Migration ecology of a re-established trumpeter swan population derived from migratory and non-migratory founders

David W. Wolfson, Randall T. Knapik, Anna Buckardt-Thomas, Laura Kearns, Brian Kiss, Steven Cordts, Taylor Finger, Tyler Harms, Sumner Matteson, Tiffany Mayo, Timothy Poole, John Moriarty, Margaret Smith, Christine Herwig, Drew Fowler, Thomas R. Cooper, John R. Fieberg, David E. Andersen

18 January, 2024

## 0.1 Abstract

### 0.1.1 Background

Individuals within a population often exhibit a continuum of movement strategies (from residency to inter-continental seasonal migration), and different movement strategies may affect fitness differently. In species such as trumpeter swans (*Cygnus buccinator*), some populations populations migrate seasonally and some are resident, and both social learning and genetics may play a role in whether individual swans migrate. Trumpeter swans were historically widespread throughout much of North America, but unregulated market hunting decimated their abundance to near extirpation in the lower 48 states by the end of the century. The Interior Population (IP) of trumpeter swans was re-established in eastern North America by releasing individuals from both migratory and non-migratory populations, but their current annual movement patterns are largely unknown. Our goal was to describe seasonal movement patterns of IP trumpeter swans and quantify the proportion of the IP that is migratory, the extent and phenology (e.g., typical departure and arrival dates) of seasonal movements, the associations between movement patterns and breeding status and breeding location, and the degree of individual and population variability in migration patterns.

### 0.1.2 Methods

We deployed 113 GPS-GSM transmitters on IP trumpeter swans in 6 U.S. states and 1 Canadian province across the current IP breeding range to quantify their annual movements. 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, and then extracted dates of migration events. We also fit a latent state model to characterize population-level associations between breeding latitude and maximum extent of migration, and linear models to quantify associations in migration phenology.

### 0.1.3 Results

Annual movements of IP trumpeter swans were highly variable. At the individual level, we classified 59% of swan-year datasets as long-distance migration (defined as moving >100km from the breeding site), 16% as regional migration (>25 km and <100 km from breeding site), and 19% as non-migratory but exhibiting local movements (<25 km from breeding site), and 6% as exhibiting multiple migration strategies across years. The relationship between breeding latitude and migration extent was best described using a 2-component mixture model in which migration extent was linearly associated with breeding latitude for 1 group of individuals and was much lower and exhibited a non-linear association with breeding latitude for a second group of individuals. Breeding latitude was a significant predictor of spring arrival date, with swans arriving earlier to territories at lower latitudes. Swans at higher latitudes tended to depart earlier in the autumn, and breeding latitude had no relationship with overall migration duration. Breeding status was a significant predictor of autumn departure date, with successful breeders leaving later in the autumn than non-breeders, but had a weak relationship with spring arrival and migration duration.

### 0.1.4 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).

## 0.2 Introduction

Migration is a behavioral mechanism widely used by all major vertebrate groups (e.g., birds, fish, mammal, herpetofauna) 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 scarce 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) and Canada [[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 the Great Lakes region of 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, but 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 has 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 inform wintering area habitat use and 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 and knowledge transfer of migratory traditions [[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 migrating individuals 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 pouplations 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.

## 0.3 Methods

### 0.3.1 Study Area

We captured IP swans 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 central Arkansas (35.5° N, 91.9° W), and as far east as central Ohio (40.6° N, 82.7° W). Capture locations occurred in a mix of Laurentian Mixed Forest, Prairie Parkland, Eastern Broadleaf Forest, and Aspen Parklands [[40](#ref-cleland1997)].

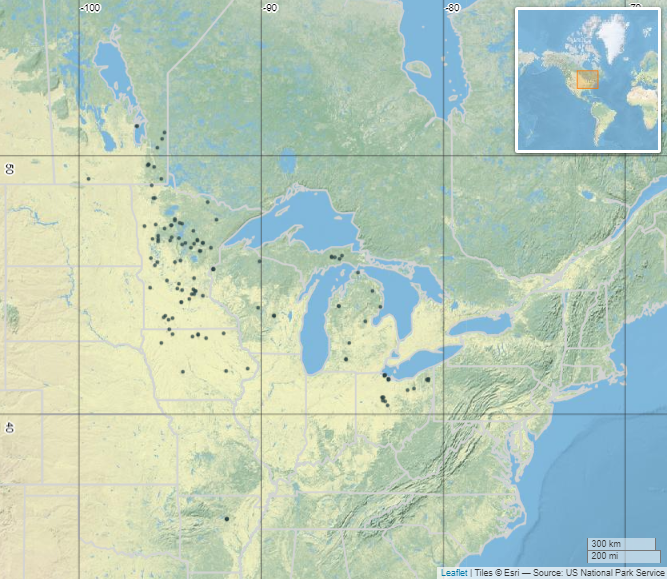


Figure 1: Capture locations for Interior Population trumpeter swans collared with GPS-GSM transmitters from July 2019–January 2022.

### 0.3.2 Capture and Handling

We captured all swans (except for 4 captured in Arkansas using snares during the winter) during the definitive prebasic molt period when adult swans replace their remiges, and are therefore flightless, 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 surface-drive motors (Gator-Tail, Loreauville, Louisiana, USA). We hand-captured swans using a shepherd’s crook pole [[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). 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.

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 Permit no. K-10-001), 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).

### 0.3.3 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 [[44](#ref-soriano-redondo2020),[45](#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, 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, and then condensed the dataset to a single average displacement value per day. 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 [[46](#ref-wolfson2022)]. The syntax of each model corresponded to an increasing number of intercepts included (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.

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.

We fit all piecewise regression models in JAGS [[47](#ref-plummer2003)] using the mcp package [[48](#ref-lindelov2020)] in Program R version 4.0.2 [[49](#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 on the Minnesota Supercomputing Institute (MSI) using a partition with 24 cores and 50GB RAM per core [[50](#ref-bengtsson2021)]. We evaluated MCMC chain convergence via the Gelman-Rubin convergence diagnostic and excluded models containing any parameters with a value of >1.1 from further consideration [[51](#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 [[52](#ref-gelman2014),[53](#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/capture locations by 1 December. We extracted spring arrival dates for individuals that moved >100 km from breeding/capture 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.

### 0.3.4 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 to 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 seeking out areas with open water closer to the location of their breeding site to survive the winter.

We use 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 :

where is the extent of migration for individual in year , conditional on the latent state for each individual, . Each latent state has a separate variance term, , depending on group assignment.

The term takes two functional forms depending on the group assignment of ; either the linear model when with and as the intercept and slope terms, and as the breeding latitude for individual in year , or the non-linear model when with , , as the intercept and slope, and as an exponential term on .

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 . 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 to a larger 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 [[47](#ref-plummer2003),[54](#ref-su2021b)]. We determined convergence of chains by assessing trace plots and using the Gelman-Rubin statistic with <1.1[[51](#ref-brooks1998)].

### 0.3.5 Migration Phenology

We visualized differences in autumn departure and spring arrival across the range of breeding latitudes using scatterplots, facetted by year, with a univariate linear model fit as a statistical smoother for each year to quantify the amount of variation latitude explained in the migration metric. We visualized differences in migration phenology between breeding classes 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, and fixed effects for sex, breeding status, and breeding latitude [[55](#ref-bates2014)]. For the LMMs fit to autumn departure dates and migration duration, the variance term for the random intercept was estimated to be 0, so instead, 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 simply the result of insufficient across-year repeated measures within the same individuals.

## 0.4 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 (Supplemental Materials deployment figure). 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 6 were cygnets at the time of capture.

### 0.4.1 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) underwent long-distance migration (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). For many swans that exhibited long-distance migration and swans breeding at higher latitudes, there was a strong association between breeding latitude (mostly between 43 and 53 degrees North latitude) and the extent of migration (Fig. 3). Many swans with breeding sites between 40 and 48 degrees North latitude, however, 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 open water or access to food.

Figure 3: Breeding/capture latitude versus extent of migration with color indicating the probability of assignment to one of 2 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.

Figure 3: Breeding/capture latitude versus extent of migration with color indicating the probability of assignment to one of 2 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.

### 0.4.2 Migration Phenology

Average departure date from breeding territories in the autumn across years for all long-distance migrants (>100 km) was 1 November with a standard deviation of 20 days, and yearly averages ranged from 25 October to 7 November (Fig. 4, Supplemental tables). 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, Supplemental tables). There was little evidence of a relationship between breeding latitude and autumn departure date (Fig. 6), but breeders left later, on average, than non-breeders or paired swans, and the difference between breeders and non-breeders was significant (Fig. 5, Fig. 6), Supplemental tables). The relationship between spring arrival (i.e., for swans that traveled >100 km during the non-breeding period and returned to within 10 km of their previous summer territory) and breeding latitude was significant, with swans returning to their territories sooner at lower latitudes. Although breeders, on average, returned earlier to their territory in the spring than paired and non-breeding swans (Fig. 5), the relationship between breeding status and spring arrival date was not significant (Fig. 6). There was no relationship between breeding latitude and migration duration (Fig. 6). Breeders, on average, had the highest migration duration, followed by paired and then non-breeding swans (Fig. 5), though the relationship between breeding status and duration was not significant (Fig. 6).

Figure 4: The 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 independent variable 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: The 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 independent variable 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). Boxplots show 75% inter-quartile range, black lines are median values for each category, and points indicate individual swan-years.

Figure 5: Migration phenology dates by breeding status (breeder, paired, and non-breeder). Boxplots show 75% inter-quartile range, black lines are median values for each category, and points indicate individual swan-years.

Figure 6: Model coefficient estimates and 95% confidence intervals (CIs) for a linear mixed model for spring arrival and linear models for 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 the baseline of female and the alternative treatment of male. The 2 covariates for breeding status represent the treatment between the baseline of succesful breeders. The 2 covariates with CIs that did not cross the vertical black line (breeding/capture latitude with spring arrival, and the difference between breeders and non-breeders with autumn departure) were statistically significant.

Figure 6: Model coefficient estimates and 95% confidence intervals (CIs) for a linear mixed model for spring arrival and linear models for 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 the baseline of female and the alternative treatment of male. The 2 covariates for breeding status represent the treatment between the baseline of succesful breeders. The 2 covariates with CIs that did not cross the vertical black line (breeding/capture latitude with spring arrival, and the difference between breeders and non-breeders with autumn departure) were statistically significant.

## 0.5 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 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 spending less time undergoing migration than non-breeders [[56](#ref-conklin2010)–[58](#ref-nilsson2013)]. Spring arrival dates were associated with both breeding latitude and breeding status, as swans likely needed to wait until shallow lakes on their breeding territories were close to ice-out dates, and successful breeders needed to arrive earlier to defend their territories from other swans (Fig. 4 and (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.

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 within close proximity of breeding locations. Autumn migration distances of swans breeding at mid-latitudes were variable, with some swans moving relatively long distances, while others only exhibited local or regional movements. These latter swans likely remained near their breeding locations during the non-breeding season as long as they were able to find open water that provided 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 [[59](#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 [[60](#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),[61](#ref-sasaki2017)]. Thus, experience and familiarity with the landscape also likely plays an important role 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 [[62](#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),[62](#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 [[63](#ref-pulido2011)]. Ultimately, our study provides a snapshot in time of current IP trumpeter swan migration patterns and population-level trends may be still stabilizing and exhibiting variation based on annual environmental conditions.

The history of IP reintroduction includes many years of anthropogenic influences, at the level of both wildlife managers and private citizens, that have likely caused considerable effects on 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 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 [[64](#ref-ellis1989)–[66](#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 [[67](#ref-satterfield2018)]. There is also increasing evidence that many local groups of swans have discovered field feeding as an additional strategy to acquire nutrients, though the timing when most field feeding occurs is not well documented [[68](#ref-varner2008),[69](#ref-baldassarre2014)].

Knowledge of current IP swan migration patterns can help inform IP swan conservation efforts by providing accurate limits of the wintering range and quantifying the 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 will need to conserve habitat during the non-breeding season for both long-distance migrants as well as residents that stay on their breeding territories year-round while also anticipating the impacts of future climate scenarios [[70](#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 [[71](#ref-nussey2005)]. The variability present in IP annual movements may position IP swans to quickly adapt to changing climate.

## 0.6 Availability of data and materials

All code necessary to reproduce the analyses are available at <https://github.com/dwwolfson/annual_mvmt> and will be archived at the Data Repository for the University of Minnesota upon acceptance.

## 0.7 Acknowledgements

We thank Dustin Arsnoe, Bruce Davis, Victoria Drake, Anthony Duffiney, David Hoffman, Steven Hogg, Joel Huener, Gary Ivey, Doug McArthur, Ciara McCarty, Luke Naylor, Mike North, Karen Rowe, Erik Thorson, and Ed Zlonis for assistance with fieldwork. We thank Barb Avers, Frank Baldwin, Wayne Brininger, Peter David, Walt Ford, David Luukkonen, Hattie Saloka for assistance with project logistics. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## 0.8 Funding

J.F. was supported by the National Aeronautics and Space Administration award 80NSSC21K1182 and received partial salary support from the Minnesota Agricultural Experimental Station. Initial funding for this project was provided in part by the Minnesota Environmental and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources (LCCMR), the U.S. Geological Survey, the Minnesota Cooperative Fish and Wildlife Research Unit, the U.S. Fish and Wildlife Service, the University of Minnesota, and the Minnesota Department of Natural Resources. Additional funding or project support was provided by the Michigan Department of Natural Resources, the Iowa Department of Natural Resources, the Canadian Wildlife Service branch of Environment and Climate Change Canada, the Cleveland Metroparks Zoo, the Great Lakes Indian Fish and Wildlife Commission, the Wisconsin Department of Natural Resources, Three Rivers Park District, the Arkansas Game and Fish Commission, and the Trumpeter Swan Society. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government, the University of Minnesota, or the State of Minnesota.

## 0.9 Author Information

### 0.9.1 Authors and Affiliations

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St Paul, MN, USA  
David W. Wolfson & John R. Fieberg

Minnesota Cooperative Fish and Wildlife Research Unit, St Paul, MN, USA  
David W. Wolfson

Michigan Department of Natural Resources, Lansing, MI, USA  
Randall T. Knapik

Iowa Department of Natural Resources, Boone, IA, USA  
Anna Buckardt-Thomas & Tyler Harms

Ohio Department of Natural Resources, Columbus, OH, USA  
Laura Kearns

Manitoba Wildlife and Fisheries Branch, Winnipeg, MB, CA  
Brian Kiss & Timothy Poole

Minnesota Department of Natural Resources, Bemidji, MN, USA  
Steven Cordts & Christine Herwig

Wisconsin Department of Natural Resources, Madison, WI, USA  
Taylor Finger & Sumner Matteson

Cleveland Metroparks Zoo, Cleveland, OH, USA  
Tiffany Mayo

Three Rivers Park District, Plymouth, MN, USA  
John Moriarty

Trumpeter Swan Society, Plymouth, MN, USA  
Margaret Smith

U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, Baton Rouge, LA, USA  
Drew Fowler

U.S. Fish and Wildlife Service, Bloomington, MN, USA  
Thomas R. Cooper

U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, St Paul, MN, USA  
David E. Andersen

### 0.9.2 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.

## References

1. Fryxell JM, Greever J, Sinclair ARE. [Why are Migratory Ungulates So Abundant?](https://doi.org/10.1086/284822) The American Naturalist. 1988;131:781–98.

2. Milner-Gulland EJ, Fryxell JM, Sinclair ARE. Animal Migration: A Synthesis. OUP Oxford; 2011.

3. Winger BM, Auteri GG, Pegan TM, Weeks BC. [A long winter for the Red Queen: Rethinking the evolution of seasonal migration](https://doi.org/10.1111/brv.12476). Biological Reviews. 2019;94:737–52.

4. Barker KJ, Xu W, Van Scoyoc A, Serota MW, Moravek JA, Shawler AL, et al. [Toward a new framework for restoring lost wildlife migrations](https://doi.org/10.1111/conl.12850). Conservation Letters. 2022;15:e12850.

5. Abrahms B, Teitelbaum CS, Mueller T, Converse SJ. [Ontogenetic shifts from social to experiential learning drive avian migration timing](https://doi.org/10.1038/s41467-021-27626-5). Nature Communications. 2021;12:7326.

6. Mueller T, Olson KA, Dressler G, Leimgruber P, Fuller TK, Nicolson C, et al. [How landscape dynamics link individual- to population-level movement patterns: A multispecies comparison of ungulate relocation data](https://doi.org/10.1111/j.1466-8238.2010.00638.x). Global Ecology and Biogeography. 2011;20:683–94.

7. Senner NR, Morbey YE, Sandercock BK. [Editorial: Flexibility in the Migration Strategies of Animals](https://doi.org/10.3389/fevo.2020.00111). Frontiers in Ecology and Evolution. 2020;8.

8. Chernetsov N, Berthold P, Querner U. [Migratory orientation of first-year white storks (Ciconia ciconia): Inherited information and social interactions](https://doi.org/10.1242/jeb.00853). Journal of Experimental Biology. 2004;207:937–43.

9. Mueller T, O’Hara RB, Converse SJ, Urbanek RP, Fagan WF. [Social Learning of Migratory Performance](https://doi.org/10.1126/science.1237139). Science. 2013;341:999–1002.

10. Sutherland WJ. Evidence for Flexibility and Constraint in Migration Systems. Journal of Avian Biology [Internet]. 1998 [cited 2023 Jun 20];29:441. Available from: <https://www.jstor.org/stable/3677163>

11. Palacín C, Alonso JC, Alonso JA, Magaña M, Martín CA. [Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard Otis tarda](https://doi.org/10.1111/j.1600-048X.2011.05395.x). Journal of Avian Biology. 2011;42:301–8.

12. Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Beck JL, Courtemanch AB, et al. [Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals](https://doi.org/10.1126/science.aat0985). Science. 2018;361:1023–5.

13. Alison R. Some previously unpublished historical records of trumpeter swans in Ontario. Canadian Field Naturalist. 1975;89:311–3.

14. Banko W. The trumpeter swan: Its history, habits, and population in the United States. North American Fauna. 1960;1–214.

15. Shea RE, Nelson HK, Gillette’ LN, King JG, Weaver DK. Restoration of Trumpeter Swans in North America: A Century of Progress and Challenges. Waterbirds. 2002;25:296–300.

16. Hansen HA, Shepherd PEK, King JG, Troyer WA. The Trumpeter Swan in Alaska. 1971;82.

17. Matteson S, Andryk T, Wetzel. Wisconsin Trumpeter Swan Recovery Plan.pdf. The Passenger Pigeon. 1988;50:119–30.

18. Baskin Y. [Trumpeter Swans Relearn Migration](https://doi.org/10.2307/1311967). BioScience. 1993;43:76–9.

19. Oyler-McCance SJ, Ransler FA, Berkman LK, Quinn TW. [A rangewide population genetic study of trumpeter swans](https://doi.org/10.1007/s10592-006-9282-y). Conservation Genetics. 2007;8:1339–53.

20. Groves DJ. The 2015 North American Trumpeter Swan Survey. U.S. Fish and Wildlife Service; 2017 p. 1–28.

21. Alerstam T, Hedenström A, Akesson S. Long-distance migration: Evolution and determinants. Oikos. 2003;103:247–60.

22. Dingle H, Drake VA. [What Is Migration?](https://doi.org/10.1641/B570206) BioScience. 2007;57:113–21.

23. Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A. [The ecology and evolution of partial migration](https://doi.org/10.1111/j.1600-0706.2011.20131.x). Oikos. 2011;120:1764–75.

24. Dawson RD, Clark RG. [Effects of Hatching Date and Egg Size on Growth, Recruitment, and Adult Size of Lesser Scaup](https://doi.org/10.1093/condor/102.4.930). The Condor. 2000;102:930–5.

25. Anderson MG, Lindberg MS, Emery RB. Probability of Survival and Breeding for Juvenile Female Canvasbacks. The Journal of Wildlife Management [Internet]. 2001 [cited 2023 Dec 28];65:385–97. Available from: <https://www.jstor.org/stable/3803090>

26. Blums P, Clark RG, Mednis A. [Patterns of reproductive effort and success in birds: Path analyses of long-term data from European ducks](https://doi.org/10.1046/j.1365-2656.2002.00598.x). Journal of Animal Ecology. 2002;71:280–95.

27. Lok T, Veldhoen L, Overdijk O, Tinbergen JM, Piersma T. [An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment](https://doi.org/10.1111/1365-2656.12706). Journal of Animal Ecology. 2017;86:998–1009.

28. Winger BM, Pegan TM. [Migration distance is a fundamental axis of the slow-fast continuum of life history in boreal birds](https://doi.org/10.1093/ornithology/ukab043). Ornithology. 2021;138:ukab043.

29. Sillett TS, Holmes RT. [Variation in survivorship of a migratory songbird throughout its annual cycle](https://doi.org/10.1046/j.1365-2656.2002.00599.x). Journal of Animal Ecology. 2002;71:296–308.

30. Rushing CS, Hostetler JA, Sillett TS, Marra PP, Rotenberg JA, Ryder TB. [Spatial and temporal drivers of avian population dynamics across the annual cycle](https://doi.org/10.1002/ecy.1967). Ecology. 2017;98:2837–50.

31. Somveille M, Rodrigues ASL, Manica A. [Why do birds migrate? A macroecological perspective](https://doi.org/10.1111/geb.12298). Global Ecology and Biogeography. 2015;24:664–74.

32. Rappole JH. The Avian Migrant: The Biology of Bird Migration. Columbia University Press; 2013.

33. La Sorte FA, Fink D, Hochachka WM, DeLong JP, Kelling S. [Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds](https://doi.org/10.1098/rspb.2014.0984). Proceedings of the Royal Society B: Biological Sciences. 2014;281:20140984.

34. La Sorte FA, Graham CH. [Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds](https://doi.org/10.1111/1365-2656.13345). Journal of Animal Ecology. 2021;90:343–55.

35. Schummer ML, Kaminski RM, Raedeke AH, Graber DA. [Weather-Related Indices of Autumn Winter Dabbling Duck Abundance in Middle North America](https://doi.org/10.2193/2008-524). The Journal of Wildlife Management. 2010;74:94–101.

36. Xu F, Si Y. [The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl](https://doi.org/10.1016/j.ecolind.2019.02.024). Ecological Indicators. 2019;101:1018–25.

37. Stafford JD, Janke AK, Anteau MJ, Pearse AT, Fox AD, Elmberg J, et al. Spring migration of waterfowl in the northern hemisphere: A conservation perspective. Wildfowl. 2014;70.

38. Lundberg P. [The evolution of partial migration in Birds](https://doi.org/10.1016/0169-5347(88)90035-3). Trends in Ecology & Evolution. 1988;3:172–5.

39. Lundberg P. [On the evolutionary stability of partial migration](https://doi.org/10.1016/j.jtbi.2012.12.017). Journal of Theoretical Biology. 2013;321:36–9.

40. Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, et al. National Hierarchical Framework of Ecological Units. Ecosystem Management Applications for Sustainable Forest and Wildlife Resources. New Haven, CT: Yale University Press; 1997. p. 181–200.

41. Eltringham SK. [Methods of capturing wild animals for marking purposes](https://doi.org/10.1007/978-1-349-03711-7_2). In: Stonehouse B, editor. Animal Marking: Recognition Marking of Animals in Research. London: Macmillan Education UK; 1978. p. 13–23.

42. Hindman LJ, Iv WFH, Walbridge HR, Hooper M, Driscoll CP. Efficient Method of Capture and Field Euthanasia of Flightless Mute Swans. Proceedings of the 16th Wildlife Damage Management Conference. Auburn, Alabama, USA; 2016. p. 55–64.

43. Lockman DC. Trumpeter Swan Mortality in Wyoming 1982-1987. Proceedings of the 11th Trumpeter Swan Society Conference. 1990. p. 12–3.

44. Soriano-Redondo A, Acácio M, Franco AMA, Martins BH, Moreira F, Rogerson K, et al. [Testing alternative methods for estimation of bird migration phenology from GPS tracking data](https://doi.org/10.1111/ibi.12809). Ibis. 2020;162:581–8.

45. van de Kerk M, Larsen RT, Olson DD, Hersey KR, McMillan BR. [Variation in movement patterns of mule deer: Have we oversimplified migration?](https://doi.org/10.1186/s40462-021-00281-7) Movement Ecology. 2021;9:44.

46. Wolfson DW, Andersen DE, Fieberg JR. [Using piecewise regression to identify biological phenomena in biotelemetry datasets](https://doi.org/10.1111/1365-2656.13779). Journal of Animal Ecology. 2022;1365–2656.13779.

47. Plummer M. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Working Papers. 2003;8.

48. Lindeløv JK. [Mcp: An R Package for Regression With Multiple Change Points](https://doi.org/10.31219/osf.io/fzqxv). OSF Preprints; 2020.

49. Team RCD. R: A Language and Environment for Statistical Computing. https://www.r-project.org/; 2022.

50. Bengtsson H. A Unifying Framework for Parallel and Distributed Processing in R using Futures. The R Journal [Internet]. 2021 [cited 2022 Dec 29];13:208. Available from: <https://arxiv.org/abs/2008.00553>

51. Brooks SP, Gelman A. [General Methods for Monitoring Convergence of Iterative Simulations](https://doi.org/10.1080/10618600.1998.10474787). Journal of Computational and Graphical Statistics. 1998;7:434–55.

52. Gelman A, Hwang J, Vehtari A. [Understanding predictive information criteria for Bayesian models](https://doi.org/10.1007/s11222-013-9416-2). Statistics and Computing. 2014;24:997–1016.

53. Vehtari A, Gelman A, Gabry J. [Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC](https://doi.org/10.1007/s11222-016-9696-4). Statistics and Computing. 2017;27:1413–32.

54. Su Y-S, Yajima M. R2jags: Using R to Run ’JAGS’. 2021.

55. Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models using Lme4. arXiv. 2014;

56. Conklin JR, Battley PF, Potter MA, Fox JW. [Breeding latitude drives individual schedules in a trans-hemispheric migrant bird](https://doi.org/10.1038/ncomms1072). Nature Communications. 2010;1:67.

57. van Wijk RE, Kölzsch A, Kruckenberg H, Ebbinge BS, Müskens GJDM, Nolet BA. [Individually tracked geese follow peaks of temperature acceleration during spring migration](https://doi.org/10.1111/j.1600-0706.2011.20083.x). Oikos. 2012;121:655–64.

58. Nilsson C, Klaassen RHG, Alerstam T. [Differences in Speed and Duration of Bird Migration between Spring and Autumn.](https://doi.org/10.1086/670335) The American Naturalist. 2013;181:837–45.

59. Åkesson S, Helm B. [Endogenous Programs and Flexibility in Bird Migration](https://doi.org/10.3389/fevo.2020.00078). Frontiers in Ecology and Evolution. 2020;8.

60. Berthold P. Genetic control of migratory behaviour in birds. Trends in Ecology & Evolution. 1991;6:254–7.

61. Sasaki T, Biro D. [Cumulative culture can emerge from collective intelligence in animal groups](https://doi.org/10.1038/ncomms15049). Nature Communications. 2017;8:15049.

62. Ransler FA, Quinn TW, Oyler-McCance SJ. [Genetic consequences of trumpeter swan (Cygnus buccinator) reintroductions](https://doi.org/10.1007/s10592-010-0137-1). Conservation Genetics. 2011;12:257–68.

63. Pulido F. [Evolutionary genetics of partial migration the threshold model of migration revis(it)ed](https://doi.org/10.1111/j.1600-0706.2011.19844.x). Oikos. 2011;120:1776–83.

64. Ellis CR, Stefan HG. [Oxygen Demand in Ice Covered Lakes as It Pertains to Winter Aeration1](https://doi.org/10.1111/j.1752-1688.1989.tb01329.x). JAWRA Journal of the American Water Resources Association. 1989;25:1169–76.

65. Slater G. Trumpeter Swan (Cygnus buccinator): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region; 2006 p. 1–39.

66. Ballard DC, Jones III OE, Janke AK. [Factors Affecting Wetland Use by Spring Migrating Ducks in the Southern Prairie Pothole Region](https://doi.org/10.1002/jwmg.22096). The Journal of Wildlife Management. 2021;85:1490–506.

67. Satterfield DA, Marra PP, Sillett TS, Altizer S. [Responses of migratory species and their pathogens to supplemental feeding](https://doi.org/10.1098/rstb.2017.0094). Philosophical Transactions of the Royal Society B: Biological Sciences. 2018;373:20170094.

68. Varner DM. Survival and foraging ecology of interior population trumpeter swans - ProQuest [PhD thesis]. Southern Illinois University Carbondale; 2008.

69. Baldassarre G. Ducks, Geese, and Swans of North America. JHU Press; 2014.

70. Reese GC, Skagen SK. [Modeling nonbreeding distributions of shorebirds and waterfowl in response to climate change](https://doi.org/10.1002/ece3.2755). Ecology and Evolution. 2017;7:1497–513.

71. Nussey DH, Postma E, Gienapp P, Visser ME. [Selection on Heritable Phenotypic Plasticity in a Wild Bird Population](https://doi.org/10.1126/science.1117004). Science. 2005;310:304–6.