

2 **Migration and the excess exposure of birds to human density in North America**

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20

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34 **ABSTRACT**

Migratory species must cross a range of landscapes that are increasingly modified by humans. A
36 key question is how migrating populations are responding to human-induced environmental
change. Here, we model the spring migration dynamics of 63 bird species in North America to
38 quantify their exposure to human population density. We find that most bird species have a
negative navigational bias, suggesting that they attempt to avoid human-dense areas during
40 migration, and yet they experience far greater human density during migration as compared to
breeding. Species that experience excess human density during migration share several key
42 traits: they tend to be nocturnal migrants, they start migrating through North America earlier in
the year, and they tend to migrate longer distances. These findings underscore that birds are
44 especially vulnerable to threats associated with human disturbance during migration, with
predictable exposures that are often elevated by 2- to 3-fold during migration.

46 **1. INTRODUCTION**

During spring migration, hundreds of bird species travel across a broad range of landscapes to
48 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
50 fragmentation, as well as altered food availability and foraging periods (Isaksson 2018). These
challenges may have important impacts on the ability of migrants to successfully reach their
52 breeding grounds. For example, window collisions and domestic cats are two major sources of
mortality for migrating birds (Loss *et al.* 2013, 2014; Machtans *et al.* 2013), artificial light
54 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 to fuel migration flight.
56 Although most studies of the impact of human activity on birds have been conducted during the
breeding phase (Faaborg *et al.* 2010), recent work reveals that some bird species occur in more
58 human-modified sites during migration as compared to other phases of the annual cycle
(Zuckerberg *et al.* 2016; Cabrera-Cruz *et al.* 2018). This raises key questions as to whether and
60 how migrating species differ in their response to human activity (Zuckerberg *et al.* 2016;
Cabrera-Cruz *et al.* 2018).

62 Here, we study the spring migration dynamics of 63 North American landbird species to
investigate how migration is influenced by human population density (HPOP). We focus on
64 HPOP because it captures a suite of human footprint effects on the landscape, including building
density, the density of roads and impervious surfaces, changes in resource availability, light and
66 noise pollution, and chemical contaminants, among other factors. We expect bird species to
differ in their responses to HPOP through multiple causal pathways. Importantly, our aim in this
68 study is not to disentangle how different mechanisms occur across species, but rather to quantify

how migrating bird species are responding to human density in general, and to investigate
70 sources of variation in their exposure. To model migration dynamics, we use data from eBird, a
community science database based on checklists submitted by hundreds of thousands of regular
72 users (Sullivan *et al.* 2009; Strimas-Mackey *et al.* 2020). These widespread observations make
eBird particularly useful for modelling the timing and trajectory of migratory populations (Fink
74 *et al.* 2011; La Sorte *et al.* 2013, 2016; Feng *et al.* 2021; La Sorte & Horton 2021). eBird
checklists also cover a wide range of HPOP in North America, with the greatest representation
76 covering sites that range between 10-10,000 persons/km² (e.g., Figure 1A inset; see also
supplement Figure S1).

78 Our first aim in this study is to estimate average levels of HPOP experienced during the
spring migration phase and breeding phase, respectively (hereafter, we refer to these estimates as
80 HPOP_{mig} and HPOP_{breed}). We also examine how these estimates relate to species differences in
breeding SSI (Julliard *et al.* 2006), an index of how specialized a species is in terms of its
82 breeding habitat. We predicted that more specialized species with a higher breeding SSI would
have lower HPOP_{mig} and HPOP_{breed}, because narrow resource requirements are less likely to be
84 met in urbanized areas (Bonier *et al.* 2007; Ducatez *et al.* 2018; Callaghan *et al.* 2019). Second,
following recent work establishing that migrating populations often use regions that differ in
86 landcover and light pollution (Zuckerberg *et al.* 2016; Cabrera-Cruz *et al.* 2018), we calculate
the average excess HPOP experienced by each species during migration as compared to
88 breeding. We also estimate each species' navigational bias with respect to HPOP, which we
define as the difference between HPOP_{mig} and a null expectation. Finally, we use a comparative
90 analysis to examine species differences in exposure to excess HPOP during migration, which we
define as the difference between HPOP_{mig} and HPOP_{breed}. We consider as predictors several traits

92 related to migration biology, including the annual timing of a species' migration through North
America, the distance the species migrates, and the time of day (nocturnal or diurnal) when
94 migration flight primarily occurs (Gauthreaux & Belser 2006; Van Doren *et al.* 2017; McLaren
et al. 2018; Adams *et al.* 2021). Overall, this is the first work to characterize how a broad range
96 of migratory bird species respond to HPOP during migration.

98 **2. MATERIALS AND METHODS**

100 *2.1 General approach*

We selected 63 migratory terrestrial bird species that are common in North America, that
102 overwinter primarily at latitudes below 40°N, and that breed primarily at latitudes above 45°N.
Given that migration behaviour can vary from year-to-year, we chose to study spring migration
104 in three successive years, 2017-19. To model migration dynamics for each species-year, we used
observations from eBird, fitting a generalized additive model (GAM) for each species-year.
106 Then, we extracted downstream estimates from the fitted species-year models to characterize a
set of responses to HPOP. All data preparation and analyses were performed in R 3.6.3 (R Core
108 Team 2020). Further details of the study species are provided in the supplement and Table S1.

110 *2.2 eBird and HPOP data*

eBird data are provided in birdwatching checklists, which contain a record of the types and
112 counts of species observed by an eBird participant. We downloaded the eBird Sampling Event
Dataset for the years 2017, 2018 and 2019, which includes meta-data for all checklists in those
114 years. As per the guidelines outlined by eBird (Johnston *et al.* 2021), we included only

‘complete’ checklists that were classified as either ‘Stationary’ or ‘Traveling’, with a duration
116 less than 300 minutes and a distance less than 5 km. ‘Complete’ checklists are those where all
species observed were reported, which is important for inferring species absences (Strimas-
118 Mackey *et al.* 2020). We limited our analysis to checklists that started between 04:00 and 20:00
local time with ten or fewer observers. If multiple observers submitted checklists for the same
120 event, we retained only one checklist. For the years we examined, 80% of checklists were
classified as complete, and of those, 98% were stationary or traveling (average duration of 65.6
122 minutes, average distance of 3.35 km).

We downloaded occurrence data for each species-year from its eBird Basic Dataset in the
124 USA and Canada for the period from January 1 to June 30. This period encompasses spring
migration as well as the pre- and post-migration periods, to ensure that we could characterize the
126 full spring migration phase for all study species. We designated sites as latitude and longitude
coordinates gridded to 0.1° and defined each species-year ‘range’ as sites with at least one
128 observation of that species. We then compiled a species-year dataset based on checklists that
occurred at those sites from January 1 to June 30, and removed sites that had fewer than 50
130 checklists from further analysis for a given species-year. The species-year datasets had an
average of 0.84 million checklists (+/- SD 0.43 million), with the smallest sample size > 96,000
132 checklists.

To determine HPOP values, we used data from the Gridded Population of the World
134 (GPW), Version 4: Population Density, Revision 11 for the year 2015 (CIESIN 2016). GPW
uses census data to model global human population densities (persons/km²) at high resolution
136 (30 arcseconds, ~1 km at the equator). Using the raster package v. 3.4-10 (Hijmans 2021), we
extracted HPOP for each unique coordinate pair in the eBird Sampling Event Dataset, gridded to

138 the nearest 0.01°, as the mean natural log-transformed human population density for a 5 km
radius around those coordinates. The 5 km radius accounts for the relative mobility of birds, as
140 well as previous work showing that artificial light affects birds primarily within this spatial scale
(Van Doren *et al.* 2017; McLaren *et al.* 2018).

142

2.3 Modelling spring migration dynamics

144 Spring migration generates a pulse in occurrence at a given location as birds arrive, and the
timing of this pulse depends on latitude as well as other site characteristics (Figure 1A-B). We
146 used GAMs to model these nonlinear dynamics. GAMs are useful for this purpose because they
sum together a series of smooth functions that allow for changes in the nonlinear landscape for
148 each cross-section of the data. We fit a separate binomial GAM for each species-year dataset
using the mgcv package v. 1.8-31 (Wood 2011), with the response variable as the binary
150 detection of a species as a function of the following predictors:

152 $\text{detection} \sim \text{te}(\text{Julian date, latitude, HPOP}) + \text{s}(\text{longitude}) + \text{s}(\text{minofday}) + \text{log}(\text{duration.minutes})$

154 The te function (tensor product smooth) models nonlinear interactions among terms with
different units of measurement (Wood *et al.* 2013), which is important because we expect the
156 effect of HPOP on occurrence to depend on latitude and date. This is illustrated in Figure 1A-B
showing an example for the bay-breasted warbler. The fitted model describes how the pulse of
158 warblers occurs first at lower latitudes, and later at higher latitudes. In addition, the fitted model
predicts that at lower latitudes in the month of April, this particular warbler species is detected
160 much more frequently in low HPOP sites as compared to high HPOP sites (Figure 1B). By late

162 May, the model predicts that this species is detected at high-latitude, high-HPOP sites prior to
164 lower HPOP areas at those latitudes (Figure 1B). These patterns differ across species; as an
additional example, we show the same plots for the cedar waxwing in the supplement (Figure
S2).

The GAMs also included the time of day when the checklist began (in minutes) and the
166 checklist duration (in minutes, log-transformed) because these two variables are known to
influence detection probability for eBird observers (Strimas-Mackey *et al.* 2020; Johnston *et al.*
168 2021). We describe the predictions of the fitted GAMs as ‘encounter rates’, or the predicted
probability that an observer will report a given species for a standardized set of observation or
170 effort parameters (Strimas-Mackey *et al.* 2020). These encounter rate values are used for
subsequent estimates of $HPOP_{mig}$ and $HPOP_{breed}$, which are described in the sections below.

172 To check the predictive accuracy of the fitted species-year GAMs, we used cross-
validation by first fitting the main GAM for each species-year using a randomly chosen training
174 subset (90% of the data). We obtained model predictions for the remaining 10% of the data and
compared model predictions with observed detections. We assessed two model performance
176 metrics: Cohen’s kappa calculated in the PresenceAbsence package v. 1.1.9 (Freeman & Moisen
2008), and the correlation for binned detection averages. Cohen’s kappa is used to evaluate
178 agreement for binary data, and is particularly useful when overall detection rates are low (Cohen
1960; Strimas-Mackey *et al.* 2020); kappa values near one indicate strong agreement. Our fitted
180 GAMs had a median kappa of 0.29 (SD = 0.07, range 0.09 to 0.45; Figure S3), with a
distribution that closely matches that of other recent eBird studies (e.g., mean of 0.31 in Strimas-
182 Mackey *et al.* 2020). Additionally, we computed the correlations between predicted and
observed detection rates averaged over space and time. We binned test data into 0.1° gridded

184 coordinates and 10-day bins, and then took the average predicted and observed detection rates
for any bins with at least 20 checklists. As further validation, the model predictions were
186 strongly correlated with observed values, with a median correlation coefficient of 0.77 (SD =
0.13, range 0.31 to 0.98; Figure S3).

188 For each species-year, we also fit a null GAM of spring migration dynamics. The null
model had the same structure as the main GAM above, but did not contain HPOP as a predictor.
190 Hence, the null model describes spring migration dynamics without modelling an explicit effect
of spatial variation in HPOP. We used the predictions of these species-year null models to
192 estimate navigational bias, as described in the sections below. Figure 1C shows an example of
the null model for the bay-breasted warbler; an additional example for the cedar waxwing is
194 shown in Figure S2 of the supplement.

196 *2.4 Estimates derived from models*

We used the fitted GAMs to estimate two key metrics for each species-year: $HPOP_{mig}$, the
198 average level of HPOP experienced during spring migration, and $HPOP_{breed}$, the average level
experienced during breeding (Figure 1D). First, we defined the beginning and end of the spring
200 migration phase for each species-year based on daily changes in the species' average latitude, as
estimated from the fitted GAM (see supplement for details of this procedure). Then, for each
202 date in a given species-year analysis, we calculated the species' daily HPOP as a weighted
average, by taking the average HPOP for all sites in the species' range, weighted by model-
204 estimated encounter rates. We calculated $HPOP_{mig}$ as the average of these daily values for the
spring migration phase, and $HPOP_{breed}$ as the average of these daily values for the breeding
206 phase. An example is shown in Figure 1D for the bay-breasted warbler. Larger values of these

metrics indicate that a species experiences greater human population densities during that
208 particular phase. Further details of these estimates are provided in the supplement.

We used the rptR package v. 0.0.22 (Stoffel *et al.* 2017) to estimate repeatability, R , of
210 $HPOP_{\text{mig}}$ and $HPOP_{\text{breed}}$, computed as the proportion of total variation attributed to differences
among species. We included year as a categorical fixed effect when estimating R . To check for
212 phylogenetic signal in both $HPOP_{\text{mig}}$ and $HPOP_{\text{breed}}$, we calculated Pagel's lambda using the
phytools package v. 0.7-80 (Revell 2012) and a phylogeny obtained from BirdTree.org (Jetz *et*
214 *al.* 2012, 2014). A value of lambda near one indicates that values are highly similar among
closely related species, whereas a value near zero indicates that trait variation is independent of
216 the phylogenetic structure.

To further describe migration and breeding ecology, we examined the association
218 between the breeding Species Specialization Index (SSI) and each of $HPOP_{\text{mig}}$ and $HPOP_{\text{breed}}$.
Breeding SSI quantifies how specialized bird species are in terms of their breeding habitat
220 (Julliard *et al.* 2006; Martin & Fahrig 2018; Di Cecco & Hurlbert 2022); larger SSI values
indicate that a species uses a narrower range of habitat types when breeding. We examined these
222 correlations for 59 species in our sample that had SSI values reported in previous work (Martin
& Fahrig 2018; Ziolkowski *et al.* 2022).

We defined a species' navigational bias as the difference between $HPOP_{\text{mig}}$ and a null
expectation. To estimate navigational bias, we computed $HPOP_{\text{null}}$ as the analog to $HPOP_{\text{mig}}$ but
226 calculated from the null model, which did not contain HPOP as a predictor (Figure 1C). Thus,
 $HPOP_{\text{null}}$ estimates the average HPOP a species experiences during its migration if we ignore
228 HPOP *per se* when modelling migration dynamics. For each species-year, we computed
navigational bias as the difference $HPOP_{\text{mig}} - HPOP_{\text{null}}$ (Figure 1D). If $HPOP_{\text{mig}}$ is greater than

230 HPOP_{null}, it indicates that a species is navigationally biased toward higher HPOP sites than
expected during its spring migration. If HPOP_{mig} is lower than HPOP_{null}, it indicates that a
232 species is navigationally biased toward lower HPOP sites than expected.

We defined a species' excess exposure to HPOP during spring migration as the difference
234 HPOP_{mig} – HPOP_{breed} (Figure 1D). Larger positive values of this estimate indicate that a species
experiences a greater excess of HPOP during spring migration, relative to breeding. In contrast,
236 negative values indicate that a species experiences less HPOP during its migration than it does
during the breeding phase. We report the fold-change by exponentiating this difference because
238 HPOP_{mig} and HPOP_{breed} are expressed on a natural log scale.

240 2.5 Comparative analysis

We used a comparative analysis to investigate sources of variation in excess exposure to HPOP
242 during migration. We fit a Bayesian phylogenetic regression model in the MCMCglmm package
v. 2.32 (Hadfield 2010) (n = 189 species-year measures from 63 species). The response variable
244 was the estimate of excess exposure to HPOP during spring migration (HPOP_{mig} – HPOP_{breed}).

As predictors, we considered several traits related to migration biology: the Julian date when the
246 species starts its northward migration within North America, the overall distance the species
migrates, and the time of day (nocturnal or diurnal) when its migration flight primarily occurs
248 (Gauthreaux & Belser 2006; Van Doren *et al.* 2017; McLaren *et al.* 2018; Adams *et al.* 2021).

Further details of these predictors are provided in the supplement. The model also included year
250 as a categorical fixed effect. The random effects included species identity to account for repeated
measures, as well as the phylogeny to account for shared ancestry. We ran 300,000 iterations
252 after a burn-in period of 3,000 with a thinning interval of 500.

254 **3. RESULTS**

256 *3.1 Species differences in HPOP estimates*

HPOP_{mig} and HPOP_{breed} are highly repeatable (HPOP_{mig}: $R = 0.77$, 95% CI = 0.67-0.85;
258 HPOP_{breed}: $R = 0.93$, 95% CI = 0.90-0.96; $n = 189$ species-year estimates from 63 species). This
demonstrates that these estimates are robust and consistent for a given species across years. We
260 did not detect significant phylogenetic signal in either trait (HPOP_{mig}: $\lambda = 0.00$, $p > .99$;
HPOP_{breed}: $\lambda = 0.32$, $p = 0.07$), indicating that species differences in HPOP are not
262 explained by shared ancestry.

264 As expected, HPOP_{breed} has a strong negative correlation with SSI ($r = -0.49$, $p < 0.0001$; see
supplement Figure S4). This indicates that bird species with more specialized breeding habitat
266 requirements breed in areas with lower average HPOP. By contrast, we found that a species'
HPOP_{mig} is not predicted by breeding habitat specialization, SSI ($r = -0.09$, $p = 0.48$, $n = 59$
268 species).

270 *3.2 Navigational bias and excess exposure to HPOP during migration*

Nearly all birds exhibit negative HPOP navigational bias (i.e., bias away from high HPOP sites
272 during spring migration; Figure 2A). A small number of bird species were found to have positive
HPOP navigational bias during migration, including the black-throated blue warbler, Nashville
274 warbler, blackpoll warbler, dickcissel, cedar waxwing, orchard oriole, Baltimore oriole, chimney
swift, and song sparrow.

276

Despite the widespread negative navigational bias, nearly all bird species experience much
278 greater HPOP during spring migration than they do during breeding (Figure 2B). On average,
species in our study experience 2.7-fold greater HPOP during migration as compared to breeding
280 (range = 0.8 to 14-fold difference). The bird species with the largest excess exposure to HPOP
during migration are the black-throated blue warbler, bay-breasted warbler, and Nashville
282 warbler (see also supplement Table S1).

284 *3.3 Comparative analysis*

Excess exposure to HPOP during migration is predicted by three key traits (Figure 3; Table S2).
286 The bird species with the greatest excess exposure are those that migrate primarily at night, start
their migration within North America earlier in the year, and tend to migrate greater distances
288 overall. Note that the relation with migration distance is relatively weak.

290 **4. DISCUSSION**

We investigated how spring migration flight of terrestrial birds is shaped by human landscape
292 alteration across North America. Our results indicate that migrating birds are navigationally
biased away from areas of high human population density, and yet they experience much greater
294 human densities during migration than they do during breeding (Figure 2). Nevertheless,
exposures to human density in North America are often elevated by 2- to 3-fold during
296 migration, as compared to breeding (Figure 2B). Taken together, these key findings highlight
how migration is a time of excess exposure to human disturbance and its associated threats (Loss
298 *et al.* 2013, 2014, 2015; Machtans *et al.* 2013; Van Doren *et al.* 2017; Korpach *et al.* 2022).

300 Our results also establish that species differ repeatably in our estimates of HPOP_{mig}, the average
level of human density experienced by a species during migration. This indicates that some
302 species may be more vulnerable than others to anthropogenic sources of mortality during
migration (Loss *et al.* 2015). Notably, neither HPOP_{mig} nor HPOP_{breed} had detectable
304 phylogenetic signal within the sample of terrestrial migratory birds in our study. This leads us to
hypothesize that variation in species-average levels of HPOP_{mig} within North America may be
306 explained primarily by geographic ranges and historic migration routes, rather than other evolved
ecological and life history traits. HPOP_{mig} had no detectable association with breeding habitat
308 specialization, although HPOP_{breed} was readily predicted by species differences in breeding
habitat specialization (with more specialized breeders using areas with lower HPOP; Bonier *et*
310 *al.* 2007; Evans *et al.* 2011; Ducatez *et al.* 2018; Callaghan *et al.* 2019; Palacio 2020; Patankar *et*
al. 2021). Importantly, this finding highlights how a species' ecological requirements during
312 migration are not necessarily the same as during breeding (Lin *et al.* 2020). There is a major lack
of information on avian ecology during migration (Faaborg *et al.* 2010). Given that birds can use
314 very different environments even throughout migration and given the documented sources of
mortality during migration (Loss *et al.* 2013, 2014, 2015; Machtans *et al.* 2013; Van Doren *et al.*
316 2017; Korpach *et al.* 2022), there is a crucial need for future research that maps out habitat and
resource requirements for many bird species throughout the annual cycle, particularly during
318 migration.

320 Although the average level of HPOP during migration was not explained by phylogeny or habitat
specialization, we found that *excess* HPOP during migration (as compared to breeding) is

322 explained by several traits (Figure 3). First, species that migrate at night are exposed to greater
excess human density. Nocturnally migrating species are known to be disoriented by artificial
324 light at night (Gauthreaux & Belser 2006; Adams *et al.* 2021), which may lead birds to spend
more time in human-modified areas. During overcast conditions, some birds may also use
326 artificial light to navigate (Weisshaupt *et al.* 2022). This may cause birds to steer towards
anthropogenically modified landscapes where they are vulnerable to light disorientation effects,
328 collisions with man-made objects, and air pollution (La Sorte *et al.* 2022b, a). For many of these
species, dark-connected skies along their migration routes may be an important resource for
330 successful navigation (Korpach *et al.* 2022).

332 Second, we found that species that begin migrating through North America earlier in the year are
exposed to greater excess human density. Early migrants include species that can overwinter at
334 higher latitudes (e.g., within North America), and those with broader physiological tolerances.
We hypothesize that these broader tolerances allow early migrants to be more flexible in terms of
336 habitat use and use of human-dense sites during migration (Bonier *et al.* 2007; Marzluff 2017;
Ducatez *et al.* 2018; Isaksson 2018; Callaghan *et al.* 2019; Patankar *et al.* 2021). Third, we found
338 a weak effect of overall migration distance: all else being equal, species that migrate farther tend
to be exposed to greater excess human density. Longer-distance migrants have a faster overall
340 pace of migration (La Sorte *et al.* 2013; Schmaljohann 2019) characterized by shorter and/or
fewer stopovers. Owing to these challenges and faster migration pace, we hypothesize that
342 longer distance migrants may be less able to choose stopover sites, which may lead to them
stopover in urban areas more often even if the conditions of these sites are less favourable.

344

Migration routes and navigational responses are the product of both genetic and cultural
346 evolution (Pulido 2007). Human development of the landscape has proceeded at a pace that far
exceeds what evolution can match. Our results indicate that the majority of terrestrial migrants
348 have a navigational bias away from human density at the population level (Figure 2A). This
response could be driven by avoidance behaviours on the part of individuals (i.e., individuals
350 avoiding cues of human-density during their migration flights and/or stopovers areas). This
response could also be driven at the population level over longer time scales, via the
352 development of migratory routes that circumvent human-dense areas when possible. It is
important to note that avoidance at the population level does not preclude attraction at the
354 individual level; these two mechanisms can co-occur even if population- and individual-level
responses are opposing, and our methods do not allow us to resolve the underlying mechanisms.
356 For example, previous work has shown that one facet of urbanization, artificial light, has both
attractive and repulsive properties depending on the spatial scale under consideration (McLaren
358 *et al.* 2018). Additionally, some bird species may continue to follow sub-optimal migration
routes if they were inherited or learned from other individuals. To fully understand the impact of
360 human landscape development on migrating birds, additional research is needed on how
individual birds are responding to human density at finer scales (Bonnet-Lebrun *et al.* 2020).

362
Our findings have implications for avian conservation. Species such as the black-throated blue
364 warbler, Nashville warbler, and blackpoll warbler, are both navigationally biased *toward* human-
dense areas and experience far greater human density during migration as compared to their
366 preferred breeding sites. These species may either be able to exploit resources in
anthropogenically modified areas, or they may be disoriented by features in these areas, such as

368 artificial light at night, that entrap them. Other species that have far greater excess exposure
combined with a navigational bias away from human-dense areas may be forced to navigate
370 through areas that they otherwise would have avoided; these include species such as the bay-
breasted warbler, ruby-crowned kinglet, and yellow-bellied flycatcher. We have provided
372 additional examples of this in the supplement (Figure S5). An important next step is to determine
whether and when the use of human-dense sites during migration can be a threat or a benefit,
374 both in the short and long term. Given that humans have modified areas that may be crucial for
migration, billions of birds may be forced to navigate highly modified landscapes despite a
376 preference to avoid them.

378

380 **FIGURE LEGENDS**

382 **Figure 1. Modeling spring migration dynamics.** An example of the modelling procedure is
shown here for the bay-breasted warbler (*Setophaga fusca*). A) North American range map for *S.*
384 *fusca*. The darker shaded regions represent the species' breeding range, and the lighter shaded
regions represent its migration range, as determined by the eBird Status and Trends Project. The
386 inset shows the distribution of HPOP for eBird checklists in the species' 2019 analysis. Notably,
the range of HPOP characteristics is broadly similar across latitudes. B) Fitted GAM of the bay-
388 breasted warbler's spring migration in 2019. Each row shows encounter rates averaged over
three latitude bands (below 35°N; 35-45°N; and above 45°N, as shown via the horizontal dotted
390 lines), and two HPOP categories (below vs. above 1,000 persons/km²). Note that latitude and
HPOP are categorized here to allow visualization of the complex model fit, but the analysis treats
392 these variables as continuous. C) Null model of bay-breasted warbler spring migration. The inset
shows the species' estimated latitudinal progress. D) Daily HPOP estimates for the bay-breasted
394 warbler in 2019. Mean values were used to calculate metrics of navigational bias and excess
exposure. Photo by Wikimedia Commons user Mdf.

396

Figure 1. Most bird species have a negative HPOP navigational bias, yet experience much
398 **greater HPOP during migration as compared to breeding.** A) Navigational bias ($HPOP_{mig} -$
 $HPOP_{null}$) during spring migration. Most species have a negative navigational bias, indicating
400 that they experience less HPOP during migration than expected based purely on latitudinal
progress. B) Excess exposure to HPOP during spring migration ($HPOP_{mig} - HPOP_{breed}$). Nearly

402 all species experience far greater HPOP during migration as compared to breeding. The sample
size for A-B is 189 species-years; the figure shows 16 avian families represented in this study.

404

Figure 3. Excess exposure to HPOP during migration is associated with several key

406 **migration traits.** Partial residual plots for the analysis of excess HPOP during migration (n =
189 species-years). Each panel shows the relationship between residual excess HPOP and a

408 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.

410 The results of this model were consistent with those of the full phylogenetic analysis. See the
supplement for additional details of this analysis.

412

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Figure 1

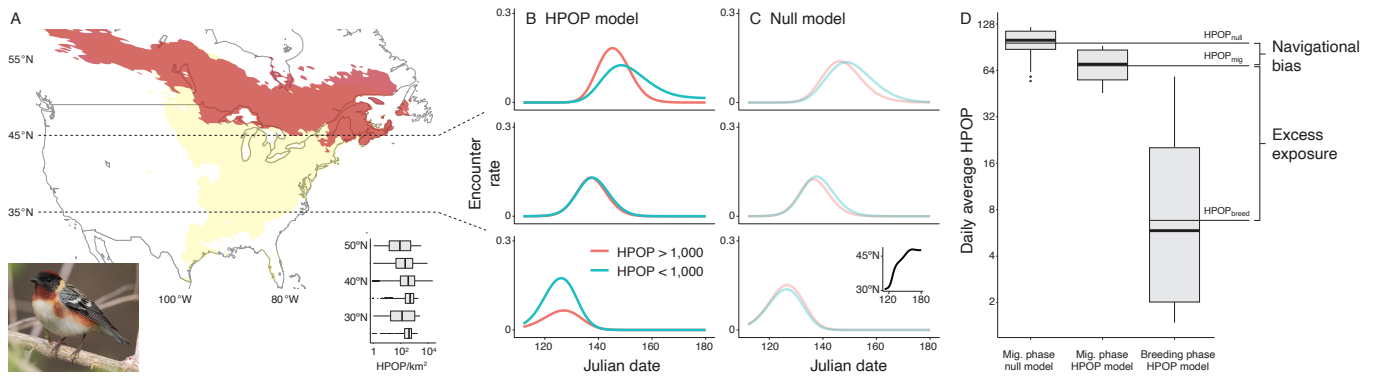


Figure 2

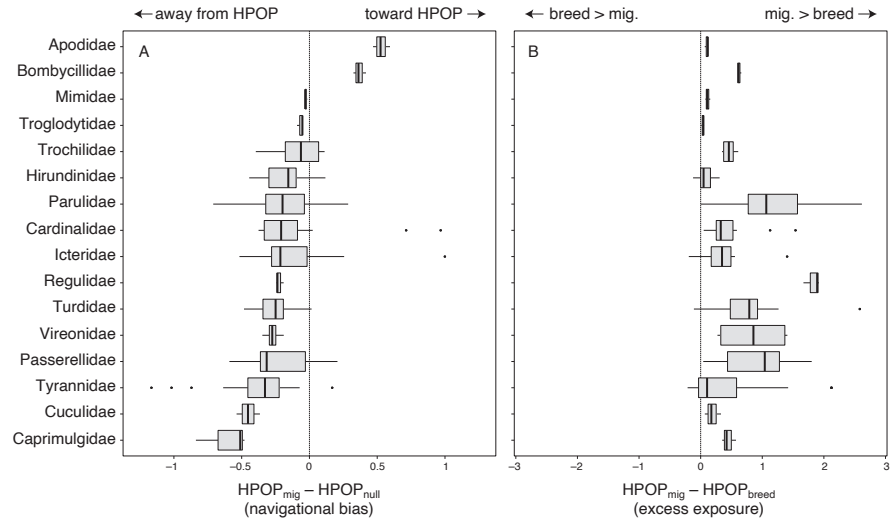


Figure 3

