Hierarchical Bayesian Model for Estimating Migratory Bird Harvest in Canada

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ABSTRACT The Canadian Wildlife Service (CWS) requires reliable estimates of the harvest of migratory game birds, including waterfowl and murres, to effectively manage populations of these hunted species. The National Harvest Survey is an annual survey of hunters who purchase Canada’s mandatory migratory game bird hunting permit. We use these survey data to estimate the number of birds harvested for each species, as well as hunting activity metrics such as the number of active hunters and days spent hunting. The analytical methods used to generate these estimates have not changed since the survey was first designed in the early 1970s. Here we describe a new hierarchical Bayesian model, which replaces the series of ratio estimators that comprised the old model. We are now using this new model to generate estimates for migratory bird harvests as of the 2019-2020 hunting season, and to generate updated estimates for all

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earlier years. The hierarchical Bayesian model uses over-dispersed Poisson distributions to model mean hunter activity and harvest (zero inflated Poisson and zero truncated Poisson, respectively). It also includes multinomial distributions to model some key components including, variation in total harvest across periods of the hunting season, the species composition of the harvest within each of those periods, and the age and sex composition in the harvests of a given species. We estimated the parameters of the main Poisson and the multinomial distributions for each year as random effects using first-difference time-series. This time-series component allows the model to share information across years and reduces the sensitivity of the estimates to annual sampling noise. The new model estimates are generally very similar to those from the old model, particularly for the species that occur most commonly in the harvest, and so the results do not suggest any major changes to harvest management decisions and regulations. However, estimates for all species from the new model are more precise and less susceptible to annual sampling error, particularly for species that occur less commonly in the harvest (e.g., sea ducks and other species of conservation concern). This new model, with its hierarchical Bayesian framework, will also facilitate future improvements and elaborations, allowing the incorporation of prior information from the rich literature and knowledge in game bird management and biology.

**KEY WORDS** Bayesian, Canada, harvest, hierarchical, JAGS, murre, open-science, recreational hunting, waterfowl

Reliable estimates of the harvest of migratory bird populations are necessary for Canada to manage populations of migratory game birds and to meet its commitments under the Migratory Bird Convention Act (Migratory Birds Convention Act, 1994, S.C. 1994, c. 22). Declining waterfowl populations in the early 1900’s was the first indication that there could be
negative effects on the sustainability of some migratory bird populations if there was no protection against excessive hunting (Nichols et al. 1995, Cooch et al. 2014). Under the Migratory Bird Convention Act, the Canadian Wildlife Service (CWS) has implemented regulations in order to prevent collapses of such populations while simultaneously allowing for recreational hunting. Management actions include designated hunting seasons, daily bag limits and possession limits.

The CWS estimates the annual recreational harvest of migratory game birds in Canada using the National Harvest Survey (NHS). The program uses information gathered from purchasers of the Migratory Game Bird Hunting Permits (MGBHP). These permits are mandatory for all non-indigenous individuals to hunt migratory game birds in Canada, and so they provide a sampling universe from which the survey can draw (Sen 1976, Cooch et al. 1978). The NHS was initiated in 1967, and after several years of fine-tuning, has been conducted annually using the same analytical methods since the mid-1970s (Sen et al. 1975). The National Harvest Survey website (https://wildlife-species.canada.ca/harvest-survey) is the central platform that annually distributes a variety of estimates related to harvests and hunting activity. For example, published estimates include: the number of active waterfowl hunters, the number of waterfowl hunting days, the number of successful hunters, species-specific harvest, and age-ratios. Providing reliable estimates is a critical part of the National Harvest Survey program since they, along with other CWS monitoring programs, are used to assess the status of migratory game bird populations in Canada (Canadian Wildlife Service Waterfowl Committee. 2020) and levels of sustainable harvest (Gilliland et al. 2009, Palumbo et al. 2020).

The analytical methods used to generate estimates of migratory game bird harvest could benefit from contemporary model-based approaches such as hierarchical Bayesian models.
Smith et al. (Dorazio et al. 2016). These model-based hierarchical approaches provide a coherent framework for sharing information through time, and among geographic strata and/or hunter groups (Cressie et al. 2009). Bayesian approaches provide both improved estimates of uncertainty and a transparent and explicit way to incorporate the ecological and sociological knowledge (Gelman et al. 2013, van de Schoot et al. 2021) that comes from the rich history of game bird population biology and harvest management in North American (Nichols et al. 1995, NAWMP 2018). Since the beginning of the survey, the estimates of harvests and hunting activity have been made using design-based equations for ratio estimates (Sen et al. 1975). This design-based approach calculated mean ratios for each stratum of a stratified random sample in a given year (Cochran 1977, Cooch et al. 1978). However, each year’s estimates were derived independently of all other years, and were therefore particularly sensitive to variation among years in response rates to the survey and the total number of hunters.

In this study, we describe a hierarchical Bayesian model that estimates annual harvest of all species of migratory game birds hunted in Canada, as well as summary estimates of hunter activity and total number of ducks, geese, and other major species groups. With this new model, we can generate estimates that are more precise and less sensitive to sampling noise, particularly for species of conservation concern or those less abundant in the harvest. We provide the full model and code required to run it in an online supplement, which greatly increases the transparency of these estimates over previous models which were never published in a formal and comprehensive way. In addition, the Bayesian framework of this new model will allow for future improvements using informative priors that incorporate the ecological and sociological knowledge that underlies the long history of waterfowl harvest management in North America (NAWMP 2018).
METHODS

Overview

The NHS is separated into two primary components: the harvest questionnaire survey (HQS), and the species composition survey (SCS). Hunters responding to the HQS provide information on the total harvest of broad groups of species (e.g., all ducks, geese, and other non-waterfowl species), where they hunted, and the total number of days spent hunting, as well as calendar information indicating how many birds in each group they harvested on each day of the season. We stratified the HQS responses based on hunter residency (Canadian vs US residents) and their previous hunting activity. Hunters responding to the SCS provide information on the species composition of their harvest by submitting wings (ducks and murres) or tail-fans (geese) that are identified to species, and if possible, aged and sexed, by waterfowl biologists. We then integrated the overall hunting information of the HQS with the species composition information of the SCS to generate estimates of the species-level harvest in each year.

Using the integrated, hierarchical Bayesian model described here, we estimated the mean group-level (e.g., all ducks) harvest of hunters using an over-dispersed, zero-inflated, Poisson distribution, and the data from the same hunter on total days (days spent hunting) as an over-dispersed, zero-truncated Poisson distribution. We used the HQS calendar responses (how many birds were harvested on each day of the season) to estimate the proportions of the total harvest that occurred within each of a series of discrete periods of the season using multinomial distributions. We then portioned this period-specific total harvest across species by integrating with the SCS data on the number of birds of each species harvested within each period using a series of additional multinomial distributions. We corrected for the period-specific portioning
because of the known decline in response rates to the SCS over the course of the season. Finally, we summed the period-specific total harvest estimates across periods to estimate the annual harvest of each species. We included in each component of the model (e.g., total harvest, total days, period-proportions of the total harvest, species proportions in a given period) an explicit random-walk time-series sub-model that shares information between sequential years. For example, the estimated mean number of days spent hunting in a given year is a function of the same value in the previous year, plus some random error. These random-effect time-series components allow the model to share some information through time, while still allowing for any shape of year-to-year change, including smooth trends (e.g., declines in overall hunting through time), annual fluctuations (e.g., seasons with very poor weather that may have reduced activity or harvest success), and step-changes (e.g., introduction of new regulations that change harvest). Finally, we transformed the per-hunter mean values for group-level and species-level harvest to population-level estimates of total harvest using information on the total size of the permit-population hunting in a given zone (i.e., the total number of permitted hunters hunting in a given zone). We apply the model separately for the province and zone where harvest-activity took place.

We randomly selected potential participants for the HQS and the SCS using records in the MGBHP database. We separated permit holders into 24 geographic hunting zones (Fig. 1) and for the HQS, we further separated them into four groups (Table 1). We selected hunters in categories A and E from the current year's permit records, while those in categories B and D are selected from the previous year's permit records. This grouping is based on their country of residence and whether or not they held a permit in previous years. The precision of the estimates
increase by grouping the hunters into one of the four groups because it takes into account differences in hunting activity and success.

We selected SCS participants differently than those in the HQS. In order to distribute plastic envelopes for the wing and/or tail samples before the start of the hunting season, we selected participants from the previous year’s MGBHP database. First, we determined a hunter’s willingness to participate in the survey by mailing a participation screening card in early July. We generated this random sample of permit holders based on survey participation history, hunting success, and permit renewal status (Table 2). We only sampled Canadian residents in the SCS because of the challenges in delivering envelopes and receiving bird-parts across international borders. Hunter selection is biased toward hunters who previously cooperated. This is beneficial because it increases the response rate, the estimate precision, and the cost efficiency of the survey. However, to limit the bias caused by repeatedly re-sampling the same hunters, we removed two-year SCS participants from the sample for at least one year.

**Hunting zones**

Due to changes over time in how permits have been purchased and hunters have been sampled for the survey, the allocation of permitted hunters and survey responses to each zone has also varied through time. Until recently, we sampled hunters based on the province and zone where they purchased their permit, because no information on the location of hunting activity was available at the time of sampling. Hunters who were sampled for the HQS indicated where they did most of their hunting. In general, the zone of purchase was predominantly the same as the zone of harvest. In recent years, many permits have been sold through an online portal where the zone of purchase is not relevant, and so we started asking hunters to indicate at the time of purchase where most of their hunting activity will take place. We then used this information to
link a permit record to a sampling zone. In the new model, we included transformation factors to
account for the proportion of hunters that were sampled in a different zone than the one in which
they hunted. These transformation factors will become less relevant once the transition to online-
sold permits is completed and we can link all permits records to hunting zones based on intended
location of hunt.

To simplify the following sections in which we detail the specific components of the model, we
use ducks as the example group. However, the model is the same for the other two groups of
species, geese and murres (in Newfoundland and Labrador Zone-1), that include calendar and
species-composition information.

**Total Harvest and Total Days**

Each HQS response includes data on the total reported number of ducks harvested by hunter \( h \),
in caste \( c \), and year \( y \), which we modeled as an over-dispersed, zero-inflated, Poisson
distribution:

\[
DUCKS_{h,c,y} \sim Poisson(\kappa_{h,c,y})
\]

We modeled the mean of the Poisson distribution with a log-link, as a function of the year-effect
\( (\alpha_y) \), an annual caste-effect \( (\beta_{c,y}) \), and an observation-level hunter-effect \( (\eta_{h,c,y}) \), plus an offset
for the log of the estimated mean number of days reported by the same hunter \( (log log (\lambda_{h,c,y})) \),
and a zero-inflation component \( (z_{h,c,y}) \), which is the outcome of a Bernoulli trial and equals 1
with estimated probability of \( (\rho_{zip,y}) \) in year \( y \). This value \( 1 - \rho_{zip,y} \) represents as the proportion
of active hunters that harvest no ducks in that year, in addition to the zero-harvests expected
from the Poisson distribution.
This extra parameter modeling zero-harvests accounts for active waterfowl hunters that only hunt one group of waterfowl (e.g., only hunt geese and not ducks).

\[ \kappa_{h,c,y} = e^{(\alpha_y + \beta_{c,y} + \eta_{h,c,y} + \log(\lambda_{h,c,y}))} * z_{h,c,y} \]

\[ z_{h,c,y} \sim \text{Bernoulli}(\rho_{h,c,y}) \]

Each HQS response also includes data on the total reported number of days spent hunting by hunter - \( h \), in caste – \( c \), and year – \( y \). We modeled these data on number of days hunting as an over-dispersed, zero-truncated, Poisson distribution:

\[ \text{DAYS}_{h,c,y} \sim \text{Poisson}(\lambda_{h,c,y}) | \text{DAYS}_{h,c,y} > 0 \]

We modeled the mean of the zero-truncated Poisson \((\lambda_{h,c,y})\) with a log-link, as a function of the year-effect \( (\gamma_y) \), an annual caste-effect \( (\delta_{c,y}) \), and an observation-level hunter-effect \( (\varepsilon_{h,c,y}) \).

\[ \lambda_{h,c,y} = e^{(\gamma_y + \delta_{c,y} + \varepsilon_{h,c,y})} \]

We modeled the year-effects for both harvest and days using a random-walk, first-difference time-series sub-model. We estimated the year-effects in the first year \((\alpha_1 \text{ and } \gamma_1)\) as fixed-effects with a zero-mean, normally-distributed prior with a variance of 10 (e.g., \( \alpha_1 \sim \mathcal{N}(0,10) \)). We estimated the remaining year-effects in year-\( y \) as random effects with a mean equal to the year-effect in the previous year and an estimated variance (e.g., \( \alpha_y \sim \mathcal{N}(\alpha_{y-1}, \sigma_{\alpha}^2) \)). We set the priors for the variance of the year-effects as weakly informative priors on the standard deviations, following Gelman et al (2006), using a half t-distribution with mean = 0, variance = 0.5 and degrees of freedom = 50 \((\sigma_{\alpha} \sim \mathcal{t}(0,0.5,50))\). This prior places approximately 95% of the prior density at values < 1.0, but includes a relatively long tail that allows for much larger values, if supported by the data. Given the common scale of parameter estimates in a log-link model such as this one, standard deviation values > 1.0 for random effects are extremely unlikely and so this
prior is only very weakly informative (Gelman et al. 2006). We used this weakly informative prior on all sigma values in the model (e.g., $\sigma_\delta$, $\sigma_\beta$, and $\sigma_\epsilon$ below).

We fixed the caste-effect parameters contributing to the days and harvest components for the caste with the largest number of hunters (caste-D) at 0 in all years, so that the remaining caste-effects were estimated as departures from the largest caste ($\beta_{1,y} = 0$ and $\delta_{1,y} = 0$). We modeled the caste-effects for the remaining castes in each year as normally distributed random-effects with a caste-specific hyperparameter mean and estimated variance ($\beta_{c,y} \sim N(B_c, \sigma_\beta^2)$ and $\delta_{c,y} \sim N(\Delta_c, \sigma_\delta^2)$). We gave the hyperparameter means ($B_c$ and $\Delta_c$) normally-distributed priors with a variance of 10 (e.g., $B_c \sim N(0,10)$).

We estimated the observation-level hunter-effect parameters for days and harvest as zero-mean, t-distributed random-effects with caste-specific variances and degrees of freedom ($\eta_{h,c,y} \sim t(0, \sigma_{\eta_c}^2, \nu_{\eta_c})$ and $\epsilon_{h,c,y} \sim t(0, \sigma_{\epsilon_c}^2, \nu_{\epsilon_c})$). Using the t-distribution to model these over-dispersion effects allows the modeled hunter-level variation to fit heavier tails than a normal distribution. We used a normal distribution in early versions of the model, but in most zones and years the empirical distributions of these hunter-level effects showed much heavier tails than a normal distribution. These heavy tails capture the influence of particularly active and successful hunters, in particular. We gave priors to the degrees of freedom parameters ($\nu_{\eta_c}$ and $\nu_{\epsilon_c}$) with gamma distributions with shape and scale set to 2 and 0.2 respectively.

We estimated the parameters of the zero-inflation for the harvest ($\rho_{zip,y}$) using a logistic regression sub-model that used a random walk time-series to track changes in these parameters over time. We estimated the logit of the first year zero-inflation parameter ($\rho_{zip,1}$) as a fixed effect in year-1 with a half-Cauchy prior following Gelman et al. (2008), which is a weakly
informative prior with a reasonable scale for logistic regression coefficients. In all subsequent years, the logit of $\rho_{zip_y}$ was a function of the value in the previous year, plus random variation.

$$\ln \left( \frac{\rho_{zip_1}}{1 - \rho_{zip_1}} \right) = \varphi_{zip_1}$$

$$\ln \left( \frac{\rho_{zip_y}}{1 - \rho_{zip_y}} \right) = \varphi_{zip_y} = N \left( \varphi_{zip_{y-1}}, \sigma_{zip}^2 \right)$$

**Correction Factors to Estimate Number of Active and Successful Hunters**

We estimated the binomial probability that a hunter in caste-c and year-y actively hunted ($\rho_{active_{c,y}}$) using the known numbers of HQS respondents who purchased a permit in that year, and the number of respondents who indicated they had $> 0$ days of hunting ($n_{active_{c,y}} \sim B \left( n_{potential_{c,y}}, \rho_{active_{c,y}} \right)$). For each caste-c, we modeled the series of $\rho_{active_{c,y}}$ values for each year using a logistic regression sub-model similar to the one used for the zero-inflation component.

$$\ln \left( \frac{\rho_{active_1}}{1 - \rho_{active_1}} \right) = \varphi_{active_1}$$

$$\ln \left( \frac{\rho_{active_y}}{1 - \rho_{active_y}} \right) = \varphi_{active_y} = N \left( \varphi_{active_{y-1}}, \sigma_{active}^2 \right)$$

In the same way, we estimated the binomial probability that a hunter in caste-c and year-y who actively hunted was successful (i.e., harvested $> 0$ birds, $\rho_{success_{c,y}}$) using the known numbers of HQS respondents who indicated they had $> 0$ days of hunting, and the number of HQS respondents who indicated they harvested $> 0$ birds ($n_{success_{c,y}} \sim B \left( n_{active_{c,y}}, \rho_{success_{c,y}} \right)$). For
each caste-\(c\), we modeled the series of \(\rho_{success_{c,y}}\) values for each year using a logistic regression sub-model identical to the one used for the proportion that were active.

\[
\ln \left( \frac{\rho_{success_1}}{1 - \rho_{success_1}} \right) = \phi_{success_1}
\]

\[
\ln \left( \frac{\rho_{success_y}}{1 - \rho_{success_y}} \right) = \phi_{success_y} = N \left( \phi_{success_{y-1}}, \sigma_{\rho_{success}}^2 \right)
\]

Similarly, we used similar time-series, logistic regression models to correct for inter-zone hunting. We modeled the annual probability that hunters sampled in a given zone would hunt mostly outside that zone (\(\rho_{leave_y}\)) and the annual probability that a hunter hunting mostly inside the zone was sampled outside that zone (\(\rho_{arrive_y}\)). We derived the data for these two sub-models from a cross tabulation of the zone of hunt and the zone of sampling for all respondents. So for a given zone and year, we modeled the probability that a hunter sampled in that zone would hunt outside the zone (\(\rho_{leave_y}\)) as a binomial distribution using the number of HQS respondents that were sampled in the zone (\(n_{sampled_z}\)) and the number of HQS respondents (\(n_{sampled_{hunted-z}}\)) sampled in the zone who hunted outside the zone (\(n_{sampled_{hunted-z}} \sim B \left( n_{sampled_z}, \rho_{leave_y} \right) \)).

We also modeled the annual values of \(\rho_{leave_y}\) and \(\rho_{arrive_y}\) using a time-series logistic model, with a structure identical to the one used for the other binomial probabilities.

We combined the correction factors for inter-zone hunting, the proportion of active hunters, and the known total number of permits purchased in each year (\(N_{c,y}\)) to estimate the total number of active hunters in a given caste and year (\(A_{c,y}\)).

\[
A_{c,y} = N_{c,y} * \left( 1 + \rho_{arrive_y} - \rho_{leave_y} \right) * \rho_{active_y}
\]

We re-scaled all mean values for hunters, castes, and species to population-level totals using the estimated number of active hunters for a given caste and year (\(A_{c,y}\)).
Derived Totals of All Group-level Harvest and Activity

We calculated the estimated mean number of days hunting waterfowl ($d_{c,y}$) for caste-$c$ and year-$y$ as a derived statistic using the exponentiated sums of the relevant parameters, plus some added variance components to account for the asymmetries in the retransformation.

$$d_{c,y} = e^{(γ_y + δ_{c,y} + 0.5 * δ_{c_c}^2)}$$

Where the term $0.5 * δ_{c_c}^2$ is an approximation of the half-variance retransformation from the mean of a log-normal distribution to the mean of the normal, accounting for the t-distributed overdispersion term in our model ($δ_{c_c}^2 ≈ δ_{c_c}^2$, where $δ_{c} = \frac{1.422 * ν_{c}^{-0.06}}{1+1.422 * ν_{c}^{-0.09006}}$). This term is an approximation because the variance of a t-distribution is undefined for some values of the degrees of freedom (Link et al. 2020). We used the same approximation suggested by Link et al. 2020, which they derived by estimating the parameters of a fitted regression model. Although this re-transformation is an area of ongoing research, we have found that it generates estimates of total harvest and activity that are on the same scale as estimates from the previous model.

Similarly, we calculated the estimated mean number of birds harvested by hunters in caste-$c$ and year-$y$ ($k_{c,y}$) using both the variance component related to days ($0.5 * δ_{c_c}^2$) and a similar variance component for harvest ($0.5 * δ_{c_h}^2$). In this case, we also included the estimated probability of a non-zero harvest to account for the zero-inflation.

$$k_{c,y} = (α_y + β_{c,y} + γ_y + δ_{c,y} + 0.5 * δ_{c_c}^2 + 0.5 * δ_{c_h}^2) * ρ_{zip,y}$$

Harvest by Species and by Age and Sex

We divide the estimates of mean total harvest by year and caste into species-specific estimates of harvest using data on the seasonal harvest patterns from the HQS calendars (daily estimates of
the number of waterfowl harvested for each respondent) and data on the species-composition information collected from the SCS. On the SCS envelopes in which wing and tail fans are received, hunters also provide information on their current year permit numbers as well as the date and location of harvest. These parts are then identified to species, and in most cases, grouped into demographic categories of age and sex by CWS biologists (Carney 1992). The SCS provides more reliable information on the species composition of the harvest in each zone and at different times of year than would be provided by asking hunters what species they harvested (Smith et al. 1974, Ahlers and Miller 2019).

For calculating the species composition, we divided the harvest season into periods to account for the declining response rates to the SCS as the season progresses (e.g., due to response-fatigue, depleted initial envelope supply, etc. Smith et al 1975). Separate estimates of the species composition in each period, combined with relatively unbiased estimates of the total harvest in these same periods allows for unbiased estimates of the overall species composition across the entire season (Cooch et al. 1978). We based the periods for a given zone and harvest group (e.g. ducks) on weekly divisions that included at least 5% of the total submitted parts. To allow the sharing of information on the seasonal patterns in harvest across years, we kept the periods consistent across all years. For ducks, we divided the season into 6 to 13 periods, depending on the length of the season in a given zone, and the distribution of the cumulative harvest across the season. In most cases, the earlier periods in a zone each represented a single week and the later periods may include more than 1 week. The final period often included many weeks, to capture the low level of hunting that continues through the winter.

The model includes three similarly structured sub-models that rely on multinomial distributions to estimate three key proportional distributions: 1) the proportions of annual harvest that
occurred in each period using the calendar data; 2) the proportion of the harvest in each period
that can be attributed to each species; and 3) the proportion of each species harvest that can be
attributed to the age and sex categories (e.g., adult-female, immature male, etc.). We then
combined these proportions with the total harvest estimates to estimate the number of birds
harvested for each species in each year, as well as the number of birds in each demographic
category for a given species.

For the sub-model for the proportional distribution of the harvest across W-periods, we used data
on the number of harvested birds reported in each period-w, by hunter-h in year-y ($DUCKS_{w,h,y}$),
and the total yearly number of harvest birds reported by the same hunter ($DUCKS_{h,y}$).

$$DUCKS_{1:W,h,y} \sim Multi\left(DUCKS_{h,y}, \rho_{period_{1:W,y}}\right)$$

We gave Dirichlet-priors to the individual probabilities for each period-w and year-y ($\rho_{period_{w,y}}$), and we estimated the parameters of the Dirichlet using a log-link, random-walk
time-series model, similar to the parameters of the logistic regression for the binomial
probabilities in the model.

$$\rho_{period_{1:W,y}} \sim Dir\left(\varphi_{period_{1:W,y}}\right)$$

$$ln\left(\varphi_{period_{w,y}}\right) = \zeta_{period_{w,y}} = N\left(\zeta_{period_{w,y-1}}, \sigma^2_{period}\right)$$

In the first year, we kept the value for $\zeta_{period_{1:1}}$ fixed at 0 for the first period and estimated as a
fixed-effect for all other periods using a normal prior with mean of 0 and a variance of 10
($\zeta_{period_{w,1}} \sim N(0,10)$).

For the sub-model for the proportional distribution of all S-species in period-w and year-y, we
used data on the number of submitted parts of each species-s, period-w, in year-y ($PARTS_{s,w,y}$),
and the total yearly number of harvest birds submitted in that period ($PARTS_{w,y}$).
We gave Dirichlet-priors to the individual probabilities for each species-s in period-w and year-y ($\rho_{\text{period}_{s,w,y}}$). We estimated the parameters of the Dirichlet using a hierarchical, log-link, random-walk time-series model, similar to the model for the period distributions. However, in this case, we included a time-series year-effect ($\tau_{s,w,y}$) as well as a random effect for the mean abundance across periods for a given species ($\phi_{s,w}$).

\[ \rho_{\text{species}_{s,w,y}} \sim \text{Dir} \left( \varphi_{\text{species}_{s,w,y}} \right) \]

\[ \ln \left( \varphi_{\text{species}_{s,w,y}} \right) = \zeta_{\text{species}_{s,w,y}} = \tau_{s,w,y} + \phi_{s,w} \]

\[ \tau_{s,w,y} \sim N \left( \tau_{s,w,y-1}, \sigma_{\tau_s}^2 \right) \]

\[ \phi_{s,w} \sim N \left( \Phi_s, \sigma_{\phi_s}^2 \right) \]

In the first year, we estimated the value for the year-effect component in each period and species as a random effect using a prior with mean = 0 and a variance specific to the period ($\tau_{s,w,1} \sim N \left( 0, \sigma_{\tau_y}^2 \right)$). For the species mean abundance component ($\Phi_s$), which is the hyperprior for the random species effect by period, we fixed it at 0 for the first species, and we estimated it as a fixed effect for all other species, using a normal prior with mean of 0 and a variance of 10 ($\zeta_{\text{period}_{w,y}} \sim N(0,10)$).

Finally, we gave Dirichlet-priors to the individual probabilities for each demographic group-d (i.e., each combination of the age and sex categories, such as adult-female, immature-male, etc.) and year-y ($\rho_{\text{demographic}_{d,y}}$), and we estimated the parameters of the Dirichlet using a log-link, random-walk time-series model, which is identical to the parameters for the distribution of harvest across the periods.
\[ \rho_{\text{demographic}_{t\cdot y}} \sim Dir \left( \varphi_{\text{demographic}_{t\cdot y}} \right) \]

\[ \ln \left( \varphi_{\text{demographic}_{d\cdot y}} \right) = \xi_{\text{demographic}_{d\cdot y}} = N \left( \xi_{\text{demographic}_{d\cdot y-1}}, \sigma^2 \xi_{\text{demographic}} \right) \]

In the first year, we set the value for \( \xi_{\text{demographic}_{1\cdot 1}} \) fixed at 0 for the first period and we estimated as a fixed-effect for all other demographic groups using a normal prior with mean of 0 and a variance of 10 (\( \xi_{\text{demographic}_{d\cdot y}} \sim N(0,10) \)).

**Final Estimates of Harvest and Activity**

Finally, for the derived estimates, we re-scaled the relevant mean values (e.g., mean harvest of ducks by caste-c in year-y, \( k_{c\cdot y} \)) to a total estimated harvest of ducks by caste-c in year-y (\( K_{c\cdot y} \)) using the estimated number of active hunters in the same caste and year (e.g., \( K_{c\cdot y} = k_{c\cdot y} * A_{c\cdot y} \)). We summed these derived estimates of harvest, days, number of successful hunters, etc. across castes, zones, and provinces to generate the full suite of estimates provided to the public in the annual analysis.

Uncertainties for each of the estimates represent summaries of the full posterior distributions. Since we estimated the zone-level analyses independently using the same MCMC process, we summed the zone-level estimates for each posterior-draw of the MCMC, to estimate the full posterior distributions of the provincial and national estimates.

We implemented the MCMC analysis in JAGS (Plummer 2003), run through R (4.0.2), using the package jagsUI (Kellner 2019). We used a burn-in of 5000 iterations, and retained 3000 posterior-draws from 3 independent chains, thinned at a rate of 1/10. We assessed convergence within and across chains by visualizing trace plots and ensuring Rhat statistics for all interpreted parameters were < 1.1 (Gelman and Rubin 1992). We archived all anonymized survey data and code required to run the analyses reported here in a public repository.
(https://github.com/AdamCSmithCWS/nhs [note: we will archive this on Zenodo, once accepted for publication]).

**Other Species**

As part of the HQS, we also collect information on the harvest of other species of migratory birds, including Wilson’s snipe, American woodcock, sandhill crane, mourning dove, American coot, rails, and band-tailed pigeon. We capture this harvest information using a simplified portion of the questionnaire that collects information on the combined harvest effort for all non-waterfowl species and the harvests of each of the above species. In order to estimate the hunting effort and harvest for each of the non-waterfowl species, we used a simplified version of the model. In this simplified model, we removed the species composition and calendar components, collapsed some of the hunter strata when samples sizes were small, and included an additional data matrix to ensure zero-harvest estimates in years when there was no allowable harvest for a particular species (i.e., a closed season in a particular zone and year). Otherwise, the components of the model that estimate harvest and activity through time are the same as they are in the main model for waterfowl and murres. We also included the complete JAGS model description and code to run this simplified version of the model in the online repository.

**Complete Estimates for 1976-2019**

We have applied this new model to all data from 1976 – 2019 and generated estimates for all species and group-level harvests, all activity measures (e.g., total hunting days), and all age and sex ratios. We archived this full set of updated estimates online (currently available in this Google Drive folder [https://drive.google.com/drive/folders/1-w1sKnOJMHprXZ-FQ7IxRM1yVmsxQI0?usp=sharing ], which will be archived formally once accepted for publication) to accompany this publication. Annual updates of these estimates will be made
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available through the Canadian Wildlife Services harvest survey results website (https://wildlife-

species.canada.ca/harvest-survey).

RESULTS

The estimates of harvest derived from this hierarchical Bayesian model are generally similar to
those from the traditional model for data-rich species, zones, and years. For example, annual
estimates of national harvests for total ducks and total geese are very similar across the entire
time-series (Fig. 2). For the species and zones that are relatively data-rich, i.e., those species that
are harvested commonly in large numbers, the two approaches generate very similar estimates
and the sharing of information through time has less influence on the estimated annual
fluctuations (e.g., mallard [Anas platyrhynchos] harvest in Saskatchewan Zone 3 and small-race
Canada goose harvest in Manitoba Zone 1; Fig. 3). By contrast, for species and zones that are
relatively data-sparse, the new hierarchical Bayesian model dampens some of the annual
fluctuations (e.g., northern pintail [Anas acuta] in Saskatchewan Zone 3; Fig. 3). Additionally in
cases with very few data, the new model generates non-zero estimates for species that happen to
be absent from the species composition survey in a given year (e.g., black scoter [Melanitta
americana] in Newfoundland and Labrador Zone 2; Fig. 3).

The hierarchical Bayesian estimates are generally more precise than the traditional estimates,
both for the data-rich species (e.g., mallard and American black duck [Anas rubripes]; Fig. 4)
and for the relatively data-sparse species (e.g., common eider [Somateria mollissima] and black
scoter; Fig. 4). In addition, the precision of the new model estimates is much more stable through
time (i.e., smaller annual fluctuations) and has grown even more precise, relative to the old
model results, especially as sample sizes of returned questionnaires and hunter-sent parts have
declined since the early 1990s. The new model harvest estimates are also more consistent from
year-to-year for data-sparse species, including species of conservation concern (Fig. 5).

With the new model, we also generate formal estimates of age ratios in the harvest, which have
estimates of uncertainty and are similarly less sensitive to annual fluctuations (Fig. 6). We
estimated the national values as ratios of age and sex specific estimates of harvest, summed
across all regions. These model based estimates of harvest ratios thereby remove a potential bias
in the old estimates. For example, national-scale age ratios for mallards from the new model are
all lower than ratios from the old model (Fig. 7). This bias in the old estimates was due to the
variation among regions in survey response rates. The old estimates gave a disproportionately
high weight to the higher age ratios in Ontario, where we have traditionally received almost three
times as many parts in relation to the total harvest, than were received in western provinces such
as Saskatchewan (Fig. 7).

DISCUSSION

This hierarchical Bayesian model represents an important advance in estimating and managing
the harvest of migratory birds. The general benefits of a hierarchical Bayesian framework are
well recognized in ecological data analysis (Cressie et al. 2009, Link and Barker 2010, Gelman
et al. 2013, Dorazio 2016), and recently in estimating harvest (Arnold 2019). By assuming that
many of the key components of the harvest in a given year are similar to that same component in
the previous year, the model allows annual estimates to vary through time, but dampens large
annual fluctuations due to sampling noise. As a result, the model generates estimates of
migratory bird harvest that are less susceptible to sampling error in a given year, particularly for
species that occur less frequently in the species composition survey (e.g., Koneff et al. 2017).
These less common species include some that have particularly important conservation and
management concerns, including harlequin duck (*Histrionicus histrionicus*) and Barrow’s goldeneye (*Bucephala islandica*): two duck species with eastern populations assessed as “special concern” by the Committee on Status of Endangered Wildlife in Canada (COSEWIC 2001 and COSEWIC 2013), but that still appear sporadically in the harvest. By contrast, the traditional analysis would estimate no harvest for less common species if no parts were submitted in a given year, such as all national estimates for harlequin duck since 2012 (Fig. 5). Harvest estimates for the most commonly harvested species are essentially the same from this new model as estimates from the traditional design-based approach, although generally more precise. This similarity suggests that there is no need to revisit past management decisions, and that these new estimates can integrate seamlessly with existing decision processes for harvest management.

This new model also provides more realistic and practical estimates of uncertainty than the traditional approach. The new model includes a coherent data-generating model based on the non-negative counts of harvested birds, days spent hunting, etc., a log-link component that ensures all predictions are non-negative. The Bayesian framework ensures that all estimates relate to the posterior distributions of the parameters that are directly of interest (i.e., number of harvested birds) and so uncertainty intervals can be interpreted as a range of values that has a high probability of containing the true value (Gelman et al. 2013, Dorazio 2016). The previous design-based estimates used ratio estimators and their standard errors, and so confidence intervals could not be directly estimated (e.g., a naïve interval would include negative numbers of harvested birds for highly uncertain or low-magnitude estimates). In addition, the new model provides a more comprehensive integration of the various sources of uncertainty, because it has explicitly defined distributions for the data and for all parameters and it propagates all uncertainty in those parameters through to all estimates of harvest, age-ratios, species
compositions, etc. (Cressie et al. 2009, Gelman et al. 2013). For example, the addition of age and
sex specific harvest estimates as a standard model output should be a useful feature for
integrating these estimates into subsequent analyses, such as Lincoln estimates of population
sizes (Alisauskas et al. 2014).

We see this model as an initial step in an ongoing evolution of our estimation and understanding
of migratory bird harvest in Canada. The hierarchical Bayesian framework provides a clear and
flexible way to customise the model, modify the prior assumptions, and add additional sources of
information. Small modifications to the priors and distributional structures of this model would
allow for stronger assumptions about species composition across years and between adjacent
periods within years. Currently, the priors on the time-series components are only weakly
informative (Gelman 2008, van de Schoot et al. 2021), but more informative priors are likely
warranted, given the deep domain-specific knowledge that exists in the waterfowl harvest
management community (Banner et al. 2020). This model framework also makes it relatively
easy to add informative covariates that might influence hunting behaviour, such as weather
conditions during peak hunting periods. Additionally, the spatial stratification provided by the
hunting zones is a useful simplification that captures a great deal of the variation in harvests
(Cooch et al. 1978). However, an inherently spatial treatment of the data could allow this model
to track the spatial variation while also sharing some information among neighbouring regions
(e.g. Morris et al. 2019) and further improve the quality of the estimates in some data-sparse
regions. For example, currently we are unable to estimate murre harvest for Newfoundland and
Labrador zone 2, because there are not enough parts or survey responses. Efforts are underway to
increase response rates for the survey and to generate more data to help fill this and other gaps.

With these additional data and by sharing information in a hierarchical framework and assuming
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that some aspects of the murre harvest are similar between the two zones, we can further improve our estimates.

One of the main areas for future improvements would be a better understanding of the variation among hunters in the species composition of their harvest. Currently, this model, as well as the traditional approach, pools all parts contributed in a given zone and period, regardless of which hunter contributed the parts. This simplification has been necessary because of the relatively low participation rate of hunters in the SCS (Cooch et al. 1978), the relatively large number of parts required to estimate species proportions in each period of the hunting season, and the complexities of coherently tracking uncertainties in the traditional model. However, this hierarchical Bayesian modeling framework provides a clear way to account for this additional source of variation. Future research could consider adding a sub-model to estimate and account for among-hunter variation. This sub-model could share information among years, seasons, and zones. It could also benefit from potential modifications to the surveys to collect additional information on hunter behaviour, such as identifying hunters that specialize on hunting seaducks or that regularly hunt in the winter. In addition, with future plans to transition the survey instrument from its current hardcopy format to an electronic format, it is hoped that individual hunters can be tracked through time as multiple years of information on each hunter would greatly improve our ability to account for the variation among hunters. Similarly, improved accounting for variations among hunters and this new modeling approach provide a coherent framework to integrate estimates of possible response bias and the uncertainty in those estimates of bias (Padding and Royle 2012).
MANAGEMENT IMPLICATIONS

With this new model and modeling framework, we have generated improved estimates of migratory game bird harvest, particularly for species that are less commonly harvested. The hierarchical nature of the new model and the time-series components that allow annual variation while sharing information through time make more efficient use of the survey data than the old model that treated each year as independent. The new model also makes it possible to estimate age and sex specific harvests that will facilitate more informed management decisions (e.g., Alisauskas et al. 2014). The Bayesian model propagates uncertainty across all the parameters in a coherent and transparent way, so that management decisions can more fully integrate that uncertainty (Nichols et al. 1995). The Bayesian nature of the new model, and the open-access code in the supplement, provides a coherent framework to incorporate the rich prior knowledge of hunting behaviour and species biology, which will facilitate future improvements and elaborations to fill more specific management information needs (Banner et al. 2020).

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Associate Editor
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.
Figure captions

Figure 1: Map of the 24 geographic hunting zones in Canada. The zones represent divisions of Canada’s provinces and territories. The provinces and territories are labeled as follows: AB = Alberta, BC = British Columbia, MB = Manitoba, NB = New Brunswick, NS = Nova Scotia, NT = Northwest Territories, NU = Nunavut*, ON = Ontario, PE = Prince Edward Island, QC = Quebec, SK = Saskatchewan, and YT = Yukon.

* there are insufficient data to fit the model in Nunavut

Figure 2. National estimates of the total harvest and total number of successful hunters for all duck species and all goose species from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical Bayesian model described here (darker line) and the old model that it replaces (lighter line). The semi-transparent ribbon surrounding each line represents the 95% credible/confidence interval on the estimates.

Figure 3. Examples of zone-level estimates of the species-specific harvest for a selection of waterfowl species that range from relatively data-rich (mallard [Anas platyrhynchos] and Canada goose: small race [mostly Branta hutchinsii a]) to relatively data-poor (black scoter [Melanitta americana] and northern pintail [Anas acuta]). Estimates are included for all years from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical Bayesian model described here (darker line) and the old model that it replaces (lighter line). The semi-transparent ribbon surrounding each line represents the 95% credible/confidence interval on the estimates. The light-grey stacked dots represent the number of individual parts for each species submitted in each year (each dot represents 10 wings or tail-fans), and the grey labels indicate the lowest
non-zero count of parts for a given species. Province and zone abbreviations are SK3 = Saskatchewan zone 3, MB1 = Manitoba zone 1, and NF2 = Newfoundland and Labrador zone 2.

\textsuperscript{a} This species identification is approximate, because taxonomy and identifications from submitted parts have changed over the course of the survey.

Figure 4. Uncertainty in national estimates of the species-specific harvest for a selection of species that are both relatively precise (e.g., mallard \textit{[Anas platyrhynchos]} and American black \textit{[Anas rubripes]} duck) and relatively imprecise (e.g., black scoter \textit{[Melanitta americana]} and common eider \textit{[Somateria mollissima]}). Estimates are included for all years from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical Bayesian model described here (darker line) and the old model that it replaces (lighter line). The CV values for the new model are lower (higher precision) in most years and the difference between the two models is increasing through time. Note: the large fluctuations in the old model results in late 1980s and early 1990s reflect annual variations in sampling rates across hunter castes and geographic strata. The light-grey stacked dots represent the number of individual parts for each species submitted in each year (each dot represents up to 200 wings or tail-fans).

Figure 5. Examples of national estimates of the species-specific harvest for a selection of species that are relatively data-poor and some are of conservation concern (e.g., harlequin duck \textit{[Histrionicus histrionicus]} and Barrow’s goldeneye \textit{[Bucephala islandica]}). The new model generates estimates for all species in all years and they fluctuate less among years. Estimates are included for all years from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical Bayesian model described here (darker line) and the old model that it replaces...
Figure 6. Examples of national estimates of the species-specific age ratios in the harvest for a selection of species that are relatively data-rich (American black duck [*Anas rubripes*], Canada goose: small race [mostly *Branta hutchinsii* a], and wood duck [*Aix sponsa*]) and relatively data-poor (canvasback [*Aythya valisineria*], greater scaup [*Aythya marila*], and Ross’s goose [*Chen rossii*]). The new model generates estimates of age ratios that are less sensitive to sampling error among years and include estimates of uncertainty. Estimates are included for all years from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical Bayesian model described here (darker line) and the old model that it replaces (lighter line). The semi-transparent ribbon surrounding each line represents the 95% credible interval on the estimates. The light-grey stacked dots represent the number of individual parts for each species submitted in each year (each dot represents approximately 10 wings or tail-fans).

Figure 7. Example of the reduced bias in estimates of national age ratios because the new model adjusts the national estimates for the harvests and number of parts submitted among hunting zones. In this example, the national age ratios for mallard (*Anas platyrhynchos*) from the old model were biased by the greater number of parts submitted / bird harvested (parts / harvest) and

\[ a \text{ This species identification is approximate, because taxonomy and identifications from submitted parts have changed over the course of the survey.} \]
the higher age ratios that tend to occur in eastern Canada (e.g., Ontario) as compared to western
Canada (e.g., Saskatchewan). The new model adjusts the national estimates for the relative
harvest and parts submission rates, and so removes this bias. Estimates are included for all years
from 1976-2019 from the Canadian National Harvest Survey, using the new hierarchical
Bayesian model described here (darker line) and the old model that it replaces (lighter line). The
semi-transparent ribbon surrounding each line represents the 95% credible interval on the
estimates. The light-grey stacked dots represent the number of individual parts for each species
submitted in each year (each dot represents 200 wings).
### Table 1: Hunter group description for the harvest questionnaire survey.

| Sample code | Description of hunter group                                      | Sample drawn from |
|-------------|------------------------------------------------------------------|-------------------|
| **A**       | Residents who did not purchase a permit in the previous year     | Current year      |
| **B**       | Residents who bought a permit year previously but not in the year prior to that | Previous year     |
| **D**       | Residents who bought a permit in the preceding 2 years          | Previous year     |
| **E**       | Non-residents                                                   | Current year      |
Table 2: Hunter categories for species composition survey.

| Sample | Description                                      |
|--------|--------------------------------------------------|
| SA     | SC, SD, SE, or SF respondent in the previous year |
| SC     | HQS respondent in the previous year who shot more than five waterfowl |
| SD     | HQS respondent in the previous year who shot one to five waterfowl |
| SE     | Renewal hunter of the previous year, not eligible for SA, SC, or SD |
| SF     | Non-renewal hunter of the previous year not eligible for SA, SC, or SD |

Summary for online Table of Contents: This new model provides improved estimates of the hunting activity and harvest of migratory game birds in Canada, as well as new estimates for age- and sex-specific harvest. The Bayesian framework and the open-source code that we provide here will facilitate ongoing improvements and elaborations of the model.