**Modeling trends of Leach’s Storm-petrel and Atlantic puffin** – updated first draft – end of February 2024

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# INTRODUCTION

Despite their presence in huge numbers on coasts and islands across the world, seabird populations present numerous obstacles to population monitoring. Seabird colonies are often large, diffuse, geographically isolated, and in some cases include a very large presence of non-breeding individuals that confound estimates of breeding totals (Mercker et al. 2021). Many seabird species also nest in burrows under soil or rock, such that variable detectability of breeders further complicates population censusing (e.g. Buxton et al. 2015, Arneill et al. 2019, Lavers et al. 2019). Seabird population monitoring has thus often been conducted sporadically and with inconsistent methods, such that combining these disparate estimates of colony size to rigorously assess population status and trend of colonial seabirds at regional scales is even more of a challenge.

Adding urgency to these estimation difficulties, numerous colonial seabird populations are declining and at risk from anthropogenic threats and ongoing environmental changes (e.g. Paleczny et al. 2015, Dias et al. 2019). In addition to long-term fisheries bycatch impacts (e.g. Anderson et al. 2011, Regular et al. 2013, Grémillet et al. 2018, Christensen-Dalsgaard et al. 2019), seabirds are now increasingly vulnerable to effects of offshore energy production, light attraction, pollution, and invasive species (e.g. Ronconi et al. 2015, Dias et al. 2019, Gilmour et al. 2023). Climate change represents a further pervasive challenge for seabirds in both their marine and terrestrial habitats (e.g. Sandvik et al. 2012, Dias et al. 2019), such that cumulative stressors can be particularly strong among widespread species (Lieske et al. 2020, Phillips et al. 2023).

In eastern Canada, Leach’s storm-petrel (*Hydrobates leucorhous*, hereafter ‘storm-petrel’) and Atlantic puffin (*Fratercula arctica*, hereafter ‘puffin’) are two burrow-nesting species of conservation concern with challenges to population monitoring. Storm-petrels are small-bodied ‘tube-noses’ that nest in small and often concealed burrows, and are active only at night at the colony. They have a broad distribution across the Northern hemisphere, including 100+ breeding colonies across eastern Canada ranging in size from a few individuals to several million (COSEWIC 2020). They are exposed to many threats to their persistence (Lieske et al. 2020, Pollet et al. 2023), showing a population decline of over 50% since the 1970s (COSEWIC 2020, d’Entremont et al. 2020, Wilhelm et al. 2015, 2020) that led to their designation in 2020 as *Threatened* by the Committee on the Status of Endangered Wildlife in Canada. Puffins have a similarly diffuse breeding distribution of 100+ colonies across the coasts of eastern Canada, also ranging in size from a few to hundreds of thousands of individuals, and can often be found on the same islands as those occupied by storm-petrels (Nettleship 1980, Wilhelm et al. 2015). But unlike storm-petrels, and in contrast to many other regions across their breeding range such as in Europe where the puffin has been listed as *Endangered* on The IUCN Red List of Threatened Species (BirdLife International 2021), the Canadian puffin population has grown in recent decades (Lowther et al. 2020), possibly linked to the closure of gill-net fisheries in the region (Regular et al. 2013). Breeding distributions for storm-petrels and puffins in Atlantic Canada are illustrated in Figure 1.

In addition to sharing widespread and overlapping breeding distributions and burrow-nesting habits, puffins and storm-petrels also both raise one single chick which fledges at night close to adult size, and is completely independent of parents after leaving the burrow (Lowther et al. 2020, Pollet et al. 2021). But these two species also show contrasting life-history traits. For example, puffins forage more locally to feed their chicks small forage fish several times a day (Harris and Wanless 2011, Pratte et al. 2017, Delord et al. 2020, Symons and Diamond 2022), compared to storm-petrels which travel hundreds of kilometers to feed over deep waters on mesopelagic lanternfish (Myctophidae), with one single trip taking several days to complete (Hedd et al. 2018, Collins et al. 2022). While young from both species spend the first few years of life at sea, puffins exhibit higher natal philopatry (reviewed in Kersten et al. 2021) compared to storm-petrels, which show high natal dispersal and can recruit in any colony across the North Atlantic (Bicknell et al. 2012, 2013). Such contrasting strategies could ultimately influence population trends in different ways even if both species are nesting in the same geographic area.

Pgph on GAMM approach (background, justification/suitability here etc)

In the context of ongoing environmental change and increasing pressures on seabirds in the North Atlantic, the objectives of this study were: (1) to provide robust regional trend estimates for Leach’s storm-petrel and Atlantic puffin in eastern Canada, (2) to illustrate the GAMM approach to modeling population trends for sporadically-censused burrow-nesting birds such as these, and (3) to explore sensitivity of trend estimates to input parameters (e.g. additive/multiplicative error, number of knots, diff approaches to determining overall regional trend from individual colonies? -need to refine wording here). [*maybe one final sentence for big picture context/implications*?]

# METHODS

## Study species and census methods

A total of X puffin and X storm-petrel colonies were surveyed at least twice between 1978 and 2023. Should we break down these numbers by province? In Newfoundland, puffins and storm-petrels can nest on the same island but rarely overlap in habitat type, showing distinct habitat preferences (e.g., storm-petrels prefer forested or fern habitat while puffins prefer grassy sloped habitat; Wilhelm et al. 2015, 2020, Bond et al. 2023). Thus, the survey approach for both species is the same, but depending on the size of the colony, methods can vary as follows.

#### Complete hole count

The approach to count all holes is the preferred method for sites where the entire island can be searched. This approach was used for all puffin colonies in Labrador as well as smaller islands in Newfoundland,, with methods previously published in Robertson and Elliot (2002a,b) and Robertson et al. (2002a). Briefly, an island-wide systematic hole count is done using a transect approach and having multiple observers walk next to each other 1-2 meters apart and count all holes encountered. For smaller islands with less than 200 holes (e.g., Bacalhao and Tinker Islands) all holes were assessed by inserting an arm (and using a wooden spoon to extend the reach if necessary) and assigning the hole as either being: 1) an extra entrance to a burrow, 2) too short to be a burrow (< 30 cm), 3) an empty burrow, 4) an occupied burrow with either an adult and/or egg and/or chick, or 5) unknown (i.e., the observer could not reach the end of the burrow to confirm it being occupied or not). If an island had more than 200 holes, hole assessments were done using a plot approach by laying a rope grid (either 3 X 3 m or 5 X 5 m) in areas occupied by the species (puffin or storm-petrel) and representative of the island. Each hole in the plot was assessed as described above. Depending on the island’s size, a range of 5-20 plots were randomly placed in different areas of the island at both the periphery and center of the colony. Hole occupancy rates were calculated as the number of occupied burrows divided by the total number of holes counted. Each plot was weighted by the number of holes assessed to calculate island-wide occupancy rates. Standard errors were based on the number of plots assessed on each island.

For Quebec puffin colonies, complete hole counts have been largely phased out to minimize disturbance and replaced by counts of adults attending the colony (on land and water). Burrow counts continue at the Betchouane Migratory Bird Sanctuary, while a system of transects and quadrats is used to estimate area of occupancy and mean occupied burrow density at the Baie de Brador Migratory Bird Sanctuary (Rail 2021, Rail and Chapdelaine 2002). Petrel colonies in Quebec generally consist of a few scattered pairs, with burrows often hidden in dense vegetation. In those conditions, hole counts are not efficient. Instead, the most recent petrel censuses have used playback at night and ARUs (automated recording units) to confirm the presence of the species, but do not provide reliable estimates of colony size in Quebec.

#### Grid or transect approach

For larger colonies where complete hole counts are not feasible, island-wide grids or transect lines set 25-100 m apart to determine the area occupied by puffins or storm-petrels and 20-80 plots were assessed to calculate occupied burrow density as described above (see also Robertson and Elliot 2002a, Robertson et al. 2002b, Pollet and Shutler 2018). This approach is suitable for islands where puffins and storm-petrels are nesting in relatively flat areas and correcting for slope is not a concern.

#### Habitat delineation

An alternative for the grid or transect approach to estimate occupied area, the use of a Geographic Information System (GIS) approach has proven to increase the efficiency of surveys and provides more accurate estimated sloped areas occupied by puffins and storm-petrels which can then be applied to the estimated occupied burrow density assessed through plots as described in the other two approaches (e.g., Wilhelm et al. 2015, 2020, d’Entremont et al. 2020, Bond et al. 2023). Briefly, estimating the habitat occupied by puffins or storm-petrels was done using a hand-held GPS and walking around the boundary of the nesting area and/or using high resolution imagery to delineate the various habitat types utilized by each species. On large and convoluted colonies where puffins and storm-petrels nest on slopes, maps of contour lines were also incorporated into the GIS approach to provide more accurate estimated areas on slopes (e.g., Wilhelm et al. 2015, 2020, Bond et al. 2023).

## Description of Hierarchical Population Model

We estimated colony- and regional-level population trajectories using hierarchical state-space models. These models decompose spatio-temporal variation in seabird counts into contributions from biological processes of interest (i.e., temporal changes in colony-level population indices) and observation processes (i.e., variation due to imprecision in survey counts).

The model assumes survey counts () arise from an over-dispersed Poisson process with mean for colony in year :

|  |  |
| --- | --- |
|  | (1) |

is a normally distributed random variable with mean equal to an expected count () and a variance term () that characterizes the magnitude of sampling error during a survey:

|  |  |
| --- | --- |
|  | (2) |

This explicitly recognizes that there are inevitable discrepancies between the numbers of birds estimated from surveys and the total number of birds that would be counted with a true colony census (i.e., is the standard error associated with a survey).

The model decomposes expected counts into contributions from two terms through a logarithmic link function:

|  |  |
| --- | --- |
|  | (3) |

where represents the general shape of each colony’s trajectory across years, and represents annual departures of population indices from the colony-level smooths (sometimes called “process variance”).

The primary goal of our analysis is to describe temporal patterns in and its variation among colonies. We accomplished this using hierarchical generalized additive mixed models (GAMMs) that fit smoothed temporal trajectories to each colony, using an approach described in Smith and Edwards (2021) where:

|  |  |
| --- | --- |
|  | (4) |

The term therefore includes effects of colony-level intercepts () and a semi-parametric “smoothed” temporal process defined by a generalized additive function (), involving the product of a series of colony-level smoothing coefficients () and a design matrix () that is constructed from a series of basis functions multiplied by a smoothness penalty. Details related to constructing are described in Appendix XX.

In our analysis, we estimated the smoothing parameters as random effects arising from a shared distribution across colonies where , following Smith and Edwards (2021). This allows the shape of colony-level trajectories to be partially conserved among colonies, if supported by the data, which can improve model predictions for colonies with sparse data. This is also a valuable feature if large-scale environmental processes (e.g., climate oscillations) affect an entire regional population in a similar way, leading to trajectories with similar shapes.

The term in equation 3 describes random annual departures from the colony-level smooths, which we modeled as:

|  |  |
| --- | --- |
|  | (5) |

These deviations can be driven by a wide variety of population processes, including random annual variation in breeding propensity or environmental effects affecting recruitment. While describes genuine year-to-year fluctuations in colony abundance around its temporal smooth, we focus inference for status and trend assessment on changes in , which represents longer-term and more persistent changes in the expected annual abundance at colonies.

Finally, our analysis included an additional sub-model to estimate the magnitude of sampling variation for in cases where estimates of were missing (i.e., where raw plot-level data to calculate this quantity were unavailable). For plot-based surveys of burrow-nesting seabirds, can be calculated via design-based estimators of spatial population totals (Horvitz and Thompson 1952). In this dataset, there was an extremely robust positive empirical relationship between and , based on surveys that had both quantities available (Figure SXX). We therefore estimated missing values of by nesting an additional linear regression within our Bayesian model:

|  |  |
| --- | --- |
|  | (6) |

## Estimation of Population Indices and Trends

For each colony, we calculated estimates of annual population index as . This definition of population index removes the effects of observation error and random annual process variation, yielding an index that is represented by each colony’s long-term temporal smooth. The addition of the term is a log-normal variance adjustment that re-scales the indices such that they are centered on the mean of the observed counts (see Sauer and Link 2011). We calculated the regional population total as the sum of annual population indices across all the colonies within each year of study, using . This naturally constructs a regional population trajectory that weights colonies according to their relative abundance; larger colonies have a stronger impact on the estimated regional population dynamics than smaller colonies.

We defined the regional population trend from year to as the geometric mean annual rate of population change over that time interval (Sauer and Link 2011), which can be expressed as an annual percent rate of change using:

|  |  |
| --- | --- |
|  | (7) |

## Bayesian model specification

We fit statistical models in a Bayesian framework using JAGS version 4.3.0 (Plummer 2003) through the jagsUI library version 1.5.2 (Kellner 2021) within the R programming language version 4.0.2 (R Core Team 2024). We used the ‘jagam’ function from the mgcv package (Wood & Wood 2015) to prepare a template for constructing hierarchical GAMs within the JAGS language, which we manually modified to incorporate colony-level random effects and observation error.

We specified vague priors on all model parameters. All variance parameters were priors of , except for process variance which we assigned a prior of ; this prior remained highly vague but improved model convergence. After a burn-in of 500,000 iterations, we stored every 2500th sample until we accumulated 2000 posterior samples from each of three MCMC chains. We assessed chain convergence by visual examination of MCMC traceplots and by evaluating that the Gelman–Rubin convergence statistic was close to 1 for all model parameters. Code and data to repeat these analyses is available at <https://github.com/davidiles/Petrel_Puffin_Trend>.

## Simulation studies

We conducted a series of simulations to confirm the statistical model could correctly estimate regional population trends with minimal bias and appropriate credible interval coverage across a range of hypothetical scenarios of population change, using only limited and imprecise survey data.

Each simulation assumed there were colonies that experienced stochastic population dynamics across a year period. Population dynamics at each colony were affected by two autocorrelated environmental covariates: 1) an “unshared” covariate that affected each colony independently, and 2) a “shared” covariate that affected all colonies simultaneously, thereby imposing correlations among all 9 trajectories. The annual expected count in each colony was modeled as: .

We simulated each environmental driver as a first-order Markov process (i.e., a random walk), starting with a value of 0, resulting in a temporal trajectory for each environmental driver that influenced the temporal dynamics at each colony. In all simulations, was modeled as . We considered two scenarios for . The first scenario omitted altogether, allowing each colony to have fully independent trajectories described entirely by . The second scenario modeled the shared environmental driver as , thereby imposing a moderate correlation among colony-level trajectories because varied more through time than .

Initial population indices for each colony were drawn from a lognormal distribution according to . We assumed each colony was surveyed in 3-6 randomly selected years across the 50-year period, with at least one survey occurring in the first and last 5 years of the simulation. Observation error was simulated according to equation 2, with parameters chosen from the posterior mean from the empirical analysis for Leach’s Storm Petrel, where Counts were then simulated as Poisson random variables using equation 1.

In each simulation, we calculated and estimated the “true” smoothed regional trajectory by fitting a GAM to the full simulated series of using the mgcv package in R. The regional trend was calculated using equation 7. We then fit the Bayesian statistical model to the simulated observed data (i.e., only 3-6 imprecise surveys at each colony), and compared the estimated trend to the true trend. We repeated this exercise 250 times for each simulation scenario. Finally, we calculated the mean bias in trend estimates, and credible interval coverage as the proportion of simulations where the 95% credible intervals on the regional trend estimates contained the “true” simulated regional trend.

## Application of GAMMs to seabird census data

* Application of GAMMs to real data
  + Dave to explore sensitivity of model results to “wiggliness” (number of knots, priors on variance in GAMM coefficients)
* Mention how we chose “which colonies to include for the regional sum” if we decide not to use all colonies, and “which years to choose for t\_start and t\_end” (e.g., if we only report trends for 1984 onwards for LESP, since Baccalieu does not have surveys prior to that date).

# RESULTS

* Summarize census data for LHSP and ATPU
* Colony-specific and regional plots of estimated abundance
* Estimates of population trend over time
* Any other applications we want to include…

*Potential figures*: Map of colonies/relative colony size (DONE already by Dave!), lots of Dave’s pretty GAMM output J

*Potential tables:* census counts at major colonies? (or redundant w GAMM model figures?)

# DISCUSSION

## Trend estimation

* Importance of accuracy and precision in population estimates generally/why this is maybe especially challenging for colonial seabirds…
* Drivers of population trends… we can see how much detail we want to go into in this paper? (e.g. ATPU new stressor: food source alteration via climate change, no longer bycatch threat to adult survival with halting of gillnetting… We probably want to provide general context/discussion based on existing literature but not go much into detail in this paper)
* Ultimately knowing the error etc will help make surveys more efficient/prioritize future monitoring (with caution, i.e. can’t necesasrily assume that parallel trends among colonies in the past will continue indefinitely into the future...?)

## Methodological considerations

* History/range of applications of GAMMs/related approaches to this kind of question
* Methodological considerations/caveats/uncertainties
* Differences in colony size/structure/pressure e.g. between QC and Atlantic: implications for model structure and/or application
* Discussion about how much faith to put in the model’s projections of pre-survey-data trends\* e.g. can discuss how GAMMs have tails that differ from the middle, and need for expert input to determine what portion of the GAMM trend to actually use for biological interpretation…

## Inferences about petrel and puffin dynamics

* ATPU vs LHSP: synchrony vs differences in dynamics across colonies, e.g. three regions (NL, Labrador, elsewhere…?) -LHSP broad trends, ATPU more colony specific
* Maybe also some exploration of how much trend interpretation changes with inclusion/exclusion of some colonies (e.g. based on largest colonies only, vs. including small ones which give more context, or sub-region information-sharing where dynamics are linked within a section of Atlantic Canada but not necessarily across the whole region) – e.g. mention also the small QC LHSP colonies as having conservation importance at margins of distribution even though they don’t represent much in terms of numbers; also changes to QC ATPU colonies too
* Also modeling/discussion of cross-spp linkages btw ATPU-LHSP: we’ll find their dynamics differ, but could be interesting to show it anyway…

## Conclusions

* Implications for monitoring/conservation of these spp in particular, including remaining information gaps (e.g. specific colonies needing updates?)
* potential to apply this same approach to looking at ATPU and LHSP Atlantic wide (i.e. including European data, where colony trends may be very different than in Canada)
* Broader implications for best practices for monitoring of similar spp/etc

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