Lost at sea: interference with navigational senses and failed social route learning may drive offshore vagrancy in passerines

William E. Brooks (✉ willbrooks.0@gmail.com)
George Mason University

Research Article

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Abstract

Background

Migratory birds possess remarkable navigational adaptations. Vagrants, few individuals who migrate to incorrect locations, offer a unique opportunity to study how navigation is accomplished. Vagrancy may occur due to external factors forcing birds off course, such as strong wings, or navigational errors. Natural disruptions in the Earth's magnetic field may cause navigational errors interfering with bird magnetoreception. Failures of other navigation tools like visual landmark recognition and social route learning may also contribute to vagrancy, but these factors are difficult to quantify.

Methods

I used eBird, a community science dataset comprising millions of bird observations, to study the relative likelihood of offshore vagrancy under different external factors including weather, geomagnetic disturbance, and solar activity using mixed effects logistic regression. Then, I studied how variation in species vagrancy propensity is driven by morphology and migration distance using multiple linear regression, or inheritances of vagrancy alleles with phylogenetic analysis.

Results

High geomagnetic disturbance and low visibility increased offshore vagrancy, and winds did not appear to blow birds off course. Most variation in offshore vagrancy stemmed species specific differences, best explained by an interaction between wing pointedness and migration. A longer migration distance was strongly correlated with increased vagrancy in birds with rounded wings, but the relationship was absent in birds with a pointed wing shape. Brown-headed Cowbirds were notably more prone to vagrancy than any other passerine.

Conclusions

External factors primarily cause vagrancy by interfering with magnetic and visual senses, rather than physically forcing birds off course. Species with longer migrations have more time to encounter these vagrancy causing events, but a more pointed wing shape may allow birds to reorient more efficiently. While migration routes are primarily genetic in passerines, I found evidence of an overlooked role of social learning in route inheritance. I contend that as a brood parasite, solitary juvenile Brown-headed Cowbirds experience more difficulty in joining migratory flocks, thus missing out on social route learning opportunities. These results clarify the relative role of different navigational adaptations in migratory birds and demonstrate the utility of studying vagrants to understand bird migration.

BACKGROUND

Migratory birds possess some of the most remarkable navigational adaptations which allow them to precisely return to breeding territories after migrating thousands of miles. Over 60 years of study have
revealed sensory, physiological, and genetic navigational adaptations (1). Many birds achieve pinpoint navigation with specialized cryptochrome proteins in the eye to sense magnetic field lines (2) and magnetite deposits in the bill to sense magnetic intensity (3, 4). Migratory routes are often encoded genetically, allowing juveniles to navigate from an endogenous migration program inherited from their parents (5–7). Yet, the importance of learning, both through experience and social interaction, is likely undervalued in our current understanding of avian navigation.

Bird navigation is not perfect: migratory birds occasionally end up in unexpected places, called vagrants. Vagrancy may be particularly revealing of the mechanisms behind avian navigation (8). External factors may drive vagrancy through interference with navigation senses. For example, natural, disruptive shifts in the Earth’s magnetic field driven by geomagnetic storms produce abnormal magnetic intensities (9) which are correlated with incorrect migration direction in lab experiments (10, 11) and increased vagrancy in free-flying birds (12, 13). Additionally, increased solar activity disrupts avian magnetoreception which may mask the effects of geomagnetic disturbance, allowing birds to migrate with natural cues (13). These results provide in situ demonstrations of the importance of magnetoreception for navigation. Visual landmarks are also likely key for navigation (8, 14), as clouds may drive vagrancy by obscuring landmarks (15). The extent that geomagnetic disturbance, solar activity, and visibly drive vagrancy may reveal the relative role that magnetoreception and visual landmarks play in migratory navigation.

However, vagrancy may also arise from winds driving birds off course, called wind drift (16, 17). A successful study of vagrancy must disentangle external factors that interfere with navigational senses from those that displace birds from their route.

Vagrancy may also occur from errors in migratory route inheritance. Vagrancy is more common in juveniles, possibly suggesting a short lifespan of birds with vagrancy mutations or naivety of younger birds (1, 18). Candidate genes regulating migration direction and timing have been identified in several species of songbird, the largest avian order (19–22), but the genetic architecture of migration still poorly known (23). Mutations in genes encoding migratory direction may misorient birds. The propagation of such mutations has been implicated in the rapid formation of new migratory routes in *Sylvia atricapilla*, *Hirundo rustica*, and *Petrochelidon pyrrhonota* (24–26). To properly evaluate the role of genetics in route inheritance in passerines, it is critical to quantify the relative contribution of social learning to route inheritance (8). Social learning is the use of inadvertent cues from other individuals as a source of information (27), as observed in large, day migrating birds, where juveniles join flocks of adults to learn migration routes (28, 29). Conventionally, it is assumed that juvenile passerines do not learn migration routes from adults because most migrate at night, making flocking difficult (6, 18). However, there are cues in passerine migration that may function in social route learning. Many nocturnally migrating passerines produce short vocalizations while migrating (nocturnal flight calls) which likely act as social cues aiding in navigation, orientation, and possibly group decision making (30, 31). Some passerines migrate diurnally in flocks, providing both visual and auditory cues (e.g. *Icteridae*, Yasukawa and Searcy 2020). The failure of a juvenile to join a migratory flock may cause them to miss out on route learning opportunities, thus leading to vagrancy.
Using vagrants to study migratory navigation presents a challenge because defining vagrancy is difficult (33). The rarity of a species at any given location is often based on observation data limited by low sampling density (e.g., survey or banding data) or inconsistent effort (e.g., community science data). Species abundance is often patchy, making it easy for local range fragments to be overlooked. Any birds dispersing from unknown range fragments may be erroneously identified as vagrants (33). Additionally, vagrants may represent the extremes of a normal curve of migration orientation, rather than true misorientation (34). To provide a clear index of vagrancy, I chose to study migratory passerines lost offshore (Fig. 1). While some migratory routes cross bodies of water (35), flying over the open ocean can be a costly mistake for a passerine. Offshore vessels document these lost passerines, presenting an opportunity to study vagrancy (36).

I studied common migratory passerines in the Western United States lost over the Pacific Ocean. I asked the questions: (1) to what extent do external factors cause vagrancy by interfering with navigational senses or displacing birds from their migration routes? And (2) what species characteristics affect vagrancy propensity? I studied the relative likelihood of offshore vagrancy under different levels of external factors including weather, geomagnetic disturbance, and solar activity. Then, I studied how the vagrancy frequency for each species varied in relation to morphology, migration route distance, and phylogenetics. My analysis revealed that external factors interfering with navigational sensing were the primary predictors of offshore vagrancy, particularly geomagnetic disturbance. The greatest variation in offshore vagrancy occurred between species. Variation between other species was best predicted by migration distance and wing pointedness. Brown-headed Cowbirds were a notable outlier, occurring offshore more often than any other species.

**METHODS**

**Data acquisition and filtering**

I sourced passerine records off the Pacific coast of North America from eBird (37), a community science platform for birdwatchers to submit observation data. The Pacific coast has broad spatial and temporal coverage from birdwatching pelagic trips, repositioning cruises, and research vessels, making an ideal study area for rare events. These data are often submitted to eBird by reliable observers like pelagic trip leaders, experienced birdwatchers, and surveyors. eBird data is submitted in georeferenced checklists containing tallies of species linked to effort data including transect distance, number of observers, and time. I downloaded the “basic” eBird dataset containing all eBird checklists submitted worldwide prior to June 2021, and filtered it using the auk package in R v4.2.1 (38, 39). I chose study species by visually inspecting records from heavily used eBird locations (> 1,000 checklists) less than 10 km from shore from southern British Columbia to southern California. I selected birds if they were present seasonally and occurred on >5% of eBird checklists in a majority of eBird locations, resulting in a set of 38 common migratory passerines. Non-migratory and rare species were not included because there are too few offshore records for analysis. I selected offshore eBird checklists submitted from southern California to southern British Columbia (32.5° – 48° latitude) from 10 km to 470 km offshore (Western boundary –
130° longitude), removing records within 10 km of land because observers occasionally combine harbor and nearshore data into one eBird checklist. I also selected onshore records up to ~60 km inland as a comparison. This served to sample 1,087,561 km² of ocean and 23,391 km² of land. Within 0.125–1° latitude slices of the sampling area (width based on sampling density, Supplementary materials Figure S1), I undersampled the land checklists to select an equal number to offshore checklists in the same band. This prevented some regions with high levels of eBird use, like cities, from being overrepresented in the set of land points.

**External drivers of offshore vagrancy**

I examined general occurrence patterns of timing and age of passerines offshore. I grouped observations by season based on prior knowledge of passerine migration timing in Western North America. Winter was considered November – March, spring April – June, summer July, and fall August – October. I performed a Pearson's chi-squared test to determine if birds were observed offshore more often in the spring or fall. I additionally calculated spherical distance of each record from shore in km. eBird checklists hold valuable descriptive data entered by users including various descriptive tags and a free text field where users may enter their comments (40, 41). I extracted keywords from field descriptions and age tags to determine the relative proportion of adults and juveniles offshore.

I acquired geomagnetic disturbance, solar activity, and weather data to as possible external factors explaining offshore vagrancy. I included geomagnetic disturbance because geomagnetic events may cause misorientation by interfering with avian magnetoreception. Following Tonelli et al. (13), I downloaded Kp (an average magnetic index from 13 globally distributed geomagnetic observatories) geomagnetic data between 1932-01-01 and 2023-01-01 from the International Service of Geomagnetic Indices (https://isgi.unistra.fr/data_download.php). I then converted Kp to ap, a numeric magnetic index more suitable for statistics. I studied solar activity because it may disrupt magnetoreception, possibly causing vagrancy or counteracting the effects of geomagnetic disturbance (13). I used daily sunspot number as a proxy for solar activity. I downloaded ‘American Relative Sunspot Number – Daily’ data between 1945-01-01 and 2023-02-05 from Laboratory for Atmospheric and Space Physics (https://lasp.colorado.edu/lisird/data/american_relative_sunspot_number_daily/). I calculated a 21-day rolling average for geomagnetic disturbance and solar activity because the effects of each may be delayed. I focused on four weather variables to study two mechanisms: wind speed and direction to test if birds are blown offshore, and visibility distance and cloud ceiling height to test if a low cloud layer may obscure the coastline causing disorientation. I used the moaa R package (42) to extract National Oceanic and Atmospheric Administration (NOAA) weather data from 55 coastal weather stations (stations listed in Supplementary Materials). I averaged hourly weather data for an entire 24-hour day for each checklist, because weather may have driven birds offshore before the time of observation. To ensure that weather recorded at onshore weather stations was comparable to checklist locations, I only used eBird data collected within 65 km from shore. I visualized all possible explanatory variables with a plot and correlation matrix to identify outliers and multicollinearity. Cloud ceiling height and visibility distance were correlated, so I removed visibility distance which had less data.
I studied how offshore vagrancy was explained by weather, geomagnetic disturbance, solar activity, or individual species differences using mixed effects logistic regression from the *lme4* package in R (43). I fitted a single model with Restricted Maximum Likelihood Estimation (REML) to estimate variance components. I used species as a random effect to determine the extent that offshore vagrancy is predicted by individual species characteristics. I used geomagnetic disturbance (ap), solar activity (sunspot count), cloud ceiling height, and wind speed (kph) as fixed effects, all standardized between 0 and 1 to ensure model convergence. At different values of each fixed effect, the average marginal predicted probability of occurrence was calculated to examine the contribution of each fixed effect while standardizing for the random effect, species, with the equation:

\[ \eta_i = X_i \beta + Z \gamma \]

This calculates the predictor \( \eta \) for a given fixed effect \( i \). The predictor matrix for that fixed effect \( X_i \) is multiplied by the fixed effect regression coefficients \( \beta \) to produce an independent predictor. Then \( Z \), a complimentary matrix to \( X \) but for the random effect, multiplied by \( \gamma \), the conditional expectation for the random effect level, is added to correct for variation introduced by the random effect. The resulting average marginal predicted probabilities were displayed graphically for all values of each fixed effect.

I analyzed wind direction differences with a Watson's two-sample test of homogeneity in the *circular* package in R (44). This test is optimized to handle circular variables, like wind direction in degrees. I performed two tests, for spring and fall, comparing the wind direction during the presence of offshore passerines and absence of offshore passerines. Seasons were separated because the impact of wind may vary by migration direction (north in spring and south in fall). A significant difference in wind direction suggests offshore vagrancy may be more likely during certain wind conditions.

### Species characteristics affecting offshore vagrancy propensity

To determine non-environmental drivers of vagrancy I studied interspecific differences in vagrancy propensity. The frequencies of each species may be heavily influenced by their overall population size. To generate a species-specific metric of offshore vagrancy propensity corrected for differences in relative commonness, I divided the overall offshore observation frequency by the overall on-land observation frequency of each species. Observation frequency is a standard eBird statistic calculated as the percent of all checklists in an area that contain a report of at least one individual of a species. The resulting index of offshore vagrancy propensity was used for all other analyses of species vagrancy propensity.

I tested whether mass, hand-wing index (HWI), or migration distance drive species differences in offshore vagrancy propensity. I downloaded mass data from EltonTraits (45). I used mass to study impacts of wind drift – lighter birds may be blown further off course by strong wind. I downloaded HWI data from the AVONET dataset (46). HWI is a measure of wing pointedness, calculated as the factor of the longest primary and secondary feather length. I included HWI because it is widely considered a proxy for dispersal ability (47), thus possibly impacting migratory ability. To estimate migration distance, I
averaged both breeding and winter latitude from North and South range extremes and longitude from East and West range extremes on range maps from Bird of the World (48), and then calculated spherical distance in km between the average breeding and winter range points. I included migration distance because birds that migrate further tend to be more prone to vagrancy (34). I performed a multiple linear regression analysis using vagrancy propensity as a response variable, normalized with a log transformation. I used mass HWI, and migration distance as explanatory variables, with an interaction term for HWI and migration distance to test if a pointed wing structure make birds more able to compensate for the effects of longer migrations.

I conducted a phylogenetic analysis to test if more related species were more likely to have similar vagrancy propensity due to the inheritance of vagrancy-causing mutations. I downloaded a phylogenetic tree subset from birdtree.org (49), made the tree ultrametric and dichotomous to meet the assumptions of standard phylogenetic analyses, and tested for phylogenetic signal of offshore vagrancy propensity with Blomberg's K using the R package phytools (50, 51).

RESULTS

I downloaded 15,466 offshore eBird checklists from 1968–2021, comprising 25,868.3 observation hours and 315,877.7 km of travel distance. Nearly 30% of checklists were submitted at 14 heavily used offshore eBird locations, the rest being distributed over 8,302 locations. Offshore passerine vagrants occurred on just 4.2% of offshore eBird checklists totaling ~ 1,371 individual birds (Fig. 2). All studied species had at least one offshore observation except hooded oriole. Mean distance offshore was 40.0 (± 27.0) km, but the furthest offshore vagrant was observed 202.7 km offshore. Offshore vagrancy overwhelmingly occurred during migration and was 37% more common in fall than in spring migration (without accounting with frequency on land; Chi-square test, \( X^2 = 18.7, \text{ df} = 1, p < 0.0001 \)). Juveniles were noted 225% more than adults (species frequencies in Supplementary materials Table S1).

External drivers of offshore vagrancy

I found geomagnetic disturbance, solar activity, and weather to all influence offshore vagrancy (Fig. 3), but with considerable variation between species. Geomagnetic disturbance appeared to be the best fixed effect predictor of offshore vagrancy. At levels of geomagnetic disturbance > 22 ap, species were predicted to be observed on 3% of eBird checklists on average. Solar activity, cloud ceiling height, and wind speed all were minor predictors of vagrancy: at values approaching 0, species were predicted to be observed on < 1% of eBird checklists on average. For all fixed effects, species response demonstrated a skewed right distribution, with a few species showing large responses to each factor, disproportionately increasing the average. Notably, the random effect, species, had the largest impact on vagrancy, meaning most of the variation in vagrancy derives from differences between species.

Wind direction related to presence and absence of offshore passerines depending on the season. In spring, winds were from the south on average regardless of passerine presence (Watson's two-sample
test of homogeneity, $U^2 = 0.263, 0.01 < P < 0.05$). In fall, the average wind direction was from the NNW (343°) when passerines were present and SSW (194°) when absent (Watson's two-sample test of homogeneity, $U^2 = 1.8704, P < 0.001$).

**Species characteristics affecting offshore vagrancy propensity**

Brown-headed cowbirds were more common offshore than all other studied species (Fig. 4). A group of three Brown-headed Cowbirds also represented the passerine recorded furthest offshore at 202.7 km off the coast of British Columbia. High vagrancy in Brown-headed Cowbirds was driven overwhelmingly by juveniles in the fall.

A multiple linear regression adequately explained species variance in offshore vagrancy propensity (Fig. 5; Multiple linear regression, $R^2 = 0.2988, F_{3, 32} = 4.836, p = 0.0036$): mass had no significant impact on vagrancy propensity ($t = -1.462, p = 0.153$), HWI and migration distance were both positively correlated with offshore vagrancy propensity ($t = 3.241, 0.0028; t = 3.675, p = 0.0009$), and HWI and migration distance had a significant negative interaction ($t = -3.572, p = 0.0011$). For birds with less pointed wings, a longer migration distance increased the likelihood of vagrancy. For birds with more pointed wings, vagrancy was equally likely at all migration distances. Vagrancy propensity was not predicted by phylogenetics. A Blomberg's K of 0.38 indicates phylogenetic repulsion, where related species are more different than expected under Brownian Motion ($K = 1$), however the relationship was not significant (Blomberg's test, $P = 0.162$; Supplementary materials Figure S2).

**DISCUSSION**

**External factors drive vagrancy through interference with navigation, rather than route perturbation**

The two best predictors of offshore vagrancy, geomagnetic disturbance and cloud ceiling height, were factors that interfere with avian senses necessary for navigation. Geomagnetic disturbance likely interferes with magnetoreception to cause misorientation. We add to growing evidence that geomagnetic disturbance is a primary driver of vagrancy (10–13), suggesting magnetoreception is a primary sensory adaptation necessary for avian navigation. Solar radiation had a weak negative impact on vagrancy, possibly supporting the suggestion by Tonelli et al. (13) that increased solar radiation masks the impact of geomagnetic disturbance. A low cloud ceiling appears to cause slightly higher rates of vagrancy, likely by obscuring the coastline from migrating passerines causing them to fly offshore, supporting the proposed role of visual landmarks in navigation (13, 14). It seems likely the association between offshore passerines and low cloud cover signals vagrancy, not increased migration in general, as cloud cover does not appear to impact migration departure (52).
I found vagrancy to not be driven by wind drift, matching previous study (16, 17). High winds and winds directing birds offshore did not increase vagrancy, and small bodied birds were not more likely to be blown off course. Instead, vagrancy was slightly more common during periods of low wind speed and tailwinds in the fall. These conditions may be associated with increased migratory departure in songbirds (53, 54), though support is mixed (52, 55, 56). Thus, it is possible that an increase in offshore vagrants simply reflects an increase in total migrants due to favorable migration conditions. This reveals the largest limitation with my approach. While land data can correct for differences in local abundance, it is not possible to know whether those birds are migrating or stopping over. This information gap may be filled by using radar data to estimate daily migrating birds. Taken together, my results suggest that external factors may primarily cause vagrancy by interfering with navigation rather than physically perturbing them from their migration route.

**Species-specific drivers of vagrancy: high vagrancy in a brood parasite indicates social route learning in passerines**

Brown-headed Cowbirds were a notable outlier in my dataset, occurring offshore significantly more than other passerines, driven overwhelmingly by juveniles in the fall. Greater vagrancy propensity in juveniles could result from high post-natal dispersal, but this explanation does not fit Brown-headed Cowbirds as they show equivalent levels of natal philopatry to other North American passerines (57). Instead, increased vagrancy in Brown-headed Cowbirds may relate to social learning and brood parasitism. Social route learning is not documented in other passerines (5, 6) but may occur via flight calls in nocturnal migrants or flocking in diurnal migrants (30, 31). Cowbirds, and several other members of *Icteridae*, migrate in flocks during the day (32, 57, 58), providing opportunities for social route learning. Unlike other members of *Icteridae*, cowbirds are brood parasites, meaning females lay eggs in other species nests allowing that species to rear their offspring for them. Thus, Brown-headed Cowbirds spend the early phase of their life completely isolated from conspecifics. Juvenile cowbirds are dependent on locating conspecific adults for learning (59), relying on fine-tuned call recognition for species recognition (60). If a juvenile cowbird is unable to locate a flock, it would be forced to rely solely on endogenous migration programming, which may be less flexible and error prone than learned navigation (7, 18). This may happen often, as juvenile cowbirds may depart hatching grounds at different times from adults, usually at high elevations and latitudes (61). I contend offshore vagrancy is more common in Brown-headed Cowbirds because juveniles are more likely to miss out on social route learning opportunities than most passerines, thus making them more prone to navigational errors.

If Brown-headed Cowbirds show reduced route learning, any expressed migration route may be a truer signal of their genetics, including any vagrancy-causing mutations. In this study, I failed to find any phylogenetic signal of vagrancy-causing alleles. Such alleles would be rare due to low survival of individuals with altered migratory routes. Thus, it is perhaps unsurprising there is no evidence from phylogenetic analyses. A focused analysis on one or few species is a better approach for identifying vagrancy genes (33). The Brown-headed Cowbird may be an ideal candidate for a genome-wide association study aimed at identifying migration genes.
Vagrancy propensity in other species was explained by an interaction between migration distance and wing pointedness. Birds that migrate further tend to be more prone to vagrancy (34), likely because more time spent migrating provides more opportunities to encounter vagrancy causing factors. However, the impact of migration distance was tempered in birds with more pointed wings and exaggerated in birds with more rounded wings. It is possible that the increased flight efficiency conferred by pointed wings (47, 62) allows these species return to normal migration routes more rapidly.

**Impacts of vagrancy**

Vagrancy may have cascading effects on bird species. Vagrants may perish in hostile environments or be isolated, unable to breed with their populations, possibly causing population decline (13). Vagrancy may also allow birds to expand their range (63), as shown by the rapid development of new wintering grounds for *Phylloscopus* warblers (64). Such expansion can shift the evolutionary trajectory of a species by causing geographic isolation and possibly speciation, or secondary contact and hybridization. Offshore vagrancy has the particularly rare outcome of allowing transoceanic expansion, including island colonization. This rare event is difficult to study, but critical for understanding of island biogeography. It may be possible to use offshore data from community science platforms to quantify the likelihood of ocean crossings for use in biogeographic and speciation modeling.

**CONCLUSIONS**

Examining offshore passerines proved a valuable approach for studying the mechanisms behind bird vagrancy and navigation.Geomagnetic disturbance appears to be the primary driver of offshore vagrancy by interfering with magnetoreception. Low visibility was also a predictor suggesting visual navigation also plays a role. Most of the variation in offshore vagrancy propensity was explained by species specific differences. I found offshore vagrancy to be significantly more common in Brown-headed Cowbirds than other passerines. As a brood parasite, solitary juvenile Brown-headed Cowbirds experience more difficulty in joining migratory flocks, thus missing out on social route learning opportunities. Future study of social learning in passerines is necessary, but presents a considerable challenge given their small size, short lifespan, and nocturnal migration. Effective approaches may leverage ever-miniaturizing tracking technology and nocturnal flight call recordings to study passerine interactions during migration. My phylogenetic analysis failed to produce evidence of selection against vagrancy causing mutations, but direct genetic study is necessary. Brown-headed Cowbirds may be a good model for studying the vagrancy genetics if they experience less social route learning.

**Abbreviations**

HWI
hand-wing index

**Declarations**
Ethics approval and consent to participate

Not applicable, this studied uses publicly available observational data.

Consent for publication

Not applicable.

Availability of data and materials

All eBird data is available for download from www.eBird.org. The R scripts for generated for this study are available in a GitHub repository.

Competing interests

The authors declare that they have no competing interests.

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No funding was required for this research.

Authors' contributions

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References


Tables

Tables 1 is available in the Supplementary Files section.

Figures
Offshore vagrancy documented from a cruise ship 80 km off the coast of Washington State. (a) A Yellow-rumped Warbler flies low over the Pacific Ocean. (b) A Yellow-rumped warbler, Wilson’s Warbler, and Lincoln’s Sparrow take refuge in an artificial plant. (c) Two deceased Wilson’s Warblers lay on the deck. (d) An unwell Yellow-rumped Warbler perches in an artificial plant. All photographs by Steve Kelling, used with permission.
Figure 2

Offshore eBird data used in this study. The raster grid shows the sampling coverage of eBird data, with the color of each cell representing the number of eBird checklists in that cell. Each triangle is a single offshore observation of a passerine.
Figure 3

**External drivers of offshore vagrancy.** Average marginal predicted probability of offshore occurrence (occurrence probability) is shown for values of each fixed effect variable calculated from the best mixed effects logistic regression model. By averaging all levels of the random effect, these results control for differences between species. Geomagnetic disturbance, solar activity, and cloud ceiling height were significantly correlated with offshore vagrancy.
Figure 4

**Species vagrancy propensity by season.** Offshore observation frequency adjusted for on-land observation frequency (adjusted observation frequency) is shown for each passerine species. Observation frequency is the percentage of all eBird checklists that contain a report of a given species. Proportion of observations in each season is overlaid. Note the high frequency of Brown-headed Cowbirds, particularly in the fall.
Figure 5

Species-wise vagrancy propensity in response to three explanatory characteristics: mass, hand-wing index (HWI), and migration distance. Each point represents a different species. Vagrancy propensity was calculated as the observation frequency offshore divided by the observation frequency on land, normalized with a log transformation. (A) Mass had no significant impact on vagrancy propensity. (B) HWI, a measure of wing pointedness which correlates to dispersal ability, had a slight positive effect on vagrancy propensity. (C) Migration distance had a clear interaction with HWI. In birds with a pointed wing shape (high HWI, demonstrated by a Swainson's thrush wing), any impact of migration distance is negated. In birds with a rounded wing shape (low HWI, demonstrated by a Wilson's Warbler), longer migration was strongly correlated with increased vagrancy propensity.
Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.png
- Offshorevagrancysupplementarymaterials.docx