Migration ecology of a re-established trumpeter swan population

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## Abstract

### Background

The Interior Population (IP) of trumpeter swans (*Cygnus buccinator*), formerly extirpated by market hunting, was re-established in eastern North America by releasing individuals from both migratory and non-migratory populations; their current annual movement patterns are largely unknown. Our goal was to describe their seasonal movements and quantify the proportion of the IP that is migratory, the extent and phenology (e.g., departure and arrival dates) of seasonal movements, and associations between movement patterns and breeding status and breeding location.

### Methods

We deployed 113 GPS-GSM transmitters on IP trumpeter swans in six U.S. states and one Canadian province across the current IP breeding range. Using data from 252 unique ‘swan-years’, we segmented the annual cycle by fitting piecewise regression models to each yearly time-series of displacement from the breeding site to estimate dates of migration events. We fit a latent state model to characterize population-level associations between breeding latitude and maximum extent of migration, and linear models to quantify associations with migration phenology.

### Results

At the individual level, 59% of swans moved to distant wintering areas (long-distance migration defined as moving >100km from the breeding site), 16% exhibited regional migration (>25 km and <100 km from breeding site), 19% exhibited non-migratory but local movements (<25 km from breeding site), and 6% exhibited multiple migration strategies across years. Migration extent was best described using a 2-component mixture model in which migration extent was linearly associated with breeding latitude for some individuals and was much lower and exhibited a non-linear association with breeding latitude for others. Swans breeding at more northern latitudes returned to their territories later in the spring than those breeding at more southern latitudes. Breeding swans departed later in the autumn and had a shorter migration duration than non-breeders, but breeding status didn’t have a strong association with arrival in the spring.

### Conclusion

IP trumpeter swans are partial migrants, with a continuum of strategies each year, from local movements to long-distance migration. Much of the variability in movement patterns was related to factors tied to natural history demands (e.g., breeding status) and response to environmental conditions (e.g., through associations with breeding latitude).

### Keywords

Trumpeter swan, migration phenology, annual movements, *Cygnus buccinator*, Interior Population, GPS telemetry, net-squared displacement, species reintroductions

## Introduction

Migration is a behavioral mechanism widely used by all major vertebrate groups (e.g., birds, mammals, fishes, reptiles, amphibians) that allows individuals to track seasonal availability of resources to increase short-term survival, and by optimizing migration phenology, maximize long-term fitness [[1](#ref-fryxell1988)–[4](#ref-barker2022)]. Despite its prevalence as an ecological process and a large body of research involving migration, how population-level migratory traditions are established is not well understood [[5](#ref-abrahms2021b)]. In part, that lack of understanding is hindered by challenges associated with making population-level inference from observations of individuals, quantifying migratory movements along a continuum of variability, and the relative scarcity of successful reintroductions of formerly rare migratory species [[6](#ref-mueller2011a),[7](#ref-senner2020)].

Similar to other large, long-lived avian species such as geese, cranes, and storks, adult swans take care of their young for the first year of life, providing food and protection, and guiding them on their first migration cycle [[8](#ref-chernetsov2004a),[9](#ref-mueller2013)]. As a consequence, cultural transmission during the first year is thought to be the primary mechanism that dictates the learned migratory strategy used in subsequent years [[10](#ref-sutherland1998),[11](#ref-palacin2011)]. Although this transfer of information is an effective mechanism for preserving migratory patterns through generations, how these trends become established after a population is reintroduced on a landscape from which it had previously been extirpated is unclear. Jesmer et al. [[12](#ref-jesmer2018)] found that newly translocated ungulate populations initially lost their migratory tendencies and it took many generations to re-establish such patterns, but that migratory trends eventually stabilized.

Trumpeter swans (*Cygnus buccinator*), the largest waterfowl species in North America, were widespread throughout much of the continent prior to European colonization [[13](#ref-alison1975)]. Due to widespread hunting for meat, skins for powder puffs, and feather quills for writing instruments, trumpeter swans were nearly extirpated in the lower 48 U.S. states and southern Canada, and reached an estimated low of 70 individuals in the 1930s [[14](#ref-banko1960)]. Low numbers of trumpeter swans led to the establishment of Red Rock Lakes National Wildlife Refuge (RRLNWR) in the confluence of Montana, Wyoming, and Idaho in 1935, which was the last vestige of a breeding swan population in the U.S. (outside of Alaska) [[15](#ref-shea2002)]. As trumpeter swan numbers at RRLNWR started to rise, this population became a source for reintroduction efforts in other parts of the historical breeding range of trumpeter swans. Trumpeter swans from RRLNWR were translocated to several U.S. states to augment and increase the abundance and distribution of the diminished Rocky Mountain Population (RMP) in the inter-Mountain West and to restore the Interior Population (IP), which had been extirpated in eastern North America [[15](#ref-shea2002)]. In the 1950s, aerial surveys in central Alaska revealed abundant numbers of trumpeter swans in the Pacific Coast Population (PCP), and this group subsequently provided the majority of swans used for reintroductions within the IP [[16](#ref-hansen1971),[17](#ref-matteson1988)]. An important distinction between these source populations is that PCP swans breeding in Alaska migrate to British Columbia and the northwestern United States each winter, whereas RMP swans from RRLNWR are non-migratory [[18](#ref-baskin1993),[19](#ref-oyler-mccance2007)].

Estimates of IP abundance have increased dramatically since reintroductions began in the 1960s, and both population size and distribution have expanded significantly [[20](#ref-groves2017)]. Trumpeter swans currently breed throughout most of the western Great Lakes region, including in Minnesota, Wisconsin, Michigan, Iowa, Manitoba, Ontario, and Ohio. Beyond estimates of population size and trends, however, there is relatively little recent information about their ecology, including seasonal movements and migration patterns. For example, it is not known what proportion of the IP remains resident on their breeding range during the winter, the extent (i.e., distance) of movement for those swans that do leave their breeding territories, the timing of migratory periods (e.g., autumn departure, spring arrival), and the magnitude of intra- and inter-individual variability in migration behavior. A more comprehensive understanding of when and where IP swans move throughout the annual cycle (especially the non-breeding season), including any differences related to breeding status or latitude will better elucidate wintering area habitat requirements and inform optimal study design for surveys to index abundance.

Many factors likely influence an individual swan’s decision to leave its breeding territory during the non-breeding season, the distance migrating individuals travel, and the degree of among-individual variability in movements for swans breeding at locations in close proximity to one another; these factors include life history requirements, knowledge transfer of migratory traditions, and inherent genetic control of migration [[21](#ref-alerstam2003)–[23](#ref-chapman2011)]. Arriving early in the spring allows individuals to re-establish and defend a breeding territory and lay and incubate eggs early during the breeding period when nest success and survival of offspring is generally highest [[24](#ref-dawson2000)–[26](#ref-blums2002)]. Similarly, there are advantages to staying on breeding territories longer in the autumn to allow cygnets time to learn to fly and develop sufficient fat reserves to migrate south for the winter [[27](#ref-lok2017),[28](#ref-winger2021)]. Survival rates of migrants are typically lowest during the non-breeding period of the annual cycle due to challenges associated with navigating relatively unfamiliar landscapes and the high energetic demand of migration [[29](#ref-sillett2002),[30](#ref-rushing2017)]. Yet, by migrating to a more temperate area during the wintering period, swans can increase their access to food and other resources that allow them to avoid harsh winter conditions in their breeding territories, thereby balancing potential costs of migration with the benefits of increased resource availability [[21](#ref-alerstam2003),[31](#ref-somveille2015)].

It is likely that the drivers of migration vary within the IP based on the location of a swan’s breeding territory. Cues for migration can include declines in food availability, which may also be affected by density-dependent intra-specific competition [[32](#ref-rappole2013)]. Swans that spend the summer at different latitudes experience varying environmental conditions that may influence arrival in spring, such as the timing of ice melt and vegetative greenness [[33](#ref-lasorte2014),[34](#ref-lasorte2021)], and departure in the autumn, such as ice formation on shallow wetlands and plant senescence [[35](#ref-schummer2010),[36](#ref-xu2019a)]. Swans breeding farther from the equator contend with shorter growing seasons and greater pressures for offspring to sufficiently develop flight before environmental conditions dictate migrating south for the winter [[37](#ref-stafford2014a)]. The ‘push’ to avoid the harsh winter conditions varies substantially throughout the IP breeding range, with concurrent implications for decisions related to migration propensity and timing. Many populations include some individuals that migrate each year while others are residents (i.e., partial migration), which can result in higher overall fitness [[23](#ref-chapman2011),[38](#ref-lundberg1988),[39](#ref-lundberg2013)]. We expected the propensity for trumpeter swans to migrate to be higher in more northern latitudes.

To better understand current movement ecology of the re-established IP trumpeter swans, we marked a sample of swans with GPS-GSM transmitters and monitored their movements over multiple annual cycles. Our primary goal was to better understand how a re-established population of trumpeter swans derived from different source populations uses a novel landscape. Our specific objectives were to quantify 1) the proportion of the IP that is migratory and the extent of migratory movements, 2) migration phenology (e.g., timing of autumn departure, spring arrival, and migration duration), and 3) associations between annual movement patterns and breeding status and breeding location.

## Methods

### Study Area

We captured IP swans from 2019–2022 throughout their current breeding distribution [[20](#ref-groves2017)] and during the breeding period, except for 4 swans captured during winter in Arkansas (Fig. 1). We deployed transmitters on IP trumpeter swans as far north and west as southern Manitoba (51.1° N, 99.7° W), as far south as Arkansas (35.5° N, 91.9° W), and as far east as Ohio (41.4° N, 80.7° W). Capture locations occurred in a mix of Laurentian Mixed Forest, Prairie Parkland, Eastern Broadleaf Forest, and Aspen Parklands [[40](#ref-cleland1997)].

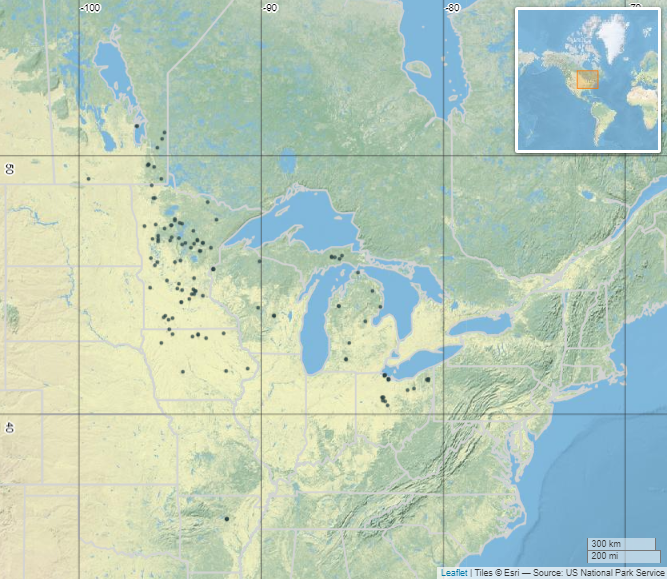


Figure 1: Capture locations of Interior Population trumpeter swans collared with GPS-GSM transmitters from July 2019–January 2022.

### Capture and Handling

We captured all swans during the definitive prebasic molt period when adult swans replace their remiges, and are therefore flightless (except for 4 captured in Arkansas using snares during the winter), using a combination of jon boats, airboats, step deck transom boats, and square-stern canoes. We primarily used long-tail mud motors (Powell Performance Fab, Hutchinson, Minnesota, USA) to navigate shallow wetlands where swans were located, though some swans were captured using boats with surface-drive motors (Gator-Tail, Loreauville, Louisiana, USA) or non-motorized canoes and kayaks. We hand-captured swans using shepherd’s crook poles or large landing nets [[41](#ref-eltringham1978),[42](#ref-hindman2016)]. We predominantly targeted adult swans, which have higher survival rates than juveniles, to maximize the longevity of telemetry data collection [[43](#ref-lockman1990)].

We marked swans with two types of collars; 55-g neck collars with GPS-GSM transmitters incorporated into the collar housing (Model OrniTrack-N62 3G, Ornitela, Vilnius, Lithuania) and 140-g GPS transmitters (Model CTT-ES400, Cellular Tracking Technologies, [CTT], Rio Grande, New Jersey, USA) that were adhered to 64-mm neck collars (Haggie Engraving, Crumpton, Maryland, USA). All collar and transmitter types weighed <3% of the marked individual’s body weight, as per animal care requirements. Both types of neck collars contained a unique alpha-numeric code for visual identification. Swans captured in Michigan were fit with CTT collars and all other swans in the study were fit with Ornitela collars. All transmitters were programmed to collect GPS locations at 15-min intervals throughout the 24-hr daily period. We leg-banded each swan with a U.S. Geological Survey butt-end aluminum band and determined sex via cloacal examination. We assigned a breeding status to each swan at the time of capture depending on if a mate and cygnet were present (‘breeder’ status), if a mate was present but no cygnets were observed (‘paired’ status), or if neither a mate nor cygnets were present (‘non-breeder’ status). Due to logistical constraints, we were unable to continuously monitor the breeding status of swans in subsequent years, and we retained the initial breeding status designation for all analyses. However, previous swan research has documented the annual probability of renesting at >90% [[44](#ref-birkhead1985),[45](#ref-ellis2007)]. We use the term breeding (e.g., breeding latitude, breeding territory) to indicate either breeding territory for successful breeders, or capture location for non-breeding swans.

### Migration Phenology Classification

Accurate quantification of migration phenology was a key objective of this study. Given the size of the dataset (~6M locations over 252 swan-years), we developed an efficient workflow to segment location data into periods of the annual cycle and estimate migration metrics. Many migration segmentation approaches are based on spatiotemporal criteria that require subjective species-specific decisions, reducing reproducibility and limiting the potential to generalize to other studies, especially given the complexity of migratory behaviors many species exhibit [[46](#ref-soriano-redondo2020),[47](#ref-vandekerk2021)].

To more objectively quantify migration phenology, we used a model-driven approach with displacement from the breeding site used to segment the annual cycle into stationary periods that correspond with breeding, stopover, and wintering areas. We first calculated annual time-series of Net-Squared Displacement (NSD) values for each swan (referred to as a ‘swan-year’ dataset), using 1 July (a time of year that swans are relatively stationary) as a cutoff date between years for individuals with multiple years of GPS data, as well as an origin point for NSD values, and then thinned datasets to contain a single averaged displacement value per day [[48](#ref-wolfson2022)]. After excluding 11 swan-year datasets with <30 days of data, we iteratively fit a series of 7 intercept-only piecewise regression models to each time-series using t-tail priors for models with more than 2 changepoints [[48](#ref-wolfson2022),[49](#ref-lindelov2020)]. The syntax of each model corresponded to an increasing number of intercepts included (from 1–7) for average displacement values throughout the time series separated by breakpoints in time where the intercept values transitioned; therefore intercepts represent stationary segments in time corresponding to periods of the annual cycle, and breakpoints are the transitions between these segments that provide information on the timing of migration events such as autumn departure and spring arrival (Fig. 2).

Figure 2: An example of extracting migration phenology metrics from a fitted piecewise regression model of an annual time-series of displacement values for an individual trumpeter swan.

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We fit all piecewise regression models in JAGS [[50](#ref-plummer2003)] using the *mcp* package [[49](#ref-lindelov2020)] in Program R version 4.0.2 [[51](#ref-rcoredevelopmentteam2022)], using 15,000 iterations and a burn-in period of 10,000. We used the *future* R package to run all scripts in parallel via the Minnesota Supercomputing Institute using a partition with 24 cores and 50GB RAM per core [[52](#ref-bengtsson2021)]. We evaluated Markov-chain Monte Carlo (MCMC) chain convergence via the Gelman-Rubin convergence diagnostic and excluded models containing any parameters with a value of >1.1 from further consideration [[53](#ref-brooks1998)]. Through extensive testing, we found that models with MCMC samples that failed to converge in distribution after 15,000 samples were typically associated with poorly fitting models (i.e., fitting a single intercept despite multiple migration periods or fitting multiple breakpoints during a stationary period). If all parameters in a model passed the threshold, we evaluated model fit and predictive performance using leave-one-out cross-validation (LOO-CV) with Pareto smoothed importance sampling to estimate the Expected Log Predictive Density (ELPD), using the *loo* package [[54](#ref-gelman2014),[55](#ref-vehtari2017)]. The ELPD values reflect the ability of the model to predict the posterior density of withheld data. We used LOO-CV to choose the ideal number of breakpoints (and thereby segments that correspond to migratory periods) for each swan-year data partition.

We qualitatively inspected the visual fit of each best-supported model (based on ELPD) for each swan-year dataset and removed 11 (out of 241 total datasets) that were obvious poor fits such that information from the breakpoints and intercepts would not adequately describe annual migration phenology. We also excluded all segments <2 km from the previous segment and all changepoints <2 days from the previous changepoint. We then extracted parameter values to represent the movement metrics of interest (Fig. 2). We extracted autumn departure dates for individuals that moved >100 km from breeding locations by 1 December. We extracted spring arrival dates for individuals that moved >100 km from breeding locations during the non-breeding season and that returned within 10 km of their previous summer territory. We estimated migration duration as the difference in time between autumn departure and spring arrival the subsequent year for all swan-year datasets that met the requirements to estimate those two terms.

### Migration Extent

An exploratory analysis of annual movement data suggested a strong linear association between breeding latitude and migration extent for many individuals, whereas others moved a much lesser extent, especially at lower latitudes. It is possible that these patterns reflect two different migratory strategies with one segment of the population consistently migrating to lower latitudes and a second segment of the population using areas with open water closer to the location of their breeding site during winter.

We used a 2-component mixture model (i.e., a model with two different groups of individuals, each following a different response pattern) to describe the relationship between breeding latitude and migration extent. Let represent the migration extent for individual in year , and let be a latent variable representing the group membership of each individual. We assumed migration extent was linearly related to breeding latitude for individuals with and was much lower and non-linearly related to breeding latitude for individuals with :

The takes one of two functional forms depending on the group assignment, ; either a linear model when with and as the intercept and slope terms, and as the breeding latitude for individual in year , or a non-linear model when with , , as the intercept and slope, and as an exponential term on . In addition, we assumed the variance of depended on the latent state .

The latent state (0 or 1) for assignment to a group (i.e., migration strategy) for each individual is modeled as:

We used normal priors for , , and , parameterized in terms of their mean and precision (). We used uniform priors for ), , , , and . We used priors partially informed by the data for the intercepts of each group, and , based on the assumption that group 1 migrates a greater extent than group 2.

We implemented the model in JAGS via the *R2jags* package using 3 MCMC chains with 30,000 iterations, a burn-in of 10,000, and a thinning rate of 10 [[50](#ref-plummer2003),[56](#ref-su2021b)]. We determined convergence of chains by assessing trace plots and using the Gelman-Rubin statistic with <1.1[[53](#ref-brooks1998)].

### Migration Phenology

We visualized observations of migration phenology across the range of breeding latitudes using scatterplots, facetted by year, with a univariate linear model fit as a statistical smoother to quantify the amount of variation in each migration metric explained by latitude. We visualized observations of migration phenology grouped by breeding status with boxplots showing the medians, inter-quartile ranges, and outliers. To test associations between predictor variables and migration phenology, we fit separate linear mixed models (LMM) using the *lme4* package to each response (autumn departure date, spring arrival date, and migration duration), with a random intercept for each individual to account for repeated measures (i.e., multiple migrations by the same individual), and fixed effects for sex, breeding status, and breeding latitude [[57](#ref-bates2014)]. For the LMMs fit to autumn departure dates and migration duration, we estimated the variance term for the random intercept to be 0, so we dropped the random effect and refit linear models with the same set of covariates. The lack of among-individual heterogeneity after accounting for fixed effects may reflect a true signal or may simply be the result of insufficient across-year repeated measures within the same set of individuals. We assessed model assumptions using the *performance* R package [[58](#ref-ludecke2021)]. To conduct post-hoc pairwise comparisons involving the categorical levels of breeding status (i.e., breeder, paired, non-breeder), we used the *emmeans* package with Tukey’s Honest Significant Difference (HSD) to adjust p-values and confidence intervals for each comparison [[59](#ref-lenth2023)]. We approximated the degrees of freedom for the HSD test of the spring arrival LMM using the Kenward–Roger method [[60](#ref-kenward1997)].

## Results

We deployed 113 collars with GPS-GSM transmitters on 126 trumpeter swans (including 13 redeployments using collars recovered from mortalities), resulting in 252 unique ‘swan-year’ telemetry datasets (Fig. S1). Of the 126 swans, 78 were female and 48 were male; 73 were breeding adults (cygnets present), 22 were adults with mates present but no cygnets observed at time of capture, 24 were non-breeding adults captured while in large groups, and six were cygnets at the time of capture (however, data from cygnets were not used in analyses).

### Migration Extent

Annual movements of IP trumpeter swans were highly variable. After filtering out 31 swan-year datasets from 27 individuals with incomplete coverage to estimate annual trends, 59% (*n*=68) of remaining IP swans (*n*=116 individuals) made seasonal movements to distant wintering areas (long-distance migration defined as moving >100 km from breeding site during the non-breeding season), 16% (*n*=19) underwent regional migration (>25 km and <100 km), 19% (*n*=22) exhibited local movements (<25 km), and 6% (*n*=7) exhibited multiple migration strategies across different years: regional and long-distance (*n*=3), and local and regional (*n*=4). The mixture model classified all individuals to a group with high likelihood, so it was unnecessary to set a user-defined threshold determining group assignment. There was a strong association between breeding latitude (mostly between 43 and 53 degrees North latitude) and the extent of migration (Fig. 3). Yet, many swans with breeding sites between 40 and 48 degrees North latitude exhibited minimal movement during the non-breeding period. We considered these individuals to exhibit local seasonal movements, with most of these swans leaving their summer territory or increasing their overall space use during the winter, likely to increase access to ice-free water or access to food.

Figure 3: Extent of migration versus breeding/capture latitude with color indicating the probability of assignment to one of two migration strategies within a 2-component mixture model describing the relationship between latitude and migration extent. Grey areas depict the 95% credible intervals for each strategy.

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### Migration Phenology

#### Autumn departure

The average autumn departure date from breeding territories across years for all long-distance (>100 km) migrants was 1 November with a standard deviation of 20 days, and yearly averages ranged from 25 October to 7 November (Fig. 4, Table S1, Table S2). Long-distance migrants at higher latitudes left territories earlier in autumn than swans at lower latitudes, though the confidence interval for the coefficient associated with breeding latitude spanned 0 ( = -1.3, 95% CI = -3.0–0.5; Fig. 6). Estimated autumn departure dates of breeding swans were, on average, 11 days (95% CI = -0.4–22.4) later than non-breeders, and 8 days (95% CI = -4.2–19.4) later than paired swans (Fig. 6, Table S3).

#### Spring Arrival

The average annual site fidelity rate for spring arrival (i.e., long-distance migrants that traveled >100 km during the non-breeding period and returned to within 10 km of their previous summer territory) was 37% for non-breeders, but surprisingly, only 50% for paired swans and 48% for successful breeders (although initial breeding status may have changed for some swans). The average spring arrival date across years was 5 March with a standard deviation of 10 days, and yearly averages ranged from 2 March to 7 March (Fig. 4, Table S4, Table S5). Swan that did return to within 10 km of the previous territory arrived earliest at southern latitudes. On average, swans arrived 5 days (95% CI = 3.9–6.4) later for every increase of 1 degree of breeding latitude (corresponding to approximately 111 km; Fig. 6). Differences in spring arrival between breeding categories were minimal, and confidence intervals spanned 0 for all two-way comparisons (breeding–non-breeder, = 2.7, 95% CI = -8.9–14.4; breeder–paired, = -3.1, 95% CI = -12.2–5.9; non-breeder–paired, =-5.9, 95% CI = -18.6–6.9; Fig. 6, Table S6).

#### Migration Duration

We did not detect an association between migration duration and breeding latitude ( = 0.2, 95% CI = -4.4–4.8; Fig. 6). Breeders had the shortest average migration duration of 125 days, 19 days (95% CI = -50.1–11.8) less than non-breeders, and 13 days (95% CI = -36.2–9.3) less than paired swans (Fig. 6, Table S9).

Figure 4: Timing of autumn departure and spring arrival as a function of breeding/capture latitude and facetted by year. Grey areas show 95% confidence intervals of linear models fit with latitude as the predictor and date as the dependent variable. R-squared values indicating the amount of variance in timing explained by latitude are superimposed on each plot.

Figure 4: Timing of autumn departure and spring arrival as a function of breeding/capture latitude and facetted by year. Grey areas show 95% confidence intervals of linear models fit with latitude as the predictor and date as the dependent variable. R-squared values indicating the amount of variance in timing explained by latitude are superimposed on each plot.

Figure 5: Migration phenology dates by breeding status (breeder, paired, and non-breeder). Boxes bound the 25th and 75th percentiles, solid lines within the boxes indicate the median, lines extend to 1.5 times the interquartile range, and points correspond to individual swan-years.

Figure 5: Migration phenology dates by breeding status (breeder, paired, and non-breeder). Boxes bound the 25th and 75th percentiles, solid lines within the boxes indicate the median, lines extend to 1.5 times the interquartile range, and points correspond to individual swan-years.

Figure 6: Model coefficient estimates and 95% confidence intervals for a linear mixed model of spring arrival and linear models of autumn departure and migration duration (defined as the number of days away from the breeding/capture territory). The covariate for sex represents the difference between males and females (the reference category). The coefficients for non-breeder and paired contrast these categories with breeders (the reference category). Blue results represent positive coefficient estimates and red results represent negative coefficient estimates.

Figure 6: Model coefficient estimates and 95% confidence intervals for a linear mixed model of spring arrival and linear models of autumn departure and migration duration (defined as the number of days away from the breeding/capture territory). The covariate for sex represents the difference between males and females (the reference category). The coefficients for non-breeder and paired contrast these categories with breeders (the reference category). Blue results represent positive coefficient estimates and red results represent negative coefficient estimates.

## Discussion

Annual movements of IP swans were highly variable in their extent and timing, with a continuum of movements exhibited each year. Much of this variability was related to factors tied to natural history demands (e.g., breeding status) and response to environmental conditions (e.g., through associations with breeding latitude). It should be noted that the degree to which annual variability in breeding status may affect inference of migration phenology has not been directly quantified. It is unclear, however, why IP swans seemed to exhibit multiple migration strategies even at similar latitudes where the effects of environmental conditions (e.g., temperature, precipitation) should also be similar. Differences in migration strategies may be influenced by other factors such as social dynamics, genetic lineage, or site-specific differences in the availability of open water and food. Fine-scale spatial variation, especially related to open water, may have a large influence on determining which swans undergo long-distance migration and which can spend the winter at higher latitudes.

The migration phenology of IP trumpeter swans appears similar to that of many other long-lived avian migrants, with breeders having the shortest migration duration (though 95% CIs for the differences in breeding status spanned 0; [[61](#ref-conklin2010)–[63](#ref-nilsson2013)]). Spring arrival dates were highly correlated with breeding latitude, as swans likely waited until shallow lakes on their breeding territories were relatively close to ice-out dates (Fig. 6). We did not, however, find an association between breeding latitude and migration duration (Fig. 6), suggesting that swans are capable of returning from wintering areas to breeding locations quickly, and that migration timing is more limited by conditions on the breeding grounds than the physiological demands of flight.

Breeding latitude was associated with the likelihood of migrating and the extent of movement during the non-breeding season (Fig. 3). Individuals that breed in the northern part of the IP range all made relatively long-distance autumn migrations. Given the severity of winter conditions at higher latitudes, options for accessing open water created by currents on rivers or anthropogenic influences (e.g., below dams, on lakes with aerators) were likely not close to breeding locations. Autumn migration distances of swans breeding at mid-latitudes were variable, with some swans moving relatively long distances, whereas others only exhibited local or regional movements. These latter swans likely remained near their breeding locations during the non-breeding season if they were able to find open water and access to food. Swans breeding at lower latitudes all remained close to their breeding locations year-round, as the local environmental conditions likely continued to provide open water and access to food.

Several factors may influence movements and migratory patterns, including transmission of migratory information between generations genetically and through social learning [[64](#ref-akesson2020)]. For some species with short lifespans (e.g., songbirds), migration is considered innate and primarily due to genetics based on observations of individuals that complete their first migrations independently without parents or other conspecifics to guide them [[65](#ref-berthold1991)]. However, for species with long generation times and high levels of parental care, such as trumpeter swans, social learning typically also plays an important role in forming migration strategies [[9](#ref-mueller2013)]. Collective knowledge has been shown to accumulate over generations to drive migration patterns and improve efficiency in flocking species with socially learned migration behaviors. In reintroduced populations of Whooping Cranes (*Grus americana*) that were initially trained (i.e., learned) to migrate by following aircraft, migratory efficiency of flocks rapidly increased when older individuals were present [[9](#ref-mueller2013),[66](#ref-sasaki2017)]. Thus, experience and familiarity with the landscape also likely play important roles in determining migratory movements. For swans, in particular, knowledge of sites with access to open water and food may be important for allowing swans to ‘escape’ migration in more northern latitudes, and this knowledge may be passed down through generations.

IP swans are unique because their reintroduction to central North America occurred relatively recently (<50 years) from a mix of source populations with varying migratory strategies [[67](#ref-ransler2011)]. Thus, there may exist heterogeneity within the population in terms of genetic makeup that influence swan movements. Although previous studies have considered genetic differences of IP source populations using microsatellites, contemporary research methods (i.e., population genomics) are needed to better evaluate the genetic structure of the IP as it relates to other trumpeter swan populations [[19](#ref-oyler-mccance2007),[67](#ref-ransler2011)]. Continued monitoring is also necessary to determine whether population-level migration characteristics (e.g., annual proportion of IP swans that migrate) are still in flux or if conditions have stabilized akin to the environmental threshold model, in which certain parts of the population are obligate residents or migrants and annual environmental conditions determine the migration threshold that dictates the outcome of facultative migrants; a population-level paradigm thought to be maintained predominantly through genetic variation [[68](#ref-pulido2011)]. Ultimately, our study provides a snapshot in time of current IP trumpeter swan migration patterns ~50 years following initial reintroduction efforts, and population-level trends may still be stabilizing and exhibiting variation based on annual environmental conditions.

In addition, the history of IP reintroduction includes many years of anthropogenic influences, at the level of both wildlife managers and private citizens, that have likely influenced migration patterns, and it is not well understood to what extent these influences may be passed down through future generations [[15](#ref-shea2002)]. Some of these influences include intentional feeding during the winter at sites of high IP swan density and lake aerators that keep lakes ice-free throughout the winter to prevent winter kill of fish [[69](#ref-ellis1989)–[71](#ref-ballard2021a)]. Although supplemental feeding has been discontinued by state and provincial management agencies throughout the IP distribution, the practice continues with some private citizens, and potential effects include not only curtailment of migration but also increased risk of pathogen transmission [[72](#ref-satterfield2018)]. There is also increasing evidence that many local groups of swans have discovered field feeding as an additional strategy to acquire resources, and this knowledge likely impacts migratory behavior, though additional research is needed to quantify the spatial extent, intensity, and timing of field-feeding in trumpeter swans. [[73](#ref-varner2008),[74](#ref-baldassarre2014)].

## Conclusions

Knowledge of current IP swan migration patterns can help inform IP swan conservation efforts by providing accurate limits of the wintering range and quantifying variability in migration strategies. Under current conditions, winter habitat for swans occurs in all but the most northerly portions of the IP breeding distribution and at mid-latitudes south of the current breeding distribution. Managers may need to conserve habitat during the non-breeding season for both long-distance migrants and residents that remain on their breeding territories year-round while also anticipating the impacts of future climate scenarios [[75](#ref-reese2017)]. It is not clear how changing climate conditions will influence future IP swan migration strategies, but currently, multiple migration strategies exist within the IP, providing a range of behavior as the basis for adaptation to changing conditions that may help offset potential negative impacts of potential asynchrony between migration phenology and environmental conditions [[76](#ref-nussey2005)]. The variability present in IP annual movements may position IP swans to quickly adapt to changing climate.

### Availability of data and materials

All R code used in this analysis are available at <https://github.com/dwwolfson/swan_migration_manuscript>. Data used to support this study are available from the corresponding author upon request.

### Abbreviations

**CI:** Confidence interval

**ELPD:** Expected log predictive density

**GPS-GSM:** Global positioning system - global system for mobile communications

**HSD:** Honest Significant Difference

**IP:** Interior Population

**LMM:** Linear mixed model

**LOO-CV:** Leave-one-out cross-validation

**MCMC:** Markov-chain Monte Carlo

**NSD:** Net-squared displacement

**PCP:** Pacific Coast Population

**RMP:** Rocky Mountain Population

**RRLNWR:** Red Rock Lakes National Wildlife Refuge

## Declarations

### Ethics approval and consent to participate

Protocols for capturing and marking trumpeter swans in U.S. states were approved by the University of Minnesota Animal Care and Use Committee (protocol no. 1905-37072A), the U.S. Fish and Wildlife Service (Research & Monitoring Special Use Permits no. K-10-001, M-20-002, and M-21-014), the U.S. Geological Survey Bird Banding Laboratory (Federal Bird Banding Permit no. 21631) and state-specific permits approved by each state wildlife agency involved. All capture and marking of trumpeter swans in Manitoba was conducted under Federal Scientific Permit to Capture and Band Migratory Birds (no. 10271), Federal Animal Care Committee approval (project 20FB02), Provincial Species at Risk Permit (no. SAR20012), and Provincial Park Permit (no. PP-PHQ-20-016).

### Consent for publication

Not Applicable

### Competing interests

The authors declare that they have no competing interests.

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### Authors’ contributions

DWW, JRF, and DEA designed the methodology; DWW, RTK, ABT, LK, BK, SC, TF, TH, SM, TM, DF, TRC, and DEA collected the data; DWW analyzed the data; DWW wrote the first draft of the manuscript which was revised primarily by JRF and DEA. All authors reviewed the manuscript and gave final approval for publication.

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