



Research



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Demography and dispersion: evaluating the causes and consequences of vagrancy in North American migratory birds

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Rare, long-distance dispersal events in animals have long been of interest to both scientists and the public. However, the reasons for the occasional appearances of animals outside of their expected range, a phenomenon known as vagrancy, have largely lacked quantitative investigation. Demography is one hypothesized mechanism, where large and growing populations are thought to result in more individuals venturing farther afield. Alternatively, navigational mishaps brought on by less-than-ideal conditions may act to disperse individuals, ultimately resulting in vagrancy, especially for migratory species. We investigate the relative importance of demographic versus dispersive forces on vagrancy using over 4.5 million banding records across a half-century from 55 North American migratory bird species. We find evidence that both demographic and dispersive forces modulate vagrancy patterns over time, with population size explaining the most variation. Furthermore, for a subset of 42 species, we find no evidence that the dispersion of populations—a measure of the average spatio-temporal rarity of all banding records in a season—is associated with population declines. The combination of demographic and dispersive vagrancy could help explain the mechanisms behind range expansion of migratory animals and the organisms they disperse, with implications for biodiversity loss in a changing world.

1. Introduction

The long-distance dispersal of organisms has long been recognized as a rare but important ecological phenomenon [1–3]. One form of long-distance dispersal can occur via vagrancy, or the appearance of an individual organism outside of its expected range. In particular, the phenomenon of vagrancy in birds has inspired ecologists for over a century, with much effort spent to uncover its causes and consequences [1,3–9]. While an abundance of theories regarding the causes and consequences of avian vagrancy have been proposed, few rigorous tests have been conducted and fewer hypotheses have strong empirical support [10–14].

One consequence of vagrancy is increased risk of mortality, as individual vagrants found far outside of their expected ranges frequently perish soon after being discovered, often due to exhaustion, disease or predation [15–17]. Although much of what we know about the fates of vagrants comes from anecdotal observations [16,17], scientific studies on birds have found evidence that vagrancy ends in death for a substantial proportion of individuals [11,18]. For example, a study comparing vagrant and within-range Red-shouldered Hawks (*Buteo lineatus*) demonstrated higher mortality rates

for vagrant individuals [18]. Events like hurricanes that lead many birds off track may be a sign of concurrent or impending mass-mortality events [11,19].

Despite dangers to the individual, vagrancy may have positive species-level impacts by facilitating colonization events [1,9,20]. Dramatic range expansions of migratory species have been observed multiple times over the last century, including colonization of the Americas by the Western Cattle Egret (*Bubulcus ibis*) from Afro-Eurasia [21,22] and the more recent range expansion of Richard's Pipit (*Anthus richardi*) in Europe [13,23]. Vagrant birds may also expand the range of sessile or otherwise geographically constrained organisms that they carry, such as arthropods, seeds and pathogens [3,12,24–26]. Because vagrancy has been implicated in both mortality events and range expansions, changing rates of vagrancy may either represent a positive sign of adaptation to a changing world [13,27] or a negative pressure on already-declining migratory species [19,28].

Two prevailing, non-mutually exclusive hypotheses exist for the processes underpinning vagrancy. The first hypothesis posits that variation in vagrancy is driven by demographic factors, where species with large and growing populations produce higher numbers of potential vagrants [6,29,30]. Empirical evidence has demonstrated a positive association between population size and vagrancy [31], as well as an association between vagrancy and high population growth rates—measured as the difference in population size between two consecutive breeding seasons [6,30]. A second hypothesis is that vagrancy results from migration gone awry. Exogenous causes like severe weather [9,11,32] or geomagnetic storms [14,33] can cause birds to be found outside of their normal migratory range. These processes likely result in an increased dispersion of migratory populations (i.e. populations are spread more diffusely over a larger area). Given their connection to exogenous factors [9], dispersive causes of vagrancy presumably vary interannually, differ in their relative importance across species and could lead to higher mortality rates (either directly or by extending the duration of migration).

Here, we test for the relative importance of demographic versus dispersive causes of vagrancy in birds by exploiting the differences in how each mechanism likely modulates vagrancy patterns. By quantifying the spatio-temporal rarity of bird occurrences—measured from a dataset encompassing over 4.5 million bird banding records—we calculate both the relative abundance of vagrants and the spatio-temporal spread of populations during spring and autumn migration for 55 North American landbird species from 1966 to 2018. We hypothesize that demographic factors, particularly population size, influence the number of vagrants through proportional changes in the number of detections both within and beyond the normal range of the species, analogous to drawing differing numbers of samples from the same probability distribution (figure 1A). Regardless of whether individual vagrants fly off course due to endogenous factors (e.g. misorientation with a genetic basis) or exogenous factors (e.g. severe weather), larger populations should produce more vagrants. Separately, we hypothesize that dispersive factors result in more vagrants by shifting the distribution of individuals from regions where they are typically common to those where they are uncommon or rare, analogous to drawing the same number of samples from two probability distributions that differ in their variances (figure 1B). Furthermore, we hypothesize that dispersive forces lead to higher mortality, which should result in a negative relationship between dispersion in both migration seasons and interannual population change. Together, our analysis is designed to assess the relationship between demographic factors, measures of population dispersion and vagrancy.

2. Methods

To investigate our hypotheses, we used a combination of bird capture records from the United States Geological Survey (USGS) Bird Banding Laboratory (BBL; [34]), population-level abundance estimates from the North American Breeding Bird Survey (BBS; [35]) and spatio-temporal models of migratory distributions from eBird Status and Trends (eBird ST; [36]). Hypotheses about the causes and consequences of vagrancy were evaluated using seasonally specific hierarchical Bayesian statistical models that we use to test for general patterns across all included study species while accounting for species-specific variation using a random effects structure.

(a) Measuring vagrancy and dispersion

Measuring any rare and extreme ecological phenomenon is challenging, and we considered different data options. Ultimately, we used BBL records from 1966 to 2018 [34] to determine annual relative vagrancy rates and population dispersion metrics for each included species, following the methods of Tonelli *et al.* [14]. However, we also considered using birdwatcher occurrence data from the citizen-science project eBird [37], but chose to use banding data, in part, due to the longer temporal scope of banding data (approximately 50 years compared with the approximately 20 years since the launch of eBird).

To assemble our species pool, we considered for inclusion all full- or partial-migrant North American landbird species likely to be routinely banded by passive efforts (i.e. excluding raptors, swifts and nightjars), except irruptive species (e.g. Pine Siskin, *Spinus pinus*; Evening Grosbeak, *Coccothraustes vespertinus*; Purple Finch, *Haemorhous purpureus*; Bohemian Waxwing, *Bombycilla garrulus*). We only included species with ranges that spanned at least three states, but no more than 45 states in the contiguous US according to range maps provided via Birds of the World [38], as we considered these geographic conditions necessary for the species to be banded regularly in the US outside of their normal ranges. All banding records and subsequent captures at a site other than where a bird was originally banded were included. We excluded site-level recaptures—both to limit pseudoreplication and because recaptures at the same site are not systematically reported to BBL (D Bystrak, 2021, personal communication). Only records in which the bird being banded was not experimentally manipulated or displaced were used. Banding records were filtered and categorized as autumn or spring migrants based on species-specific migratory dates using

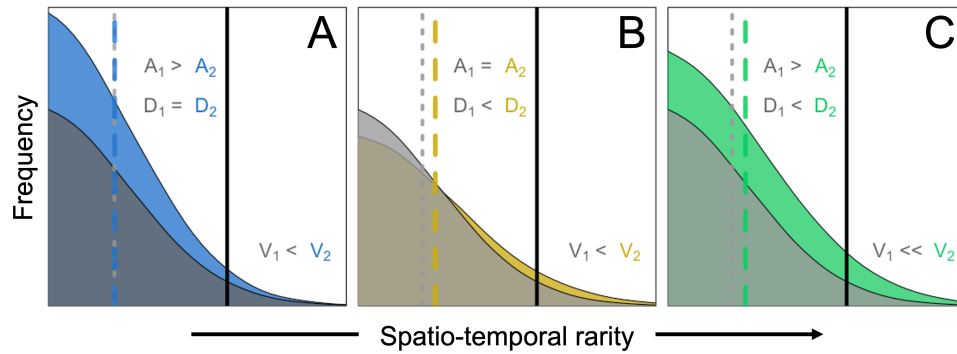


Figure 1. Theoretical model of demographic and dispersive vagrancy. Here, we suggest that vagrancy trends can be explained as the tail of a distribution representing the spatio-temporal rarity of species records. Vagrancy rates (V)—represented here as the area under the curve to the right of an arbitrary vagrancy cutoff (black line)—can be altered either by a changing abundance (A) of a species population (panel A), analogous to drawing more values from a truncated normal distribution, or the changing dispersion (D) of spatio-temporal rarity records (panel B), analogous to increasing the variance of the distribution. Concurrent increases in population size and dispersion may interact to drive even greater vagrancy rates (panel C).

the modelled data product eBird Status and Trends [36]. We further limited our analysis to species that had at least 100 banding records for each migration season in at least 30 years within the study period. In all, this resulted in the inclusion of 50 species, totalling 3 227 894 banding records and 2379 species-year values for the autumn, and a largely overlapping set of 47 species totalling 1 580 827 banding records and 2184 species-year values for the spring. A full list of the 55 species included in the analysis is presented in electronic supplementary material, S2.

(b) Population size and interannual population change

We used survey-wide BBS indices from 1966 to 2019 for species-level estimates of population size and interannual population change [35]. Population size is measured as the survey-wide species index for each year ($N_{i,t}$). For each species, we centred yearly population size estimates by subtracting the mean index value from each value. We calculated interannual population change ($r_{i,t}$) as the log of the ratio in population size between successive years,

$$r_{i,t} = \log\left(\frac{N_{i,t+1}}{N_{i,t}}\right) \quad (2.1)$$

for species i and year t . When analysing the output of our model, we back-transformed this metric to represent the population change in raw per cent terms. Measures of population change derived from BBS population size estimates represent additional information about the population size between two annual survey periods. The true population size during the autumn and spring migration periods following the initial breeding season is the product of the breeding population size, breeding productivity and mortality. Population growth, as measured as the difference between breeding population size in two consecutive summers, thus provides a rough estimate for the difference between the surveyed population size and the true population size for the intra-survey period. For example, if population growth was measured as +10%, the population size during that autumn migration season is likely to be roughly 10% greater than a year in which the population growth rate was 0%.

We assessed potential multicollinearity in the demographic model covariates via correlation tests. Measures of population size and growth were very weakly correlated in our autumn (Pearson's R : -0.16) and spring datasets (Pearson's R : -0.08), indicating minimal potential problems of multicollinearity.

(c) Vagrancy and dispersion

For each banding record, we calculated a continuously scored, numeric vagrancy index based on the date and location of capture (figure 2A,B), following Tonelli *et al.* [14]. To determine spatio-temporal rarity, we compared the location of each banding record to the expected weekly spatial distribution of relative abundance for each species according to eBird Status and Trends [36]. We chose to use this approach to account for the fact that the rarity of a species occurrence in a given location will change throughout the year. In some cases, this approach will lead to a high score if a species is identified within its range but outside of the expected time window for occurrence. For example, Rufous Hummingbirds exhibit an elliptical migration, migrating up the west coast of the US in the spring and then through the Intermountain West during the autumn. With our method, an occurrence record of Rufous Hummingbird in Colorado during spring migration will score higher on the vagrancy index scale compared with a record in the autumn. Furthermore, a record of the same species in Colorado very late during autumn migration would be scored higher on the vagrancy index than a record during peak autumn migration.

For each species, we then took the 1% of records across all years with the highest spatio-temporal rarity index values and gave these records a binary classification of being vagrants (v_i). Determination of what constitutes a vagrant varies widely [10,31,39], but here our method aims to identify a fixed percentage of occurrences across the full time series that have the highest spatio-temporal rarity relative to the entire capture record for each species. We performed sensitivity analyses on the 1% cutoff (testing 0.5 and 5%) and found qualitatively similar results in all cases. We then z-scored the logged number of vagrants

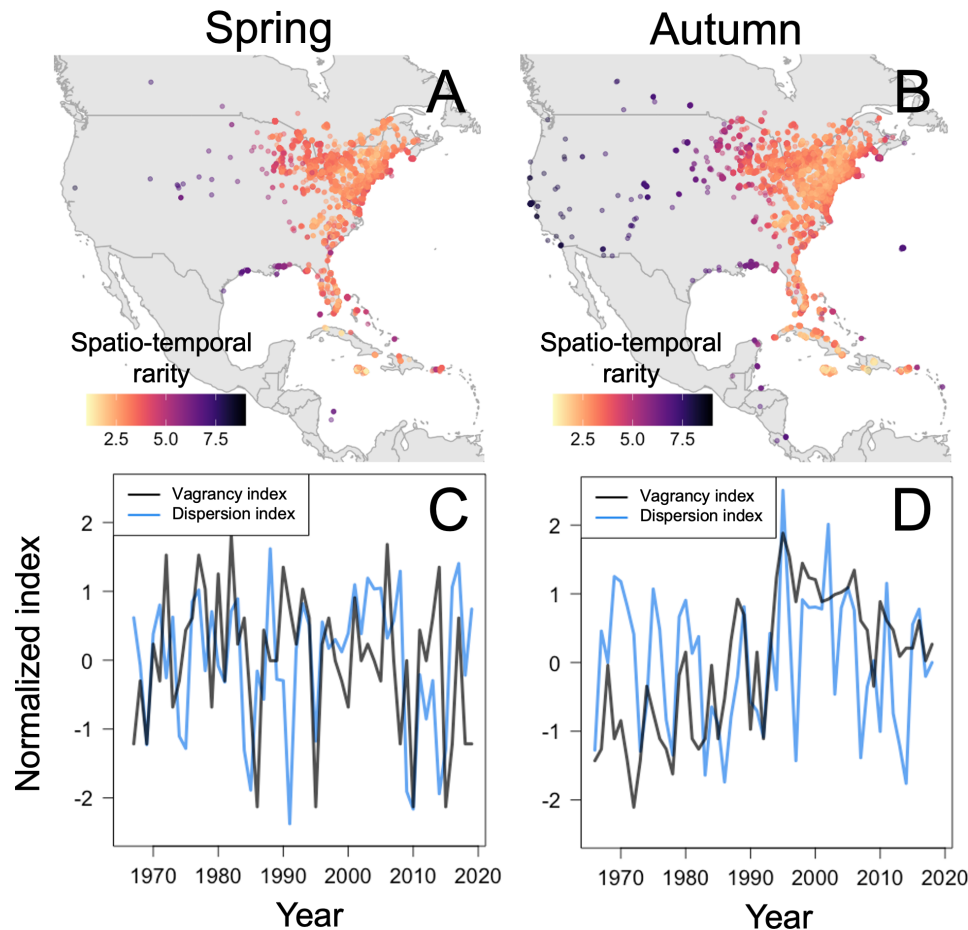


Figure 2. Measures of vagrancy and dispersion at the species level were derived from measures of spatio-temporal rarity of individual banding records. The spatio-temporal rarity of banding records for all years in the spring (A) and autumn (B) migration seasons was calculated for each species following Tonelli *et al.* [14]. The example shown here is for the Black-throated Blue Warbler (*Setophaga caerulea*) in the spring (A, C) and autumn (B, D). We then used derived rarity values to construct relative species-level, year-specific indices of vagrancy (black lines; C, D) and temporally smoothed indices of dispersion (blue lines; C, D) independently for both the spring (C) and autumn (D) migration seasons.

(adding 1 to all counts of vagrants to avoid taking the log of 0) to produce a relative metric of vagrancy ($V_{i,t}$) for each species i in year t (figure 2C,D). We used a log transform as is standard when modelling population abundance. When analysing the output of our models, we back-transformed this metric to the actual number of vagrants expected for each species.

To calculate population dispersion—the average spatio-temporal rarity of banding records in each year and season ($D_{i,t}$)—we first calculated the mean of the log-transformed vagrancy index values of banding records for each species in each season ($d_{i,t}$). Depending on the hypothesis being tested, we either excluded or included vagrant records in our calculations of dispersion. Changing species ranges (i.e. range contractions or expansions) or changing spatial patterns of banding effort (e.g. increasing banding effort in the western US) could potentially influence trends in measures of dispersion over the study period. Taking a conservative approach, we detrended dispersion estimates by calculating a flexible spline (degrees of freedom = 4) for each species' calculated dispersion values and then subtracted the fit spline estimates from the true dispersion values (i.e. leaving only the spline residuals, electronic supplementary material, figure S1). This effectively removes longer-term trends in dispersion for each species that may result from artefacts of sampling. We then z-scored this detrended dispersion metric within species to create a relative measure of dispersion for each species (figure 2C,D). With these transformations, $D_{i,t}$ represents the detrended spatio-temporal rarity of all capture records for each species (i) in each year (t) on a relative scale.

We also calculated uncertainty in population dispersion for each species and year using bootstrapping, simulating 100 resamples of $D_{i,t}$ where the sample size for each species-year was equivalent to the number of records included in the calculation of the metric. We then calculated the standard deviation of the population dispersion metric for each species-year value and incorporated that uncertainty downstream into our models.

(d) Bayesian models

We fitted two independent Bayesian models to investigate our hypotheses that: (i) demographic and dispersive measures are positively associated with vagrancy, and (ii) population dispersion during migration is positively associated with population declines. We employed a flexible Bayesian approach to estimate species-level effects through a varying-intercepts, varying-slopes, random effects structure, analogous to linear mixed effect models. To control for the effect of the number of banding records on vagrant detection, we also included an effort variable representing the total number of records for all species in the analysis during a given year. Uninformative priors were used for parameters in all the models employed here.

(e) Cause model: effects of demographic factors and dispersion on vagrancy

We modelled normalized, species-specific time series of relative vagrancy ($V_{i,t}$) as a function of population size ($X_{1,i,t}$), population change ($X_{2,i,t}$) and population dispersion ($X_{3,i,t}$). We controlled for the effect of effort (θ_i), measured as the total number of banding records across all species in a year. We modelled the extent of vagrancy for each species in each year as a normally distributed variable,

$$V_{i,t} \sim \text{Normal}(\alpha_i + \theta_i * \text{eff}_t + \beta_{1,i} * X_{1,i,t} + \beta_{2,i} * X_{2,i,t} + \psi_i * X_{3,i,t} + \omega_{1,i} * X_{3,i,t} * X_{1,i,t} + \omega_{2,i} * X_{3,i,t} * X_{2,i,t}, \sigma_i), \quad (2.2)$$

where α_i represents the species-level intercept, $\beta_{1,i}$ represents the effect of population size, $\beta_{2,i}$ represents the effect of population change and ψ_i represents the effect of dispersion on vagrancy. We also included two interaction terms to account for the potential combinatory effects of dispersion with population size ($\omega_{1,i}$) and dispersion with population change ($\omega_{2,i}$, figure 1C). Each term is modelled hierarchically with a normal hyper-distribution, with the mean representative of the cross-species effect of the metric of interest on vagrancy. To avoid circularity in our model, population dispersion was calculated using all banding records except those determined to be vagrants by our 1% cutoff.

(f) Per cent variance calculations

To determine the relative impact of dispersion, population size and population change on vagrancy, we calculated the per cent variance explained by each covariate (Bayesian R^2) across the study period using a method designed for Bayesian models [40]. To determine the relative impact of each factor across the entire study period, we calculated the variance of the predicted relative vagrants ($g_{rep,t}$) and the unexplained variance (ϵ_t) and then calculated the per cent variance explained by each of the coefficient-covariate pairs. For example:

$$g_{rep,t} = \beta_{1,i} * X_{1,i,t} \quad (2.3)$$

$$\epsilon_t = y_t - g_{rep,t} \quad (2.4)$$

$$\frac{\sigma_{g_{rep}}}{\sigma_{g_{rep}} + \sigma_{\epsilon}} \quad (2.5)$$

where σ represents the variance of the metrics of interest (e.g. $\sigma_{g_{rep}}$ is the variance of g_{rep}).

(i) Consequence model—impact of population dispersion on population trajectory

Our second model examines the relationship between population change ($r_{i,t}$) and dispersion in the two migratory seasons (spring = $X_{1,i,t}$, autumn = $X_{2,i,t}$) using a linear mixed effects model fitted in a Bayesian context. We modelled population change for each species in each year as t -distributed

$$r_{i,t} \sim \text{Student's } t(\alpha_i + \eta_{1,i} * X_{1,i,t} + \eta_{2,i} * X_{2,i,t}, \nu, \sigma), \quad (2.6)$$

where α_i is the species-level intercept, $\eta_{1,i}$ is the effect of spring dispersion and $\eta_{2,i}$ is the effect of autumn dispersion. We used a Student's t -distribution rather than a normal distribution in order to account for outlier years where populations experience pronounced decline or growth [41], necessitating greater weight in the distributional tails. Each term was modelled hierarchically with hyper-parameter means (μ_{α} , μ_{η_1} , μ_{η_2}) representing the cross-species effect of population dispersion in each migration season (spring, autumn) on population change. We used data from the spring and autumn, including years in which at least 100 records were present for both migration seasons. In all, this resulted in 1932 species-year records for 42 species. For this model, population dispersion was calculated using all records for each species in each year, with vagrant records included and detrended as detailed above.

All models were fitted using the rstan package [42] to interface with stan [43] using R v. 4.2.1 [44]. We analysed model output using MCMCvis [45]. Our results report effect sizes and their associated uncertainty, denoted by 89% credible intervals, as well as the proportion of the posterior distribution that overlaps zero (i.e. $\text{pr}(\beta < 0) = X$).

3. Results

(a) Demographic effects on vagrancy

Across species, we found that population size is positively associated with vagrancy during both migration seasons (spring, median $\mu_{\beta_1} = 0.96$, 89% CrI = 0.51 to 1.41, $\text{pr}(\mu_{\beta_1} > 0) = 1$; autumn, median $\mu_{\beta_1} = 1.02$, 89% CrI = 0.42 to 1.59, $\text{pr}(\mu_{\beta_1} > 0) = 1$; equation (2.1), table 1). As hypothesized, the effect of population size leads to roughly proportional changes in vagrancy in either season (e.g. a 5% increase in population size leads to a 5% increase in vagrancy; figure 3A). Population size explained 2.2% of the variance in vagrancy for a typical species for the spring migration season (range across species: 0.04 to 39.7%) and 5.6% of the variance (range across species: 0.5 to 69.6%) for the autumn (electronic supplementary material, tables S1 and S2).

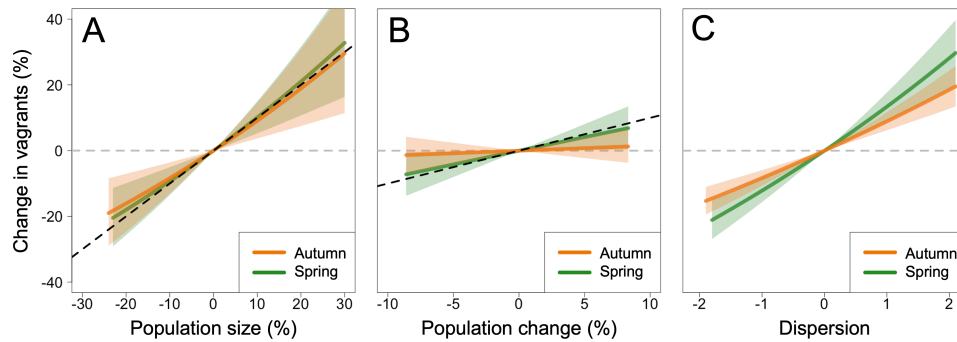


Figure 3. Vagrancy is associated with both demographic change and dispersion. Relative impact of population size (A), population change (B) and dispersion (C) on the expected change in the number of vagrants detected during the spring (green) and autumn (orange) migration season. Mean species effects are represented with solid lines, with coloured polygons representing 89% credible intervals. Lines are plotted over realistic ranges (encompassing 95% of values). The black dashed lines (A, B) represent the theoretical expectation that changes in population size and interannual population change—a proxy for the number of first-year birds in the population—lead to proportional changes in the number of vagrants.

Table 1. Parameter estimates (posterior median and 89% credible intervals) from the cause model, testing for relationships between population size, population growth and dispersion on vagrancy in both autumn and spring migration. Proportions of the posterior greater than 0 for positive medians ($p > 0$) or less than 0 for negative medians ($p < 0$) are also reported. Bolded parameters indicate where 89% of the posterior was greater than (or alternatively less than) 0.

season	parameter estimates				
	pop. size, μ_{β_1}	pop. change, μ_{β_2}	dispersion μ_{ψ}	pop. size \times dispersion, μ_{ω_1}	pop. change \times dispersion, μ_{ω_2}
spring	0.96 (0.51, 1.41) $\text{pr}(\mu_{\beta_1} > 0) = 1$	0.81 (0.05, 1.59) $\text{pr}(\mu_{\beta_2} > 0) = 0.96$	0.13 (0.09, 0.16) $\text{pr}(\mu_{\psi} > 0) = 1$	0.28 (0.03, 0.52) $\text{pr}(\mu_{\omega_1} > 0) = 0.97$	0.21 (-0.62, 1.03) $\text{pr}(\mu_{\omega_2} > 0) = 0.66$
autumn	1.02 (0.37, 1.59) $\text{pr}(\mu_{\beta_1} > 0) = 1$	0.18 (-0.54, 0.93) $\text{pr}(\mu_{\beta_2} > 0) = 0.66$	0.1 (0.07, 0.13) $\text{pr}(\mu_{\psi} > 0) = 1$	-0.01 (-0.22, 0.2) $\text{pr}(\mu_{\omega_1} < 0) = 0.52$	0.05 (-0.55, 0.67) $\text{pr}(\mu_{\omega_2} > 0) = 0.56$

The effect of population change (measured as the change in survey-wide population size between consecutive breeding seasons) on vagrancy was strongly supported for the spring migration season (median spring $\mu_{\beta_2} = 0.81$, 89% CrI = 0.05 to 1.6, $\text{pr}(\mu_{\beta_2} > 0) = 0.96$, equation 2.1, table 1), but not supported for the autumn (median autumn $\mu_{\beta_2} = 0.18$, 89% CrI = -0.54 to 0.93, $\text{pr}(\mu_{\beta_2} > 0) = 0.66$, equation 2.1, table 1). Population change explained much less of the variance across species compared with population size, with a median of 0.04% (range: 0.01 to 0.61%) in the spring and 0.05% (range: 0 to 2.9%) in the autumn (electronic supplementary material, tables S1 and S2).

(b) Effects of dispersion on vagrancy

We found that increased dispersion of migratory populations is associated with increases in vagrancy in both the spring (median spring $\mu_{\psi} = 0.13$, 89% CrI = 0.09 to 0.16, $\text{pr}(\mu_{\psi} > 0) = 1$, equation 2.1, table 1) and autumn (median autumn $\mu_{\psi} = 0.10$, 89% CrI = 0.070 to 0.13, $\text{pr}(\mu_{\psi} > 0) = 1$, equation 2.1, table 1, figure 3). Across all species, dispersion explained a median of 1.7% (range: 0.45 to 7.89%) of variation in the spring and 1.1% (range: 0.75 to 1.51%) in the autumn (electronic supplementary material, tables S1 and S2).

(c) Combinatory effects on vagrancy

Consistent with our hypothesis that the effects of dispersion on vagrancy would increase with larger population size and growth, we found strong support for a positive interaction between population size and population dispersion on vagrancy during spring migration (spring median $\mu_{\omega_1} = 0.28$, 89% CrI = 0.03 to 0.52, $\text{pr}(\mu_{\omega_1} > 0) = 0.97$), meaning that the effect of greater dispersion was amplified when population sizes were larger. In contrast, we found no support for an interaction between population change between consecutive breeding seasons and dispersion during the spring migration season (spring median $\mu_{\omega_2} = 0.21$, 89% CrI = -0.62 to 1.03, $\text{pr}(\mu_{\omega_1} > 0) = 0.66$, equation 2.1, table 1) and no support for either interaction effect for the autumn migration season (median $\mu_{\omega_1} = -0.01$, 89% CrI = -0.22 to 0.20, $\text{pr}(\mu_{\omega_1} < 0) = 0.52$, median $\mu_{\omega_2} = 0.05$, 89% CrI = -0.55 to 0.67, $\text{pr}(\mu_{\omega_1} > 0) = 0.56$, equation 2.1, table 1).

(d) Consequences of dispersion on subsequent demographic rates

Using a separate Bayesian model, we found no support for a cross-species negative association between dispersion and population change during either the spring (spring effect, $\mu_{\gamma_1} = -0.00013$, 89% CrI = -0.0011 to 0.00091 , $\text{pr}(\mu_{\gamma_1} < 0) = 0.60$, equation 2.6) or the autumn (autumn effect, $\mu_{\gamma_2} = -0.00011$, 89% CrI = -0.0012 to 0.0013 , $\text{pr}(\mu_{\gamma_2} < 0) = 0.51$, equation 2.6).

4. Discussion

The causes and consequences of vagrancy have long been a source of speculation [1] but the topic has found renewed interest given how variation in vagrancy might influence the ability of species to respond to climate change or may be a function of the demographic status of species [9,46,47]. In this context, the long-distance dispersal of migratory birds has been suggested as either a positive sign of adaptation to changing environments or a negative aberration from ‘normal’ that leads to excess mortality. Here, we find that vagrancy rates are explained, to different degrees, by both demographic and dispersive forces. The influence of both forces on vagrancy rates has important implications for understanding the future ecological consequences of this extreme phenomenon.

(a) Vagrancy and mortality

Migration seasons are the deadliest periods for many species [48–50], and any deviation from an optimal route that extends migration either temporally or spatially could increase the chance of mortality. Although there is some evidence that vagrancy is often fatal for individuals [16,18,19], we find no evidence that species-wide measures of demographic declines occur following migration seasons with increased measures of population dispersion. It is possible that we did not find evidence for this because the population change metric used in this study represents the difference between population sizes across two consecutive breeding seasons, rather than a direct measure of within-migration mortality. Because of this, our population change metric conflates productivity and mortality and likely introduces substantial noise that may make finding strong evidence for an effect unlikely.

Alternatively, there may be little to no biologically meaningful effect for a species-wide effect of dispersion on population change. The estimated 89% credible intervals for the mean species-level effect on dispersion on population change ranged from -0.11% to $+0.09\%$ per +1 s.d. increase for the spring and from -0.12% to $+0.13\%$ for the autumn—both small effect sizes independent of uncertainty—indicating that any effect of dispersion on population change is likely to be marginal.

The effect of dispersive factors on mortality rates may also be undetectable at the species level because vagrancy affects only certain breeding populations or because vagrancy often results in sub-lethal effects. For example, a hurricane over the Gulf of Mexico leading to an increase in the number of vagrant birds may be the cause of substantial mortality [19], but only on the small subset of the population directly impacted by the hurricane. Future work to document and test for drivers of dispersive vagrancy and their effects on mortality could help identify risks to migrating birds.

(b) Ecological consequences of vagrancy

Vagrancy can lead to range expansions both of migrating species and the organisms they carry. Although vagrancy and associated dispersal events may be relatively rare, the ecological impacts of unusual long-distance movements can be substantial [12,24]. For example, avian vagrants have been suggested to facilitate the colonization of a species into newly suitable areas [13,22,51]. We found a strong, positive relationship between population size and vagrancy—in some species, explaining up to 69% of the variation in vagrancy rates (e.g. for the Ruby-throated Hummingbird, *Archilochus colubris*). For the majority of species in either migration season, demography explained a much greater proportion of the variation in vagrancy, particularly among species with larger fluctuations in population size over the study period (electronic supplementary material, figure S2). The explanatory power of demography suggests that, especially over longer time scales, changes in vagrancy patterns are likely to be most dramatic in species with large changes in population size.

If vagrancy does influence the likelihood of colonization events, species with large and growing populations may be more likely to colonize new areas. In contrast, species with small and shrinking populations may see a smaller probability of colonization events. Although we do not measure or test the impact of vagrancy rates on range expansion at the species level, previous evidence suggests that some common and widespread birds like Richard’s Pipit and Cattle Egret produce large numbers of vagrants—sometimes leading to the development or rapid expansion of new migratory routes or wintering populations [13,22,52]. If species experiencing demographic booms are the most likely to produce vagrants and colonize new areas, there is the potential for biodiversity loss through a ‘rich-get-richer’ scenario, where species with large populations continue to expand while smaller populations do so less frequently. Novel competitive interactions between species that are expanding their ranges may exacerbate this trend through negative effects on native species, like the example of a single vagrant Peregrine Falcon (*Falco peregrinus*), potentially displaced by tropical storms or aided by ship traffic [53], predated nearly 10% of the adult population of the endangered MacGillivray’s Prion (*Pachyptila macgillivrayi*) on St. Paul Island in a single season [54].

5. Conclusion

Here, we demonstrate that long-distance dispersal in migratory birds results from two distinct processes: demographic factors that lead to more detections proportional to population size and, separately, dispersive factors that lead to a greater spatio-temporal spread of populations during migration seasons. Regardless of whether individuals become vagrants because of endogenous or exogenous causes, the clear link between demographic factors and long-distance dispersal events suggests that species that are more abundant may be more likely to expand their range or that of the organisms they disperse, such as plant seeds [55], fish eggs [56], parasites [25,57] and pathogens [24]. Similarly, the probability of the ecological consequences of vagrancy are likely to be heightened in years during which populations are more dispersed by environmental factors.

Although our analysis is limited to North American landbirds, our methodology could be applied in the future to investigate vagrancy patterns in other bird species as well as in other animals that exhibit vagrancy, such as insects, mammals and reptiles [3,58]. One potentially fruitful topic of future study is determining whether the relative effects of demographic and dispersive factors differ between species groups excluded here, such as non-migratory Old-World passerines, seabirds or trans-oceanic vagrants. For a future analysis, integration of data from international banding datasets or birdwatcher checklists via databases like eBird could provide wider spatial and taxonomic coverage. Regardless of the method of study, incorporating the expected proportional impact of population sizes on vagrancy rates can help to isolate and quantify the effects of specific dispersive factors on vagrancy. Uncovering the factors responsible for dispersive vagrancy across these species could help predict how patterns of vagrancy and its ecological consequences, such as the range expansions of plants and pathogens dispersed by migratory animals, are likely to change into the future.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code are archived on Zenodo [59].

Supplementary material is available online [60].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. B.T.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; C.Y.: formal analysis, methodology, writing—review and editing; M.W.T.: conceptualization, formal analysis, methodology, project administration, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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