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Research article

Evaluation of breeding distribution and chronology of North American scoters

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North America's scoter species are poorly monitored relative to other waterfowl. Black *Melanitta americana*, surf *M. perspicillata*, and white-winged *M. deglandi* scoter abundance and trend estimates are thus uncertain in many parts of these species' ranges. The most extensive source of waterfowl abundance and distribution data in North America is the Waterfowl breeding population and habitat survey (WBPHS). Although the WBPHS effectively monitors most species, both its timing and geographic coverage may preclude accurate scoter monitoring. Therefore, our goal was to better define when and where scoters breed to help interpret survey results and optimize potential supplemental survey efforts for scoters. We integrated satellite telemetry tracking data from scoters marked at multiple molting, staging, breeding, and wintering areas along the Atlantic and Pacific coasts to quantify continent-wide breeding chronology and distribution. We also examined possible drivers of variation in timing of arrival, length of stay, and departure at nesting locations. We documented a northwest to southeast distribution of estimated breeding sites across Alaska and Canada. On average, scoters arrived at nest sites on 1 June. Surf scoters and Pacific black scoters arrived earliest and departed earliest. Pacific-wintering black and white-winged scoters began breeding earlier than Atlantic-wintering birds. Additionally, birds arrived at nesting locations earlier in years with earlier snowmelt, and later snowmelt reduced lengths of stay for males. Breeding chronology also varied by age group, with adults arriving earlier than subadults. Our study is the first to comprehensively describe spatial variation in timing of breeding of both Atlantic and Pacific populations of all three scoter species across North America. Our results increase our understanding of how current surveys enumerate scoters and will inform possible supplemental efforts to improve continental monitoring of scoter populations.

Keywords: aerial surveys, breeding chronology, continental distributions, Melanitta spp., satellite telemetry, scoters

Introduction

Scoter (*Melanitta* spp.) breeding abundance and distribution is poorly documented relative to other North American waterfowl (Environment and Climate Change Canada 2019). Limited data suggest that black *Melanitta americana*, surf *M. perspicillata* and white-winged scoter *M. deglandi* numbers have fluctuated in the past 30–60 years (Bowman et al. 2015, Environment and Climate Change Canada 2019, Anderson et al. 2020, Bordage and Savard 2020, Brown and Fredrickson 2020). However, estimates are uncertain in many parts of these species' ranges, making it difficult to evaluate the need for and response to management actions (Bowman et al. 2015). Therefore, there is a need to improve abundance and trend estimate accuracy for North American scoters (Sea Duck Joint Venture 2015a,b,c).

Breeding season surveys are one method for acquiring improved scoter abundance estimates. Relative to breeding surveys, wintering and staging surveys have additional error due to aggregated and temporally-variable bird distributions, co-occurrence of similar looking species, limited information on detection and availability processes, and more numerous disturbances (Silverman et al. 2012, 2013, Garrettson et al. 2020). Therefore, the Sea Duck Joint Venture (SDJV) has invested heavily in projects to improve breeding survey reliability and accuracy for scoters (Sea Duck Joint Venture 2015d, 2020), which are identified among the highest priority sea duck species for monitoring (Sea Duck Joint Venture 2017).

The Waterfowl Breeding Population and Habitat Survey (WBPHS) provides the most extensive and long-term estimates of breeding waterfowl numbers in North America (Smith 1995). The WBPHS, however, is not optimal for providing reliable scoter estimates. First, WBPHS fixed-wing surveys do not cover the entire boreal and sub-Arctic scoter breeding ranges (Takekawa et al. 2011, Brook et al. 2012, Bowman et al. 2015). Second, WBPHS transects are typically surveyed beginning in early May in southern latitudes, and mid-May to early-June in northern latitudes (Environment and Climate Change Canada 2021). This timing may not coincide with the breeding chronology of scoters and creates the potential for double counting, which could result in biased indices of populations and breeding distributions. Finally, because scoter species are difficult to differentiate in aerial fixed-wing surveys and have overlapping breeding ranges, a large proportion of scoters are not identified to species by the WBPHS (except in Alaska since 1993, Smith 1995, Anderson et al. 2020), and accurate methods to correctly assign scoters to species have not been developed. In light of perceived population declines (Sea Duck Joint Venture 2015a,b,c) and the importance of accurate harvest management of scoters, the SDJV identified research and monitoring priorities for black, surf, and white-winged scoters that included better defining breeding ranges, optimizing timing of breeding surveys, and developing methods to identify scoters to the species level (Sea Duck Joint Venture 2015a,b,c).

In this study, we used continent-wide satellite telemetry data from black, surf and white-winged scoters to chronicle timing and location of scoter breeding across Canada and Alaska. Better understanding distribution and population status of scoters has been identified as a key priority by the SDJV (Sea Duck Joint Venture 2007, 2008, 2022). Our goal was to address these priorities by providing key information about when and where scoters breed to help inform potential future monitoring efforts. Our study is the first to provide a detailed description of the distribution and timing of breeding of Atlantic and Pacific populations of all three scoter species across North America. Because sea ducks often arrive at breeding sites as sites become snow free (Takekawa et al. 2011, Petersen and Savard 2015), we tested the hypothesis that snow-free date influences scoter breeding chronology. Given that satellite telemetry information provided locations for many individuals across the annual cycle, we also explored how breeding chronology differed among species and how it was related to an individual's age and wintering site.

Material and methods

Satellite telemetry

We compiled Platform Transmitter Terminal (PTT; Microwave Telemetry Inc., Columbia, MD, USA or Telonics, Mesa, Arizona, USA) data for 70 black scoters, 113 surf scoters and 83 white-winged scoters captured between 1999 and 2019. Details regarding capture locations and sample sizes are given in Lamb et al. (2019, 2020a, 2022). In general, we captured both sexes of adult (> 2 years old) and subadult (1–2 years old) scoters at sites in the Great Lakes and along the Atlantic and Pacific coasts during scoter molting, staging, and wintering periods (August–March). On the Atlantic coast, no birds were captured south of Pamlico Sound, North Carolina, and on the Pacific coast, no birds were captured in Oregon or northern California. Therefore, sampled scoters may not represent the entire range of these species' wintering locations (see Table 1 for a summary of the number of tagged birds by species, origin, and sex; raw data are available on the Dryad Digital Repository at doi.org/10.5061/dryad.bk3j9kdfr).

Specific methods for scoter capture, implantation, transmitter programing, and data filtering are described in Lamb et al. (2022). Detailed transmitter duty cycles are given in De La Cruz et al. (2009) and Lamb et al. (2019, 2022). We processed and filtered location data as described in Bowman et al. (2021).

Scoter arrival dates, lengths of stay, and departure dates at breeding sites were determined from time-stamped position estimates in PTT datasets. For individuals detected in multiple years, arrival dates, lengths of stay, and departure dates were determined for every year that an individual was detected. In total, 223 individuals were detected in only one year, 39 individuals were detected in two years, and four individuals were detected in three years (see Supporting information for summary of the number of birds tagged and detected over time). To estimate breeding locations, data were filtered to include detections from 20 April to 1 July of each year (a range bracketing the suspected nesting period of North American scoters; Takekawa et al. 2011, Anderson et al. 2020, Bordage and Savard 2020, Brown and Fredrickson 2020). We identified every location recorded between 20 April and 1 July where an individual bird was recorded for at least nine days (typically three duty-cycles) with points recorded within 20 km of one another within the potential breeding range of each species (Takekawa et al. 2011). We then identified the centroid of the 20 km area where each bird was detected as the estimated nesting location, and all detections within 20 km of this centroid were considered movements within the nesting location.

We classified arrival date as an individual's first detection at the estimated nesting location, departure date as the last detection at the estimated nesting location, and length of stay as the number of days between arrival and departure. We calculated arrival dates for males and females but minimum length of stay and departure dates for males only. This was done for two reasons. First, female lengths of stay and departure dates are dependent on their breeding status. Whether females were prospecting, successfully laid a clutch, successfully raised a brood, and/or moulted with the brood will affect the amount of time spent at nesting locations (Savard et al. 2007, Lepage et al. 2020). Female lengths of stay and departure dates therefore exhibit high variability and complicated distribution patterns. As it was not possible to determine female breeding status with the current dataset, inclusion of additional data would be needed for a biologically informative analysis of female length of stay and departure dates. Second, paired males typically depart prior to females (about three weeks after arrival at breeding sites; Savard et al. 2007), and males are more easily observed than females, which are often missed during aerial surveys. Therefore, under standard waterfowl breeding population survey protocol, nesting female presence is inferred from observations of males, where indicated breeding pairs are calculated from counts of actual pairs, lone males, and males in flocks of two to four individuals (Canadian Wildlife Service and US Fish and Wildlife Service 1987, Smith 1995). Male length of stay and departure dates are thus more informative for timing aerial surveys.

Implantation with PTTs can delay an individual's migration in the year of implantation compared to the following year (Lamb et al. 2020b, 2022, Forstner et al. 2022), and as a result, nesting dates estimated from satellite telemetry data may be later in the year of implantation. In a preliminary analysis, however, we found no differences in arrival timing between the year of tagging and subsequent years (see Supporting information for analysis details and results). Therefore, we included all years with PTT detection data in our analysis.

Table 1. Number of PTT-tagged individuals that contributed data to this study. Sample sizes are broken down by species (BLSC = black scoter, SUSC = surf scoter, WWSC = white-winged scoter), wintering origin, sex (f = female, m = male), and number of individual birds (n).

Species	Origin	Sex	n
BLSC	Atlantic	f	24
		m	8
	Pacific	f	29
		m	9
SUSC	Atlantic	f	38
		m	13
	Pacific	f	58
		m	4
WWSC	Atlantic	f	28
		m	4
	Pacific	f	43
		m	8

Snow-free date estimation

We estimated snow-free date at each estimated nesting location using the National Oceanic and Atmospheric Administration (NOAA) National Snow and Ice Data Center's Ice Mapping System (IMS) snow cover maps (US National Ice Center 2008). We downloaded daily snow cover data for Canada and Alaska for the years of our study at a spatial resolution of 24 km. Snow-free date was defined for each 24 km square as the third consecutive day of the year (DOY) with no snow. We then calculated snow-free date for each year at each estimated nesting location as the mean DOY of snowmelt within a 24 km buffer around each nesting location centroid.

Evaluation of tag implantation

We further evaluated whether PTT implantation delayed PTT-marked birds by comparing PTT-marked and unmarked individuals. We collected brood observation data for unmarked scoters from various sources. We collected

Labrador brood data from unpublished reports (Barrow 1982, LGL Limited 2008) and unpublished survey data from the Canadian Wildlife Service (CWS). Québec data came from various reports and publications (Consortium Gauthier and Guillemette – G.R.E.B.E. 1990, Benoit et al. 1994, 1996, Morneau 1998, Benoit 2005, Morrier et al. 2008) and unpublished CWS survey data. Information on northern Ontario broods came from Brook et al. (2012). Fisher (USFWS) provided a large dataset of brood observations collected in Alaska from 1990–1993. For all data sources, broods were observed on lakes, rivers, or wetlands, and aged by observers in the field using standard brood aging protocols for waterfowl (Gollop and Marshall 1954, Lesage et al. 1997). These data were not necessarily always collected using standardized survey protocols and some observations were made opportunistically. We recognize the limitations of such information, but these observations represent the best information available for these difficult-to-study species and serve as a useful independent point of comparison to unmarked birds. All brood data used for analysis are available from the Dryad Digital Repository at doi.org/10.5061/dryad.bk3j9kdfr.

We estimated nest initiation dates (i.e. date the first egg was laid) by back-dating from the date of brood observation, using the median age of each duckling plumage age class (from Gollop and Marshall 1954, adjusted for surf scoters according to Lesage et al. 1997), a laying rate of one egg per day and a mean clutch size of seven eggs. In total, nest initiation dates were estimated for 452 black, surf, and white-wing scoter broods observed between 1989 and 2012 (see Supporting information for summary of brood observation numbers by species, province/state, and year). Previous work on Pacific surf scoters suggested that estimated breeding location arrivals precede nest initiation by 1–7 days (De La Cruz et al. 2009). Therefore, if individuals implanted with PTTs are delayed in migration compared to untagged conspecifics, then arrival dates of PTT-marked individuals may be similar or up to one week later than nest initiation dates of unmarked birds.

Statistical analyses

We evaluated whether variation in arrival and departure dates differed by species, wintering origin (Atlantic or Pacific), an interaction between species and wintering origin, age class (one-year-old subadult, two-year-old subadult, or adult), and/or snow-free date using linear mixed effects models (LMMs). Lamb et al. (2021) found sex-related differences in migration timing in Atlantic black scoters. We thus included sex as a covariate in our analysis of arrival date to further account for this factor. All candidate models included a random effect for year to control for between-year variation and a random effect for animal identity to account for repeated measurements for some individuals. For analyses of birds detected in multiple years, we adjusted age at breeding for each year of detection. For instance, individuals tagged as one-year-old subadults were classified as two-year-old subadults in their second year of detection, and individuals tagged as two-year-old subadults were classified as adults in their second year of detection (see Table 2 for summary of sample sizes used in statistical analyses, with age classes adjusted for detection year).

We also evaluated whether minimum length of stay at estimated breeding locations differed by species, wintering origin, an interaction between species and wintering origin, age class, and/or snow-free date using generalized linear mixed effects models (GLMMs) with log-link functions and Poisson distributions. Similar to the previous analysis, we adjusted age at breeding for each year of detection for the birds detected in multiple years; we also included a random effect for year to control for between-year variation and a random effect for animal identity to account for repeated measurements for some individuals in all candidate models.

Next, we created predictive maps of scoter arrival timing. As a whole, estimated scoter breeding locations closely followed the delineation of the Taiga ecoregion, with additional detections in the Hudson Plains ecoregion and along the northwest coast of Alaska (Fig. 1). We predicted each species' arrival timing across this area using the best-supported model for scoter arrival dates, based on lowest Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002), and annual snowmelt data. First, we created a polygon for prediction (hereafter 'prediction

Table 2. Sample sizes included in statistical analyses. Sample sizes are broken down by species (BLSC = black scoter, SUSC = surf scoter, WWSC = white-winged scoter), wintering origin, sex (f = female, m = male), age class at breeding (Subadult 1 = one-year-old subadult, Subadult 2 = two-year-old subadult), and number of bird-years (n). Sample sizes differ from numbers shown in Table 1, as some individuals contributed multiple years of data.

Species	Origin	Sex	Age at breeding	n
BLSC	Atlantic	f	Subadult 1	1
			Subadult 2	8
			Adult	26
		m	Adult	11
	Pacific	f	Subadult 1	6
			Subadult 2	15
			Adult	16
		m	Subadult 2	6
			Adult	5
SUSC	Atlantic	f	Subadult 2	8
			Adult	33
		m	Subadult 1	2
			Subadult 2	5
			Adult	6
	Pacific	f	Subadult 2	8
			Adult	58
		m	Subadult 2	1
			Adult	3
WWSC	Atlantic	f	Subadult 1	1
			Subadult 2	2
			Adult	29
		m	Adult	5
	Pacific	f	Subadult 1	1
			Subadult 2	18
			Adult	31
		m	Subadult 2	2
			Adult	6

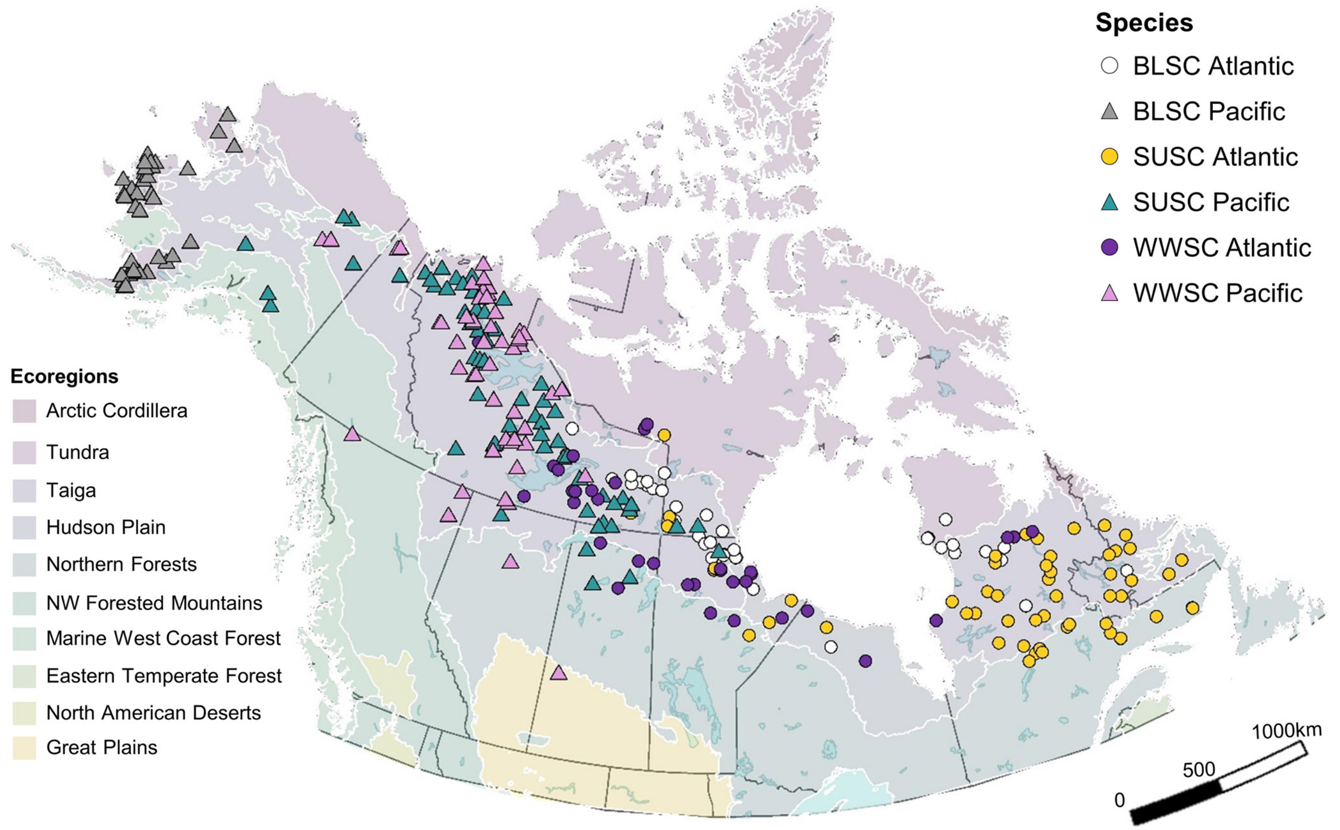

Figure 1. Continental distribution of North American black scoter (BLSC), surf scoter (SUSC), and white-winged scoter (WWSC) estimated nesting locations determined from PTT-tagged birds marked on Atlantic or Pacific wintering, staging, and molt sites between 1999 and 2020. Background colours indicate Level I North American Ecoregions (included for illustration). Level 1 ecoregion shapefile from the US Environmental Protection Agency (USEPA 2010).

polygon'). We downloaded Level 1 ecoregion shapefiles from the US Environmental Protection Agency (USEPA 2010). We drew a 100 km buffer around the Taiga and Hudson Plains ecoregions to account for scoters potentially nesting in ecoregion transition zones. We then extended this polygon to include PTT-estimated breeding locations along the northwest Alaskan coast. We used the same polygon for all three species. Next, we estimated arrival dates for each species across the prediction polygon. To do this, we overlaid the prediction polygon with a hexagonal grid (Strimas-Mackey 2020). Snow cover data had a spatial resolution of 24 km; we thus generated grids where each hexagon had an apothem (i.e. distance from the hexagon centre to side) of 24 km. Using annual snowmelt rasters from 2010 to 2020, we generated a new raster showing mean snowmelt date for this period (roughly the last 10 years of this study), which was used to determined mean snow-free date within each hexagonal grid cell. We then used each hexagon's estimated mean snow-free date in our best-supported model to estimate arrival dates in each hexagon. For prediction, we held wintering origin at Atlantic, age at adult, sex at male, and year and animal identity at zero (i.e. reference levels). All spatial analyses were completed using the 'sf' (Pebesma 2018) and 'raster' (Hijmans 2021) packages.

We used LMMs to investigate whether nest initiation date varied by species, wintering origin, and an interaction between species and wintering origin using the brood observation dataset. We assumed that scoters observed in Alaska wintered on the Pacific coast and that scoters observed in eastern Canada (Ontario, Québec, and Labrador) wintered on the Atlantic coast, an assumption corroborated by estimated nesting location distributions of Pacific and Atlantic PTT-marked birds (Fig. 1). All models included a random intercept for year, and we added a variance structure for origin (varIdent) to account for heterogeneity (Zuur et al. 2009). We did not include animal identity as a random effect in these models, since each individual was only included once.

We used LMMs to assess whether arrival dates of PTT-marked individuals were delayed relative to nest initiation dates of unmarked individuals. For this comparison, PTT data were spatially filtered to only include detections where brood observations also occurred (i.e. Alaska, Newfoundland and Labrador, Ontario, and Québec; Supporting information). We merged filtered PTT and brood observation data and added a variable to the combined dataset to denote whether values originated from marked or unmarked birds. Forstner et al. (2022) showed that barrow's goldeneye *Bucephala islandica* arrival and departure timing were only affected in the year of implantation. Therefore, we only used PTT data from the year of tag deployment to evaluate whether tag implantation caused delays. The global model included arrival/nest initiation date as a response variable, and we included species, wintering origin, an interaction between species and wintering origin, and whether an individual was marked as fixed effects. All models included random intercepts for year. We did not include animal identity as a random effect in these models since each individual was only included once. We added a variance structure for origin (varIdent) to account for heterogeneity (Zuur et al. 2009).

Finally, we determined the percent of estimated breeding locations within the survey area of the WBPHS. We downloaded WBPHS stratum boundaries from the US Fish and Wildlife Service Catalog (https://ecos.fws.gov/ServCat/Reference/Profile/142628). For each species, we then determined the number of estimated breeding locations falling within WBPHS strata relative to the total number of estimated breeding locations. We completed this analysis using the 'sf' package (Pebesma 2018).

In all analyses, snow-free date was encoded as a continuous variable and was rescaled to have a mean of zero and SD of one. All other predictors were encoded as factors. We did not include nest location (i.e. latitude and longitude) in our models, as it was correlated with snow-free date (latitude: $r^2 = 0.19$, $p = 0.001$; longitude: $r^2 = 0.38$, $p < 0.0001$). For models that included arrival, nest initiation, departure, or minimum length of stay as a response variable, we first evaluated support for each individual predictor in a single factor model. Then, for single factor models with AIC_c values < 2 of the AIC_c of the null (i.e. intercept only) model, we also evaluated support for all possible factor combinations and, for models that included species and wintering origin, we also evaluated the interaction between species and wintering origin. In this way, our analysis of arrival date considered support for 39 candidate models, minimum length of stay and departure date analyses considered support for 11 candidate models, and our analysis of nest initiation date considered support for five candidate models. Examination of whether PTT implantation delayed scoter breeding compared two candidate models: the global model and a model without the factor indicating whether an individual was marked. In all models, inclusion of spatial and temporal autocorrelation structures did not improve model fits, as determined by AIC_c (Burnham and Anderson 2002).

We completed all analyses in R ver. 4.0.3 (www.r-project.org). We ran LMMs in 'nlme' (Pinhero et al. 2021) and GLMMs in 'lme4' (Bates et al. 2015). LMMs run using 'nlme' and 'lme4' produced the same results in preliminary analyses. We completed model selection using 'bbmle' (Bolker et al. 2021). AIC_c scores were used for model selection, and models with $\Delta AIC_c \leq 2$ were considered of equivalent model fit (Burnham and Anderson 2002). We considered predictors to have influenced a response when 85% confidence limits (85% CL) around parameter estimates from the most parsimonious model did not overlap zero, as determining predictor importance using 85% CL is compatible with using AIC for model selection (Arnold 2010). All data used for analysis are available from the Dryad Digital Repository at doi.org/10.5061/dryad.bk3j9kdfr.

Results

Spatial distribution

Satellite telemetry data revealed a northwest to southeast distribution of Atlantic and Pacific scoter estimated breeding sites across North America, with most individuals breeding in the Taiga ecoregion (Fig. 1). Pacific scoters tended to breed in Alaska and western Canada, and Atlantic scoters tended to breed in eastern Canada, with some mixing of individuals of different wintering origins in the middle of the continent (Fig. 1). For birds of Pacific origin, black scoters were only detected breeding in Alaska, whereas surf and white-winged scoters were more widely distributed, with most breeding individuals concentrated in the Northwest Territories and fewer individuals detected in eastern Alaska, Yukon, British Columbia, Alberta, and Saskatchewan. For birds of Atlantic origin, scoters of all three species were detected breeding in the Northwest Territories, Nunavut, Manitoba, Ontario, and Québec, with white-winged scoters also detected in Saskatchewan, and black and surf scoters also detected in Labrador.

Male and female arrival dates

Mean arrival date across all species was 1 June ± 9 days (± SD; range: 20 April–26 June; Table 3, see Supporting information for estimated breeding chronology summary statistics results by province/state). The best-supported model for scoter arrival date included snow-free date, species, wintering origin, an interaction between species and wintering origin, age, and sex (Akaike weight [w] = 0.81), while all remaining models received less support ($\Delta AIC_c > 3.1$, $w < 0.18$; Table 4). Surf scoters and Pacific black scoters arrived earliest at estimated nesting locations (estimated mean arrival date was 28 May). Atlantic black scoters arrived approximately nine days later, on average (6 June). Overall, white-winged scoters arrived latest, with estimated mean arrival dates of 2 June and 9 June for Pacific and Atlantic birds, respectively (Fig. 2a). Adult scoters arrived 5.1 days earlier than one-year-old subadults and 1.6 days earlier than two-year-old subadults (Fig. 2b). Arrivals were positively associated with snow-free dates, such that arrivals were one day later for every five-day delay in snowmelt (Fig. 2c). Additionally, males arrived 2.0 days earlier than females (Fig. 2d); however, the strength of effect was relatively weak (a model without sex was nearly equivalent to the best-supported model, and the 85% confidence interval [CI] around sex was very close to zero and overlapped zero at broader CIs; see Table 5 for summary of all PTT parameter estimate and 85% CL values).

Using mean snow-free dates for the last 10 years (2010–2020), the best-approximating model for scoter arrival dates predicted a trend toward earlier arrivals at more southern and

Table 3. Atlantic- and Pacific-wintering black scoter (BLSC), surf scoter (SUSC), and white-winged scoter (WWSC) estimated nesting location arrival dates, minimum lengths of stay, and departure dates determined from PTT-marked individuals, and nest initiation dates determined from brood observations. Arrivals were determined using male and female birds, and lengths of stay and departures were determined using males only (see Supporting information for a summary of arrival dates, lengths of stay and departure dates by province/state).

Origin	Species	Arrival				Length of stay (days)				Departure				Nest initiation			
		Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n
Atlantic	BLSC	8 June	23 May	26 June	46	21	9	29	11	27 June	13 June	6 July	11	4 June	7 May	2 July	25
	SUSC	30 May	14 May	15 June	54	23	10	83	13	21 June	2 June	17 August	13	3 June	6 May	22 June	114
	WWSC	8 June	30 May	22 June	37	25	11	46	5	30 June	18 June	18 July	5	20 June	14 June	29 June	20
Pacific	BLSC	25 May	20 April	21 June	48	29	14	68	11	16 June	7 June	27 June	11	14 June	13 May	8 July	144
	SUSC	29 May	16 May	21 June	70	17	9	20	4	14 June	9 June	22 June	4	2 June	11 May	24 June	129
	WWSC	3 June	19 May	21 June	58	20	9	40	8	25 June	11 June	3 July	8	2 June	11 May	22 June	50

more western nesting locations for black, surf, and white-winged scoters (Fig. 3; a dataset of arrival date predictions are available on the Dryad Digital Repository at doi.org/10.5061/dryad.bk3j9kdfr). For black scoters, earliest arrival dates were predicted for nesting locations near the Alaskan coast. For all species, latest arrival dates were predicted for areas of higher elevation and large, inland lakes.

Male lengths of stay and departure dates

Male scoters spent an average of 23 ± 14 days at estimated breeding locations (range: 9–83; Table 3). Snow-free date was retained in the best-ranked model to explain variation in scoter minimum length of stay ($w = 0.60$). All remaining models received less support than the best-performing model ($\Delta AIC_c \geq 2.0$, $w \leq 0.22$; Table 6). Scoters stayed at estimated nesting locations for fewer days in years with later snowmelts (Table 5, Fig. 4).

On average, male scoters departed nest locations on June 22 ± 12 days (range: 2 June – 17 August 17; Table 3). The best-ranked model to explain variation in male departure dates from estimated nesting locations retained species, wintering origin, the interaction between species and wintering origin, and age ($w = 0.96$). All other models received less support ($\Delta AIC_c > 6.0$, $w \leq 0.04$; Table 7). Male surf scoters and Pacific black scoters departed earliest from estimated nesting locations (estimated mean departure date was approximately June 15). Male Atlantic black scoters departed approximately 12 days later (27 June), on average. Overall, male white-winged scoters departed latest, with estimated mean departure dates of 25 June and 30 June for Pacific and Atlantic birds, respectively (Fig. 5a). Adult males departed 12 days earlier than male one-year-old subadults and at the same time as male two-year-old subadults.

Evaluation of tag implantation

For unmarked scoters, nest initiation dates based on brood observations ranged from 5–6 May to 7–8 July (Table 3). The best-supported model to explain variation in nest initiation dates retained species, wintering origin, and the interaction between species and wintering origin ($w = 1.0$; Supporting information). Other models received less support ($\Delta AIC_c > 67$, $w < 0.001$). Estimated mean nest initiation dates were similar for surf scoters from both wintering areas (4–6 June). For black and white-winged scoters, nest initiation dates differed between wintering areas, such that Atlantic black scoters and Pacific white-winged scoters initiated nesting at the same time as surf scoters, but nest initiation dates were later for Pacific black scoters (16 June) and Atlantic white-winged scoters (20 June, Supporting information).

Finally, we examined whether tag implantation delayed PTT-marked individuals. The best-supported model retained whether a bird was marked or unmarked ($w = 1.0$; Supporting information). Arrival dates of PTT-marked individuals were 7.1 days earlier than nest initiation dates of unmarked individuals (Supporting information).

Table 4. Model selection results for 39 candidate models examining factors that influence variations in estimated nesting location arrival dates of PTT-marked scoters. AIC_c = Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c = difference in AIC_c from the best-approximating model, w = Akaike weight, cond. R^2 = conditional R^2 (proportion of variance explained by fixed and random effects), marg. R^2 = marginal R^2 (proportion of variance explained by fixed effects only). See Table 2 for summary of sample sizes included in this analysis.

Fixed effects	AICc	ΔAICc	weight	cond. R^2	marg. R^2
snow + species + origin + species:orgin + sex + age	2074.5	0.0	0.807	0.94	0.45
snow + species + origin + species:origin + age	2077.5	3.1	0.174	0.94	0.45
snow + species + origin + species:origin + sex	2082.4	7.9	0.015	0.93	0.44
snow + species + origin + species:origin	2085.3	10.8	0.004	0.93	0.43
snow + species + origin + sex	2099.9	25.4	< 0.0001	0.93	0.41
snow + species + origin + age	2100.5	26.0	< 0.0001	0.93	0.40
snow + species + origin	2104.2	29.7	< 0.0001	0.93	0.39
snow + species + sex + age	2110.1	35.7	< 0.0001	0.92	0.33
snow + species + age	2112.1	37.6	< 0.0001	0.92	0.33
snow + species + sex	2114.0	39.6	< 0.0001	0.92	0.33
snow + species	2116.1	41.6	< 0.0001	0.92	0.33
species + origin + species:origin + sex + age	2133.7	59.3	< 0.0001	0.92	0.32
snow + origin + sex + age	2137.8	63.4	< 0.0001	0.92	0.29
species + origin + species:origin + age	2138.3	63.8	< 0.0001	0.92	0.30
species + origin + age	2140.7	66.3	< 0.0001	0.92	0.28
species + origin + sex	2142.3	67.9	< 0.0001	0.92	0.28
species + origin + species:origin + sex	2144.4	70.0	< 0.0001	0.92	0.29
snow + origin	2145.2	70.8	< 0.0001	0.92	0.28
snow + sex + age	2147.6	73.2	< 0.0001	0.91	0.22
species + origin + species:origin	2148.5	74.1	< 0.0001	0.92	0.27
snow + age	2149.2	74.7	< 0.0001	0.91	0.22
snow + sex	2152.6	78.1	< 0.0001	0.91	0.22
snow	2154.2	79.8	< 0.0001	0.91	0.21
species + origin + sex + age	2166.6	92.1	< 0.0001	0.91	0.21
species + origin + sex	2170.6	96.1	< 0.0001	0.91	0.20
species + origin + age	2172.3	97.9	< 0.0001	0.91	0.18
species + origin	2176.3	101.8	< 0.0001	0.91	0.18
species + sex + age	2184.3	109.8	< 0.0001	0.91	0.12
species + age	2187.5	113.1	< 0.0001	0.91	0.11
species + sex	2188.7	114.3	< 0.0001	0.91	0.11
species	2192.2	117.7	< 0.0001	0.91	0.10
origin + sex + age	2196.1	121.6	< 0.0001	0.90	0.11
origin + sex	2200.0	125.5	< 0.0001	0.90	0.11
origin + age	2201.6	127.1	< 0.0001	0.90	0.09
origin	2205.6	131.2	< 0.0001	0.90	0.09
age + sex	2212.2	137.7	< 0.0001	0.90	0.02
age	2215.6	141.1	< 0.0001	0.90	0.01
sex	2217.5	143.1	< 0.0001	0.89	0.01
intercept only (only includes random effects)	2221.3	146.8	< 0.0001	0.89	0.00

Discussion

Breeding chronology

Most scoters arrived at estimated nesting locations at the end of May and initiated nesting in early June. Between 2000 and 2022 in WBPHS strata where PTT-tagged birds were detected (Supporting information), aerial transects were conducted from 15 May to 15 June, on average (US Fish and Wildlife Service Catalog, https://ecos.fws.gov/ServCat/Reference/Profile/142670). Our results indicate that 95% (297/313) of PTT-marked scoters arrived at estimated nesting locations between 1 May and 15 June (hence, 5% arrived after 15 June), and 24% (116/482) of unmarked scoters initiated nesting after 15 June. With respect to timing, this suggests most individuals should be present and available to be counted within the WBPHS survey window. However, for a small proportion of individuals, mismatch between WBPHS and scoter arrival and nest initiation increases potential for under- or overestimating breeding distributions and abundance if uncorrected WBPHS data are used to generate estimates, as some scoters may be missed, counted multiple times on migration, or counted on migration and breeding areas (Schummer et al. 2018). Our results are similar to other studies evaluating late-nesting waterfowl species, such as scaup (*Aythya* spp.), which suggest that WBPHS timing may be early for some individuals (Finger et al. 2016, Schummer et al. 2018).

We note, however, that most tags had duty cycles of three days, with a few having duty cycles of up to five days. Therefore, PTT-determined arrival dates and departure dates may be up to five days later or earlier, respectively, than a

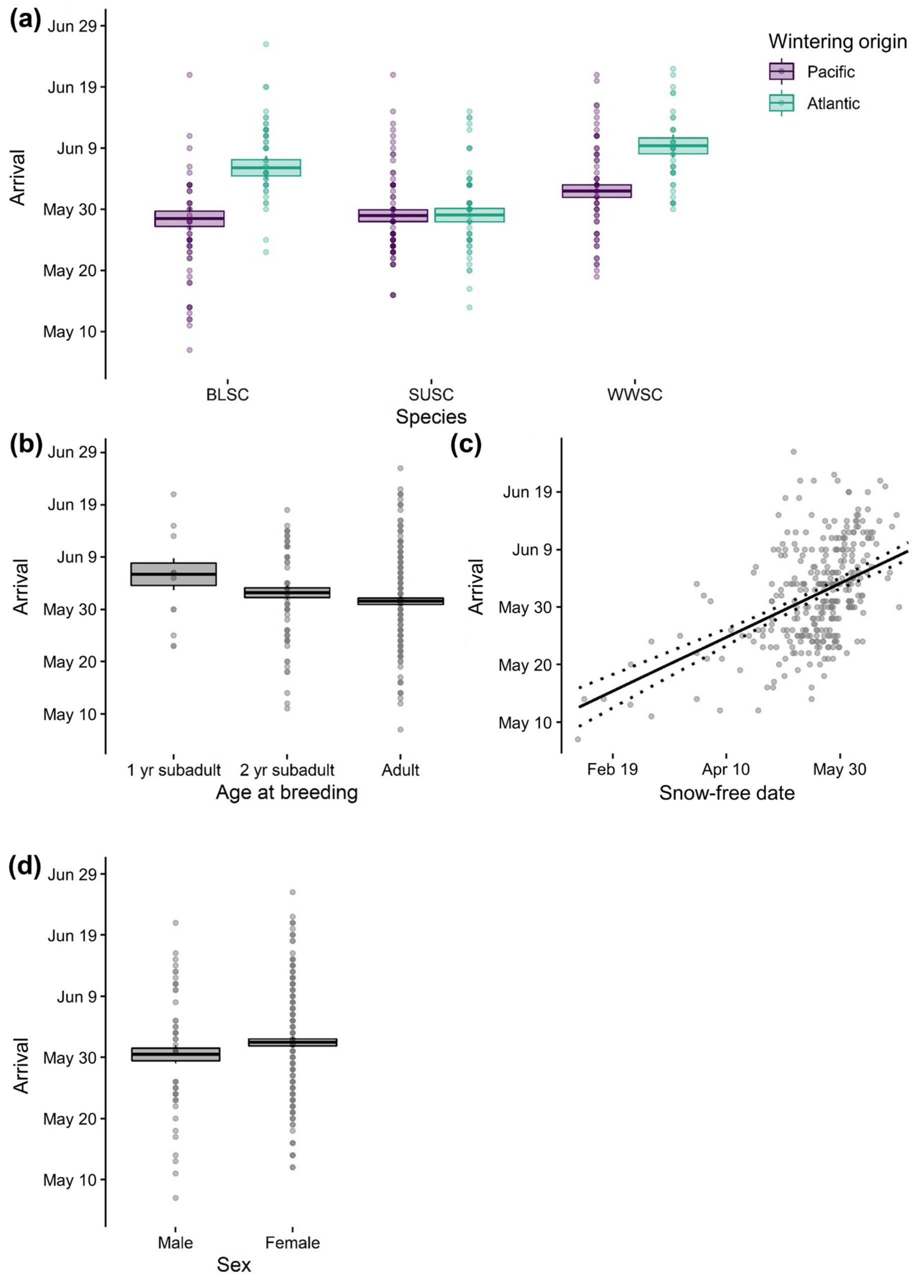

Figure 2. Estimated nesting location arrival dates of PTT-marked scoters varied by species (BLSC = black scoter, SUSC = surf scoter, WWSC = white-winged scoter) and wintering origin (Atlantic = green, Pacific = purple; a), age at breeding (b), snow-free date (c), and sex (d). In panels (a, b and d), boxes show model-predicted means ± SE, with vertical lines indicating 85% confidence intervals. In panel c, line indicates model-predicted means ± an 85% confidence interval. In all panels, circles indicate raw values for individual birds. See Table 1–2 for sample sizes.

bird's actual arrival or departure. Lengths of stay may thus be underestimated, and our estimates represent the minimum lengths of stay of these three species. Furthermore, our study assumes that PTT-tagged birds were breeding if they were at one location for nine or more days between a certain period of the breeding season. We acknowledge that nonbreeders (e.g. unpaired males, non-breeding females) may have remained at a site for more than nine days even if they were not nesting. However, it was not possible to definitively confirm whether breeding occurred at sites identified as nesting locations using PTT detection data. Therefore, our comparison with WBPHS survey dates should be interpreted with caution.

We observed a positive relationship between snow-free date and scoter arrivals, with later arrivals in years and nesting locations with later snowmelts. Scoters typically follow spring thaw on northward migration, which allows them to arrive at nesting locations as soon as possible after snowmelt (Takekawa et al. 2011). Indeed, most PTT-tagged scoters in

Table 5. Parameter estimates (β) and 85% confidence limits (85% CL) for covariates in the best-supported models explaining variations in PTT-marked scoter arrival dates, lengths of stay, and departure dates from estimated nesting locations. Subadult 1 = one-year-old subadult, Subadult 2 = two-year-old subadult. Asterisks indicate β values for which 85% CL did not overlap zero. See Table 2 for summary of sample sizes included in analyses.

Response	Parameters in best-ranked model	β	lower 85% CL	upper 85% CL
Arrival date	species – SUSC	−7.7*	−10	−5.4
	species – WWSC	3.6*	1.0	6.2
	origin – Pacific	−8.3*	−11	−5.6
	Age – Subadult 1	5.1*	2.0	8.3
	Age – Subadult 2	1.6*	0.15	3.1
	Sex – Male	−2.0*	−3.5	−0.42
	Snow-free date	0.19*	0.16	0.22
	species (SUSC): origin (Pacific)	8.2*	5.1	11
	species (WWSC): origin (Pacific)	1.0	−2.5	4.5
	Intercept	130*	125	136
Length of stay	Snow-free date	−0.22*	−0.29	−0.15
	Intercept	3.0*	2.9	3.1
Departure date	species – SUSC	−12*	−17	−7.0
	species – WWSC	3.4	−2.5	9.3
	origin – Pacific	−11*	−17	−6.0
	Age – Subadult 1	12*	2.6	21
	Age – Subadult 2	−0.2	−4.2	3.8
	species (SUSC): origin (Pacific)	11*	2.3	19
	species (WWSC): origin (Pacific)	6.1	−1.8	14
	Intercept	178*	175	181

our study arrived at estimated nesting locations shortly after snowmelt (Supporting information). Although early arrival is generally associated with greater reproductive performance (Lepage et al. 2000, Newton 2008), there are costs associated with arriving too early, including harsher climatic conditions, lack of open water and lower food availability, and increased rates of nest predation and parasitism (reviewed in Bêty et al. 2004). Therefore, scoters, like many other ground-nesting Arctic-breeding birds (Reed et al. 2004, Liebezeit et al. 2014), adjust their migration schedules to arrive shortly after breeding habitats become snow-free.

Timing of snowmelt could thus be used to help predict yearly scoter arrival dates and thereby optimize timing of a supplemental survey for breeding scoters. Currently, WBPHS timing changes annually in relation to latitude- and weather-related factors, such as bird migration and breeding patterns and ice break-up (Environment and Climate Change Canada 2021). Numerous factors influence snowmelt timing, including spring temperatures and winter snow accumulation, which, in turn, are influenced by factors like wind and topography (Frei and Henry 2021). Therefore, using snowmelt dates would add additional predictive power to the development and operation of large-scale surveys.

Across Canada, snow cover duration is decreasing due to later snow onset, earlier spring melt, and reduced seasonal snow accumulation (Derksen et al. 2019). Birds have shown a variety of responses to warming temperatures, including changes in diet, habitat selection, and migratory behaviour (Dunn and Winkler 2010). Our data suggest that scoters could respond to earlier snowmelt by advancing breeding location arrivals and nest initiations. Interestingly, we saw a negative relationship between snowmelt timing and lengths of stay for male scoters. Therefore, in years and locations with later snowmelt, male scoters arrived later, shortened their lengths of stay, and departed at the same time as in years with early snowmelts. This suggests that either male scoters may have a relatively fixed molt migration schedule or that they leave nesting locations soon after breeding to seek better conditions (e.g. more abundant food resources) elsewhere.

We found differences in estimated breeding chronology among scoter species. Overall, surf scoters and Pacific black scoters arrived earliest and departed earliest, whereas white-winged scoters and Atlantic black scoters arrived latest and departed latest. Additionally, brood observations of unmarked birds suggest that Pacific black scoters and Atlantic white-winged scoters initiated nesting latest. Dissimilar migratory patterns among scoter species have been reported previously. Atlantic-wintering black scoters (Lamb et al. 2021) and Pacific-wintering surf scoters (De La Cruz et al. 2009, Takekawa et al. 2011) are dispersed in winter and more concentrated during migration and breeding, whereas Atlantic-wintering white-winged scoters are more concentrated during winter and dispersed during migration (Meattey et al. 2018, Lepage et al. 2020). Identifying differences in migration and breeding timing is important for increasing our understanding of the comparative ecology of North American scoters. However, given the overlap among species' estimated breeding chronology, it will be impossible to rely on interspecies differences in timing to differentiate among scoter species during fixed-wing surveys, and other methods will be needed to determine species-specific abundance and trends.

Estimated breeding timing was earlier in Pacific black and white-winged scoters relative to Atlantic birds, and male Pacific black and white-winged scoters had earlier departure dates. Spring advancement due to climate change is more pronounced in the Pacific relative to the Atlantic coast (Descamps et al. 2019) and may be advancing scoter breeding more in Pacific- relative to Atlantic-wintering birds. Differences in estimated breeding chronology between Atlantic and Pacific scoters may be related to numerous other factors (e.g. wintering area variation in prey availability [e.g. herring spawn on Pacific coast; Lok et al. 2008, 2012], predation risk [Jonker et al. 2010], weather patterns [Takekawa et al. 2011, Imlay et al. 2018], contaminant exposure [Fort et al. 2014, Gurney et al. 2014]). Additionally, differences in migration distance could impact breeding location arrival and departure dates (Howard et al. 2018, Schmaljohann 2019). Indeed, arrival and departure to breeding locations by Atlantic black scoters varies by longitude, where individuals breeding farther west (i.e. individuals with greater migration distances) arrive later, stay longer, and depart later than individuals breeding farther east

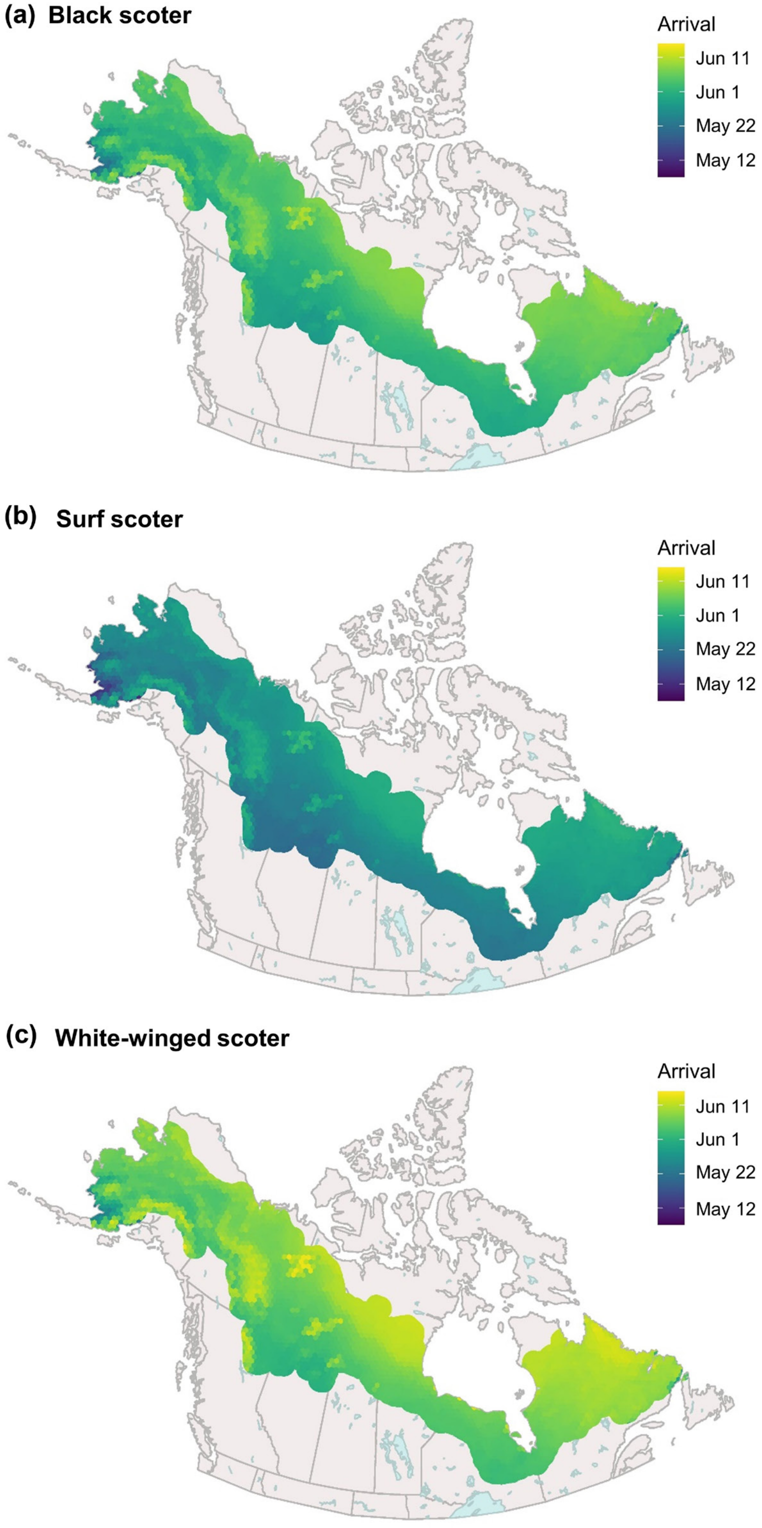

Figure 3. Map of model-predicted nesting location arrival dates of black, surf, and white-winged scoters. Predictions were made across a polygon covering a 100 km buffer around the Taiga and Hudson Plains ecoregions, extended to include PTT-estimated scoter nesting locations along the northwest coast of Alaska. Predictions were generated using the 11-year snow-free date average from 2010–2020 within each cell of a hexagonal grid with 24 km apothems (i.e. distance from hexagon centre to side). Map colours indicate arrival date, with more blue colours indicating earlier arrivals, and more yellow colours indicating later arrivals. Note that maps do not depict predicted breeding ranges, as the map includes areas outside of the presumed breeding range of certain species (e.g. black scoters do not breed across the entire continent; Bordage and Savard 2020), and birds do not nest at every location within the area where predictions were made (e.g. on mountains and large lakes, along the St. Lawrence River shoreline).

Table 6. Model selection results for 10 candidate models examining the factors that influence variations in minimum length of stay of PTT-marked male scoters at estimated nesting locations. AIC_c = Akaike's information criterion corrected for small sample sizes, ΔAIC_c = difference in AIC_c from the best-approximating model, w = Akaike weight, cond. R^2 = conditional R^2, marg. R^2 = marginal R^2. See Table 2 for sample sizes of males included in this analysis.

Fixed effects	AICc	ΔAICc	weight	cond. R^2	marg. R^2
snow	365.4	0.0	0.597	0.79	0.22
snow + origin	367.4	2.0	0.221	0.79	0.22
snow + species	368.5	3.1	0.124	0.79	0.26
snow + species + origin	370.2	4.8	0.053	0.79	0.26
snow + species + origin + species:origin	375.3	10.0	0.004	0.79	0.28
intercept only (only includes random effects)	384.5	19.2	< 0.0001	0.77	0.00
species	384.6	19.2	< 0.0001	0.77	0.10
origin	386.3	20.9	< 0.0001	0.77	0.01
species + origin	387.0	21.6	< 0.0001	0.77	0.10
age	387.9	22.5	< 0.0001	0.77	0.03

(Lamb et al. 2021). However, surf scoters wintering along the Pacific Coast show highly synchronous breeding regardless of wintering origin or differences in spring migration distance (De La Cruz et al. 2009, Takekawa et al. 2011), and previous tracking of white-winged scoters tagged along the Atlantic Coast found no relationship between migration duration and total migration distance (Meattey et al. 2018).

These results may also reflect intrinsic differences in migration strategies between Atlantic and Pacific scoter populations. At a breeding site in Saskatchewan, white-winged scoters from Atlantic wintering areas had later nest initiation dates than individuals from Pacific wintering areas (Gurney et al. 2014). However, there was no difference in clutch size or nest success, suggesting that later breeding was not associated with lower reproductive success, as is often observed in Arctic-breeding birds (Lepage et al. 2000, Weiser et al. 2018), and notably in northern-breeding scoter species with relatively slow-maturing ducklings (Traylor and Alisauskas 2006, Brown and Fredrickson 2020). Instead, Atlantic white-winged scoters had a higher mid-incubation body mass, which suggested that these birds may have used a different migration strategy, where they migrated more slowly and gained greater nutrient stores en route to Saskatchewan (Gurney et al. 2014). Indeed, the broad range of nest initiation dates (30–50 days) based on brood observations suggests that there is no strong selection for timing of nesting in scoters. Therefore, key priorities to fill gaps in our knowledge of scoter biology include: 1) identifying drivers of variation in breeding chronology between Atlantic- and Pacific-wintering birds and among scoter species and 2) examining whether surf and white-winged scoters exhibit differences in breeding chronology where Atlantic- and Pacific-wintering populations overlap within the breeding range.

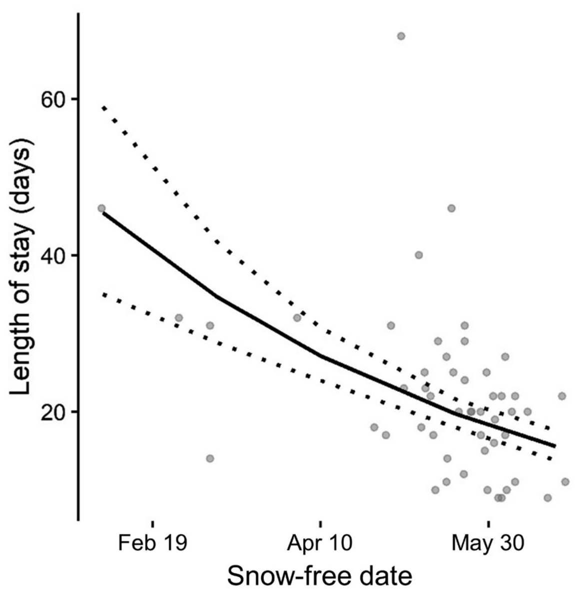

Figure 4. Minimum length of stay of male PTT-marked scoters at estimated nesting locations varied by snow-free date. Line indicates model-based predictions ± an 85% confidence interval. Circles indicate raw values for individual birds. See Table 1–2 for sample sizes.

In our study, adults arrived earlier than one-year-old and two-year-old subadults. Work in other species suggests that adults typically arrive at breeding areas before juveniles (Devries et al. 2008, Newton 2011, Briedis et al. 2019). This is consistent with the assumption that scoters breed for the first time at two to three years of age (Anderson et al. 2020, Bordage and Savard 2020, Brown and Fredrickson 2020). Savard et al. (2007) suggested that surf scoter subadults likely remain in marine habitats throughout the summer; however, terrestrial isotopic signatures in immature male surf scoters suggest that subadult males may spend time in inland waters prior to molt (Budge and Gilliland 2007). Studies in surf, black, and white-winged scoters demonstrate that males, subadults, and non-breeding females typically leave breeding areas and begin post-breeding remigial molt before breeding females (Savard et al. 2007, Meattey et al. 2018, Lepage et al. 2020, Gilliland and Savard 2021, Lamb et al. 2021). There is also evidence of differing habitat use among sexes, age groups, and between successful and unsuccessful breeders (Iverson et al. 2004, Meattey et al. 2018, Lepage et al. 2020, Lamb et al. 2021).

Our finding that males arrived at breeding locations two days earlier than females is unexpected, but may suggest that at least some marked males were unpaired. Scoters pair on their wintering grounds (Eadie and Savard 2015), and paired males should arrive on breeding sites at the same time as females (Savard et al. 2007). In our dataset, three male

Table 7. Model selection results for 11 candidate models examining the factors that influence variations in departure dates of PTT-marked male scoters from estimated nesting locations. AIC_c = Akaike's information criterion corrected for small sample sizes, ΔAIC_c = difference in AIC_c from the best-approximating model, w = Akaike weight, cond. R^2 = conditional R^2, marg. R^2 = marginal R^2. See Table 2 for sample sizes of males included in this analysis.

Fixed effects	AICc	ΔAICc	weight	cond. R^2	marg. R^2
species + origin + species:origin + age	338.0	0.0	0.914	0.93	0.29
species + origin + age	389.9	6.2	0.041	0.92	0.28
species + origin + species:origin	344.4	6.4	0.040	0.92	0.22
species + origin	352.6	14.6	0.002	0.97	0.18
species + age	352.9	14.9	0.001	0.99	0.17
species	362.0	23.9	0.0002	1.00	0.12
origin + age	365.0	26.9	< 0.0001	1.00	0.08
age	367.5	29.5	< 0.0001	1.00	0.06
origin	373.2	35.1	< 0.0001	1.00	0.07
intercept only (only includes random effects)	377.5	39.5	< 0.0001	1.00	0.00
snow	382.0	44.0	< 0.0001	1.00	0.03

black scoters arrived very early relative to other individuals (20 April, 6 May and 11 May; distribution of male arrival dates was left-skewed; Supporting information). We suspect that these early arriving males were unpaired at the time of marking and shifted mean male arrival dates nearly two days earlier relative to females. We note, however, that the effect of sex was relatively weak and was not important enough to affect our conclusions. We also note that although we did not have sufficient data to adequately analyze female lengths of stay and departure dates, a future, more detailed analysis with additional data focusing specifically on females is warranted to better understand the breeding biology of scoter species.

Understanding interspecific and demographic differences in migration timing and habitat use is valuable, as it has implications for how survey data are used to estimate annual breeding duck abundance, where breeding pair presence is inferred

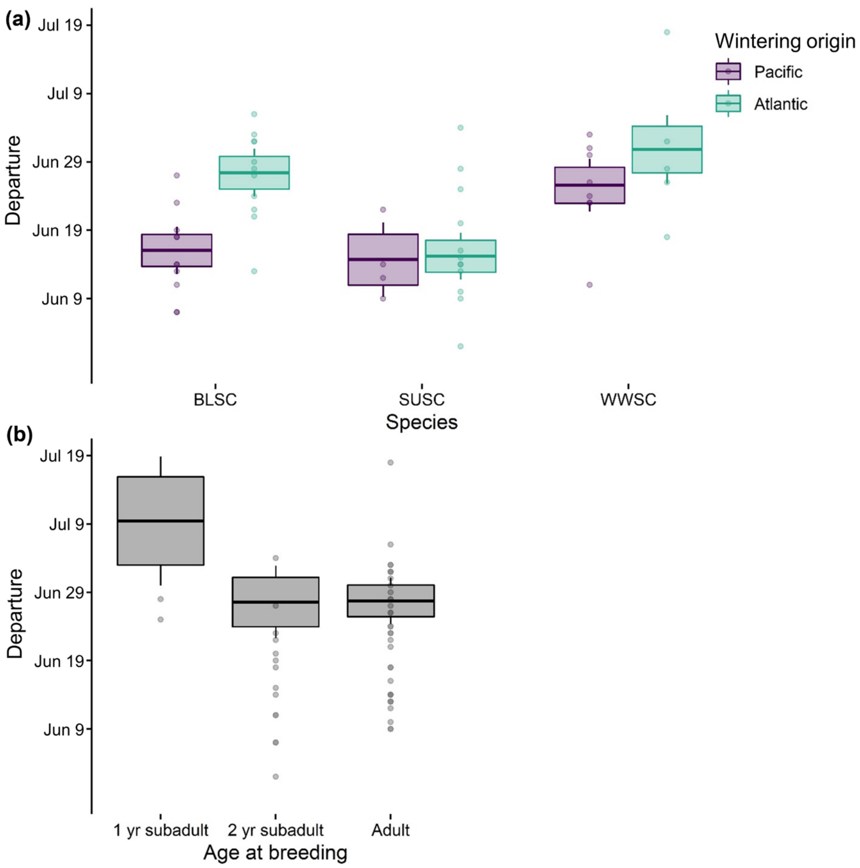

Figure 5. Departure dates of male PTT-marked scoters from estimated nesting locations varied by species (BLSC = black scoter, SUSC = surf scoter, WWSC = white-winged scoter) and wintering origin (Atlantic = green, Pacific = purple; a) and age at breeding (b). Boxes show model-predicted means ± SE, with vertical lines indicating 95% confidence intervals. See Table 1–2 for sample sizes.

from lone males and males in groups of less than five individuals (Canadian Wildlife Service and US Fish and Wildlife Service 1987, Smith 1995). It is also important from a conservation perspective, as different segments of scoter populations could be exposed to dissimilar environmental and ecological pressures (Iverson et al. 2004, Lamb et al. 2021), and better understanding these pressures and their impacts on scoter populations can inform decisions to help mitigate risks.

Spatial distribution

Our analyses provide further information regarding scoter breeding distribution across North America. Together, the Traditional and Eastern WBPHS survey areas covered approximately 50% of PTT-estimated black scoter breeding locations and 70% of PTT-estimated surf and white-winged scoter breeding locations (Supporting information). In particular, scoter breeding sites in the westernmost part of the Northwest Territories, in Nunavut, and in northern Manitoba, Québec, and Labrador are not covered by the WBPHS. WBPHS population estimates may be inaccurate for species that breed in large numbers outside of survey strata boundaries (Smith 1995, US Fish and Wildlife Service 2019). Completing a one-time survey of the full breeding distribution would help understand what fraction of continental scoter populations (i.e. no. of individuals) is currently sampled by the WBPHS.

White-winged and surf scoters had relatively wide breeding ranges. Our results support previous satellite telemetry studies showing core breeding regions in the Northwest Territories for Pacific surf scoters (Takekawa et al. 2011) and in northern Québec and Labrador for Atlantic surf scoters (Perry et al. 2006, Sea Duck Joint Venture 2015a). Additionally, our findings corroborate previous studies showing high densities of Pacific white-winged scoters in the Northwest Territories (Brown and Fredrickson 2020), and an association between Atlantic wintering areas and white-winged scoter nest sites in the Northwest Territories, northern Saskatchewan, Manitoba, Ontario, and Québec (Meattey et al. 2018, Lepage et al. 2020). Along with these previous studies, our results suggest that presumed breeding ranges for white-winged scoters could be expanded further east (Supporting information). Pacific and Atlantic white-winged and surf scoters breeding distributions slightly overlapped in the middle of the continent, and genetic data suggest that there is or has been recent gene flow and connectivity between Atlantic and Pacific populations in both species (Sonsthagen et al. 2019). Despite partial sympatry between breeding ranges of Atlantic- and Pacific-wintering white-winged and surf scoters, these populations would likely benefit from separate monitoring and management programs because Pacific- and Atlantic-wintering white-winged scoter populations showed differences in arrival timing on the breeding grounds, these populations are largely demographically distinct, and their breeding and wintering grounds have distinct ecological characteristics and pressures (Sea Duck Joint Venture 2015a, Lepage et al. 2020).

Conversely, black scoters were less widely distributed, and Atlantic- and Pacific-wintering populations showed distinct breeding distributions (Bordage and Savard 2020, Bowman et al. 2021). Pacific black scoters bred only in Alaska, while Atlantic black scoters bred in the Northwest Territories, Nunavut, and in northern Manitoba, Ontario, Québec and Labrador. This supports the need to revise black scoter range maps to include breeding areas west of Hudson Bay (Bowman et al. 2021, Supporting information). Recent satellite telemetry work by Bowman et al. (2021) found that Atlantic and Pacific black scoter populations show no overlap at any stage of their annual cycle. Moreover, recent genetic analyses revealed elevated levels of genetic divergence between Alaskan and Atlantic sampling sites (Sonsthagen et al. 2019). Together, these results suggest that there are two separate populations of black scoters in North America, and Bowman et al. (2021) recently discussed the evidence for separate monitoring and management programs for western and eastern black scoter populations.

Evaluation of tag implantation

Previous studies found that sea ducks implanted with satellite transmitters nest later and at lower rates in the year captures occurred compared to subsequent years (Lamb et al. 2020b). However, in our study, a preliminary assessment revealed no difference in arrival dates between the year of tagging and subsequent years in individuals with multiple years of data. Furthermore, in the year of implantation, PTT-marked birds arrived at their breeding sites an average of seven days earlier than nest initiation dates of unmarked birds. This is similar to the difference of 1.0–7.3 days between arrival at breeding areas and nest initiation in PTT-marked Pacific surf scoters observed by De La Cruz et al. (2009). This suggests that PTT-marked individuals had adequate time between arrival and nesting to initiate nesting at the same time as unmarked birds. However, black scoters nesting in the Yukon-Kuskokwim Delta, Alaska, between 2003 and 2016 arrived ~ one month before nest initiation dates previously reported for black scoters between 2001 and 2004 in this area (Schamber et al. 2010), and earlier studies report 30–36 days between arrival and nesting in white-winged scoters in Saskatchewan (Brown and Brown 1981) and Alberta (Vermeer 1969), respectively. However, variations between arrival and nest initiation by species, location, and/or year are not well understood in scoters. Conversely, Lamb et al. (2020b) found that breeding site attendance was lower following PTT implantation. It is therefore possible that newly tagged birds deferred migration to breeding areas and reproduction, in which case implantation-related changes in migration timing in the year of implantation would not be reflected in our dataset. Observations comparing PTT-marked and unmarked birds in the field would be required to explicitly determine the accuracy of PTT-derived phenology information. We note that there were no brood observation data from the centre of the breeding range, where most PTT-marked birds nested, and that nest initiation dates may be later in the centre of the breeding range because scoters migrate farthest to reach this area (Lamb et al. 2021; however, see discussion regarding migration distance and arrival timing above). We also note that all brood observation data came from breeding birds, whereas the breeding status of PTT-marked birds was unknown, and some data may have come from non-breeders. Previous work suggests that non-breeding scoters, which are less time constrained than breeding birds, may arrive later (Savard et al. 2007, Lepage et al. 2020); therefore, arrival dates of PTT-marked birds may be biased late. Nevertheless, in our sample, transmitter implantation did not delay birds to the extent that arrivals of marked birds were later than nest initiation dates of unmarked birds. Timing of scoter arrival and lengths of stay at breeding locations should therefore be reliable enough to assist in development of a breeding survey that targets scoter species.

Conclusions

Logistical difficulties and expense associated with monitoring efforts in boreal and Arctic regions (Mallory et al. 2018) are major limitations to expanding current survey protocols and to implementing novel survey programs and techniques (Sea Duck Joint Venture 2007, Schummer et al. 2018). As a result, abundance estimates for breeding scoters remain uncertain in many parts of their range due to a lack of effective monitoring programs (Anderson et al. 2020, Bordage and Savard 2020, Brown and Fredrickson 2020). To address this information gap, the SDJV recommended a two-pronged approach, which included 1) large-scale telemetry studies, to accurately determine scoter distributions and 2) the development of geographically expanded waterfowl surveys, to help improve estimates of sea duck breeding population sizes (Sea Duck Joint Venture 2007, 2008, 2014, 2022). Our study directly addressed the first part of this strategy by combining satellite telemetry data for all North American scoter species from both Atlantic and Pacific wintering areas to identify breeding distributions of all three species. Our results also indirectly addressed the second component of the strategy by providing predictions of the timing of scoter arrival on the breeding grounds, which can help inform the development of future monitoring programs that are optimally timed for those species. Until future surveys are developed, WBPHS data represent the most consistent sub-sample of the breeding distributions of scoters, and it will therefore serve as an index of scoter breeding populations. Further work to establish the full spatial and temporal representation of this sample will aid in defining its utility.

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Permits – All capture, handling, and marking of scoters was conducting following the Animal Care and Use Committee guidelines at each investigator's institution or organization, with permits from the Canadian Wildlife Service, US Fish and Wildlife Service, USGS Bird Banding Laboratory, Secretarı´a de Medio Ambiente y Recursos Naturales (SEMARNAT), and multiple states and territories.

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Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bk3j9kdfr (Bianchini et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Anderson, E. M., Dickson, R. D., Lok, E. K., Palm, E. C., Savard, J.-P. L., Bordage, D. and Reed, A. 2020. Surf scoter (*Melanitta perspicillata*), version 1.0. – In: Rodewald, P. G. (ed.), Birds of the World. Cornell Laboratory of Ornithology, https://doi.org/10.2173/bow.sursco.01.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. – J. Wildl. Manage. 74: 1175–1178.

Barrow, W. R. 1982. A summary of Labrador waterfowl banding, 1947–1982. – Canadian Wildlife Service Internal Report.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Benoit, R. 2005. Complexe de la Romaine. Étude de la faune aviaire. Sauvagine et autres oiseaux aquatiques. Report Presented to Hydro-Québec Équipement, Direction Développement de projets et Environnement. – Foramec.

Benoit, R., Reed, A. and Lalumière, R. 1994. Étude de la sauvagine sur la côte nord-est de la baie James – 1993. – Report Presented to the Service Écologie, Société d'Énergie de la Baie James.

Benoit, R., Lalumière, R. and Reed, A. 1996. Étude sur la Bernache cravant et la Macreuse à ailes blanches (côte nord-est de la baie James – 1995). – Report Presented to the Service Écologie, Société d'Énergie de la Baie James.

Bêty, J., Giroux, J.-F. and Gauthier, G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). – Behav. Ecol. Sociobiol. 57: 1–8.

Bianchini , K. 2023. Data from: Evaluation of breeding distribution and chronology of North American scoters. – Dryad Digital Repository. https://doi.org/10.5061/dryad.bk3j9kdfr.

Bolker, B., R Development Core Team and Gine-Vazquez, I. 2021. bbmle: tools for general maximum likelihood estimation (1.0.24) [Computer software]. – https://github.com/bbolker/bbmle.

Bordage, D. and Savard, J.-P. L. 2020. Black scoter (*Melanitta americana*), ver. 1.0. – In: Poole, A. F. (ed.), Birds of the world. Cornell Laboratory of Ornithology, https://doi.org/10.2173/bow.blksco2.01.

Bowman, T. D., Gilliland, S. G., Schamber, J. L., Flint, P. L., Esler, D., Boyd, W. S., Rosenberg, D. H., Savard, J.-P. L., Perry, M. C. and Osenkowski, J. E. 2021. Strong evidence for two disjunct populations of black scoters *Melanitta americana* in North America. – Wildfowl 71: 179–192.

Bowman, T. D., Silverman, E. D., Gilliland, S. G. and Leirness, J. B. 2015. Status and trends of North American sea ducks: reinforcing the need for better monitoring. – In: Savard, J.-P. L., Derksen, D. V., Esler, D. and Eadie, J. M. (eds), Ecology and conservation of North American Sea ducks. – CRC Press, pp.1–28.

Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Liechti, F., Meier, C. M., Procházka, P. and Hahn, S. 2019. A full annual perspective on sex-biased migration timing in long-distance migratory birds. – Proc. R. Soc. B 286: 20182821.

Brook, R. W., Abraham, K. F., Middel, K. R. and Ross, R. K. 2012. Abundance and habitat selection of breeding scoters (*Melanitta* spp.) in Ontario's Hudson Bay Lowlands. – Can. Field Nat. 126: 20–27.

Brown, P. W. and Brown, M. A. 1981. Nesting biology of the white-winged scoter. – J. Wildl. Manage. 45: 38–45.

Brown, P. W. and Fredrickson, L. H. 2020. White-winged scoter (*Melanitta deglandi*), ver. 1.0. In: Rodewald, P. G. (ed.), Birds of the World. – Cornell Laboratory of Ornithology, https://doi.org/10.2173/bow.whwsco2.01.

Budge, S. and Gilliland, S. G. 2007. Diet of surf scoters molting in eastern North America. Sea Duck Joint Venture annual report no. 92. – US Fish and Wildlife Service, https://seaduckjv.org/pdf/studies/pr92.pdf.

Burnham, K. and Anderson, D. 2002, Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Canadian Wildlife Service and US Fish and Wildlife Service. 1987. Standard operating procedures for aerial waterfowl breeding ground population and habitat surveys in North America. – Canadian Wildlife Service and US Fish and Wildlife Service.

Consortium Gauthier and Guillemette – G.R.E.B.E.1990. Complexe Grande-baleine. Avant-projet Phase II. Étude de l'avifaune et du castor: écologie des Macreuses à bec jaune (*Melanitta nigra*) et à front blanc (*M. perspicillata*) en période de reproduction sur le territoire du complexe Grande-Baleine. Final report presented to Hydro-Québec, vice-présidence Environnement. Saint-Romuald, Québec.

De La Cruz, S. E. W., Takekawa, J. Y., Wilson, M. T., Nysewander, D. R., Evenson, J. R., Esler, D., Boyd, W. S. and Ward, D. H. 2009. Spring migration routes and chronology of surf scoters (*Melanitta perspicillata*): a synthesis of Pacific coast studies. – Can. J. Zool. 87: 1069–1086.

Derksen, C., Burgess, D., Duguay, C., Howell, S., Mudryk, L., Smith, S., Thackeray, C. and Kirchmeier-Young, M. 2019. Changes in snow, ice, and permafrost across Canada. – In: Bush, E. and Lemmen, D. S. (eds), Canada's Changing Climate Report. Government of Canada, pp. 194–260.

Descamps, S., Ramírez, F., Benjaminsen, S., Anker-Nilssen, T., Barrett, R. T., Burr, Z., Christensen-Dalsgaard, S., Erikstad, K. E., Irons, D. B., Lorentsen, S. H., Mallory, M. L., Robertson, G. J., Reiertsen, T. K., Strøm, H., Varpe, Ø. and Lavergne, S. 2019. Diverging phenological responses of Arctic seabirds to an earlier spring. – Global Change Biol. 25: 4081–4091

Devries, J. H., Brook, R. W., Howerter, D. W. and Anderson, M. G. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). – Auk 125: 618–628.

Dunn, P. O. and Winkler, D. W. 2010. Effects of climate change on timing of breeding and reproductive success in birds. – In: Møller, A. P., Fiedler, W. and Berthold, P. (eds), Effects of climate change on birds. Oxford Univ. Press, pp. 108–119.

Eadie, J. M. and Savard, J.-P. L. 2015. Breeding systems, spacing behavior, and reproductive behavior of sea ducks. – In: Savard, J.-P. L., Derksen, D. V., Esler, D. and Eadie, J. M. (eds), Ecology and conservation of North American Sea ducks. CRC Press, pp.325–368.

Environment and Climate Change Canada. 2019. Population status of migratory game birds in Canada, vol. 52. – Canadian Wildlife Service Waterfowl Committee. http://publications.gc.ca/collections/collection_2020/eccc/CW69-16-52-2019-eng.pdf.

Environment and Climate Change Canada. 2021. Waterfowl breeding population and habitat survey [Program descriptions]. – https://www.canada.ca/en/environment-climate-change/services/bird-surveys/waterfowl/breeding-population-habitat-survey.html.

Finger, T. A., Afton, A. D., Schummer, M. L., Petrie, S. A., Badzinski, S. S., Johnson, M. A., Szymanski, M. L., Jacobs, K. J., Olsen, G. H. and Mitchell, M. A. 2016. Environmental factors influence lesser scaup migration chronology and population monitoring. – J. Wild. Manage. 80: 1437–1449.

Forstner, T. M., Boyd, W. S., Esler, D., Bowman, T. D., Schamber, J. L., McAdie, M., Thompson, J. E. and Green, D. J. 2022. Migratory connectivity and variation in migratory phenology within the Pacific population of Barrow's goldeneye (*Bucephala islandica*). – Avian Conserv. Ecol. 17: 7.

Fort, J., Robertson, G. J., Grémillet, D., Traisnel, G. and Bustamante, P. 2014. Spatial ecotoxicology: migratory Arctic seabirds are exposed to mercury contamination while overwintering in the northwest Atlantic. – Environ. Sci. Technol. 48: 11560–11567.

Frei, E. R. and Henry, G. H. R. 2021. Long-term effects of snowmelt timing and climate warming on phenology, growth, and reproductive effort of Arctic tundra plant species. – Arct. Sci. e-First 8: 1–22.

Garrettson, P. R., Kruse, K. L., Moser, T. J. and Groves, D. J. 2020. Exploratory surveys of migratory birds breeding in the Western and Central Canadian Arctic 2005–2011. – J. Fish Wildl. Manage. 11: 321–340.

Gilliland, S. G. and Savard, J.-P. 2021. Variability in remigial moult chronology and nutrient dynamics of surf scoters *Melanita perspicillata*. – Wildfowl 71: 193–220.

Gollop, J. B. and Marshall, W. H. 1954. A guide for aging duck broods in the field. – Mississippi Flyway Council Technical Section Report.

Gurney, K. E. B., Wood, C. J., Alisauskas, R. T., Wayland, M., DeVink, J.-M. A. and Slattery, S. M. 2014. Identifying carry-over effects of wintering area on reproductive parameters in white-winged scoters: an isotopic approach. – Condor 116: 251–264.

Hijmans, R. J. 2021. raster: geographic data analysis and modeling (3.5-11). – https://CRAN.R-project.org/package=raster.

Howard, C., Stephens, P. A., Tobias, J. A., Sheard, C., Butchart, S. H. M. and Willis, S. G. 2018. Flight range, fuel load and the impact of climate change on the journeys of migrant birds. – Proc. R. Soc. B 285: 20172329.

Imlay, T. L., Mills Flemming, J., Saldanha, S., Wheelwright, N. T. and Leonard, M. L. 2018. Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. – Ecosphere 9: e02166.

Iverson, S. A., Smith, B. D. and Cooke, F. 2004. Age and sex distributions of wintering surf scoters: implications for the use of age ratios as an index of recruitment. – Condor 106: 252–262.

Jonker, R. M., Eichhorn, G., Langevelde, F. van and Bauer, S. 2010. Predation danger can explain changes in timing of migration: the case of the barnacle goose. – PLoS One 5: e11369.

Lamb, J. S. et al. 2019. Spatially explicit network analysis reveals multi-species annual cycle movement patterns of sea ducks. – Ecol. Appl. 29: e01919.

Lamb, J. S. et al. 2020a. Assessing year-round habitat use by migratory sea ducks in a multi-species context reveals seasonal variation in habitat selection and partitioning. – Ecography 43: 1842–1858.

Lamb, J. S. et al. 2020b. Implanted satellite transmitters affect sea duck movement patterns at short and long timescales. – Condor 122: duaa029.

Lamb, J. S., Gilliland, S. G., Savard, J.-P. L., Loring, P. H., McWilliams, S. R., Olsen, G. H., Osenkowski, J. E., Paton, P. W. C., Perry, M. C. and Bowman, T. D. 2021. Annual-cycle movements and phenology of black scoters in eastern North America. – J. Wildl. Manage. 85: 1628–1645.

Lepage, D., Gauthier, G. and Menu, S. 2000. Reproductive consequences of egg-laying decisions in snow geese. – J. Anim. Ecol. 69: 414–427.

Lepage, C., Savard, J.-P. L. and Gilliland, S. G. 2020. Spatial ecology of white-winged scoters (*Melanitta deglandi*) in eastern North America: a multi-year perspective. – Waterbirds 43: 147–162.

Lesage, L., Reed, A. and Savard, J.-P. L. 1997. Plumage development and growth of wild surf scoter *Melanitta perspicillata* ducklings. – Wildfowl 47: 205–210.

LGL Limited 2008, Waterfowl in the lower Churchill River area. Report prepared for Minaskuat Inc. and Newfoundland and

Labrador Hydro. – Lower Churchill Hydroelectric Generation Project.
Liebezeit, J. R., Gurney, K. E. B., Budde, M., Zack, S. and Ward, D. 2014. Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors. – Polar Biol. 37: 1309–1320.
Lok, E. K., Kirk, M., Esler, D. and Boyd, W. S. 2008. Movements of pre-migratory surf and white-winged scoters in response to pacific herring spawn. – Waterbirds 31: 385–393.
Lok, E. K., Esler, D., Takekawa, J., De La Cruz, S. E. W., Boyd, W., Nysewander, D., Evenson, J. and Ward, D. 2012. Spatiotemporal associations between Pacific herring spawn and surf scoter spring migration: evaluating a 'silver wave' hypothesis. – Mar. Ecol. Prog. Ser. 457: 139–150.
Mallory, M. L., Gilchrist, H. G., Janssen, M., Major, H. L., Merkel, F., Provencher, J. F. and Strøm, H. 2018. Financial costs of conducting science in the Arctic: examples from seabird research. – Arct. Sci. 4: 624–633.
Meattey, D. E., McWilliams, S. R., Paton, P. W. C., Lepage, C., Gilliland, S. G., Savoy, L., Olsen, G. H. and Osenkowski, J. E. 2018. Annual cycle of white-winged scoters (*Melanitta fusca*) in eastern North America: migratory phenology, population delineation, and connectivity. – Can. J. Zool. 96: 1353–1365.
Morneau, F. 1998. Utilisation des réservoirs par la sauvagine pour la reproduction. Report presented to the Service hydraulique et environnement. – Hydro-Québec.
Morrier, A., Lesage, L., Reed, A. and Savard, J.-P. L. 2008. Étude sur l'écologie de la Macreuse à front blanc au lac Malbaie, Réserve des Laurentides – 1994-1995. Technical Report Series no. 301. – Canadian Wildlife Service.
Newton, I. 2008. The migration ecology of birds. – Academic Press, Elsevier.
Newton, I. 2011. Migration within the annual cycle: species, sex and age differences. – J. Ornithol. 152: 169–185.
Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. – R J. 10: 439–446.
Perry, M. C., Kidwell, D. M., Wells, A. M., Lohnes, E. J. R., Osenton, P. C. and Altmann, S. H. 2006. Characterization of breeding habitats for black and surf scoters in the eastern boreal forest and subarctic regions of Canada. – In: Hanson, A., Kerekes, J. and Paquet, J. (eds). Limnology and waterbirds 2003. Canadian Wildlife Service Technical Report Series no. 474, pp. 80–89.
Petersen, M. R. and Savard, J.-P. L. 2015. Variation in migration strategies of North American sea ducks. – In: Savard, J.-P. L., Derksen, D. V., Esler, D. and Eadie, J. M. (eds), Ecology and conservation of North American sea ducks, vol. 46. CRC Press. https://pubs.er.usgs.gov/publication/70147373.
Pinhero, J., Bates, D., Sarkar, D. and R Core Team 2021. nlme: linear and nonlinear mixed effects models (3.1-153). – https://CRAN.R-project.org/package=nlme.
Reed, E. T., Gauthier, G. and Giroux, F. 2004. Effects of spring conditions on breeding propensity of greater snow goose females. – Anim. Biodivers. Conserv. 27: 35–46.
Savard, J.-P. L., Reed, A. and Lesage, L. 2007. Chronology of breeding and molt migration in surf scoters (*Melanitta perspicillata*). – Waterbirds 30: 223–229.
Schamber, J. L., Broerman, F. J. and Flint, P. L. 2010. Reproductive ecology and habitat use of Pacific black scoters (*Melanitta nigra americana*) nesting on the Yukon-Kuskokwim Delta, Alaska. – Waterbirds 33: 129–139.
Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: a cross-continental analysis. – Movem. Ecol. 7: 25.
Schummer, M. L., Afton, A. D., Badzinski, S. S., Petrie, S. A., Olsen, G. H. and Mitchell, M. A. 2018. Evaluating the waterfowl breeding population and habitat survey for scaup: evaluating the WBPHS for scaup. – J. Wild. Manage. 82: 1252–1262.
Sea Duck Joint Venture 2007. Recommendations for monitoring distribution, abundance, and trends for North American sea ducks. – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2008. Sea Duck Joint Venture strategic plan 2008–2012. – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2015a. Species status summary and information needs: surf scoter (*Melanitta perspicillata*). – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2015b. Species status summary and information needs: black scoter (*Melanitta americana*). – US Fish and Wildlife Service, Canadian Wildlife Service
Sea Duck Joint Venture 2015c. Species status summary and information needs: white-winged scoter (*Melanitta fusca*). – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2015d. SDJV project no. 141: Canadian barrenlands experimental breeding sea duck survey, year 2. – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2017. Sea duck joint venture implementation plan for January 2017 through December 2019. – US Fish and Wildlife Service, Environment and Climate Change Canada, p. 28.
Sea Duck Joint Venture 2020. SDJV project no. 154: integrating fixed-wing and helicopter survey platforms to improve detection and species identification of North American Breeding Scoters. – US Fish and Wildlife Service, Canadian Wildlife Service.
Sea Duck Joint Venture 2022. Sea duck joint Venture strategic plan 2022–2031. – US Fish and Wildlife Service, Canadian Wildlife Service.
Silverman, E. D., Leirness, J. B., Saalfeld, D. T., Koneff, M. D. and Richkus, K. D. 2012. Atlantic coast wintering sea duck survey, 2008–2011. – US Fish and Wildlife Service.
Silverman, E. D., Saalfeld, D. T., Leirness, J. B. and Koneff, M. D. 2013. Wintering sea duck distribution along the Atlantic Coast of the US. – J. Fish Wildl. Manag. 4: 178–198
Smith, G. W. 1995. A critical review of the aerial and ground surveys of breeding waterfowl in North America. – In: Opler, P. A. (ed), Biological science report, vol. 5. US Fish and Wildlife Service.
Sonsthagen, S. A., Wilson, R. E., Lavretsky, P. and Talbot, S. L. 2019. Coast to coast: high genomic connectivity in North American scoters. – Ecol. Evol. 9: 7246–7261.
Strimas-Mackey, M. 2020. Fishnets and honeycomb: square vs hexagonal spatial grids. – https://strimas.com/post/hexagonal-grids/.
Takekawa, J. Y., De La Cruz, S. W., Wilson, M. T., Palm, E. C., Yee, J., Nysewander, D. R., Evenson, J. R., Eadie, J. M., Esler, D., Boyd, W. S. and Ward, D. H. 2011. Breeding distribution and ecology of Pacific Coast Surf Scoters. – In: Wells, J. V., (ed.), Boreal birds of North America: a hemispheric view of

their conservation links and significance. University of California Press, pp. 41–64.

Traylor, J. J. and Alisauskas, R. T. 2006. Effects of intrinsic and extrinsic factors on survival of white-winged scoter (*Melanitta fusca deglandi*) ducklings. – Auk 123: 67–81.

US Environmental Projection Agency 2010. NA_Eco_Level1. – US EPA Office of Research & Development – National Health and Environmental Effects Research Laboratory.

US Fish and Wildlife Service 2019. Waterfowl breeding population and habitat survey. – https://migbirdapps.fws.gov/mbdc/databases/mas/aboutmas.htm.

US National Ice Center 2008. IMS Daily Northern Hemisphere snow and ice analysis at 1 km, 4 km, and 24 km resolutions, ver. 1. – NSIDC: National Snow and Ice Data Center.

Vermeer, K. 1969. Some aspects of the breeding of the white-winged scoter at Miquelon lake, Alberta. – Blue Jay 27: 72–73.

Weiser, E. L. et al. 2018. Life-history tradeoffs revealed by seasonal declines in reproductive traits of Arctic-breeding shorebirds. – J. Avian Biol. 49: e01531.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. – Springer.