Migrating birds vary in their navigational response to human population density

by

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Abstract

Long-distance migratory species often cross a range of human-modified landscapes. A key question is how animal populations are responding to these human-induced changes. Here, we use community science data to model the spring migration dynamics of 63 bird species in North America with the goal of understanding how migration is associated with variation in human population density (HPOP). We find that most migrating bird species demonstrate a negative navigational response to HPOP, yet nearly all bird species experience much greater HPOP during migration as compared to breeding. We show that species differ repeatably in their navigational response to HPOP, and that this variation can be explained by variation in breeding ecology and the pace of migration. These findings underscore how birds may be particularly vulnerable to the effects of HPOP during migration, as the average level of HPOP experienced during migration is 2.7-fold greater than that of breeding.
**Co-authorship**

Chapter 1 is a general introduction to bird migration, written in a popular science style without references, as approved by my thesis advisory committee.

Chapter 2 is a manuscript co-authored with my supervisor Dr. Roslyn Dakin, who helped design the study, prepared the data, performed the modelling and model validation, and provided extensive editing and feedback. Chapter 2 is formatted for submission to a peer-reviewed journal, and it includes an introduction with references.
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Chapter 1: Migration – A time of wonder and danger

Early in the spring, when the snow has just started to melt, you may notice a change in the air – the sudden appearance of birdsong. Where did these birds come from? It seems like only yesterday the air was quiet. This sudden appearance is caused by the fascinating phenomenon of long-distance migration, where animals, such as birds, travel up to thousands of kilometers twice a year in response to changing weather conditions. What is so tremendous about bird migration is that most of these long-distance migrants can fit in the palm of your hand, and travel using one of the most demanding forms of movement – flight. Despite this seemingly impossible feat, billions of North American birds migrate every year. How does long-distance migration work? What challenges do birds face while migrating? In this article, I will explore these questions, as well as discuss the role of my MSc research in learning how bird migration is affected by human activity.

1.1 The fascinating biology of bird migration

The first question you may have about migration is why do birds undertake these extensive journeys? During the winter, when the weather up north turns cold and harsh and food is difficult to find, it is clear why migrants return to their wintering grounds in the south. But why not stay down south? Well, spring migration has a primary benefit: it allows birds to capitalize on resources, while experiencing reduced competition from neighbours. During the breeding period, birds require large amounts of food in order to rear their offspring. This increases the competition for resources in the south. Meanwhile,
in the north, plants and insects begin emerging in abundance, thus creating a surplus of resources that migrants can exploit.

Food is also crucial during migration. Birds store fuel in the form of fat deposits under their skin. These fat deposits are visible on the bird, and can be used to non-invasively assess the bird’s energetic state. The high metabolic demand of migration means that fat deposits are quickly depleted, and birds rely on stopover areas along the way to rest and refuel for the next leg of their journey. The types of sites birds choose for their staging grounds are highly variable, and depend on the species’ resource requirements. Many stopovers occur before and after geographic barriers, such as the Gulf of Mexico, where many birds need to prepare for and recover from a long, non-stop flight over water. Birds can stay at stopovers for several days before they move on. The length of time a bird stops over and how many stopovers a bird makes will contribute to its overall length of migration. Typically, birds spend less time migrating during the spring than they do during the fall. This is because they are racing to reach their breeding grounds to find the best breeding habitats and food sources. For this same reason, in some species, males depart earlier than females, particularly during the spring.

Most long-distance migrants are nocturnal migrants, which means they fly by night and stopover during the day. Nocturnal migration has several advantages: First, the air currents are calmer, which makes for a more energy-saving flight. Second, it is generally safer since many predators hunt by day and rest at night. Lastly, the air is cooler at night, which can help remove excess body heat. Another hypothesis is that nocturnal migration may optimize the amount of time for foraging since migrants can search for food throughout the day. Despite these advantages, some songbirds do migrate by day
(diurnal migration). The reasons why are not entirely clear, but some hypotheses are that diurnal migrants have more time to sleep, they can hunt while they fly (e.g., catching insects from the air), and/or can quickly locate suitable stopover sites during flight, as compared to having to re-orient in a new place every morning. Note that when flying over major water bodies, like the Gulf of Mexico, birds will fly by both day and night.

So how do birds find their way across these vast distances, year after year? As humans, we have our maps, compasses, and GPS devices to find our way around, but birds clearly do not have this technology, which makes their navigational ability all the more impressive. The exact trajectory a species takes is dictated by both genetics and learning. Though research is still being done on exactly how birds navigate, there are several established mechanisms: First, birds use landmarks to find their way. For example, the major flyways that birds use tend to follow coastlines (e.g., Pacific and Atlantic flyways), mountains (e.g., Central flyway), and rivers (e.g., Mississippi flyway). Second, birds use celestial cues like the sun and stars to orient themselves. Third, other senses like smell and magnetoreception, the detection of the Earth’s magnetic field, are essential for navigation. The receptors for magnetoreception are likely proteins found in birds’ eyes that may act as a visual filter according to the bird’s orientation.

1.2 A time of danger

Despite the wonder we attribute to bird migration, it is also riddled with many dangers, which make it the most vulnerable time in a bird’s annual cycle. Many birds never reach their destination. First and foremost, migration is exhausting. Some songbirds can fly over 500 km in a single day, and when crossing large water bodies, they can fly
for several days without rest. This means that when birds land, they are vulnerable to predators, and can easily starve or be in bad shape for breeding if they cannot find enough food. This intense workout also means a serious risk of overheating – hence why flying at night can be an advantage. Birds can also be blown off course during inclement weather, and though at least some species can re-orient themselves using magnetoreception, this may delay their arrival to the breeding grounds and affect their ability to find a territory and mate.

On top of these inherent physiological and behavioural challenges, birds must also deal with dangers imposed by humans. Humans have greatly altered Earth’s terrestrial environment; for example, we have constructed cities and suburbs that billions of birds must move through to reach their breeding or wintering grounds. Though urban areas have many benefits for birds, like feeders and nesting cavities, they also pose their own challenges. One of the greatest, and maybe unexpected, killers of migrating birds, is domestic cats, which hunt and kill billions of birds every year, and injure countless others. During migration, birds are already tired and vulnerable, and cats are natural-born hunters. Even with the ability to fly, birds do not stand a chance.

The second leading cause of death for migrating birds is collisions with buildings and other large human-made structures like wind turbines. Window collisions are estimated to cause over a billion bird deaths annually in the United States and Canada alone. It may seem odd that birds are flying into these large and seemingly obvious structures, though there are several reasons why this occurs. First, most birds’ eyes are oriented to the sides, and thus have a much narrower binocular visual field (area of overlap between the two eyes) than humans do. For many birds, the areas on the retina
with highest acuity (“fovea”) occur laterally. Birds may also fixate their gaze down or to the sides as they are flying, and consequently may not be paying attention to their direction of travel. These differences in anatomy and behaviour could cause a bird to not notice large, human-made objects. Further, lights at night can blind and disorient birds so that they end up in urban areas, where they are more likely to collide with windows in the morning. The reason why windows are so dangerous is because they reflect sky and vegetation, which can deceive birds into thinking there is a space they can fly through. These collisions often kill birds on impact, and can also cause internal injuries that later prove fatal or make birds even more susceptible to predation.

The last major human challenge that I will describe is habitat loss and fragmentation. Humans have decimated many natural habitats like forests and wetlands. It is well known that loss of breeding and wintering grounds can contribute to mortality and affect breeding fitness in songbirds. But what about the loss of land along migration routes? Many bird species experience more light pollution during migration than during other phases of their annual cycle, which suggests that they experience greater human activity during migration as well. But can birds not just fly over urban areas? Well, remember that birds must stopover to replenish their fat supplies. If the staging areas they use are gone or severely altered, they may not be able to acquire the energy they need to finish their journey. Urban areas can, however, provide benefits for some migrants; primarily, bird feeders and vegetation in gardens can supplement birds’ diets to help them along. The issue is that not all birds will visit backyard feeders, and feeders might not provide all the food birds require.
1.3 Help from far and wide

It is no secret that the global human population has rapidly expanded. And with all the changes we have made to natural habitats along migration routes, it begs the question of how birds are responding to these changes as they migrate. For example, birds seem able to depart earlier in response to climate change and potentially light pollution. Can they also alter their migration paths to avoid or utilize the human areas they come across? To answer this question, we need to track birds as they migrate, which is notoriously difficult to do because migration is transient and covers a very broad range of locations.

Traditionally, we have tracked birds using banding, where experienced scientists put a metal band with a unique number around a bird’s leg, and then record important information about the individual, such as its species, age, sex, weight, and where and when it was banded. With hundreds of thousands of birds banded every year across North America, and over a hundred years of data, banding provides important information about bird movements, such as providing first insights into species’ migration trajectories, showing how migration timing varies with age, sex and season, and how first arrival dates have changed over time in response to climate change. Some limitations are that banding occurs at specific sites, and individuals are rarely re-captured. An exciting and relatively new way of tracking birds is to use geolocators - tiny, dime-sized tags that are placed on a bird’s back. By recording light levels throughout the day, geolocators provide information on the bird’s location throughout its journey. The caveat for this technology is that the bird needs to be re-captured in order to recover the data. It is also expensive and time-consuming to track many individuals, and weather and vegetation can cause
errors in the data. To solve the problem of re-capture, one can track birds en masse using Weather Surveillance Radar. Radar detects radio waves that are reflected by objects in the atmosphere, such as birds taking off during migration. The downside of radar data is that they cannot identify different individuals or typically even species, meaning the conclusions we draw are very general. For example, radar towers across North America have provided insight into the number of birds in the airspace, average flight altitudes of birds in general, and how bird densities change near urban areas.

One promising avenue for tracking multiple species over vast distances is eBird, a project by Cornell University. In eBird, birders record their observations, which can then be used by scientists. With birders all across the world and over a billion records made thus far, eBird has incredible spatial and temporal coverage. There are, of course, some important features of eBird observations that must be considered when interpreting any results derived from these data. For one thing, the number of birds an observer detects will be influenced by that person’s level of experience, how long they search, the time of day they go out, and how many people are searching. eBird addresses this by having birders provide this information and by encouraging short (<2 minute) birding sessions. Some other features of the data include the fact that certain locations and times of year are more popular for birding, and the same individual bird may be recorded numerous times, especially for rare species. Again, the scientists at eBird try to control this bias by vetting suspicious observations.

With its large number of observers and broad spatial coverage, eBird has the potential to provide insight into previously untestable questions. For example, how are birds responding to human activity across the entire continent? Do different species have
different responses and if so, why? Answering these questions could give us a holistic view on how vulnerable birds are to human activity during migration, and allow us to predict which species are especially vulnerable. In my thesis, I aimed to answer these questions using eBird data for 63 migratory bird species. To measure human activity, I used human population density (HPOP). HPOP is the number of people per km$^2$, and is useful since it captures many aspects of human activity – wherever there are more people, there are likely also more buildings, roads, lights, and noise. Hence, any association with HPOP could be driven by the numerous factors associated with HPOP. I used modelling to develop metrics of migration behaviour in response to HPOP, and found two key results: First, nearly all species were biased away from HPOP during migration, meaning they associated less with these areas than expected based on their location.. And yet, most species also experienced much higher HPOP during migration than during breeding. This is an interesting finding because it shows that migration may be a time when birds are especially vulnerable to the dangers of human activity. Second, some species had a more positive navigational response to HPOP than others – these species tended to have slower-paced migrations and breed in forests and/or areas with greater HPOP.

Altogether, these findings are important for broadening our understanding of bird migration behaviour. They can also help us predict which types of species may be especially vulnerable to human-caused changes to the landscape. For example, species that both experience high levels of HPOP during migration yet have a negative navigational response, include the yellow-bellied flycatcher, fox sparrow, black-throated green warbler, blackburnian warbler, and Townsend’s warbler. These species may be particularly vulnerable to areas with high human presence and to future land
development. It is our hope that with these findings, we can better understand how birds are changing their migration in response to human development of the landscape. This could in turn help us design our cities to be more bird-friendly, and to know which species we should prioritize for conservation.

1.4 Conclusion

Whether the birds you see are passing through or arriving at the end of a long journey, migration is an incredible behaviour that is both rewarding and dangerous. As humans, we have the potential to hinder migrants, or aid them on their journey. By studying the response of birds to human activity across a broad scale, we can begin to understand how to help them come back year after year so we can experience the wonder of their songs.

1.5 Further reading


Chapter 2: Migrating birds vary in their navigational response to human population density

2.1 Introduction

During spring migration, hundreds of bird species travel across a broad range of landscapes to their breeding grounds. Migrants are faced with key physiological and behavioural challenges, including human-imposed obstacles such as artificial light, window collisions, habitat loss and fragmentation, as well as altered food availability and foraging periods (Isaksson 2018). These challenges may have important impacts on the ability for migrants to successfully reach their breeding grounds. For example, window collisions and domestic cats are major sources of mortality for migrating birds (Loss et al. 2013, 2014; Machtans et al. 2013), artificial light fragments the aerial landscape and impairs navigation (Van Doren et al. 2017; Korpach et al. 2022), and loss of stopover areas can limit access to resources necessary for flight. Despite these important implications, research on how human activity affects bird migration is lacking. Recent work has found that some migrant bird species may use human-modified landscapes more during fall and spring migration as compared to other periods of their annual cycle (Zuckerberg et al. 2016; Cabrera-Cruz et al. 2018). To what extent is this pattern driven by navigational bias to urban areas? How do species differ in their response to human activity on the landscape?

Here, we investigate how spring migration dynamics of birds in North America are associated with variation in human population density (HPOP), which is defined as the number of people per square kilometer (Fig. A1). We expect HPOP to capture many
aspects of human activity and influence on the landscape, such as chemical and sensory pollution, anthropogenic structures, and the extent of impervious surfaces. Hence, any association with HPOP will be the result of numerous aspects that accompany human presence. In North America, lower and mid-latitudes generally have higher human population densities that many birds must traverse to reach their breeding grounds (Fig. A1). We model migration dynamics for 63 migratory species using data from eBird, a community science database with hundreds of millions of bird sightings from across the globe (Sullivan et al. 2009; Strimas-Mackey et al. 2020). With this vast number of observations, eBird is particularly useful for modelling the timing and trajectory of migratory population dynamics (Fink et al. 2011; La Sorte et al. 2013, 2016; Feng et al. 2021; La Sorte & Horton 2021). eBird occurrence data are provided in birdwatching checklists, which contain a record of the types and counts of species observed during a single sampling event. The ability to submit ‘complete’ checklists (where all species observed are documented) helps with inferring species absences, while additional data including checklist duration and number of observers can be used to account for variation in sampling effort (Strimas-Mackey et al. 2020). eBird sites encompass a wide range of HPOP, with the greatest representation covering sites that have between 10-10,000 persons/km² (e.g., Fig. 1A).
Figure 1. Modeling spring migration dynamics. A) Example of the distribution of HPOP values for eBird checklists in the ruby-throated hummingbird’s 2019 range. Note that HPOP is on a log-scale, and the axes show back-transformed values. B) Example of model-estimated encounter rates for the ruby-throated hummingbird on March 31, 2019. At this time, ruby-throated hummingbirds have arrived at lower latitudes (high encounter rates; red dots), but are rare and absent at mid- and higher-latitude sites (low encounter rates; blue dots). C) Daily average HPOP estimates for the ruby-throated hummingbird in 2019. The horizontal dotted lines show HPOP$_{mig}$, HPOP$_{null}$, and HPOP$_{breed}$. We used the differences in these estimates to calculate navigational bias, and to compare the migration and breeding phases as shown.

In this study, our first aim was to test whether migration dynamics are influenced by HPOP for a broad range of migratory landbird species. To do this, we compared generalized additive models (GAMs) of spring migration dynamics with and without HPOP included as a predictor. GAMs sum together a series of smooth functions to allow for irregular curves for each cross-section of the data. This allows us to model migration dynamics for each species using a nonlinear landscape of predictor variables. Migration is expected to generate a pulse in occurrence for a given latitude with respect to date, and GAMs allow us to model how this pulse may vary with other predictors, such as HPOP. Second, we used the predictions from the fitted GAMs to estimate each species’
navigational bias for HPOP during spring migration, which we define as the extent to which the species is found in areas with more or less HPOP than predicted by a null model. We also compared the average level of HPOP that each species experiences during migration with that of its breeding phase. We examined whether species differ repeatably in these estimates of navigational bias and experience of HPOP, and whether this variation can be explained by phylogeny.

Our final aim was to ask what determines species differences in navigational bias for HPOP. Using a comparative analysis, we tested several predictions about traits that may explain navigational bias, as follows. First, we expected that species that breed in high HPOP areas would be more tolerant of HPOP during migration. Second, we predicted that generalist species would be less negatively biased toward HPOP during migration than habitat specialists or forest breeding species. This is because habitat specialists and forest-breeding species have specific resource requirements that may not be met in urban areas. Additionally, habitat generalists are known to be more tolerant of urban areas than habitat specialists (Bonier et al. 2007; Ducatez et al. 2018; Callaghan et al. 2019). Third, we predicted that species that breed at higher latitudes would be more positively biased toward HPOP during migration, owing to the increased challenge of longer-distance migration. Fourth, we predicted that navigational bias would be associated with variation in the duration of migration. While we did not have a prediction for this trait, we expect migration duration to be determined by a species’ use of stopover sites, which may determine navigational behaviour. Finally, we predicted that nocturnally migrating species would be more positively biased toward HPOP than diurnally migrating species, because artificial light at night is known to disorient nocturnal
migrants, and trap them in urban areas (Gauthreaux & Belser 2006; Van Doren et al. 2017; McLaren et al. 2018; Adams et al. 2019). Additional details of these predictions are summarized in the appendix (Table A1). Overall, this is the first work to characterize how a broad range of migratory bird species respond to HPOP during migration.

2.2 Methods

2.2.1 Data preparation

To sample species for this study, we selected long-distance migratory bird species that overwinter primarily at latitudes below 40°N and breed primarily above 45°N. See the appendix for further details on selection criteria and a list of the 63 species (A1; Table A2). We downloaded the eBird Sampling Event Dataset filtered to include the years 2017-2019. The Sampling Event Dataset, which includes all checklists submitted to eBird, is necessary for estimating species absences. As per the guidelines outlined by eBird (Johnston et al. 2021), we included only ‘complete’ checklists (where all species observed were reported) that were classified as either ‘Stationary’ or ‘Traveling’, with a duration less than 300 minutes and a distance less than 5 km. Checklists were limited to those with ten or fewer observers, and we retained only one checklist for each group ID. Checklists were also limited to diurnal events that started between 04:00 and 20:00 local time. For the years we examined, 80% of checklists were classified as complete, and of those, 98% were stationary or traveling. Complete checklists had an average duration of 65.6 minutes, and an average distance of 3.35 km.

Next, for each species, we downloaded occurrence data from the eBird Basic Dataset in the USA and Canada for the period from January 1 to June 30 in our three
study years, 2017, 2018 and 2019. The period from January to June encompasses spring migration as well as the pre- and post-migration periods. Migration phenology and behaviour can vary from year-to-year. By including multiple years, we aimed to evaluate whether estimates derived from models are repeatable.

All data preparation steps and analyses were performed in R 3.6.3 (R Core Team 2019). For each species-year, we merged the eBird occurrence records with the Sampling Event Dataset using the unique Sampling Event Identifier. We defined sites in this merged dataset as latitude and longitude coordinates gridded to 0.1°. We then defined each species’ range for a given year as the sites with at least one observation of that species during the period from January to June. Note that a gridding of 0.1° was chosen to ensure an ample number of non-detections. Checklists that occurred at sites outside of a species’ range for a given species-year, and sites within a species’ range that had fewer than 50 checklists, were filtered from the analysis. The average sample size of species-year datasets was approximately 0.84 million checklists (+/- SD 0.43 million), with the smallest sample size > 96,000 checklists.

To quantify HPOP, we used data from the Gridded Population of the World (GPW), Version 4: Population Density, Revision 11 (CIESIN 2016). GPW models global human population densities (persons/km²) at high resolution (30 arc-second; ~1 km at equator) using census data from between 2005 and 2014. GPW produces estimates at 5-year intervals between 2000 and 2020. We downloaded the raster file of population density estimates for 2015. Using the raster package v. 3.4-10 (Hijmans 2021), we extracted HPOP as the mean log-transformed human population density for a 5 km radius around each coordinate pair in the eBird Sampling Event Dataset, with latitude and
longitude coordinates gridded to the nearest 0.01°. The 5 km radius accounts for the relative mobility of birds and eBird observers, as well as previous work showing that artificial light affects birds primarily within this spatial scale (Van Doren et al. 2017; McLaren et al. 2018).

2.2.2 Modelling migration dynamics

To model migration dynamics, we fit a separate GAM for each species-year dataset using the mgcv package v. 1.8-31 (Wood 2011). The response variable was the binary detection of a species as a function of checklist location and date. We fit a separate migration model for each species-year. Models were fit with a binomial distribution and with the discrete argument set to true. The structure of the most saturated model, which included HPOP as a predictor, is as follows:

\[
\text{detection} \sim \text{te(date, latitude, HPOP)} + s(\text{longitude}) + s(\text{minofday}) + \log(\text{duration.minutes})
\]

where detection of a species in a given checklist is modelled as a function of tensor product (te) smooth functions for the checklist Julian date, latitude, and log-transformed human population density, smooth functions (s) for checklist longitude and the time of day when the checklist began (minofday), and a parametric term for duration of the checklist session in minutes (duration.minutes, log-transformed). Tensor product smooths are used to model smooth interaction terms with different units of measurement (Wood et al. 2013), which is important because we expect the effect of HPOP to depend on latitude and date. Time of day and checklist duration are two checklist variables known to influence detection probability for eBird observers (Strimas-Mackey et al.)
2020; Johnston et al. 2021). Additional details of the model fitting procedure are provided in the appendix (A2).

We used cross-validation to test the predictive accuracy of each species-year migration GAM. For a given species-year, we first fit the migration GAM using a randomly chosen subset representing 90% of the data. After fitting the model to these training data, we obtained model predictions for the remaining 10% of the data and compared these predicted detection rates (detected or not) with observed values. We assessed two performance metrics: Cohen’s kappa, and the correlation coefficients for binned detection averages. Cohen’s kappa is used to evaluate the agreement between model predicted detections, and observed detection values, corrected for random chance agreement (Cohen 1960). Kappa values near one indicate strong agreement, whereas values near zero indicate that agreement is no better than expected by chance. Kappa performs well when there is a class imbalance, which is useful because detection probabilities for a given species in eBird are low (Strimas-Mackey et al. 2020). We used the PresenceAbsence package v. 1.1.9 (Freeman & Moisen 2008) to calculate the maximum kappa for each model. Additionally, we computed correlation coefficients for the predicted and observed average detection rates, binned in space and time. For this analysis, we binned test data into 0.1° grid 10-day bins, and then took the average predicted and observed detection values for each bin that had at least 20 checklists. We then determined the Pearson’s correlation coefficient between predicted and observed bin averages.

To determine whether HPOP influences migration dynamics, we compared each species-year migration model to a corresponding null model. The null model had the
same structure as the most saturated model described above, but did not contain HPOP as a predictor. Hence, the null model describes migration dynamics under the assumption that migration behaviour is not affected by variation in HPOP per se. We took the difference in AIC values between these two candidate models (\( \Delta \text{AIC} = \text{null model AIC} – \text{HPOP model AIC} \)). A positive value of \( \Delta \text{AIC} \) indicates that the model with HPOP has greater support. We calculated Akaike’s weight, \( w \), as a measure of the strength of the evidence that HPOP is associated with migration dynamics.

2.2.3 Deriving metrics from fitted migration models

For each species-year, we used the fitted migration GAMs to estimate the average level of HPOP experienced at two phases in the annual cycle: HPOP\text{mig}, and HPOP\text{breed}, and we additionally estimated HPOP\text{null} as a comparison with HPOP\text{mig} (Fig. 1B). First, we defined the beginning and end of the migration phase for a given species-year based on estimated daily changes in average latitude, as derived from the fitted migration model (see S3 in the appendix for details of this procedure). The breeding phase was defined as beginning on the first day after the migration phase and ending on June 30th. For each date starting from the beginning of the migration phase, we calculated daily HPOP as a weighted average, by taking the average HPOP for all sites in the species’ range weighted by model estimates for site-specific encounter rates (Fig. 1B). An encounter rate is the predicted probability that an observer will report a given species for a standardized set of observation or “effort” parameters (Strimas-Mackey et al. 2020). We then calculated HPOP\text{mig} as the average of these daily values for the migration phase, and HPOP\text{breed} as the average of these daily values for the breeding phase. Larger values of HPOP\text{mig} and
HPOP\textsubscript{breed} indicate that a species experiences greater human population densities during that phase. We also calculated HPOP\textsubscript{null} for the migration phase using estimates from the null model. HPOP\textsubscript{null} is the average HPOP during migration in a model that assumes migration is not influenced by HPOP. See the appendix for further details and validation of these metrics (A4-A6).

To quantify a species’ navigational bias for human-influenced sites, we took the difference HPOP\textsubscript{mig} – HPOP\textsubscript{null} (Fig. 1C). If HPOP\textsubscript{mig} is greater than HPOP\textsubscript{null}, it indicates that encounter rates are biased toward high HPOP sites during migration. Alternatively, if HPOP\textsubscript{mig} is lower than HPOP\textsubscript{null}, it indicates that encounter rates are biased toward low HPOP sites.

To compare the amount of HPOP experienced during migration and breeding, we took the difference, HPOP\textsubscript{mig} – HPOP\textsubscript{breed} (Fig. 1C). We calculated the fold-change by taking the ratio of back-transformed values (HPOP\textsubscript{mig}/HPOP\textsubscript{breed}, expressed in persons/km$^2$). A 2-fold change would indicate that a species experiences twice as much HPOP during migration as it does during breeding, whereas a 0.5-fold change would indicate that a species experiences half as much HPOP during migration as it does during breeding.

2.2.4 Species differences in migration metrics

We used the rptR package v. 0.0.22 (Stoffel et al. 2017) to evaluate whether annual estimates of species’ navigational bias and HPOP\textsubscript{mig} were repeatable (i.e., do species differ consistently in these measures?). In this analysis, species was the random effect and we included year as a categorical fixed effect. To estimate phylogenetic signal in
navigational bias and $H\text{POP}_{\text{mig}}$, we calculated Pagel’s lambda using the phytools package v. 0.7-80 (Revell 2012) and a phylogeny obtained from BirdTree.org (Jetz et al. 2012, 2014). A value of lambda near one indicates that trait values are highly similar among closely related species, whereas a value near zero indicates that trait variation is independent of the phylogenetic relationships among species.

To investigate sources of variation in navigational bias, we used a comparative analysis based on a Bayesian phylogenetic regression model in the MCMCglmm package v. 2.32 (Hadfield 2010) ($n = 189$ species-year measures from 63 species). The fixed effect predictors included a species’ breeding habitat and the time of day when it migrates (see section A7 in the supplement for details on how these traits were measured) as well as $H\text{POP}_{\text{breed}}$, average breeding latitude, and the duration of migration in days estimated from the GAM for each species-year. The model also included year as a categorical fixed effect. The random effect structure included species identity to account for repeated measures, as well as the phylogeny to account for shared ancestry. We ran 100,000 iterations after a burn-in period of 3,000, with a thinning interval of 500.

2.3 Results

2.3.1 Migration is influenced by human population density

The fitted GAMs performed well (Fig. 2A), with a median deviance explained of 0.32 (SD = 0.08, range 0.12 to 0.46) and a median kappa of 0.29 (SD = 0.07, range 0.09 to 0.45). This distribution of kappa values closely matches that of other recent studies of bird migration dynamics (e.g., mean of 0.31 in Strimas-Mackey et al., 2020). Model predictions in the cross-validation analysis were also strongly correlated with observed
values, with a median correlation coefficient of 0.77 (SD = 0.13, range 0.31 to 0.98). All models with HPOP received much stronger support than their corresponding null models (lower AIC; all Akaike weights > 0.99; Fig. 2B), consistent with the hypothesis that HPOP broadly influences migration across species.

Figure 2. Birds alter their migration behaviour in response to HPOP. A) Metrics of model performance for saturated models that include HPOP as a predictor. B) Distribution of ΔAIC values comparing the saturated models to null models that did not include HPOP (n = 189 species-year models, grouped by family). Models with HPOP were universally better supported, indicating that HPOP broadly influences spring migration. C) Distributions for navigational bias and the difference between HPOP_{mig} and HPOP_{breed} (n = 189 species-years). Most birds show a negative bias to HPOP while migrating, yet the level of HPOP experienced during migration is much greater than that of breeding. A small number of species were found to be positively biased toward HPOP during migration, including the black-throated blue warbler, Nashville warbler, blackpoll warbler, dickcissel, cedar waxwing, orchard oriole, Baltimore oriole, chimney swift, and song sparrow. Red lines indicate the medians.

Navigational bias was negative for nearly all species-years (Fig. 2C), indicating that most bird species (54/63) are biased away from HPOP during migration. Despite this strong negative response, nearly all species (58/63) experience much greater HPOP during migration than they do during breeding (Fig. 2C). On average, we estimate that birds experience 2.7-fold greater HPOP during migration as compared to breeding (range
= 0.8 to 1.4-fold difference). The species with the largest excess of HPOP during migration are the black-throated blue warbler, bay-breasted warbler, and Nashville warbler.

### 2.3.2 Variation among species

Navigational bias was moderately repeatable (R = 0.59, 95% CI = 0.42 to 0.70, p < 0.0001), indicating consistent species differences in this trait. The average level of HPOP experienced during migration, HPOP\textsubscript{mig}, was also highly repeatable (R = 0.77, 95% CI = 0.68 to 0.85, p < 0.0001). We did not detect significant phylogenetic signal for either trait, indicating that closely related species respond similarly to HPOP (HPOP\textsubscript{mig}: \( \lambda = 0.23, p = 0.42 \); Navigational bias: \( \lambda < 0.0001, p > 0.99 \)).

A comparative analysis of navigational bias revealed that variation is explained by three key traits (Fig. 3; Fig. A3; Table A4). As expected, navigational bias is positively associated with HPOP\textsubscript{breed}, indicating that more urban-tolerant breeders are less positively biased towards HPOP when migrating. Second, forest-breeding species are less negatively biased toward HPOP than are habitat specialist and habitat generalist species. Third, species with longer-duration migrations are more positively biased toward HPOP. This indicates that species that migrate slowly and/or stopover more often associate less with HPOP during migration than expected based on location. We did not detect an association between navigational bias and average breeding latitude or the time of day when a species migrates.
Figure 3. Navigational bias for HPOP is associated with breeding ecology and the pace of migration. Partial residual plots for the comparative analysis of navigational bias (n = 189 species-years). Each panel shows the relationship between residual navigational bias and a given predictor, after accounting for other predictors in the model. For visualization purposes, these partial residual plots were generated from a model that does not account for phylogeny. The results of this simpler model were consistent with those of the full phylogenetic analysis. See the appendix for additional details of this analysis.

2.4 Discussion

These findings provide a broad, comparative analysis of how migrating birds are responding to the many factors associated with human activity. Our results indicate that most migrating birds are negatively biased toward HPOP, and yet they experience much greater HPOP during migration than they do during breeding. This indicates that migration is a time of heightened exposure to the well-documented threats associated with high human population density. Our results also show that species differ repeatably in navigational bias, and that variation in this trait can be explained by breeding ecology and the pace of migration. Hence, some species may be particularly vulnerable to mortality as a result of anthropogenic causes during migration.

For all species-years, we found that migration dynamics across the North American landscape were associated with variation in HPOP. This was an expected finding since lower latitudes tend to have greater HPOP than the higher latitudes where
most migrants breed. This finding is also consistent with previous research showing an association between human activity and avian distributions across broad geographic scales, particularly during migration (Mason et al. 2021; Schrimpf et al. 2021). We found this association to be driven by navigational bias to HPOP during migration, indicating that bird populations may be able to alter their migration trajectories in response to contemporary changes to the landscape. Note that we found signs of navigational bias at a broad spatial and population scale. Previous work has shown that one facet of HPOP, artificial light, has both attractive and repulsive properties depending on the spatial scale under consideration (McLaren et al. 2018). Though the disorientation effects associated with light are not the same as navigational bias to HPOP, it is possible that birds may also respond differently to HPOP at a smaller geographic scale. A small number of species were found to have a positive navigational bias toward HPOP during migration, including the black-throated blue warbler, Nashville warbler, blackpoll warbler, dickcissel, cedar waxwing, orchard oriole, Baltimore oriole, chimney swift, and song sparrow.

Our results indicate that the vast majority of bird species experience much greater HPOP during migration than they experience during breeding, indicating that billions of birds must migrate through areas with high human influence to reach their breeding grounds. This finding is consistent with previous research showing that some bird species use sites with higher human influence and greater light pollution during migration than during non-migratory seasons (Zuckerberg et al. 2016; Cabrera-Cruz et al. 2018). Birds are already vulnerable during migration because of physiological and behavioural challenges associated with these long flights. Our results suggest that migrating birds may also be especially vulnerable to challenges caused by humans. Given that the very
highest density HPOP sites are underrepresented in eBird data, migrating birds may experience even higher human activity than we estimate here.

We found repeatable species differences in both navigational bias and HPOP\textsubscript{mig}. Neither trait had phylogenetic signal, indicating that they may be explained by broad differences in species’ geographic ranges and in habitat and resource requirements rather than phylogenetic position. This work establishes for the first time that some species are consistently more vulnerable and responsive to HPOP during long-distance migration. One avenue for future work is to determine whether certain individuals within a species are also more affected.

We found that species differences in navigational bias could be explained by three ecological traits. First, species that breed in high HPOP areas showed a less negative bias to HPOP while migrating. Second, forest-breeding species had a less negative bias to HPOP than either habitat specialist or generalist species, suggesting that forest breeders may be better able to exploit urban and suburban resources (Archer \textit{et al.} 2019). One caveat is that our sample of generalists are almost exclusively aerial insectivores, meaning that we cannot disentangle the effects of these two traits. We did not detect a difference in navigational bias when comparing habitat generalists and specialists; both were overall negatively biased on average, suggesting that generalists may prefer sites with lower HPOP during migration (Bonier \textit{et al.} 2007; Ducatez \textit{et al.} 2018; Callaghan \textit{et al.} 2019). Third, we found that species with slower paced migrations were less negatively biased to HPOP than species with faster paced migrations. Slower migrants use stopovers more often and/or for longer periods, and may thus have more choice in stopover sites. We therefore hypothesize that slow migration and the frequent use of stopovers may be
associated with a greater ability to exploit urban and suburban resources. Variation in navigational bias was not explained by breeding latitude or time of day of migration.

Our study describes variation in a species’ experience of and navigational response to HPOP during migration. This raises important questions for future work about the association between these traits and population declines. For example, species with a strong negative navigational bias, yet experience high $HPOP_{mig}$ include the yellow-bellied flycatcher, fox sparrow, black-throated green warbler, blackburnian warbler, and Townsend’s warbler; these species may be particularly vulnerable to high HPOP and to future land development. We have provided further description of a potential categorization in the appendix (A6; Fig. A2).

Our findings demonstrate that for birds, long-distance migration dynamics are influenced by the many facets of human population density, with species varying in their navigational response to HPOP. Most species had a negative navigational bias to HPOP, yet nearly all birds experience much greater HPOP during migration than during breeding. Navigational bias is explained by species differences in breeding habitat, $HPOP_{breed}$, and the pace of migration. These findings fill an important gap by examining how HPOP is associated with migration behaviour for many species across a broad spatial scale. This work may also have implications for bird conservation. For example, human development of the landscape is likely proceeding at a pace that evolution cannot keep up with. Some bird species may continue to follow sub-optimal migration routes if they were inherited or learned from other individuals. Future work should determine whether differences in navigational bias during migration are beneficial for fitness or survival, both in the short and long term.
2.5 References


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distribution dynamics with spatiotemporal exploratory models: Discovering patterns


3.4-13.


Figure A1. Distribution of human population densities (HPOP) across the United States and Canada. Coloured points represent sites gridded to the nearest 0.01°. Grey regions were not sampled in this study. Inset: Example of the distribution of HPOP values for eBird checklists in the ruby-throated hummingbird’s 2019 range. Note that HPOP is on a log-scale, and the legend and axes show back-transformed values.
Table A1. Predictions for the comparative analysis of navigational bias. A predicted positive direction indicates that we expect species with higher values of that trait to be more positively biased towards HPOP during migration. Note that we did not have a prediction for duration of migration.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Hypothesis</th>
<th>Predicted direction for the relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>HPOP_{breed}</td>
<td>Species that experience high HPOP while breeding will likely also experience high HPOP during migration.</td>
<td>Positive</td>
</tr>
<tr>
<td>Breeding habitat – specialist category, forest category</td>
<td>Habitat specialists and forest-breeding species have specific habitat requirements that may not be found in urban areas.</td>
<td>Negative</td>
</tr>
<tr>
<td>Average breeding latitude</td>
<td>Species breeding at higher latitudes may travel farther distances, which may make urban benefits like feeders especially useful.</td>
<td>Positive</td>
</tr>
<tr>
<td>Duration of migration</td>
<td>Since species with slower-paced migrations may have more choice of stopover sites, they may either be able to make better use of urban areas or be able to avoid them.</td>
<td>NA</td>
</tr>
<tr>
<td>Nocturnal migration</td>
<td>Disorientation by light pollution at night may disorient birds and trap them in urban areas.</td>
<td>Positive</td>
</tr>
</tbody>
</table>

HPOP_{breed} is the average level of HPOP experienced by a species during the breeding phase.
A.1 Species selection criteria

To sample species for this study, we began by considering all migratory bird species that breed in North America. We then selected species using four main criteria. First, we focused on landbirds. Hence, we ruled out waterbirds (such as ducks or geese, *Anatidae*) and pelagic species. Second, we prioritized species that are common and broadly-distributed in North America and that have estimated population sizes in the millions based on recent estimates from Rosenberg et al. (2019). This criterion was important for our ability to obtain robust estimates of migratory dynamics using eBird citizen science data. Third, since nocturnal migration is far more common among long-distance migrants than diurnal migration, species were also chosen to try to attain a balance of nocturnal and diurnal migrants. Lastly, we selected species so that our sample encompassed a wide range of families. Fig. 2B in the main text shows the list of 16 families represented in our sample.
Table A2. Species sampled in this study and estimates of key traits including navigational bias and HPOP\textsubscript{mig}. Species are ordered by phylogeny (Jetz et al. 2012, 2014). HPOP\textsubscript{mig} is the average level of HPOP experienced during the migration phase.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>COMMON NAME</th>
<th>TIME OF DAY OF MIGRATION</th>
<th>BREEDING HABITAT</th>
<th>NAVIGATIONAL BIAS</th>
<th>HPOP\textsubscript{MIG}</th>
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<td>Habitat generalist</td>
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<td>1.4</td>
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<td>Dendroica virens</td>
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</tr>
<tr>
<td>Dendroica townsendi</td>
<td>Townsend's warbler</td>
<td>Nocturnal</td>
<td>Forest-breeding</td>
<td>-1.5</td>
<td>2.3</td>
</tr>
<tr>
<td>Setophaga ruticilla</td>
<td>American redstart</td>
<td>Nocturnal</td>
<td>Forest-breeding</td>
<td>-0.09</td>
<td>3</td>
</tr>
<tr>
<td>Dendroica magnolia</td>
<td>Magnolia warbler</td>
<td>Nocturnal</td>
<td>Forest-breeding</td>
<td>-0.2</td>
<td>5.5</td>
</tr>
<tr>
<td>Wilsonia citrina</td>
<td>Hooded warbler</td>
<td>Nocturnal</td>
<td>Forest-breeding</td>
<td>-1</td>
<td>2.4</td>
</tr>
<tr>
<td>Wilsonia pusilla</td>
<td>Wilson's warbler</td>
<td>Nocturnal</td>
<td>Forest-breeding</td>
<td>-0.1</td>
<td>2</td>
</tr>
<tr>
<td>Name</td>
<td>Color Description</td>
<td>Breeding Habitat</td>
<td>Breeding Schedule</td>
<td>Night Activity</td>
<td>Day Activity</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>---------------------------------</td>
<td>------------------</td>
<td>-------------------</td>
<td>----------------</td>
<td>--------------</td>
</tr>
<tr>
<td>Mniotilta varia</td>
<td>Black-and-white warbler</td>
<td>Forest</td>
<td>Nocturnal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seiurus noveboracensis</td>
<td>Northern waterthrush</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.9</td>
<td>3.1</td>
</tr>
<tr>
<td>Oporornis philadelphia</td>
<td>Mourning warbler</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.2</td>
<td>4.5</td>
</tr>
<tr>
<td>Geothlypis trichas</td>
<td>Common yellowthroat</td>
<td>Habitat</td>
<td>Nocturnal</td>
<td>-0.7</td>
<td>0.7</td>
</tr>
<tr>
<td>Vermivora peregrina</td>
<td>Tennessee warbler</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.3</td>
<td>4.8</td>
</tr>
<tr>
<td>Vermivora ruficapilla</td>
<td>Nashville warbler</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>0.2</td>
<td>6.3</td>
</tr>
<tr>
<td>Spiza americana</td>
<td>Dickcissel</td>
<td>Habitat</td>
<td>Nocturnal</td>
<td>1.7</td>
<td>3.3</td>
</tr>
<tr>
<td>Passerina cyanea</td>
<td>Indigo bunting</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.7</td>
<td>0.6</td>
</tr>
<tr>
<td>Pheucticus ludovicianus</td>
<td>Rose-breasted grosbeak</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.8</td>
<td>1.2</td>
</tr>
<tr>
<td>Piranga rubra</td>
<td>Summer tanager</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-0.9</td>
<td>0.8</td>
</tr>
<tr>
<td>Tachycineta bicolor</td>
<td>Tree swallow</td>
<td>Habitat</td>
<td>Diurnal</td>
<td>-1</td>
<td>-0.09</td>
</tr>
<tr>
<td>Riparia riparia</td>
<td>Bank swallow</td>
<td>Habitat</td>
<td>Diurnal</td>
<td>-1</td>
<td>-0.2</td>
</tr>
<tr>
<td>Progne subis</td>
<td>Purple martin</td>
<td>Habitat</td>
<td>Diurnal</td>
<td>-0.5</td>
<td>0.7</td>
</tr>
<tr>
<td>Petrochelidon pyrrhonota</td>
<td>Cliff swallow</td>
<td>Habitat</td>
<td>Diurnal</td>
<td>-0.04</td>
<td>0.5</td>
</tr>
<tr>
<td>Hirundo rustica</td>
<td>Barn swallow</td>
<td>Habitat</td>
<td>Diurnal</td>
<td>-0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Coccyzus americanus</td>
<td>Yellow-billed cuckoo</td>
<td>Forest</td>
<td>Nocturnal</td>
<td>-1.4</td>
<td>0.6</td>
</tr>
</tbody>
</table>
A.2 eBird variables influencing detection probability

Several properties of eBird checklists are known to influence detection probabilities (Strimas-Mackey et al. 2020; Johnston et al. 2021). For example, the time of day when a checklist begins can affect detectability because birds have different activity patterns that vary throughout the day. Most birds are much more active during early morning and evening than during mid-day, making them more noticeable to a human observer. Additionally, the duration of the checklist observation session also affects detection probability. In general, the ability to detect a given species increases with session duration.

A.3 Defining the migration phase

Many of the long-distance migrant species in our sample overwinter in Central and South America and are not yet present in North America during the period from January-March. Additionally, different species arrive in North America at different times. Therefore, to ensure that any further estimates were only calculated for dates when a species is present in reasonable numbers, we determined the first date when the cumulative number of checklist detections in the United States or Canada reached 5% of the total number of checklist detections for that species-year. For any days prior, we deem the species as not yet present in large enough numbers to estimate encounter rates.

Next, for each species-year, we used encounter rate estimates to define the dates of the beginning and end of the migration phase, and the beginning of the breeding phase. To define the migration phase, we examined changes in average daily latitude estimates. We calculated each average daily latitude as a weighted average, by taking the mean of
the latitude coordinates for all sites in the species’ range weighted by model-estimated site encounter rates for a given date. We then defined the migration phase as beginning on the first day on which the change in the species’ average latitude was at least +5 km relative to the previous day (i.e., the average latitude for the species had moved at least 5 km northward). We defined the migration phase as ending when the species’ average latitude change fell below +5 km/day, or the 150th day of the year (May 30), whichever date was earlier. Breeding was defined as starting on the first day after the end of migration. For each species-year, we calculated the duration of migration in days by subtracting the last Julian date of the migration phase from the first Julian date of the migration phase. We calculated average breeding latitude by averaging the daily latitudes for dates within the breeding phase.

One species, the song sparrow, never met the +5 km/day threshold for migration; it has a maximum average daily latitude change of +3-4 km/day. We therefore defined the migration phase for the song sparrow as beginning on the first date when it had +0 km/day latitudinal change, and ending on the last date when it met this threshold, or the 150th day of the year, whichever was earlier.

A.4 Sensitivity analysis for migration threshold

The threshold of +5 km/day described above was chosen to represent consistent northward progress. However, in reality, population movement is a continuum. We therefore performed a sensitivity analysis to test whether \( HPOP_{mig} \), \( HPOP_{breed} \), \( HPOP_{null} \), and the duration of migration were sensitive to changes in the +5 km/day threshold. We re-calculated these metrics using three alternative thresholds: +4 km/day, +6 km/day, and
+10 km/day, and examined Pearson’s correlations to compare the metric values obtained in these different threshold scenarios. The results of this sensitivity analysis demonstrated that HPOP\textsubscript{mig}, HPOP\textsubscript{breed}, and HPOP\textsubscript{null} are all highly robust to changes in the migration threshold (all correlation coefficients > 0.98; see Table A3). Migration duration was slightly more sensitive to changes in the threshold (e.g., correlation coefficients between 0.79-0.98), but this is not surprising given that migration duration is directly defined by the threshold. Notably, even the largest changes in the threshold still yielded a correlation coefficient of 0.79 for migration duration, and 0.98-0.99 for the other metrics.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Alternative threshold (km/day)</th>
<th>Correlation with values obtained with + 5 km/day threshold (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>HPOP\textsubscript{mig}</td>
<td>4</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.98 (0.97 to 0.98)</td>
</tr>
<tr>
<td>HPOP\textsubscript{breed}</td>
<td>4</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td>HPOP\textsubscript{null}</td>
<td>4</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>&gt;0.99 (&gt;0.99 to &gt;0.99)</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.98 (0.98 to 0.99)</td>
</tr>
<tr>
<td>Duration of migration</td>
<td>4</td>
<td>0.89 (0.86 to 0.92)</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>0.98 (0.98 to 0.99)</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.79 (0.73 to 0.84)</td>
</tr>
</tbody>
</table>

A.5 Validating metrics using eBird Status and Trends (ebirdst)

As an additional validation for our GAM procedure, we compared migration metrics HPOP\textsubscript{mig} and HPOP\textsubscript{breed} calculated from our GAMs to analogous metrics calculated using a different modelling procedure, the eBird Status and Trends project (hereafter, ebirdst Data Products). ebirdst Data Products are publicly available estimates of species
occurrence that use models controlling for biases in eBird data (i.e., encounter rates) and are provided at a weekly temporal scale and 2.96 km spatial resolution (Fink et al. 2020). For each of the 63 species in our study, we used the ebirdst package v. 0.3.2 (Strimas-Mackey et al. 2021) to obtain weekly average encounter rates for each site in the species’ 2019 range (as defined in section 2.1 of the main text). Note that 2019 was the only year provided at the time we accessed ebirdst Data Products that corresponds to one of our sample years. We also obtained weekly average encounter rates using our fitted 2019 GAMs. We defined migration and breeding weeks using the designations described above (Section A3). We then calculated HPOP\textsubscript{mig} and HPOP\textsubscript{breed} for each species, from both ebirdst models and our GAM-based estimates. We then checked the Pearson’s correlation for HPOP\textsubscript{mig} and HPOP\textsubscript{breed} values derived under these two different modelling frameworks.

For both metrics, we found strong correlations: for HPOP\textsubscript{mig}, the correlation was 0.84, and for HPOP\textsubscript{breed}, the correlation was 0.95. Hence, we conclude that our models capture similar migration dynamics as the models used in ebirdst. Moreover, this analysis provides further support that species variation in these two traits (HPOP\textsubscript{mig} and HPOP\textsubscript{breed}) is generalizable across modelling frameworks. Note that our GAM-based modelling approach provides two important advantages specific to our research aims within this study. First, we modelled observations on a daily basis, which provides additional temporal resolution (by contrast, the estimates provided in ebirdst are weekly). Second, for each species, we repeated our modelling procedure on three separate spring migration years (2017, 2018, and 2019), which provides a check on the stability and repeatability of downstream estimates.
A.6 Migration HPOP dynamics

The average HPOP experienced by each species fluctuates over the course of the annual cycle (Fig. A2). Based on visual inspection of these time series, we identified four general patterns:

1. Species with a negative navigational bias to HPOP during migration, but experience much greater HPOP during migration than they do during breeding (e.g., black-and-white warbler; Fig. A2A; n = 12 species).

2. Species that do not appear to have a strong navigational bias, and experience greater HPOP during migration than they do during breeding (e.g., American redstart; Fig. A2B; n = 25 species).

3. Species with a negative navigational bias to HPOP during migration, and experience similar HPOP during migration as they do during breeding (e.g., bank swallow; Fig. A2C; n = 14 species).

4. Species that do not appear to have a strong navigational bias, and experience similar HPOP during migration as they do during breeding (e.g., barn swallow; Fig. A2D; n = 12 species).
Fig. A2. Examples of the dynamics of HPOP during migration and breeding. A) Black-and-white warbler, B) American redstart, C) bank swallow, and D) barn swallow. In each panel, the dark lines show the daily estimates for the average level of HPOP experienced. The semi-transparent lines show the expectations from null models. The migratory and breeding phases are denoted by the background shading.

A.7 Breeding habitat and daily timing of migration

We obtained information on species’ breeding habitat from Rosenberg et al. (2019), who compiled the primary breeding biome assigned to each species in the Avian Conservation Assessment Database (ACAD; Partners in Flight, 2021). Because some of the breeding biome categories in Rosenberg et al. (2019) are relatively rare, we collapsed their designations into three breeding habitat categories for our analyses:
1. Forest-breeding species (Eastern forest, Western forest, Boreal forest, and forest
generalists (occur in two or more types of forest) from Rosenberg et al. (2019),
2. Habitat specialists (grassland, wetland, and arctic tundra species), and
3. Habitat generalists (defined by the ACAD as species that use three or more
   habitats).

Some birds may become trapped in areas with high HPOP because of artificial light at
night. We also investigated whether the use of diurnal versus nocturnal migration flight
predicts navigational bias for HPOP during migration. Using the Birds of the World
database (Billerman et al. 2020), we classified each species as either an exclusive
nocturnal migrant (species that migrate only at night) or diurnal/mixed migrants (species
that migrate only during the day or during a mix of times). In Birds of the World, the
primary source of information on daily migration timing comes from tower kills, which
indicate nocturnal migration. If migration timing information was not available from
Birds of the World, we referred to the All About Birds website (Cornell Lab of
**Table A4. Analysis of navigational bias during migration.** Posterior means for the categorical predictors ‘breeding habitat’ and ‘daily timing of migration’ depict pairwise comparisons between each level and the reference level (bold). Also provided are the 95% credible intervals (CI), effective sample sizes, and pMCMC values (** indicates pMCMC < 0.01).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Type of trait</th>
<th>Posterior mean</th>
<th>95% CI</th>
<th>Effective samples</th>
<th>pMCMC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Migration period (duration)</td>
<td>Species-year</td>
<td>0.0052</td>
<td>0.0035, 0.0071</td>
<td>114</td>
<td>&lt;0.005 **</td>
</tr>
<tr>
<td>Average breeding HPOP</td>
<td>Species-year</td>
<td>−0.86</td>
<td>−1, −0.74</td>
<td>200</td>
<td>&lt;0.005 **</td>
</tr>
<tr>
<td>Breeding habitat – Habitat generalists to <strong>forest-breeding</strong></td>
<td>Species</td>
<td>−0.38</td>
<td>−0.72, −0.12</td>
<td>150</td>
<td>&lt;0.005 **</td>
</tr>
<tr>
<td>Breeding habitat – Habitat specialists to <strong>forest breeding</strong></td>
<td>Species</td>
<td>−0.42</td>
<td>−0.71, −0.16</td>
<td>200</td>
<td>0.02 *</td>
</tr>
<tr>
<td>Breeding habitat – Habitat generalists to <strong>habitat specialists</strong></td>
<td>Species</td>
<td>0.058</td>
<td>−0.3, 0.44</td>
<td>200</td>
<td>0.77</td>
</tr>
<tr>
<td>Average breeding latitude</td>
<td>Species-year</td>
<td>−0.0052</td>
<td>−0.028, 0.017</td>
<td>200</td>
<td>0.67</td>
</tr>
<tr>
<td>Daily timing of migration – Nocturnal to <strong>diurnal</strong></td>
<td>Species</td>
<td>−0.18</td>
<td>−0.39, 0.12</td>
<td>295</td>
<td>0.20</td>
</tr>
</tbody>
</table>
Fig. A3. Analysis of navigational bias during migration. As in the main text Fig. 3, this plot shows partial residual plots from an analysis that does not account for phylogeny (n = 189 species-years). Each panel shows the relationship between navigational bias and one predictor, after accounting for the other predictors in the model. The full phylogenetic analysis is reported in Table A4.

A.8 References


