Annual movement trends of Interior Population Trumpeter Swans decades after reintroduction from migratory and non-migratory populations

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## 0.1 Abstract

## 0.2 Background

### 0.2.1 Biological intro to migration in long-lived avian species

Migration is a behavioral mechanism widely used by all major vertebrate groups (e.g. birds, fish, mammal, herpetofauna) that allows individuals to optimize seasonal availability of resources to increase short-term survival, and by optimizing migration phenology, maximize long-term fitness ([Fryxell et al. 1988](#ref-fryxell1988), [Milner-Gulland et al. 2011](#ref-milner-gulland2011), [Winger et al. 2019](#ref-winger2019), [Barker et al. 2022](#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 ([Abrahms et al. 2021](#ref-abrahms2021b)). In part, that lack of understanding is hindered by the difficulty of 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 ([Mueller et al. 2011](#ref-mueller2011a), [Senner et al. 2020](#ref-senner2020a)).

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 ([Chernetsov et al. 2004](#ref-chernetsov2004a), [Mueller et al. 2013](#ref-mueller2013)). As a consequence, cultural transmission during the first year is thought to be the primary mechanism that dictates the learned migration patterns used in subsequent years ([Sutherland 1998](#ref-sutherland1998)).

Although this transfer of information is an effective mechanism for preserving migratory patterns through generations, it is unclear how these trends become established when a population has been re-established on a landscape from which it had been extirpated. Jesmer et al. ([2018](#ref-jesmer2018)) found that newly translocated populations initially lost their migratory tendencies and that it took many generations to re-establish such patterns.

### 0.2.2 History of Trumpeter Swans in North America

Trumpeter swans (*Cygnus buccinator*), the largest waterfowl species in North America, were widespread throughout the continent prior to European colonization during the century ([Alison 1975](#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 ([Banko 1960](#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 ([Shea et al. 2002](#ref-shea2002)). During this period, a cryptic (i.e., not recognized as trumpeter swans but thought to be tundra swans [*Cygnus columbianus*] until properly identified in 1959 ([Hansen et al. 1971](#ref-hansen1971))) population of trumpeter swans existed in southern Alaska.

### 0.2.3 History of IP TRUS comeback in NA

As trumpeter swan numbers at RRLNWR started to rise, this flock was used as a source population for reintroduction efforts in other parts of the historical breeding range. Many states translocated trumpeter swans from RRLNWR to augment and boost the abundance and distribution of the diminished Rocky Mountain Population (RMP) or to restore the Interior Population (IP), which had been completely extirpated ([Shea et al. 2002](#ref-shea2002)). In 1959, aerial surveys in Alaska discovered a previously unknown population of over a thousand Pacific Coast Population (PCP) swans ([Hansen et al. 1971](#ref-hansen1971)). Additional surveys in 1968 tallied 2,848 swans, confirming that the population was growing, and that there were sufficient abundance to provide swans for translocations, including to states conducting reintroduction efforts within the IP ([Matteson et al. 1988](#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 the Tri-State area are non-migratory ([Baskin 1993](#ref-baskin1993), [Oyler-McCance et al. 2007](#ref-oyler-mccance2007)).

### 0.2.4 Current IP conditions

Estimates of IP abundance have increased dramatically since reintroductions began in the 1960s, and both population size and distribution has expanded significantly ([Groves 2017](#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 (onset in the fall, settlement during winter, arrival in the spring), and the magnitude of intra- and inter-individual variability in migration behavior.

### 0.2.5 Drivers/Why to migrate (or not)

Many factors may influence the decision to leave the breeding territory during the non-breeding season, how far to migrate for those that leave, and why there may be high among-individual variability even for those breeding at similar locations, including energetics of flight, life history requirements, and knowledge transfer of migratory traditions ([Alerstam et al. 2003](#ref-alerstam2003), [Dingle and Drake 2007](#ref-dingle2007), [Chapman et al. 2011](#ref-chapman2011)). The energetic cost of migration for a given distance traveled increases non-linearly with the overall weight of the bird, and therefore swans, one of the heaviest avian species to migrate, do so at considerable expense ([Pennycuick 1989](#ref-pennycuick1989), [Berthold 2001](#ref-berthold2001), [Newton 2010](#ref-newton2010)). Conversely, according to the ‘Thermal Tolerance’ or ‘Body Size’ hypothesis, greater body mass conveys both a higher basal metabolic rate ability to fast, therefore better withstanding harsh winter conditions, and the tendency to migration should decrease with increasing body size ([Ketterson and Nolan Jr. 1976](#ref-ketterson1976), [Fudickar et al. 2013](#ref-fudickar2013)). Additionally, due to the novelty of persisting in relatively unfamiliar landscapes and the high energetic demand of migration, the non-breeding period typically has the lowest survival rates throughout the annual cycle ([Sillett and Holmes 2002](#ref-sillett2002), [Rushing et al. 2017](#ref-rushing2017)). Alternatively, migrating to a more temperate area during the wintering period can provide access to food and other resources that allow trumpeter swans to avoid the harshness of winter in the breeding territory ([Somveille et al. 2015](#ref-somveille2015)).

Differences in migratory habits may also be due to breeding status, which conveys unique life history requirements, such as early arrival in the spring to defend a breeding territory, lay and incubate eggs, and to stay on the territory late enough in the fall that cygnets learn to fly and develop sufficient fat reserves to migrate south for the winter; all requirements that non-breeding swans will not experience (cite sources).

It is also 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 available food resources, which may also be affected by density-dependent intra-specific competition ([Rappole 2013](#ref-rappole2013)). Swans that spend the summer at different latitudes will experience varying environmental conditions, such as timing of vegetative greenness or the freeze-up of water on shallow wetlands, which blocks access to submerged vegetation (cite sources). The ‘push’ to avoid the harsh elements of winter will vary substantially throughout different portions of the IP breeding range, and we’d expect the consequences on movement trends to vary concurrently (cite cources).

### 0.2.6 Objectives

To address current information needs, we marked a sample of IP swans with GPS-GSM transmitters to evaluate their movement throughout the annual cycle. Specifically, we will quantify 1) the proportion of IP that is migratory and the extent of those movements, 2) migration phenology, 3) the role of breeding status and breeding location on annual movement patterns, and 4) the degree of individual and population variability in migration patterns. Ours is primarily a descriptive study of how a re-established population of trumpeter swans uses a novel landscape.

## 0.3 Methods

### 0.3.1 Study Area

Our study area for swan captures is approximately the current breeding and wintering distribution of IP trumpeter swans (Groves 2017). We captured all swans on their breeding range except for 4 swans captured on their wintering grounds 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 ([Cleland et al. 1997](#ref-cleland1997)).

Figure 1: Deployment locations for Interior Population trumpeter swans collared with GPS-GSM transmitters from July 2019–January 2022. Darker red dots indicate capture sites with multiple swans collared.

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### 0.3.2 Capture and Handling

We captured all swans (except for 4 captured 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 although some swans were captured using surface-drive motors (Gator-Tail, Loreauville, Louisiana, USA). We hand-captured swans using a shepherd’s crook pole ([Eltringham 1978](#ref-eltringham1978), [Hindman et al. 2016](#ref-hindman2016)). We predominantly targeted adult swans, which have higher survival rates than juveniles, to maximize the longevity of telemetry data collection ([Lockman 1990](#ref-lockman1990)).

We marked swans with two types of neck 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 Minnesota Department of Natural Resources (Special Permit no. 19017), the Michigan Department of Natural Resources (Threatened and Endangered Species Permit TE 175), the U.S. Fish and Wildlife Service (Research & Monitoring Special Use Permit no. K-10-001), and the U.S. Geological Survey Bird Banding Laboratory (Federal Bird Banding Permit no. 21631). 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).**Need permit info from WI, IA, AR, and OH?**

### 0.3.3 Migration Phenology Classification

To quantify migration phenology throughout the annual cycle, we first calculated yearly time-series of Net-Squared Displacement (NSD) values for each swan, using July 1 as a cutoff date between years for individuals with multiple years of GPS data, and then condensed the dataset to a single average NSD value per day. After excluding swan-year datasets with less than 30 days of data, we iteratively fit a series of 7 intercept-only piecewise regression models to each time-series ([Wolfson et al. 2022](#ref-wolfson2022)). The syntax of each model corresponded to an increasing number of intercepts included (1-7) for average NSD 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. We fit all piecewise regression models in JAGS ([Plummer 2003](#ref-plummer2003)) using the mcp package ([Lindeløv 2020](#ref-lindelov2020)) in Program R version 4.0.2 ([Team 2022](#ref-rcoredevelopmentteam2022)), using 15,000 iterations and a burn-in period of 10,000. We ran all scripts in parallel using the future package on a partition of the Minnesota Supercomputing Institute (MSI) with 48 cores and 50GB RAM per core ([Bengtsson 2021](#ref-bengtsson2021)). We evaluated MCMC chain convergence via the Gelman-Rubin convergence diagnostic and excluded any model containing a parameter with a value of >1.1 from further analyses ([Brooks and Gelman 1998](#ref-brooks1998)). 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 ([Gelman et al. 2014](#ref-gelman2014), [Vehtari et al. 2017](#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 dataset by selecting the model with the best ELPD value.

We qualitatively inspected the visual fit of each model chosen by 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 be able to describe the annual migration phenology (link to Supplemental Materials). For models that passed visual inspection (230 out of 241), we extracted parameter values to represent the movement metrics of interest **(reference all of these metrics in a table?)** after first applying a series of criteria thresholds to strengthen the biological connection of the breakpoints and intercept values from the fitted models. **(include these in the supplemental as well?)**.

### 0.3.4 Summary of Migratory Trends

We devised a flexible workflow that could accommodate a wide breadth of variability in annual movements (because we’re fitting to individual years of data from each swan instead of a bigger pooled dataset) but still allow for population-level inference. For all swan-year datasets that had >30 points and had the best-fitting model pass visual inspection for **text to refer to passing fit and biological relevance check**, we derived a number of movement metrics to describe annual movement trends by creating an algorithm to exclude erroneous segments and changepoints that didn’t represent biologically meaningful transitions between different segments of the annual movement cycle. We excluded all segments <2 km from the previous segment and all changepoints <2 days from the previous changepoint. We extracted fall departure dates for individuals that moved >100 km from breeding/capture territories by 1 December. We extracted spring arrival dates for individuals that moved >100 km from breeding/capture territories during the nonbreeding season and that returned within 10 km of their previous summer territory. We estimated migration duration as the difference in time between fall departure and spring arrival the subsequent year for all swan-year datasets that met the requirements to estimate those two terms. **(link to Supp Materials for rulesets?)**

### 0.3.5 Latent State Model for Migration Extent

We modeled the relationship between breeding latitude and migration extent (defined as max displacement from breeding territory during the non-breeding season) using a state-space formulation for assignment in one of two migration ‘strategy’ categories, either a linear relationship between breeding latitude or a quadratic relationship in which swans at lower latitudes do not travel long distances but make greater movements at higher latitudes. We excluded 6 swan-year datasets that had large dispersal movements during the summer because our focus was on movements during the non-breeding season. The underlying latent migration strategy for each individual was modeled as:

where is the latent state (0 or 1) for assignment to a migration strategy, is the overall mean of ()and is an individual-specific random effect () with precision (). The model likelihood is as follows:

where is the extent of migration for individual in year , and are separate precision parameters for each latent state, , , and are the intercept and slope for the linear model, is the breeding latitude for individual in year , and , , and are the parameters in the non-linear model when . We used normal priors for , , and . We used uniform priors for ), , , and . We implemented the model in JAGS via the rjags R package using 3 MCMC chains with 20,000 iterations, a burn-in of 10,000, and a thinning rate of 10 ([Plummer 2003](#ref-plummer2003), [Su and Yajima 2021](#ref-su2021b)). We determined convergence of chains by assessing trace plots and using the Gelman-Rubin statistic with <1.1([Brooks and Gelman 1998](#ref-brooks1998)).

### 0.3.6 Variability in Annual Movements

We estimated the consistency of migration phenology by calculating among-individual variation, within-individual variation, and repeatability (defined as the proportion of the total variance accounted for by differences among groups) of fall departure dates, spring arrival dates, and migration duration using two analytical approaches. When possible, we fit a linear mixed model (LMM) with restricted maximum likelihood, which is robust to unbalanced designs and accounts for repeated measures ([Nakagawa and Schielzeth 2010](#ref-nakagawa2010)). If fit LMMs were singular, we quantified summary statistics of migration metrics using simple sample means and variances.

For each of three migration phenology response terms, we fit separate models in which are the observations of the migration metric (e.g. spring arrival date) for the th individual () during the th year, is the overall population mean, is a random effect for individuals, and is a random within-individual error term. When there was sufficient variability in the variance-covariance structure of random effects to avoid model singularity, we also included as a vector of covariates for individual and year that include breeding status and sex to control for confounding effects that will otherwise inflate the total phenotypic variance ([Matuschek et al. 2017](#ref-matuschek2017), [Bates et al. 2018](#ref-bates2018)).

The variance of random effects, , specified as individual swan ID, quantifies among-individual variation. The variance remaining in model residuals, , represents within-individual variation. Repeatability, , is defined as the proportion of total phenotypic variance in the population, , that is due to among-individual variation.

We fit LMMs with restricted maximum likelihood estimation using the lme4 R package and conducted parametric bootstrapping with 1000 iterations to quantify the uncertainty in adjusted repeatability estimates using the rptR R package ([Bates et al. 2015](#ref-bates2015), [Stoffel et al. 2017](#ref-stoffel2017)). For any metrics that produced singular fits using LMMs, we were not able to estimate repeatability. We instead estimated variability in timing for a migration metric and reporting the population average and standard deviation, and estimated among-individual variability by calculating the time spans for each year for a given migration metric and reporting the average across years with a standard deviation.

**Include a supplemental file that shows the thresholds for each rule in the script that pulls out the movement summary information. In the main text, briefly allude to the ruleset without laying everything out in a lot of detail?**

## 0.4 Results

### 0.4.1 Capture/deployment/data stuff

We deployed 113 collars with GPS-GSM transmitters on 126 trumpeter swans (including 13 redeployments using collars recovered from mortalities). Of these, 78 were female and 48 were male; 73 were breeding adults (cygnets present), 22 were adults with mates present but no cygnets at time of capture, 24 were non-breeding adults captured while in large groups, and 6 were cygnets at the time of capture.

We collected 252 unique ‘swan-year’ telemetry datasets. We excluded 19 datasets due to insufficient temporal data coverage and 11 datasets due to a lack of piecewise regression model convergence.

Figure 2: An overview of GPS telemetry data received from all collared IP trumpeter swans. Each line represents the period of data collection from a single collared swan. The grey regions indicate periods of collar deployment. The black lines are 1 January of each year. Number of deployments (including redeployments) by state/province are: Michigan (n=14), Minnesota (n=56), Manitoba (n=11), Iowa (n=12), Ohio (n=20), Wisconsin (n=9), and Arkansas (n=4).

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### 0.4.2 Main text of results

#### 0.4.2.1 Proportion of IP that is migratory, and the extent of migratory distance:

Annual movements of IP trumpeter swans were highly variable. For swans that underwent long-distance migration (**add in x out of x went >xx km?**), there was a strong correlation between breeding/capture latitude (mostly between 43 and 53 degrees latitude) and the extent of migration during the non-breeding season (Fig. 3). However, many swans with breeding/capture sites between 40 and 48 degrees latitude showed minimal movement during the non-breeding season and can be considered resident or exhibiting short-distance regional movements.

Figure 3: Breeding/capture latitude versus extent of migration (furthest distance from breeding territory during the nonbreeding season) for 187 ‘swan-year’ datasets representing annual migration cycles.

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#### 0.4.2.2 Latent-state model:

**What text to add about the latent state model that adds to what is shown from the figure?** Show a histogram of the state assignment probabilities to show that it’s very bimodal? Posterior predictive checks of the model?

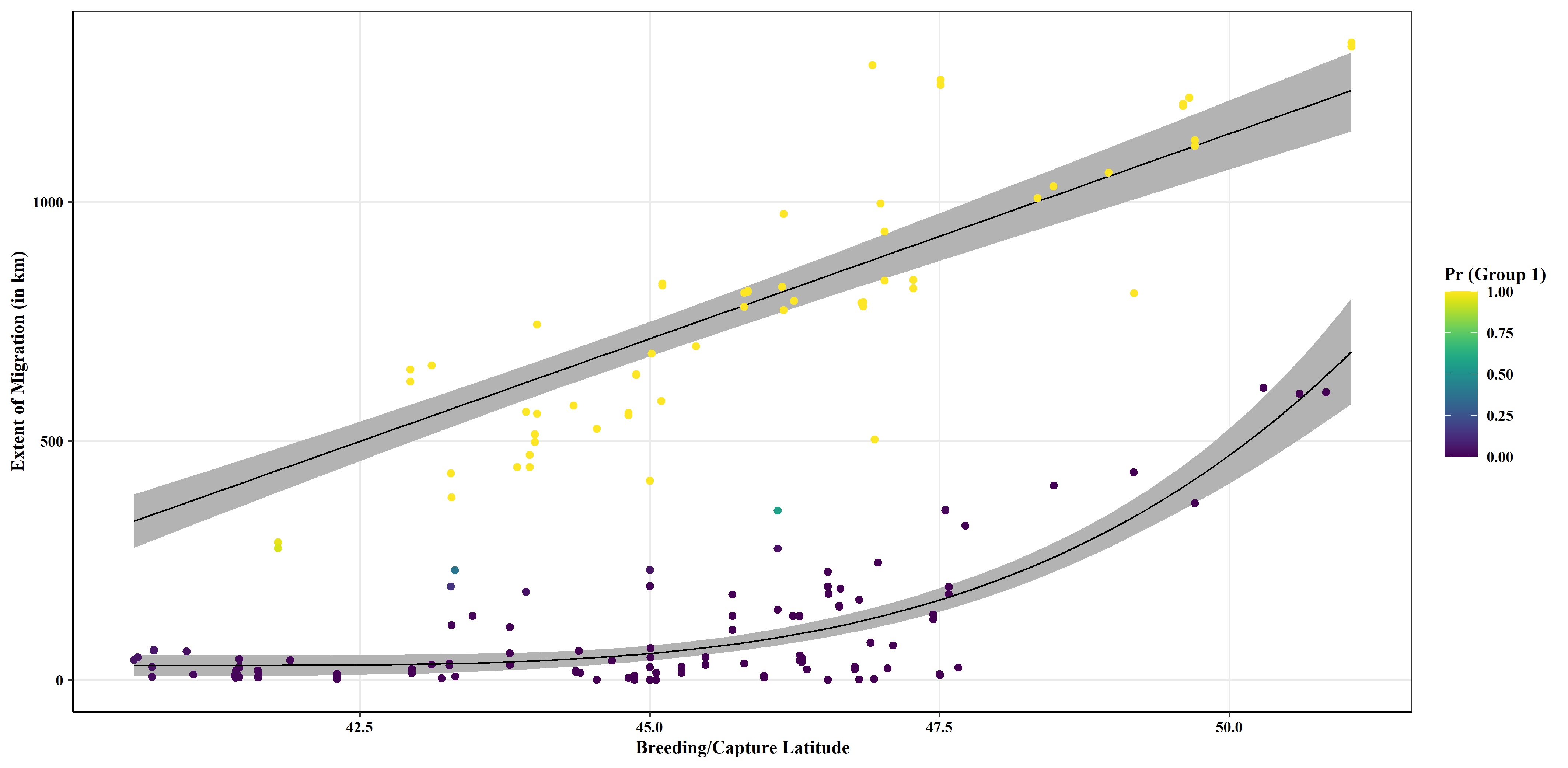


Figure 4: Breeding/capture latitude versus extent of migration datasets color coded by the probability of assignment to one of 2 migration strategies as determined by a latent state model with 2 functional forms to model the relationship between latitude and migratino extent. Grey areas are the 95% credible interval posteriors for the fit of each latent state.

#### 0.4.2.3 Migration phenology, relationships to breeding and latitude, and variability:

##### 0.4.2.3.1 Fall departure:

Dates of departure from breeding territories in the fall by long-distance migrants (>100km) were variable, with the overall average departure date across years on November 1st with a standard deviation of 20 days (Table 1), and yearly averages ranged from October 25 to November 7 (Table 2).

Table 1: Migration phenology of fall departures by long-distance migrants. 'Swan-year' datasets were only considered if individuals moved >100km from breeding/capture territories by December 1.

| **Number of Swans** | **Number of Swan-Years** | **Average Fall Departure** | **Standard Deviation (in days)** | **Earliest Departure** | **Latest Departure** |
| --- | --- | --- | --- | --- | --- |
| 64 | 91 | November 01 | 20 | September 01 | December 04 |

Table 2: Fall departures of long-distance migrants by year. 'Swan-year' datasets were only considered if individuals moved >100km from breeding/capture territories by December 1.

| **Year** | **Number of Swans** | **Average Fall Departure** | **Standard Deviation (in days)** | **Earliest Departure** | **Latest Departure** |
| --- | --- | --- | --- | --- | --- |
| 2019 | 7 | October 31 | 7 | October 21 | November 08 |
| 2020 | 38 | October 25 | 20 | September 01 | November 24 |
| 2021 | 30 | November 06 | 20 | September 22 | December 04 |
| 2022 | 16 | November 07 | 10 | October 07 | November 16 |

We found little to no evidence of a relationship between breeding latitude and date of fall departure (Fig. 5), but breeders and cygnets left later, on average, than non-breeders or paired swans, and non-breeders had much higher variability in timing than the other breeding categories (s.d.=30 for non-breeders and s.d.=10 for each other category) (Fig. 6, Table 3). **Should we not report variability in this way given that there is the other methods on it now?**

Figure 5: The timing of fall departure and spring arrival 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 dates explained by latitude is superimposed for each plot.

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Figure 6: Insert caption for timing vs breeding status figure here…

Figure 6: Insert caption for timing vs breeding status figure here…

Table 3: Fall departures of long-distance migrants by breeding status

| **Breeding Status** | **Number of Swans** | **Number of Swan-Years** | **Average Fall Departure** | **Standard Deviation (in days)** | **Earliest Departure** | **Latest Departure** |
| --- | --- | --- | --- | --- | --- | --- |
| breeder | 33 | 50 | November 04 | 10 | September 30 | December 04 |
| non\_breeder | 12 | 19 | October 24 | 30 | September 01 | November 24 |
| paired | 13 | 16 | October 27 | 10 | September 30 | November 20 |

##### 0.4.2.3.2 Spring arrival

Dates of spring arrival for swans that traveled >100 km during the nonbreeding season and returned to within 10 km of their previous summer territory were more consistent than fall departure dates, with the overall average spring arrival date of March 5 and a standard deviation of 10 days (Table 4), and yearly averages ranged from March 2 to March 7 (Table 5).

Table 4: Migration phenology of spring arrivals by long-distance migrants

| **Number of Swans** | **Number of Swan-Years** | **Average Spring Arrival** | **Standard Deviation (in days)** | **Earliest Arrival** | **Latest Arrival** |
| --- | --- | --- | --- | --- | --- |
| 42 | 63 | March 05 | 10 | February 06 | April 11 |

Table 5: Spring arrivals of long-distance migrants by year

| **Year** | **Number of Swans** | **Average Spring Arrival** | **Standard Deviation (in days)** | **Earliest Arrival** | **Latest Arrival** |
| --- | --- | --- | --- | --- | --- |
| 2020 | 4 | March 02 | 20 | February 08 | March 23 |
| 2021 | 27 | March 05 | 7 | February 26 | March 23 |
| 2022 | 24 | March 07 | 20 | February 07 | April 11 |
| 2023 | 8 | March 05 | 20 | February 06 | April 08 |

#### 0.4.2.4 Variation and repeatability:

Due to parameters near the boundary of the feasible parameter space, we were unable to estimate variability estimates using a LMM framework for fall departure timing. Using a non-model-based approach, we estimated the average within-individual difference in fall departure to be 21 days (s.d.=18 days) and the average among-individual variability (defined as the time span between the first and last migrant) to be 53 days (s.d.= 30 days). For spring arrival timing, we fit a LMM including fixed effects of sex and breeding status and swan ID as a random effect. Repeatability of spring arrival timing was 0.67 (SE=0.123, CI=[0.38,0.85]) and among-individual variation (var=137, sd=11.8) was greater than within-individual variation (var=67, sd=8.2). For migration duration, we fit an intercept-only LMM with swan ID as a random effect. Repeatability of migration duration was 0.086 (SE=0.22, CI=[0,0.69]) and among-individual variation (var=38, sd=6.2) was much lower than within-individual variation (var=408, sd=20.2).

**Weird to give an average of differences for the non-model based and the squared standard deviation for the model-based? Should I not give the average and just square the s.d. for fall departure for both within and among?**

**Include a reference to the full table of all parameter output?**

Figure 7: Insert caption for duration vs breeding status figure here…

Figure 7: Insert caption for duration vs breeding status figure here…

| **Migration Metric** | **Number of Migratory Tracks** | **Number of Swans** | **Within-individual Variance** | **Within-individual Standard Deviation** | **Among-individual Variance** | **Among-individual Standard Deviation** | **Repeatability** | **Repeatability Standard Error** | **Repeatability Lower Confidence Limit** | **Repeatability Upper Confidence Limit** |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Fall Departure | 85 | 58 | 21.622 | 18.170 | 53.00 | 30.000 |  |  |  |  |
| Spring Arrival | 63 | 42 | 137.710 | 11.730 | 67.73 | 8.230 | 0.670 | 0.123 | 0.376 | 0.845 |
| Migration Duration | 41 | 32 | 38.330 | 6.191 | 408.83 | 20.219 | 0.086 | 0.220 | 0.000 | 0.686 |

## 0.5 Discussion

### 0.5.1 Summarize main take-aways and the bigger relevance

**Provide brief summary of all results before going through easch section in more detail?** Our study finds that IP swans exhibit partial migration and were highly variable in the extent and timing of their annual movement habits, with a continuum of strategies each year including residency, short-distance local movement, regional migration, and long-distance migration. Much of this variability can be explained by factors tied to natural history demands and response to environmental conditions such as breeding status and breeding location.

Breeding latitude had a strong relationship with the likelihood to migrate 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. Autumn migration distances of swans breeding at mid-latitudes were variable, with some swans moving considerable distances and some swans remaining near their breeding locations during the non-breeding season. Swans breeding at lower latitudes all remained relatively near their breeding locations.

The relationship between breeding latitude and migratory patterns did not appear to be consistent among all individuals, and the latent state model fit suggests there may be multiple migration strategies; one in which all swans migrate with a straightforward relationship between latitude and distance, and another in which swans persist near the breeding area during the winter except at higher latitudes, in which they migrate but much lower distances than the first strategy (Fig. 4). It is unclear why these two groups seem to have distinct movement patterns. The effects of local environmental conditions should be relatively similar for swans at similar latitudes, so differences are likely due to other factors such as social dynamics, genetic lineage, and internal physiology.

### 0.5.2 Ecology and evolution of migration (drivers and how are patterns passed on thru generations in general)

Once established, the mechanisms that underlie transmission of migratory information between generations can be influenced both genetically and through social learning ([Åkesson and Helm 2020](#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 ([Berthold 1991](#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 habits ([Mueller et al. 2013](#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, although 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 ([Mueller et al. 2013](#ref-mueller2013), [Sasaki and Biro 2017](#ref-sasaki2017)).

### 0.5.3 Now bring it back to IP swans specifically

IP swans are unique because their reintroduction to the greater Midwest occurred relatively recently (<50 years) from a mix of source populations with varying migratory habits ([Ransler et al. 2011](#ref-ransler2011)). Thus, there may exist heterogeneity within the population in terms of internal physiological state and genetic makeup. Continued monitoring is needed to determine whether IP partial migration habits 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 ([Pulido 2011](#ref-pulido2011)). Partial migration is common among migratory species for which a mix of life-history strategies maximizes the overall fitness of the population, though this can be highly influenced by density-dependent effects such as competition for limited resources ([Chapman et al. 2011](#ref-chapman2011)).

### 0.5.4 Broader significance of differences in timing between latitude or breeding status and repeatability

The observed patterns of migration phenology by IP trumpeter swans corresponds with those of many other long-lived avian migrants ([Conklin et al. 2010](#ref-conklin2010), [van Wijk et al. 2012](#ref-vanwijk2012b)). Spring arrival dates were strongly associated with both breeding latitudes and breeding status (Fig. 5 and Fig. 6). Trumpeter swans, being the largest species of waterfowl in North America, have high energetic demands to produce young while also meeting their own physiological requirements, and optimal timing of arrival on breeding grounds in the spring to defend territories with adequate resources is necessary ([Kokko 1999](#ref-kokko1999)). Like most avian migrants, breeders spent less time undergoing migration than non-breeders, though breeding latitude had no relationship with migration duration (Fig. 7; Nilsson et al. ([2013](#ref-nilsson2013))).

### 0.5.5 Broader significance of IP partial migration

Ultimately, this study provides only a snapshot in time of current IP trumpeter swan migration patterns and population-level trends may be still stabilizing overall as well as experiencing annual variation based on environmental conditions each year. The history of IP reintroduction includes many years of anthropogenic influences, at the level of both wildlife manager and private citizen, that have likely cause considerable effects on migration patterns, and it is not well understood to what extent these influences may be passed down through future generations (cite sources). Some of these include intentional feeding during the winter at sites of high IP swan density and lake aerators that keep portions of lake ice-free throughout the winter to prevent winter kill of fish ([Ellis and Stefan 1989](#ref-ellis1989), [Slater 2006](#ref-slater2006), [Ballard et al. 2021](#ref-ballard2021a)). Although most supplemental feeding has been discontinued by state agencies, the practice continues with many private citizens, and potential impacts include not only curtailment of migration but also increased risk of pathogen transmission ([Satterfield et al. 2018](#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 needs more study ([Varner 2008](#ref-varner2008), [Baldassarre 2014](#ref-baldassarre2014)).

Potential contributing reasons for partial migration: - Spectrum of environmental conditions along the latitudinal gradient of IP breeding range  
- Potential delays due to initiation of migration trends for the first time in reintroduced areas being limited by intergenerational transfer of knowledge? - Potential “lag effects” of genetic lineage from RMP vs PCP?

## 0.6 Conclusion

## 0.7 Data availability

## 0.8 Acknowledgements

## 0.9 Funding

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