribution of burrows and the high proportion of plots having zero counts, which amplified residuals in the lowest-density bins during cross-validation across bootstrapped iterations. Whereas Bird et al. (2022) found that model-based estimators can yield unbiased population estimates when burrow density responds predictably to habitat structure, our findings suggest that this advantage weakens in systems with more discrete colony structure and extensive zero counts. The elevated zero-inflation and fine-scale heterogeneity at Alder Island likely constrained model performance, contributing to the modest negative bias and greater uncertainty observed for CAAU.

Despite the consistency in overall abundance estimates between approaches, the precision of our estimates was generally low. High variance in burrow density among plots, and the bootstrap-based resampling procedure that incorporated this spatial heterogeneity, contributed to wider confidence intervals. This procedure effectively simulated repeated random surveys, reflecting the uncertainty inherent in plot-based sampling and the systematic transect design used in both years. Although wider confidence intervals may appear less precise, they provide a transparent and realistic measure of uncertainty, which is critical for designing future surveys and comparing results across sites, species, or years.

Species-specific patterns emerged when comparing data from 1985 and 2023. For ANMU, burrow density in 2023 was higher than in 1985, yet occupancy was lower, resulting in fewer occupied burrows. Burrow-nesting seabirds will often reuse the same burrow for multiple years, and burrows can retain their structure when unoccupied (Gaston, 1992). Thus, burrow density reflects longer-term accumulation, whereas burrow occupancy rate reflects breeding activity in the current year. ANMU, in particular, are known to shift their preferred nesting areas over periods from years to decades,

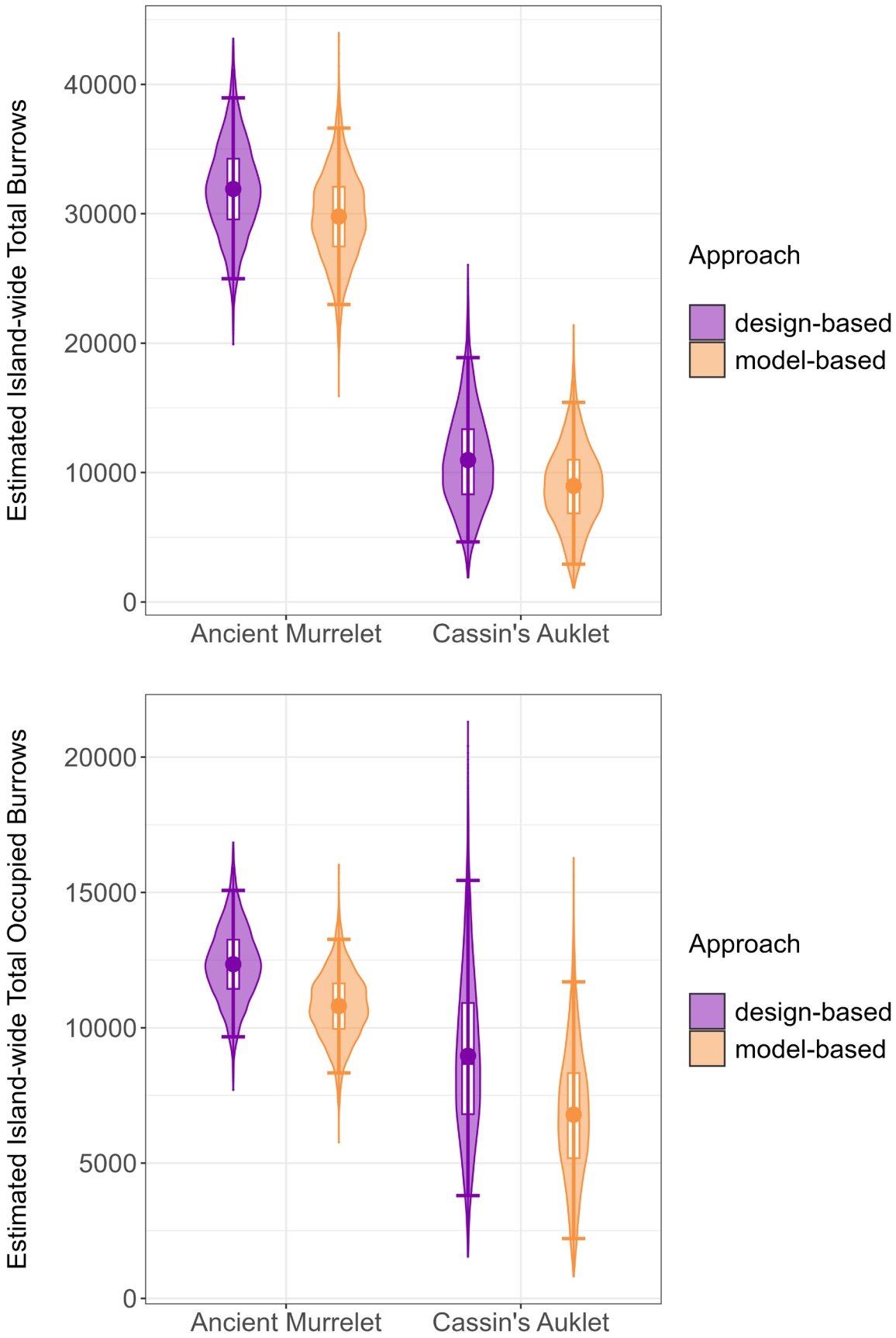


Fig. 6. Estimates of total and occupied burrows of Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* on Alder Island, British Columbia, Canada, derived using design-based and model-based approaches. Distributions show the mean estimate (point), interquartile range (box), 95% confidence intervals (horizontal bars), and the full distribution of bootstrap predictions (violin plot).

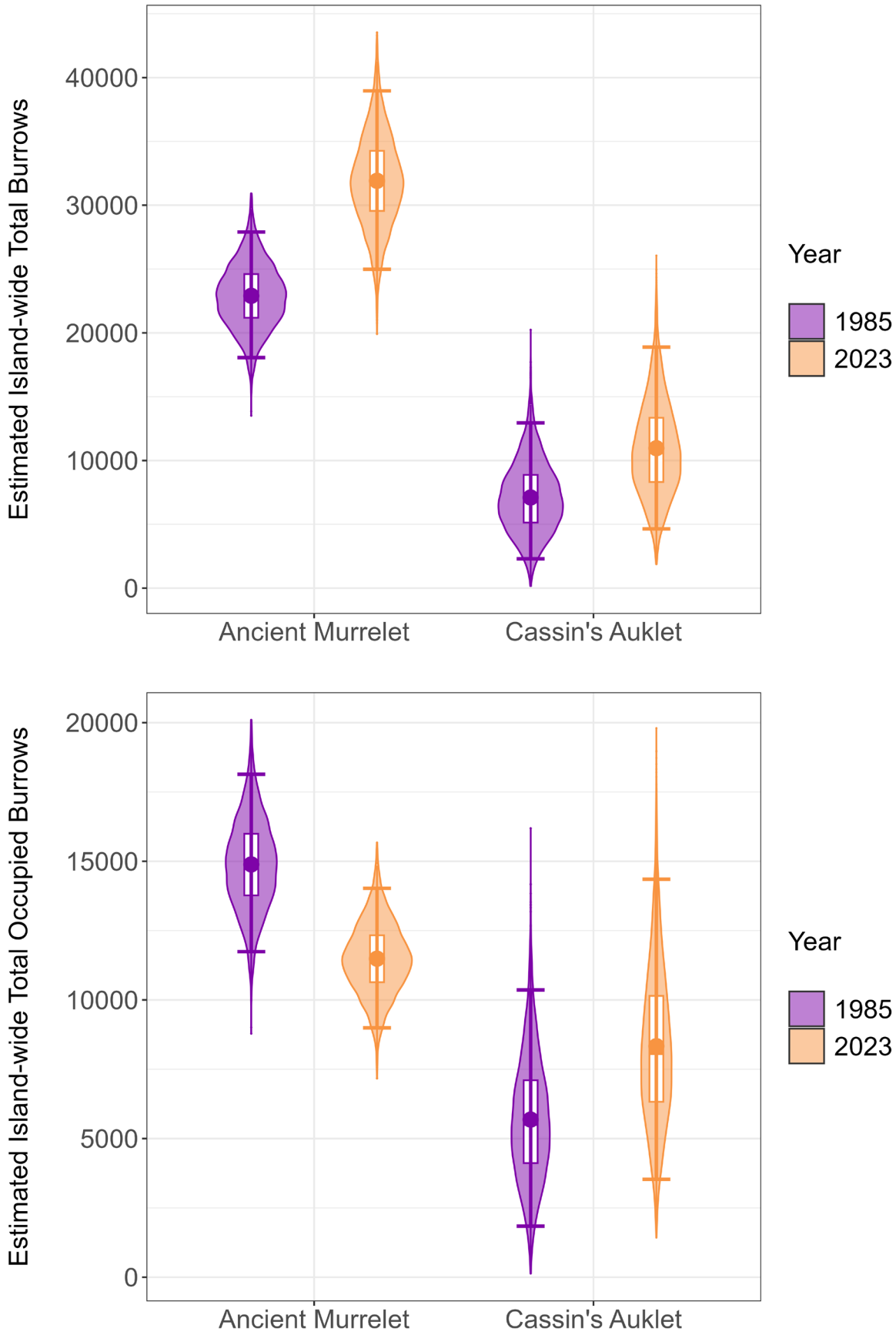


Fig. 7. Estimates of total and occupied burrows of Ancient Murrelets *Synthliboramphus antiquus* and Cassin's Auklets *Ptychoramphus aleuticus* on Alder Island, British Columbia, Canada, in 1985 and 2023, using a bootstrap design-based approach. Distributions show the mean estimate (point), the interquartile range (box), 95% confidence intervals (horizontal bars), and the full distribution of bootstrap predictions (violin plot).

potentially in response to changes in forest structure or as burrows become enlarged or degraded through repeated use (Gaston, 1992). This underscores the importance of evaluating both burrow density and occupancy when estimating colony size. The stark difference in ANMU occupancy rate (0.65 in 1985 vs. 0.36 in 2023) may indicate low breeding propensity (i.e., the proportion of breeding-age females that make a nesting attempt) in 2023 rather than a definitive population decrease. Notably, 2023 occupancy was determined across plots spread throughout the colony, rather than concentrated in one area as in 1985, providing a more representative island-wide view. Field observations also suggest lower-than-average nesting activity for ANMU at some Haida Gwaii colonies in recent years (L. Wilson, personal observation), and the 1985 occupancy rate was consistent with average values from other BC colonies (Rodway et al., 1988). This lower occupancy rate, an indication of reduced breeding effort, may also reflect climate-driven oceanographic and food-web changes. Seabirds are experiencing wide-spread declines, both globally and specifically in BC, often linked to these large-scale processes (Caroll et al, 2015; Gaston et al., 2009; Hipfner et al., 2020). If occupancy had remained closer to long-term averages, total occupied burrows in 2023 might have matched or exceeded 1985 estimates. Ongoing monitoring, including increased field effort towards ascertaining occupancy rates, will be critical to determine whether 2023 represents an anomalous year or the onset of a longer-term trend.

In contrast, CAAU burrow density was higher in 2023 than 1985 and occupancy rates remained consistent (0.80 vs. 0.76), resulting in a greater number of occupied burrows. The spatial extent of areas with burrows also seemingly expanded, with burrows now present in areas not previously thought to be occupied. CAAU can nest in both rock crevices and surface burrows near the forest edge, potentially allowing expansion into newly suitable or previously underused habitat. This expansion is encouraging and may reflect recovery from past pressures, potentially aided by conservation interventions in Gwaii Haanas, such as invasive predator control, which have benefitted both ANMU and CAAU on other islands in the region (Bergman & Halpen, 2017; Regehr et al., 2007). The stability of occupancy rates suggests that this increase reflects genuine population growth rather than temporary variation in breeding effort.

Comparing our results to Rodway et al. (1988) highlights the impact of differing methodological assumptions about colony area and sampling scope. The 1985 estimates were based on manually delineated "colony" boundaries specific to each species, with extrapolation limited to plots within those areas. In contrast, our design-based analysis assumed that all non-rocky, vegetated terrain on Alder Island was potentially suitable for nesting for both species and included all plots, including those with zero burrows. This broader definition likely produced more conservative abundance estimates but allowed a more comprehensive and comparable assessment across years and methods.

Our treatment of occupancy in cross-year comparisons also warrants consideration, particularly for ANMU, where occupancy differed substantially between years. Because only a single occupancy estimate was available for 1985, occupied burrow totals for both years were derived using mean occupancy values rather than propagating uncertainty in occupancy. As a result, the confidence intervals for occupied burrows reflect uncertainty in burrow density but not occupancy and are therefore likely narrower than if full occupancy uncertainty were included. Consequently, the degree of overlap between years is likely underestimated, and differences in occupied burrow estimates should be interpreted with appropriate caution.

The model-based approach, by incorporating habitat covariates and spatial predictions of abundance, effectively delineated suitable nesting areas across the island, providing a data-driven colony boundary. Importantly, our transect layout was not aligned with any strong environmental gradient, and comparisons of habitat metrics between sampled plots and island-wide values indicate that our design captured the full range of conditions, lending confidence to the representativeness of our survey and model-based approach. These spatial predictions facilitate comparison with design-based estimates and also delineate probable colony extent, a key strength of the model-based approach that supports long-term monitoring and management planning.

Looking ahead, our findings highlight several other practical applications of the model-based approach. Although our model-based estimates were slightly less precise and potentially biased low relative to the design-based estimates, the predictive spatial distributions provide valuable complementary information that can refine future survey designs, reduce sampling effort required while achieving target precision, and guide spatially explicit management actions (Bird et al., 2022). Both analytical frameworks rely on how well sampled plots capture the range of habitat conditions and burrow densities, emphasizing the importance of strategic site selection given the logistical challenges of accessing plots in steep terrain and dense vegetation. For Alder Island and other Haida Gwaii colonies, the next step is to refine survey design to improve precision and efficiency. Spatially continuous model predictions can inform the placement of additional plots to most effectively reduce uncertainty, following the recommendations of Pearson et al. (2013) for optimally allocating sampling effort to maximize power while minimizing field effort and cost. For example, Alder Island is a relatively small island compared to some other islands in Haida Gwaii with ANMU colonies. Although ANMU burrows are found over most of Alder Island, they are less likely to occur in the interior of larger islands. Therefore, sampling effort might need to be constrained to a reasonable zone to optimize survey design.

For other ANMU and CAAU colonies in Haida Gwaii, direct transferability of our models would be limited because models calibrated using Alder Island data capture local habitat–density relationships that may not generalize and, therefore, should not be applied directly to other colonies. However, our model-based approach demonstrates how LiDAR-derived habitat data and plot-level surveys can be combined to design spatially balanced sampling schemes and robustly estimate uncertainty. Testing the model-based approach on a larger island with robust data would provide an opportunity to assess broader applicability of the modeling framework, refine covariate selection, and better understand the limits of model extrapolation.

The value of using a model-based approach that incorporates LiDAR-derived habitat covariates depends on survey objectives as well as logistical and financial constraints. In this study, LiDAR data were available from a pre-existing survey, enabling model-based estimation without additional acquisition costs. Where such data are already available, integrating habitat covariates into model-based approaches provides clear benefits, including

spatially explicit predictions of burrow density, improved delineation of colony extent, and the ability to optimize future sampling design. In contrast, where no high-resolution habitat data exist, the costs of acquiring LiDAR data must be weighed against the expected gains in inference. We would suggest that LiDAR-informed model-based approaches are most valuable in systems with strong habitat–density relationships and heterogeneous spatial structure, where design-based sampling alone may miss key gradients or require substantially greater sampling effort to achieve comparable precision.

Model-based approaches using habitat covariates, such as those derived via LiDAR, are particularly useful when survey objectives include mapping colony extent, identifying high-density areas, or informing spatially explicit management and impact assessments. For example, spatial distribution mapping can support the Haida Nation's interest in understanding potential impacts of tourism, development, marine industrial activity, and climate change by identifying colony extent and relative distribution, highlighting areas of vulnerability to spatially explicit threats. In more homogeneous systems, or where the higher priority is to estimate total abundance rather than spatial distribution, design-based approaches may provide sufficiently robust estimates without the additional cost of LiDAR acquisition.

Where the primary objective is repeated estimation for trend detection at key sites, simpler design-based monitoring frameworks may be more efficient and cost-effective. Future work should consider whether survey designs prioritize precise estimates of colony size or the detection of change over time, as these objectives inherently require different spatial allocations of field effort (Buxton et al., 2016). If the primary objective is to derive reliable estimates of abundance for both total burrow counts and occupied burrows, future surveys should consider increasing sample size and ensuring that plots sampled for occupancy rate are representative. Ideally, occupancy would be determined for all burrows within sampled plots, allowing spatial variation in occupancy and potential habitat- or density-dependent effects to be incorporated into models. In practice, however, achieving sufficient spatial coverage of occupancy data to support such modelling is likely infeasible. Determining occupancy is logistically challenging and often uncertain (e.g., 72% of nearly 300 burrows checked on Alder Island in 2023 were inaccessible for confidently assigning occupancy status), resulting in sparse and potentially biased data. Consequently, occupancy observations are unlikely to be available at the spatial resolution or sample size required to parameterize and validate spatially explicit occupancy models, particularly in large or complex colonies. As a result, occupancy is more realistically treated as a colony-level parameter, estimated from a limited, representative subset of burrows rather than modelled as a spatially varying process.

Altogether, our results demonstrate that model-based and design-based frameworks are complementary tools that address different aspects of colony estimation. Design-based approaches provide robust and comparable estimates of abundance, particularly for repeated monitoring, whereas model-based methods incorporate habitat covariates (e.g., LiDAR-derived metrics) to generate spatially explicit predictions of burrow density and colony extent. The value of the model-based approach depends on data availability and system characteristics, with the greatest benefit in heterogeneous landscapes where strong habitat–density relationships exist. In more homogeneous systems, or where the primary objective is to estimate total abundance, design-based approaches alone may be sufficient and more cost-effective. Survey design should therefore be guided by study objectives, balancing the need for precise abundance estimates against the benefits of spatial inference.

ACKNOWLEDGEMENTS

We are grateful for the leadership of the Gwaii Haanas Archipelago Management Board, who direct all conservation work in Gwaii Haanas and support the diverse partnerships that make projects like this possible.

Fieldwork for this project in 2023 was a demanding and collaborative effort that relied on the in-kind expertise of several biologists. We would like to thank Jonas Prevost (Council of the Haida Nation); Rian Dickson (Laskeek Bay Conservation Society); Erica McClaren (Government of British Columbia); Vivian Pattison (Environment and Climate Change Canada [ECCC]); Glen Keddie; and Charlotte Houston, Elin Price, and Chavonne Guthrie (Gwaii Haanas) for their dedicated effort. All fieldwork was carried out under ECCC Animal Care Permit 19LW02, ECCC Scientific Permit SC-BC-2021-0005.01, and Parks Canada Agency Research and Collection Permit GHNPR-2023-45384.

Data collection in 2023 was funded by the Gwaii Haanas Terrestrial Program, as well as the Canadian Wildlife Service's Marine Unit (MU), Species at Risk Unit (SAR), Conservation Partnership Unit (CPU), and Canada's Oceans Protection Plan (OPP). Special thanks to Megan Willie (MU), Kerry Woo (SAR), Ailish Murphy (CPU), and Greg McClelland (OPP), who assisted with funding; Janet Kwok, who assisted with contracting; and Nicole Skeleton, Laura Boettcher, and Barbara Wojtaszek, who assisted with permits. We are grateful for the logistics and support provided by the Gwaii Haanas technical team, who maintain the vessels and cabins so critical to the success of this project. Additional logistical support was provided by Eric Pineault, James Bulbrook, and Nigel Pearson. Data collection in 1985 was led by Michael Rodway and Moira Lemon, who are now retired from the Canadian Wildlife Service. We are very grateful for their early contributions to conducting the coast-wide inaugural colony inventories and for developing the ECCC-CWS BC Seabird Colony Monitoring Program and specifically for their work at Alder Island in 1985. We also express our gratitude for their feedback throughout the process of developing this study. We are grateful for the comments from reviewers, whose efforts helped us to improve our paper.

AUTHOR CONTRIBUTIONS

Conceptualization: SEG, DTI, PS, JB, LW. Formal analysis: SEG, DTI. Funding acquisition: PS, LW. Investigation: all coauthors. Methodology: all coauthors. Project administration: SEG, PS, LW. Writing—original draft: SEG. Writing—review & editing: all coauthors.

REFERENCES

Bergman, C., & Halpen, L. (2017, February 22–25*). Acoustic monitoring of seabirds before and after rat eradication on Haida Gwaii* [Conference presentation and published abstract]. 44th Annual Meeting of the Pacific Seabird Group, Greater Tacoma Convention and Trade Center, Tacoma, WA, United States.

Bird, J. P., Terauds, A., Fuller, R. A., Pascoe, P. P., Travers, T. D., McInnes, J. C., Alderman, R., & Shaw, J. D. (2022), Generating unbiased estimates of burrowing seabird populations. *Ecography*, *2022*(7), Article e06204. https://doi.org/10.1111/ecog.06204

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press. https://doi.org/10.1093/oso/9780198506492.001.0001

Burger, A. E., & Powell, D. W. (1989). Diving depths and diet of Cassin's Auklet at Reef Island, British Columbia. *Canadian Journal of Zoology*, *68*(7), 1572–1577. https://doi.org/10.1139/z90-232

Buxton, R. T., Gormley, A. M., Jones, C. J., & Lyver, P. O. (2016), Monitoring burrowing petrel populations: A sampling scheme for the management of an island keystone species. *Journal of Wildlife Management*, *80*(1), 149–161. https://doi.org/10.1002/jwmg.994

Carroll, M. J., Butler, A., Owen, E., Ewing, S. R., Cole, T., Green, J. A., Soanes, L. M., Arnould, J. P. Y., Newton, S. F., Baer, J., Daunt, F., Wanless, S., Newell, M. A., Robertson, G. S., Mavor, R. A., & Bolton, M. (2015). Effects of sea temperature and stratification changes on seabird breeding success. *Climate Research*, *66*, 75–89. https://doi.org/10.3354/cr01332

Campbell, M. J., Dennison, P. E., Hudak, A. T., Parham, L. M., & Butler, B. W. (2018). Quantifying understory vegetation density using small-footprint airborne lidar. *Remote Sensing of Environment*, *215*, 330–342. https://doi.org/10.1016/j.rse.2018.06.023

Clark, T. J., Matthiopoulos, J., Bonnet-Lebrun, A. S., Campioni, L., Catry, P., Marengo, I., Poncet, S., & Wakefield, E. (2019). Integrating habitat and partial survey data to estimate the regional population of a globally declining seabird species, the sooty shearwater. *Global Ecology and Conservation*, *17*, Article e00554. https://doi.org/10.1016/j.gecco.2019.e00554

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., & Böhner, J. (2015). System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geoscientific Model Development*, *8*(7), 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015

Committee on the Status of Endangered Wildlife in Canada. (2014). *COSEWIC assessment and status report on the Cassin's Auklet (Ptychoramphus aleuticus) in Canada*. https://species-registry.canada.ca/index-en.html#/documents/E0FQsZAxthNkQQhHSUGVz

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Domalik, A. D., Hipfner, J. M., Sudholme, K. R., Crossin, G. T., & Green, D. J. (2018). At-sea distribution and fine-scale habitat use patterns of zooplanktivorous Cassin's auklets during the chick-rearing period. *Marine Biology*, *165*, Article 177. https://doi.org/10.1007/s00227-018-3434-8

Environment and Climate Change Canada. (2018*). Management plan for the Ancient Murrelet (Synthliboramphus antiquus) in Canada*. Species at Risk Act Management Plan Series. Environment and Climate Change Canada.

Environment and Climate Change Canada. (2023). *British Columbia seabird colony inventory*. Government of Canada Open Data Portal. https://open.canada.ca/data/en/dataset/cc3c0551-1bf7-47cf-9510-f2df2de55730

Gaston, A. J. (1992). *The ancient murrelet: A natural history in the Queen Charlotte Islands*. T. & A. D. Poyser.

Gaston, A. J., Bertram, D. F., Boyne, A. W., Chardine, J. W., Davoren, G., Diamond, A. W., Hedd, A., Montevecchi, W. A., Hipfner, J. M., Lemon, M. J. F., Mallory, M. L., Rail, J.-F., & Robertson, G. J. (2009). Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. *Environmental Reviews*, *17*(1), 267–286. https://doi.org/10.1139/A09-013

Gaston, A. J., Carter, H. R., & Sealy, S. G. (1993). Winter ecology and diet of Ancient Murrelets off Victoria, British Columbia. *Canadian Journal of Zoology*, *71*(1), 64–70. https://doi.org/10.1139/z93-010

Government of Canada. (2018). *Gwaii Haanas Gina 'Waadluxan KilGuhlGa Land-Sea-People Management Plan*. Archipelago Management Board, Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site.

Hedley, S. L., & Buckland, S. T. (2004). Spatial models for line transect sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*(2), 181–199. https://doi.org/10.1198/1085711043578

Hipfner, J. M., Galbraith, M., Bertram, D. F., & Green, D. J. (2020). Basin-scale oceanographic processes, zooplankton community structure, and diet and reproduction of a sentinel North Pacific seabird over a 22-year period. *Progress in Oceanography*, *182*, Article 102290.

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2022). *dismo: Species distribution modeling* (Version 1.3-9) [R package]. CRAN package repository. https://CRAN.R-project.org/package=dismo

Horvitz, D. G., & Thompson, D. J. (1952). A generalization of sampling without replacement from a finite universe. *Journal of the American Statistical Association*, *47*(260), 663–685.

International Union for Conservation of Nature. (2025). *The IUCN Red List of Threatened Species*. Version 2025-2. https://www.iucnredlist.org

Mattivi, P., Franci, F., Lambertini, A., & Bitelli, G. (2019). TWI computation: A comparison of different open source GISs. *Open Geospatial Data, Software and Standards*, *4*(1), Article 6. https://doi.org/10.1186/s40965-019-0066-y

Okado, J., & Watanuki, Y. (2023). Flight altitudes of chick-rearing Rhinoceros Auklets *Cerorhinca monocerata* measured by GPS logger. *Marine Ornithology*, *51*(1), 113–118. http://doi.org/10.5038/2074-1235.51.1.1517

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A. F., Miller, P. I., & Louzao, M. (2012). Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation*, *156*, 94–104. https://doi.org/10.1016/j.biocon.2011.11.013

Oppel, S., Hervías, S., Oliveira, N., Pipa, T., Silva, C., Geraldes, P., Goh, M., Immler, E., & McKown, M. (2014). Estimating population size of a nocturnal burrow-nesting seabird using acoustic monitoring and habitat mapping. *Nature Conservation*, *7*, 1–13. https://doi.org/10.3897/natureconservation.7.6890

Parks Canada Agency. (2016). *Multi-species action plan for Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site*. Species at Risk Act Action Plan Series. Parks Canada Agency.

Parks Canada Agency. (2025). *SGin Xaana Sdiihltl'lxa: Night birds returning*. https://parks.canada.ca/pn-np/bc/gwaiihaanas/nature/conservation/restauration-restoration/retour-return

Pattison, V., Bone, C., Cowen, L. L. E., O'Hara, P. D., & Wilson, L. (2023). Characterizing Ancient Murrelet *Synthliboramphus antiquus* movement behaviour during breeding-season foraging trips using hidden Markov models. *Ibis*, *165*(3), 924–943. https://doi.org/10.1111/ibi.13173

Pearson, S. F., Hodum, P. J., Good, T. P., Schrimpf, M., & Knapp, S. M. (2013). A model approach for estimating volony size, trends, and habitat associations of burrow-nesting seabirds. *The Condor*, *115*(2), 356–365. https://doi.org/10.1525/cond.2013.110207

Paleczny, M., Hammill, E., Karpouzi, V., & Pauly, D. (2015). Population trend of the world's monitored seabirds, 1950–2010. *PLOS One*, *10*(6), Article e0129342. https://doi.org/10.1371/journal.pone.0129342

R Core Team. (2024). *R* (version 4.3.1) [Computer software]. The R Foundation for Statistical Computing. https://www.r-project.org/

Regehr, H. M., Rodway, M. S., Lemon, M. S., & Hipfner, J. M. (2007). Recovery of the Ancient Murrelet *Synthliboramphus antiquus* colony on Langara Island, British Columbia, following eradication of invasive rats. *Marine Ornithology*, *35*(2), 137–144. http://doi.org/10.5038/2074-1235.35.2.744

Ridgeway, G. (2020). *gbm: Generalized boosted regression models* (Version 2.1.8) [R package]. CRAN package repository. https://CRAN.R-project.org/package=gbm

Rodway, M. S., Lemon, M. J. F., & Kaiser, G. W. (1988). *British Columbia seabird colony inventory: Report 1—East Coast Moresby Island* (Canadian Wildlife Service Pacific and Yukon Region Technical Report Series No. 50). Canadian Wildlife Service.

Sealy, S. G. (1975). Feeding ecology of the ancient and marble murrelets near Langara Island, British Columbia. *Canadian Journal of Zoology*, *53*, 418–433. https://doi.org/10.1139/z75-055

Scott, D., Moller, H., Fletcher, D., Newman, J., Aryal, J., Bragg, C., & Charleton, K. (2009). Predictive habitat modelling to estimate petrel breeding colony sizes: Sooty shearwaters (*Puffinus griseus*) and mottled petrels (*Pterodroma inexpectata*) on Whenua Hou Island. *New Zealand Journal of Zoology*, *36*(3), 291–306. https://doi.org/10.1080/03014220909510156

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer.

Vermeer, K., Fulton, J. D., & Sealy, S. G. (1985). Differential use of zooplankton prey by Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands. *Journal of Plankton Research*, *7*(4), 443–459. https://doi.org/10.1093/plankt/7.4.443