

The influence of population growth and wind on vagrancy in a North American passerine

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Understanding the causes of vagrancy among migratory bird species is of increasing importance as climate change threatens species' survival. Vagrancy may serve to safeguard populations from environmental change through expansion of their geographic ranges. To dissect underlying causes of vagrancy, we analysed data on occurrence of vagrant Ash-throated Flycatchers *Myiarchus cinerascens* to the east coast of North America and population growth within their core breeding range, to test to what extent vagrancy is driven by population growth and the production of young that have a proclivity to explore new places. We also tested to what extent vagrancy is related to drift by prevailing winds, through analysis of synoptic weather maps of North America. Our analyses aimed to quantify which factors most strongly influence interannual variation in the number of Ash-throated Flycatchers reaching the east coast of North America. We obtained records of vagrants from 'North American Birds', population data from the North American Breeding Bird Survey (BBS), reproductive success from Monitoring Avian Productivity and Survivorship (MAPS) databases, and synoptic weather maps from the NOAA NCEP North American Regional Reanalysis database. We found that vagrancy was predominantly explained by the growing breeding population size as indexed by BBS data. In addition, we found significant effects of annual production of young within the breeding range, as well as three measures of air circulation across North America. Our models indicated an important role of population growth, with additional effects of reproductive success and predominant airflow affecting the incidence of vagrancy. Years of high reproductive success bring larger numbers of Ash-throated Flycatchers to the east, and this number is enhanced when weather conditions are especially favourable.

Key words: vagrancy, long-distance movement, population growth, airflow, entrainment

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Birds, like other organisms, frequently engage in long-distance dispersal, regularly appearing far outside of their historical distributions (Grinnell 1922, Hengeveld 1989, Howell *et al.* 2014). These individuals are often referred to as 'vagrants' (Kot *et al.* 1996). Because birds are conspicuous, relatively easy to identify and popular among amateurs, there is a much larger body of published data available on vagrancy among birds than for other organisms (North American Birds, British Birds

and other regional publications). Theories to account for the occurrence of vagrants, however, are conflicting and in general weakly supported (DeBenedictis 1971, DeSante 1973, Newton 2008), and the vast geographical scope over which vagrancy occurs makes it difficult to quantify.

We use the term 'vagrant' throughout to emphasize long-distance movement to areas outside of the known species' range, without regard to whether or not the

individuals that move subsequently breed (though many vagrants do; e.g. Hengeveld 1989, Johnson 1994, Veit *et al.* 2016). Thus, our use of the word ‘vagrant’ differs from the conventional ecological use of the word ‘dispersal’ in not implying subsequent breeding. Under this definition, vagrancy can occur at any time of year, and may or may not result in range expansion.

Vagrancy has been proposed to arise from a suite of factors, ranging from faulty internal mechanisms such as inheritance of an incorrect compass orientation (Rabøl 1969, DeSante 1973, Diamond 1982, Thorup 1998, 2004, Thorup *et al.* 2012), to external drivers such as displacement by wind or weather systems (Baker 1977, Elkins 1979). Errors in compass orientation have been thought to result from either mirror-image misorientation (DeSante 1973) or reverse migration (Rabøl 1969), however, no direct support yet exists for either mechanism due to difficulty in testing for orientation errors of individual vagrants. Statistical support for mirror-image misorientation remains weak (despite Diamond 1982), and existence of reverse migration is based on the untested assumption (Newton 2008) that birds flying in a counterintuitive direction have made a mistake (the word ‘misorientation’ itself implies a faulty mechanism).

Extensive time series on numbers of vagrants appearing at any one place show that many vagrant species tend to appear in episodic irruptions (e.g. Veit 1990, Patten & Marantz 1996, Hamilton *et al.* 2007, White & Kehoe 2014), with larger than usual numbers of vagrants occurring in given years. This kind of variability through time suggests a link to population growth, as bird populations often fluctuate episodically

as well (Perrins *et al.* 1991, Böhning-Gaese *et al.* 1994). Though vagrants have been considered aberrant, publications on patterns of vagrancy do point out that birds that appear as vagrants belong to large and growing populations (McLaren 1981), and even show statistically significant relationships between population size and the tendency to appear as vagrants (DeBenedictis 1971, Patten & Marantz 1996).

Within this paper we do not test whether vagrancy is deliberate. Instead, our analysis builds models to assess the relative contributions of both population growth, production of young and prevailing wind direction to the annual occurrence of vagrants. Ash-throated Flycatchers *Myiarchus cinerascens*, a southwestern North American species (Figure 1) that winters from Mexico to Honduras, are particularly suitable for this analysis because virtually all east coast records have occurred since about 1960, so that the process of vagrancy is carefully documented within the literature (American Birding Association (ABA), NYOSOA's journal ‘The Kingbird’, the New England birding journal ‘Bird Observer’; see Table S1). They are also rare enough anywhere on the East Coast that we are confident that most Ash-throated Flycatchers have been reported.

We hypothesize that the number of vagrant Ash-throated Flycatchers appearing on the East Coast each autumn is statistically related to the growth of their population in the west, the number of young being produced within the breeding range in the previous summer (i.e. large numbers of vagrants are the result of large numbers of young being produced), and to the occurrence of weather patterns that favour eastwards and north-eastwards movement. We do not know the

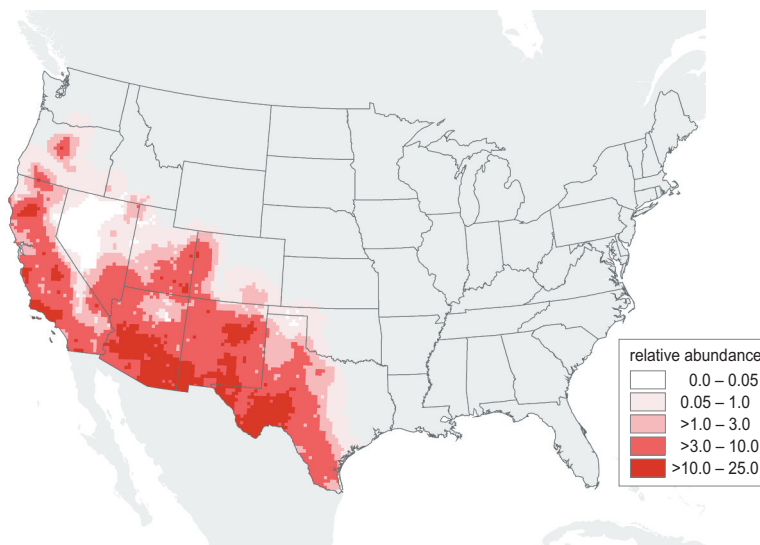


Figure 1. Distribution and relative abundance of Ash-throated Flycatchers during the breeding season, based on average counts from the interval 2011–2015 on each route. Image reproduced with permission from the North American Breeding Bird Survey (BBS; Sauer *et al.* 2017).

exact route any of these birds used to travel across North America. However, we can hypothesize that they, like other southwestern North American species that occur on the east coast as vagrants, travel eastwards during persistent periods of generally south-westerly winds, often ahead of low pressure systems and cold fronts, during the 3 to 4-day time frame over which these weather conditions persist (Bagg 1970, Able 1972, 1974, Heil 1981, Brinkley & Lehman 2003, Sullivan & Wood 2005, Brinkley 2011, Farnsworth & Iliff 2012). This expands upon hypotheses proposed by Brinkley & Lehman (2003), and others (e.g. Bagg 1970), in which eastwards movement of western North American vagrants have been speculated to result from eastward entrainment by south-westerly airflow extended across eastern North America over a roughly 2 to 4-day period.

Our approach differs from previous quantitative analyses in that we suppose that vagrants do not differ fundamentally in behaviour from non-vagrants. Instead, we suspect what we see as vagrancy here is the end result of larger than average numbers of birds spreading outwards while exploring for potential new habitat (Baker 1978).

It is increasingly important to understand the mechanism of vagrancy in birds (Ogden 2016). Birds and other organisms are constantly and increasingly changing their distributions, and these changes are contingent upon vagrancy (Kokko & López-Sepulcre 2006, Jiguet & Barbet-Massin 2013). Furthermore, increasing proportions of species that have become endangered require that we understand the role of vagrancy for the persistence of these species (Sugden & Pennisi 2006, Hodgson *et al.* 2016). The spread of diseases that affect both humans and wildlife has also been linked to vagrancy by birds (Smith *et al.* 1996, Morshed *et al.* 2005), including potential intercontinental transport (Reed *et al.* 2003). Vagrants have not been explicitly examined for pathogens, but long-distance movement facilitates spread, and identification of this link is important. By gaining an understanding of these movements through research, we can better predict range expansions and aid in conservation efforts for a variety of species.

METHODS

We extracted data on vagrant Ash-throated Flycatchers in eastern North America between Newfoundland and Florida from August to January, which are available from the years 1956 to 2014, from 'North American

Birds' (NAB, ABA; Table S1) and its predecessors 'American Birds' and 'Audubon Field Notes' (Figure 2A). Ash-throated Flycatchers vacate the breeding grounds by late July, therefore August to January captures the entirety of the non-breeding season in which flycatchers would be vagrant to eastern North America. We chose to focus on the East Coast, and not include records from inland sites, both because the coast provides somewhat of a barrier to further travel for vagrants, and also because of the less intensive coverage of areas removed from the coast, especially in earlier years. Each bird recorded was listed as a single record based on its detection date (Table S1). The detection date of each bird will be interpreted as its arrival date throughout. There is no way of knowing exactly when an Ash-throated Flycatcher arrives at a particular location. However, Ash-throated Flycatchers are conspicuous, and easily found, so it seems unlikely that detection dates are more than a day or two different from the dates the birds actually arrived. The geographical scope of our study follows the geographical designations outlined in NAB. NAB divides the eastern United States into sub-regions as follows: (1) Atlantic Provinces and St. Pierre et Miquelon, (2) Quebec, (3) New England, (4) Hudson–Delaware, including New York, New Jersey and Delaware, (5) Middle Atlantic, including Maryland, D.C., and coastal Virginia, (6) Southern Atlantic, including North and South Carolina and coastal Georgia, and (7) Florida, from which we included only East Coast records (i.e. we excluded the panhandle region). All vagrants identified to age were hatching year birds (19.4%; NAB, ABA).

To evaluate the quality of data from the online observations database 'eBird', we extracted all available records of vagrant Ash-throated Flycatchers (eBird Basic Dataset 2013) and compared these records to those in NAB. Upon comparison, we found that the time series of NAB records is comparable to eBird records ($r = 0.88$, $P < 0.001$; Figure 2A). While eBird contains some records NAB lacks, we excluded eBird records from our analysis due to the following caveats that come with using eBird. First, eBird was not established until 2002. Any records prior to this year are not available on eBird, except for the few that have been opportunistically added. NAB, however, began compiling records in 1946, so all known records of Ash-throated Flycatchers have been recorded. Second, eBird does not have a consistent method of distinguishing whether two or more reports pertain to one or more individual birds, resulting in many single birds being listed multiple times by multiple observers. A single bird can have more than twenty reports for the same

day. NAB editors, on the other hand, use multiple sources of information from local experts (local publications, state records committees, observers who were present at the sightings) to assess whether any two records are of the same bird. In the few instances where there were multiple records in NAB that were not annotated as being separate birds, we defined ‘separate’ occurrences as two individuals at the same location separated by at least 5 days with no sightings.

While difficulty arises in distinguishing among *Myiarchus* species, most vagrant records of Ash-throated Flycatchers are supported by clear photographs or collected specimens that have been examined by local and national rarities committees (Table S1). The vast majority of eastern records of Ash-throated Flycatchers occur after mid-October, long after the locally common Great Crested Flycatchers *Myiarchus crinitus* have departed for the winter (Cardiff & Dittmann 2002, Farnsworth & Iliff 2012, Miller & Lanyon 2014; Figure 2B, Table S1). Great Crested Flycatchers disappear from their breeding grounds in eastern North America by September. To test for confusion between species, we derived records of Great Crested Flycatchers using the same methods outlined above, and compared timing of records to Ash-throated Flycatcher vagrancy (Figure S1). If there were numerous records of late autumn Great Crested Flycatchers before 1980, it is possible these could have been misidentified Ash-throated Flycatchers, but there is no such pattern of occurrence of *Myiarchus* before the increase of Ash-throated Flycatchers during the 1990s (Figure S1). Indeed, the numbers of Great Crested Flycatchers seen do not decrease concurrent with the increase in Ash-throateds, and do not differ statistically from 1956 to 2014 (Figure S2). Annotations of this species seen in late autumn in the 1950s and 1960s also specifically state that they “were carefully examined to ensure they were not one of the western species”. Thus, the record of occurrence of these two species strongly suggests that the recent increase of Ash-throated Flycatchers is real and not an artefact of past misidentification.

Increasing observation effort is also not responsible for the increasing trend shown in Figure 2A, as many species of vagrants to the East Coast have been shown to decline over the same period that Ash-throated Flycatchers have been increasing (Veit 1990, 2000, van den Berg & Bosman 2001, White & Kehoe 2014). To show that increasing numbers of vagrants are not the result of increased birder effort, we re-examine Veit’s (2000) results that show long term decreases and increases of vagrants from western North America to the East Coast. This multi-species analysis compares

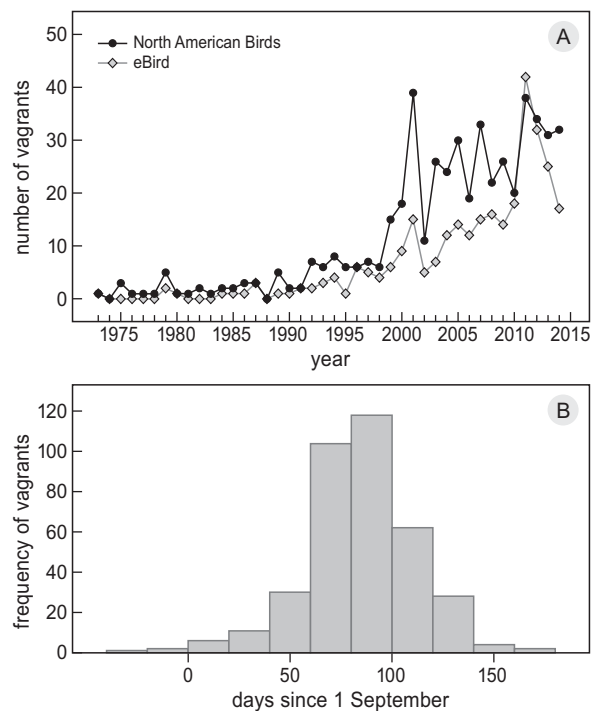


Figure 2. (A) Records of Ash-throated Flycatchers from North American Birds (NAB) and eBird during autumn migration (August–January) in eastern coastal North America (Newfoundland to Florida) in 1956–2014. All records are single birds on their detection date. The records from NAB and eBird are significantly correlated ($r = 0.88$, $P < 0.001$). (B) Seasonal occurrence of vagrant Ash-throated Flycatchers on the U.S. East Coast in 1956–2014, based on NAB data.

patterns of vagrancy of six western North American species to patterns of vagrancy of Ash-throated Flycatchers to Massachusetts. Methods were derived from Veit (2000). The scope of this analysis only covered Massachusetts because there is a general issue with collecting data on vagrant birds: if a species appears too frequently as a vagrant, their occurrence is no longer quantified in the literature, while some vagrants appear so infrequently (e.g. Hermit Warbler *Setophaga occidentalis*) that there are not enough data to allow analysis. The western North American species whose trajectories we present here – Western Kingbird *Tyrannus verticalis*, Western Tanager *Piranga ludoviciana*, Black-headed Grosbeak *Pheucticus melanocephalus*, Lark Sparrow *Chondestes grammacus*, Clay-coloured Sparrow *Spizella pallida* and Yellow-headed Blackbird *Xanthocephalus xanthocephalus* – are rare enough in Massachusetts that almost every bird observed was reported. At the scale of the entire East Coast, however, NAB editors tend to report an “average

abundance” of individuals, and each individual editor’s idea of ‘average’ is seemingly quite variable. Thus, we use occurrence in Massachusetts for these other western species to compare temporal pattern of occurrence with that of the Ash-throated Flycatcher. We calculated Pearson correlation coefficients at a Bonferroni corrected significance level $\alpha = 0.008$.

Using annually summarized Ash-throated Flycatcher sightings, we sought to develop a model that would correlate vagrancy to both population growth and to airflow. BBS (North American Breeding Bird Survey) and MAPS (Monitoring Avian Productivity and Survivorship) provide independent estimates of population growth and reproduction; BBS and MAPS use transect and mistnetting methodologies (respectively), thus yielding different estimates of reproduction. MAPS provides a direct measure of reproduction through capture of young birds (see below). We included wind directions in our model to ask whether the numbers of vagrants occurring in the east could be explained on the basis of prevailing winds (e.g. south-westerly winds across the continent: Bagg 1970, Brinkley & Lehman 2003, Farnsworth & Iliff 2012).

North American Breeding Bird Survey (BBS) data

BBS data consists of annual indices of abundance of bird species during the height of the avian breeding season (June for most of the United States; Pardieck *et al.* 2017). Indices are obtained via roadside surveys. Each survey route is 39.4 km long, and all birds seen or heard are counted at stop intervals of 0.8 km. BBS data were available from the years 1968–2011.

BBS annual indices are calculated at three spatial scales: (1) the division of the entire continent into thirds (Eastern, Central, Western), (2) ecogeographic strata (Robbins *et al.* 1986, Veit 2000), and (3) individual states. For our analyses, we first used the entire non-subdivided dataset on Ash-throated Flycatchers: (1) the entire United States. We then chose fifteen distinct study regions among the three different scales to determine if we could ascribe vagrancy on the East Coast to any particular portion of the breeding range (Böhning-Gaese *et al.* 1994). These study regions included (2) western North America (general breeding range of Ash-throated Flycatchers), (3) the south-western states of Colorado, Utah, Arizona, and New Mexico, (4) the Great Basin, (5) the Sonora and Mojave deserts, (6) the Southern Rockies, (7) the Intermountain West, and the individual states of (8) Arizona, (9) California, (10) Colorado, (11) Idaho, (12) Nevada, (13) New Mexico, (14) Oregon, (15) Texas, and (16) Utah (Figure 4).

For each study region, we estimated regression coefficients between numbers of vagrants in year t and the annual indices of abundance in year t . Abundance in year t served as a predictor of population size for Ash-throated Flycatchers in the breeding range. We used Bonferroni-corrected $\alpha = 0.0167$ for our significance tests. Vagrant data were log-transformed.

We also calculated differenced BBS data (BBS Difference), on the premise that: BBS index in year $(t+1)$ – BBS index in year t , is an estimate of the number of young produced in year t (Veit 1997). This estimate relies on the assumption that the difference in population between years results from number of young produced. However, the difference in index between years may also capture emigration and immigration between different breeding populations, as well as adult winter survival between years. Hatching year (HY) birds are not counted in BBS roadside surveys, i.e. birds that are born and undergo their first migration in year t are not counted until year $t + 1$, therefore, the abundance of HY birds produced in year t are reflected in the abundance of year $t + 1$. While we do not know how changes in abundance are partitioned among over-winter mortality, immigration and reproduction, we assume that large positive changes on a continent-wide scale primarily reflect reproduction. By correlating vagrants in year t to the difference in BBS indices (BBS Difference), we can relate vagrants to population growth in the breeding range.

Monitoring Avian Productivity and Survivorship (MAPS) data

Data from MAPS banding stations consists of banding records of all Ash-throated Flycatchers mist-netted at these stations during the MAPS banding season (May–August). It includes information related to their age, sex, body condition and reproductive status. MAPS banding stations where Ash-throated Flycatchers had been captured limited the extent of our analyses to the individual states of Arizona, California, Colorado, New Mexico, Nevada, Oregon, Texas, Utah, as well as the Sonora region, and the averaged data over all MAPS stations per year (the breeding range surveyed by MAPS, hereafter ‘Total’). MAPS data were available from the years 1989–2014.

We extracted annual indices of reproductive success from MAPS as follows: To provide an estimate of reproduction for each station, ratios of hatch-year (HY) birds (MAPS age 2) to after-HY birds (MAPS ages 1 and 5) were calculated. Only unique birds were included in the analysis – recaptures of the same bird at the same station in a given year were excluded. The ratios of HY

to after-HY birds for each station were averaged over each state (each banding station was weighted equally regardless of number of birds captured) to provide a number of fledged chicks per adult for each state for each year: the Fledge Rate. Subareas with less than three nonzero Fledge Rates were excluded from further analysis, however, Total still reflects data from every location where MAPS data was taken.

Prevailing Wind Direction

Ash-throated Flycatchers, and other southwestern birds, have been theorized to occur in the eastern United States as a result of entrainment within broad-scale south-westerly winds across the continent (Bagg 1970, Brinkley & Lehman 2003, Farnsworth & Iliff 2012). That is, they are thought to arrive on winds blowing from the southwest. Though there is recent theoretical support for this idea (Elkins 2005, Newton 2008), and it appears in ecological texts (Ricklefs & Relyea 2014), quantitative analyses of this scope have never been performed (Table S4). We used two different approaches to assess the influence of prevailing winds upon flycatcher occurrence in the east, quantifying airflow in two different ways, to create two airflow variables to include within our model: (1) number of days with appropriate south-westerly winds each autumn (Airflow), and (2) mean wind direction (taken from NPEC NARR daily maps) measured at three different locations during three days prior to the occurrence of each vagrant at the East Coast, where the three points were taken as lying along a straight line between the geographic centre of Arizona and the location on the East Coast where the vagrant was found. Quantification of Airflow (1) was used to estimate how many occurrences there are per autumn season where conditions are appropriate for transporting south-western birds north-eastwards, i.e. conditions described by Brinkley & Lehman (2003) and Farnsworth & Iliff (2012). These conditions were continuous south-westerly winds (within 35° of 225° true) extending from Texas to New England. Mean wind direction (2) then provided a second way of estimating whether, for each Ash-throated Flycatcher at the East coast, wind conditions along the shortest route from the breeding ground were appropriate for entraining birds eastwards. We chose Arizona as the starting point because that is the centre of abundance for nesting Ash-throated Flycatchers in North America, as well as the area with the strongest population growth as determined from BBS data (Figure 1). Data were taken from the years 1956–2013 for Airflow, and 1989–2011 for the Average Wind Direction.

AIRFLOW

To quantify number of days with appropriate winds, we counted days of continuous south-westerly airflow (i.e. blowing from the direction of $190\text{--}260^\circ$) across southern North America, from Texas to the East Coast (approximately Chesapeake Bay; Figure 5). This is the route most likely to be traversed by Ash-throated Flycatchers on their way to the East Coast, and covers altitudes at which these birds are likely to be flying, i.e. <1000 m (Able 1973, Elkins 2004, Newton 2008). Data were extracted from surface weather maps for North America and archived data on continent wide airflow from the Daily Weather Maps (www.lib.noaa.gov/collections/imgdocmaps/daily_weather_maps.html) within National Oceanographic and Atmospheric Administration (NOAA) archives (Richardson 1990, Elkins 2004). Maps were examined each day of autumn migration from 1 September through 30 December, for the years 1956–2013. An integer estimate was extracted for each autumn season. We hypothesized that large numbers of days with south-westerly airflow would lead to large numbers of Ash-throated Flycatchers in the east, under the premise that birds choose nights with tailwinds to migrate or disperse (Able 1973), so that Ash-throated Flycatchers ought to appear on the East Coast when south-westerly winds prevail across the southern United States, as suggested for Cave Swallows *Petrochelidon fulva* and other species by Bagg (1970), Able (1972, 1974), Heil (1981), Brinkley & Lehman (2003) and Farnsworth & Iliff (2012).

AVERAGE WIND DIRECTION

Since we have no data on where vagrant Ash-throated Flycatchers initiate their eastward flight, nor on where they stop along the way, we could not realistically model the trajectories of individual birds, as in McLaren *et al.* (2012). Nevertheless, we can ask whether, if Ash-throated Flycatchers begin their journey to the East Coast three days before they are detected on the East Coast, the winds along that projected route are appropriate to carry them in an easterly direction. Ash-throated Flycatchers could plausibly follow patterns of south-westerly airflow from within the breeding range to reach the East Coast (Farnsworth & Iliff 2012). While flight speed of passerines ranges widely, a flight speed of $20\text{--}30$ km/h ($5.6\text{--}8.3$ m/s) is a reasonable estimate for Ash-throated Flycatchers (Elkins 2004, translating to approximately 700 km per 24-h period, under the implication that birds are traveling continuously (Brinkley & Lehman 2003, Farnsworth & Iliff 2012).

We extracted data from NCEP North American Regional Reanalysis (NARR) databases (www.esrl).

noaa.gov/psd/data/gridded/reanalysis/), which utilizes component wind data to provide surface maps with wind direction and wind speed. Using the 'Daily Average NCEP NARR Composites' page (www.esrl.noaa.gov/psd/cgi-bin/data/narr/plotday.pl). We extracted records of wind direction at three different points, in the direction from which the wind was blowing, clockwise from North. Wind direction was recorded 700 km along a straight line towards Arizona from the location where the vagrant was recorded, 24 h prior to the arrival date. Wind direction was then recorded 48 h prior to arrival at 1400 km towards Arizona from the arrival location, and 72 h prior to arrival at 2100 km towards Arizona from the arrival location, to obtain three separate measurements of wind direction. Annual mean values of wind direction (mean per year over all individual vagrants) were calculated for each 24-h period to obtain the variables Average Wind 1, Average Wind 2, and Average Wind 3. Data were collected at both the 1000 and 900 mb levels, which span the range of elevations (ground level to 1000 m) through which most migrating passerines travel (Elkins 2004). The data upon which this analysis is based used 376 vagrant records (from 1989–2011) \times three geographical locations per record \times two altitudinal levels, for 2256 maps of vectored wind direction at a continent-wide scale. This is, by far, the largest database, to our knowledge, ever used in an analysis to address influence of wind direction upon the occurrence of vagrant birds. Numerous authors (e.g. Bagg *et al.*) have proposed this mechanism of travel, and we feel it is prudent to test this idea within our models.

Arizona was taken as the starting point for each vagrant, because it is the abundance centroid of the entire breeding population in the western United States, based on BBS data (Figure 1), and is also the largest source of population growth within the breeding range (Figure 4). Since previous studies have shown that vagrant individuals are correlated with regions of high population growth in their breeding ranges (Veit 1997, 2000), we theorized that Arizona is the origin of most vagrant Ash-throated Flycatchers to the east coast, rather than other areas of the breeding range with lower levels of population growth (i.e. Texas and surrounding states).

Last, to test whether wind direction could explain arrival on the east coast, we calculated the difference between an individual bird's hypothesized bearing and the prevailing wind direction along the most direct route necessary to arrive at the sampled location. We tested the null hypothesis that these differences had a mean of 0. If vagrants at the east coast are arriving due

to entrainment, the predominant difference should be 0. That is, to arrive at Massachusetts from Arizona, an individual bird should follow a bearing of 72° and ideally would migrate with a wind direction of 252°.

To assess whether we should treat our circular variables (the direction variables, where wind direction of 0 = wind direction of 360°) in a circular regression, we implemented 'gam' (from package 'mgcv'; Wood 2012) with circular prediction terms (the bs = 'cc' smoother with 10 knots, where knots are anchor points for smoother parameterization; Wood 2012). This procedure yielded no quantitative difference from our GLM.

Model selection

Using these rates, we built general linear models of the form Vagrants = Reproduction (MAPS, Fledge Rate) + Reproduction (BBS Difference) + Population Size (BBS Index) + Airflow + Average Wind 1 + Average Wind 2 + Average Wind 3 + Error. Data included in the model were from years 1989 to 2011, because this was the only timeframe for which our population variables, MAPS and BBS data, overlapped. We used both Poisson and Negative Binomial distribution of errors, as numbers of vagrants were leptokurtic (Table S2, S3). Insignificant model terms were removed from the model using stepwise backward elimination (using stepAIC from package MASS; Ripley *et al.* 2017). The best model was chosen based on the lowest Akaike Information Criterion (AIC), and was only considered to be the best model if the lower AIC differed from the next-higher AIC by more than two units (Table 2, 3; Burnham & Anderson 2002). In cases where the AIC difference was less than two, the models were examined to determine whether they differed from the best model by one parameter and had similar maximized log-likelihood values. If both criteria were true, the larger model could not be supported and cannot compete as the best model. After selecting the best model, we performed a post-hoc analysis to evaluate whether the predictors in the best model were significantly related to the dependent variable. All analyses were conducted using R (R Core Team 2014).

RESULTS

Multi-species Analysis

The temporal trends in the occurrence of western birds on the U.S. East Coast differed among species (as found by Veit 2000). Occurrence of Western Kingbirds was negatively ($P = 0.03$) correlated with the occurrence of Ash-throated Flycatchers in Massachusetts, therefore

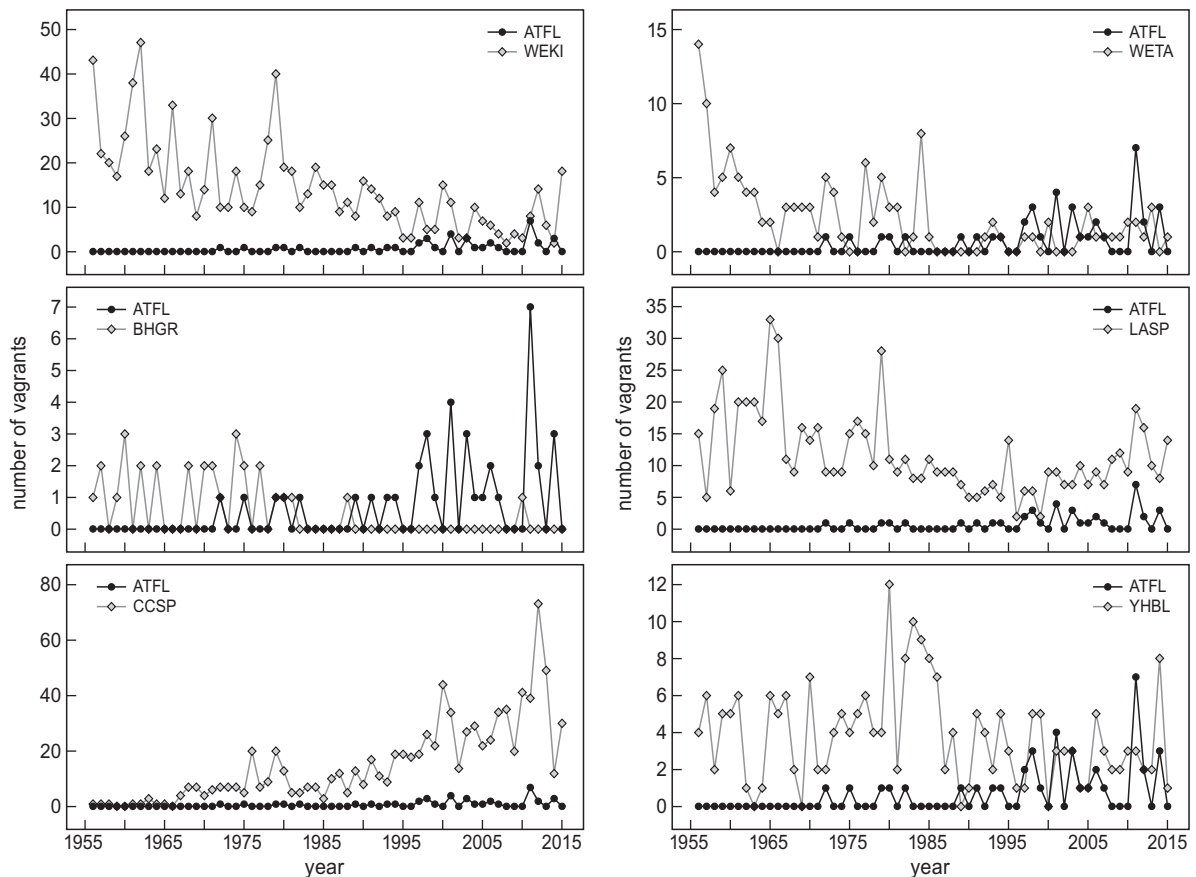


Figure 3. Multi-species analysis comparing patterns of vagrancy of six western North American species to patterns of vagrancy of Ash-throated Flycatchers (ATFL) in 1956–2014. Records cover Massachusetts, and were extracted from Bird Observer. The species analysed were Western Kingbird (WEKI), Western Tanager (WETA), Black-headed Grosbeak (BHGR), Lark Sparrow (LASP), Clay-coloured Sparrow (CCSP) and Yellow-headed Blackbird (YHBL). Correlations are as follows: WEKI ($r = -0.28$, $P = 0.03$), WETA ($r = -0.22$, $P = 0.09$), BHGR ($r = -0.23$, $P = 0.08$), LASP ($r = -0.08$, $P = 0.54$), CCSP ($r = 0.44$, $P < 0.001$) and YHBL ($r = 0.004$, $P = 0.97$). Bonferroni corrected significance level: $\alpha = 0.008$. Note difference in scale of y-axis for each species.

Western Kingbirds actually declined despite the increase of observers over this time period in contrast to Ash-throated Flycatchers (Veit 1990, 2000, van den Berg & Bosman 2001, White & Kehoe 2014), whereas the occurrence of Clay-coloured Sparrows was positively correlated with that of Ash-throated Flycatchers ($P < 0.001$). The four other species were not correlated with Ash-throated Flycatchers (Figure 3). These temporal trajectories of vagrancy of seven species of passerines occurring on the East Coast indicate independent and species-specific patterns, rather than increasing birder effort.

Longer-term, BBS roadside surveys (1968–2011)

Vagrancy on the East Coast was significantly correlated with indices of abundance at every study region ($P < 0.001$; Figure 4), with significantly increasing

positive trends, with the exception of Nevada ($P = 0.214$; Table 1). Many of the sixteen study regions are subsets of each other, so the tests are not independent of each other, but we present these data for comparison to our second set of models below.

Shorter-term, model selection

Of the ten areas where MAPS banding was conducted, Colorado, Nevada, and the Sonora region had fewer than three nonzero Fledge Rates (0, 2 and 2, respectively) and were thus excluded from model selection. The seven remaining areas analysed were Arizona, California, New Mexico, Oregon, Texas, Utah and the Total of all of the states (Table 2, 3; Table S2, S3).

At the 1000 mb level (pressure at ground level; Table 2), California, New Mexico, Oregon and Utah were best modelled by BBS Difference and BBS Index,



Figure 4. Sixteen study regions within three different spatial scales were analysed for correlations between reproduction in that portion of the breeding range based on BBS data and vagrancy on the East Coast. The study regions within which this study was conducted were: (1) United States, (2) western North America, (3) the southwestern states of Colorado, Utah, Arizona and New Mexico, (4) the Great Basin, (5) the Sonora and Mojave deserts, (6) the Southern Rockies, (7) the Intermountain west, and the individual states of (8) Arizona, (9) California, (10) Colorado, (11) Idaho, (12) New Mexico, (13) Nevada, (14) Oregon, (15) Texas and (16) Utah.

Table 1. Coefficients of determination (r^2) for linear regression analysis comparing breeding abundance (estimate of population size) in each study region in the year t (BBS Index) within three different spatial scales to number of vagrants on the East Coast in year t . Vagrant data were log-transformed. The Bonferroni corrected α is 0.0167. Significant values are printed in bold.

	Study region	Linear regression	
		R^2	P
Annual indices of abundance	United States	0.82	<0.001
	Western North America	0.89	<0.001
	Southwestern States	0.80	<0.001
	Great Basin	0.81	<0.001
	Sonora & Mojave Deserts	0.69	<0.001
	Southern Rockies	0.79	<0.001
	Intermountain West	0.79	<0.001
	Arizona	0.67	<0.001
	California	0.21	<0.010
	Colorado	0.82	<0.001
	Idaho	0.50	<0.001
	Nevada	0.01	0.214
	New Mexico	0.81	<0.001
	Oregon	0.75	<0.001
	Texas	0.81	<0.001
	Utah	0.71	<0.001

while Texas was best modelled by BBS Difference, BBS Index and Average Wind 2. Arizona and Total (the data averaged over all MAPS stations per year) were best modelled by six of the seven predictors, excluding Average Wind 3. All the selected models used a negative binomial distribution of errors. Maximum likelihood pseudo- R^2 -values were also included to explain how much variation in number of vagrants is explained by the predictors in question (Table 2). ‘Total’ was modelled best, having the highest pseudo- R^2 -value of 0.24, while least of the variation was explained in California (pseudo- R^2 = 0.02).

At the 900 mb level (pressure at 1000 m), the results were qualitatively similar (Table 3). New Mexico and Utah resulted in the same models as the 1000 mb level, and were best modelled by BBS Difference and BBS Index. California was best modelled by BBS Difference, BBS Index, Average Wind 1 and Average Wind 3, and Oregon had two competing models: the same model as the 1000 mb level including BBS Difference and BBS Index, and a competing model with Fledge Rate, BBS Difference and BBS Index. Arizona and Total were best modelled by four of the seven predictors, excluding all average wind direction variables. ‘Total’ was modelled best with a pseudo- R^2 value of 0.22, while California was the least-well modelled (pseudo- R^2 = of 0.07).

For all states, BBS Index explained most of the variance in numbers of vagrants. Fledge Rate was an important predictor for Arizona and Total, but not other states (with the exception of the competing model for Oregon). This disparity indicates that Fledge Rate is still an important factor in predicting the number of vagrants, however, low sample sizes may have contributed its infrequent selection. Though BBS data is a key predictor of the number of vagrants, MAPS data still holds weight in predicting how many vagrant flycatchers will appear on the East Coast of North America in a given year. BBS Difference was frequently selected, though the sign of its coefficient varied across areas. Overall, reproductive data was significantly predictive of numbers of vagrants in the Ash-throated Flycatcher (Tables 1, 2 and 3).

South-westerly airflow was rarely chosen in the models, and in those cases (Arizona and Total), only after demography was accounted for. Upon further investigation of the residuals in these two cases, a

single year (2011; Figure S3) within the airflow dataset was driving the significance of airflow within these models. Removal of this year resulted in selection of different models in which airflow was no longer selected. At the 1000 mb level, the new model for Arizona included the predictors Fledge Rate, BBS Difference, BBS Index and Average Wind 2, while for Total, the new model included the predictors Fledge Rate and BBS Index. At the 900 mb level, the new model for Arizona included the predictors Fledge Rate, BBS Difference and BBS Index, while for Total, the new model included the predictors Fledge Rate and BBS Index. Further, days of south-westerly airflow are not significantly correlated with the number of vagrants in 1956–2013 ($y = 0.14x + 7.47$, $r^2 = -0.016$, $P = 0.79$; see Figure S3). In our dataset there was only weak support for measures of wind support, and population growth had a much larger effect size in explaining the occurrence of vagrant Ash-throated Flycatchers (Table 2, 3, Figure 5).

Table 2. Model selection for eight breeding regions of the Ash-throated Flycatcher in the United States from 1989–2011 for wind directions were obtained from the 1000 mb level (approximately at ground level). Models were built from the form Vagrants = Reproduction (MAPS, Fledge Rate) + Reproduction (BBS Difference) + Population Size (BBS Index) + Airflow + Average Wind Direction 1 + Average Wind Direction 2 + Average Wind Direction 3 + Error. Effect sizes ($SS_{\text{predictor}}/SS_{\text{total}}$) and parameter estimates are given after P -values. ns indicates not significant. AIC shows the value for the best model for the region.

Region	Distribution	Predictor 1 (P)	Predictor 2 (P)	Predictor 3 (P)	Predictor 4 (P)	Predictor 5 (P)	Predictor 6 (P)	AIC	Maximum-likelihood pseudo- R^2 (best model only)
AZ	Neg. Binomial	Fledge Rate ($P < 0.001$), 0.15, 0.70	BBS Diff ($P < 0.001$), 0.006, 0.15	BBS Index ($P < 0.001$), 0.48, 0.30	Air Flow ($P < 0.01$), 0.01, 0.09	Wind 1 (ns), 0.001, 0.01	Wind 2 (ns, $P < 0.1$), 0.008, -0.01	151	0.20
CA	Neg. Binomial	BBS Diff ($P < 0.05$), 0.07, -0.69	BBS Index (ns, $P < 0.1$), 0.08, -0.69					174	0.02
NM	Neg. Binomial	BBS Diff ($P < 0.001$), 0.06, 0.31	BBS Index ($P < 0.001$), 0.68, 0.36					141	0.21
OR	Neg. Binomial	BBS Diff ($P < 0.001$), 0.07, 12.59	BBS Index ($P < 0.001$), 0.62, 11.76					150	0.16
TX	Neg. Binomial	BBS Diff (ns, $P < 0.1$), 0.02, -0.39	BBS Index ($P < 0.001$), 0.63, 0.62	Wind 2 (ns), 0.01, -0.004				149	0.18
UT	Neg. Binomial	BBS Diff (ns), 0.002, 0.44	BBS Index ($P < 0.001$), 0.42, 0.68					165	0.07
Total	Neg. Binomial	Fledge Rate (ns, $P < 0.1$), 0.02, 1.08	BBS Diff ($P < 0.05$), 0.01, 0.23	BBS Index ($P < 0.001$), 0.65, 0.84	Air Flow ($P < 0.05$), 0.01, 0.05	Wind 1 (ns, $P < 0.1$), 0.01, 0.01	Wind 2 (ns, $P < 0.1$), 0.01, -0.01	144	0.24

The average wind direction was also rarely chosen in the models. At the 1000 mb level, wind direction was chosen for Arizona, Texas and Total, only after demographic variables were accounted for. Upon further investigation, we found that Average Wind 1 and Average Wind 2 are not significantly correlated with the number of vagrants in 1956–2013 ($y = -0.09x + 34.89$, $r^2 = 0.011$, $P = 0.28$ and $y = -0.08x + 31.31$, $r^2 = 0.007$, $P = 0.30$, respectively). Examination of residuals shows that two particular years, 2001 and 2011, carry the inclusion of these predictors in the best model. At the 900 mb level, wind direction was only chosen for California, however, California was the least-well modelled. We tested for correspondence between flight direction from Arizona to the East Coast and prevailing wind direction, and found a significant difference (Rayleigh test; $P = 0.001$); that is, our wind support analysis provided no indication that birds followed prevailing wind from Arizona to the East Coast in the three-day window prior to their arrival.

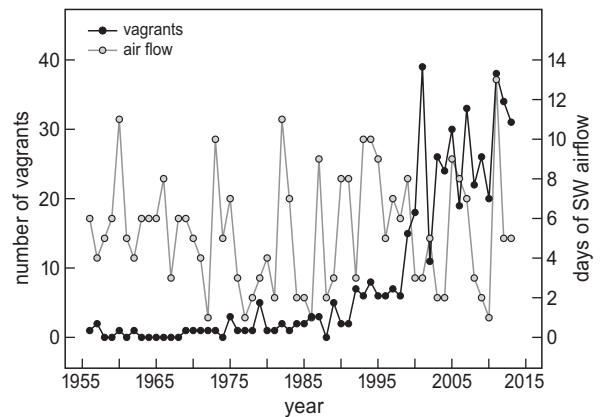


Figure 5. Number of vagrants compared to days of south-westerly airflow in 1956–2013. Days of south-westerly airflow were compiled from NOAA archives, and represent an integer estimate of days of continuous south-westerly airflow across southern North America, from Texas to the East Coast during autumn migration (1 September – 30 December).

Table 3. Model selection for eight breeding regions of the Ash-throated Flycatcher in the United States from 1989–2011 for wind directions obtained from the 900 mb level (approximately at 1000 m altitude). Models were built from the form Vagrants = Reproduction (MAPS; Fledge Rate) + Reproduction (BBS Difference) + Population Size (BBS Index) + Airflow + Average Wind Direction 1 + Average Wind Direction 2 + Average Wind Direction 3 + Error. Effect sizes ($SS_{\text{predictor}}/SS_{\text{total}}$) and parameter estimates are given after P -values. ns indicates not significant. AIC shows the value for the best model for the region.

Region	Distribution	Predictor 1 (P)	Predictor 2 (P)	Predictor 3 (P)	Predictor 4 (P)	AIC	Maximum-likelihood pseudo- R^2 (best model only)
AZ	Neg. Binomial	Fledge Rate ($P < 0.001$), 0.15, 0.72	BBS Diff ($P < 0.001$), 0.01, 0.16	BBS Index ($P < 0.001$), 0.48, 0.28	Air Flow ($P < 0.01$), 0.01, 0.08	150	0.18
CA	Neg. Binomial	BBS Diff ($P < 0.01$), 0.07, -0.89	BBS Index (ns, $P < 0.1$), 0.08, -0.66	Wind 1 ($P < 0.01$), 0.03, -0.01	Wind 3 ($P < 0.01$), 0.11, 0.01	169	0.07
NM	Neg. Binomial	BBS Diff ($P < 0.001$), 0.06, 0.30	BBS Index ($P < 0.001$), 0.68, 0.36			141	0.21
OR	Neg. Binomial	BBS Diff ($P < 0.001$), 0.07, 12.56	BBS Index ($P < 0.001$), 0.62, 11.76			150	0.16
TX	Neg. Binomial	BBS Diff (ns), 0.02, -0.39	BBS Index ($P < 0.001$), 0.63, 0.63			149	0.17
UT	Neg. Binomial	BBS Diff (ns), 0.002, 0.44	BBS Index ($P < 0.001$), 0.42, 0.68			165	0.07
Total	Neg. Binomial	Fledge Rate (ns), 0.03, 1.02	BBS Diff ($P < 0.05$), 0.002, 0.28	BBS Index ($P < 0.001$), 0.42, 0.79	Air Flow ($P < 0.05$), 0.01, 0.05	144	0.22

DISCUSSION

Our model selection showed that population size explained most of the variation in occurrence of vagrant Ash-throated Flycatchers on the East Coast of North America. In addition, reproductive indices were more frequently selected than our quantifications of airflow. For all models, the index of population size itself (BBS Index) had a larger effect than either measures of reproductive success upon vagrancy. Nevertheless, our measures of reproductive success (Fledge Rate) remained significant even after population size was factored out (Table 2, 3). Also, BBS Difference was frequently selected. The sign was positive for the core breeding range in Arizona, but negative in some other regions. We conclude that in years when larger numbers of young are produced in the core of the breeding range, larger numbers of young are seen along the east coast. This suggests that vagrancy is linked to population growth in the breeding range (Figure 6), and sometimes to external factors such as wind-driven events. Number of vagrants increase when there are more individuals available to travel.

In our models the effect of wind was always secondary in effect size to population growth. This is not to say that airflow never contributes to patterns of vagrancy or migration in passerines. In some years, an increased number of days of south-westerly airflow did impact numbers of vagrants. Especially the year 2011 added support for airflow to our models, when a high number of days with south-westerly airflow coincided with the second largest number of Ash-throated Flycatchers in the east (Figure 5). There was also a significant effect of wind upon vagrancy for Arizona, Texas and Total (Table 2, 3), after reproductive variables were accounted for. Our interpretation of airflow in these instances is that, when eastwards dispersal is already underway due to elevated population growth, tailwind sometimes contributes to vagrancy, but is not essential for vagrancy to occur (Williamson 1963).

2011 was also an interesting year in that there were a record number of vagrant Ash-throated Flycatchers on the east coast between September and early October, a month earlier than the usual November peak. All individuals seen were juvenile birds that had not yet undergone their post-fledging moult. Farnsworth & Iliff (2012) hypothesize that these early movements may have resulted from a severe drought that impacted Texas, the Great Plains and the southwest in October of that year, causing juveniles to leave moult-migration grounds early in an attempt to find suitable regions to moult. This hypothesis alludes to the complexity of

movements in passerines, and other variables that may have small effects on individual trends. Our data suggest that the high number of vagrant individuals in 2011 was also driven by a good breeding year (high BBS difference), but the earlier timing of individuals may have resulted from poor environmental conditions.

The variation in abundance of other western vagrant birds to Massachusetts supports the role of population dynamics in driving the frequency of vagrancy among species (Figure 3). It is difficult to explain these temporal trajectories on the basis of weather, since favourable winds for causing eastwards movement of one western species ought to be favourable, to some extent, for the other species as well, even allowing for interspecific differences in migratory peaks. This is not what the data show; each species has its own pattern of variation through time, and for each species, that variation is significantly related to population growth (Veit 1997, 2000).

An emerging phenomenon from previous vagrant analyses is the prevalence of a spatial association between vagrancy and reproductive success. Numbers of vagrant individuals are correlated with regions of high population growth within the breeding range (Veit 1997, 2000). For example, the number of vagrant Western Kingbirds in Massachusetts each year is significantly correlated with the reproductive success of Western Kingbirds on the eastern Great Plains in the same year, but less correlated with reproductive success elsewhere (Veit 2000). Similarly, for Ash-throated Flycatchers, model analysis revealed that the number of vagrants each year was significantly correlated with Fledge Rate in Arizona (Figure 6), but not for any other

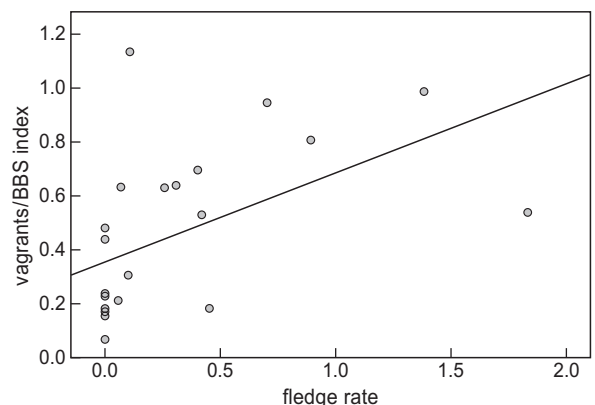


Figure 6. Vagrant Ash-throated Flycatchers divided by BBS Index (population size) versus Fledge Rate. Data for Arizona (see Tables 2 and 3). $r^2 = 0.23$, $P = 0.012$. Years with higher production of young were correlated with higher numbers of vagrants on the east coast.

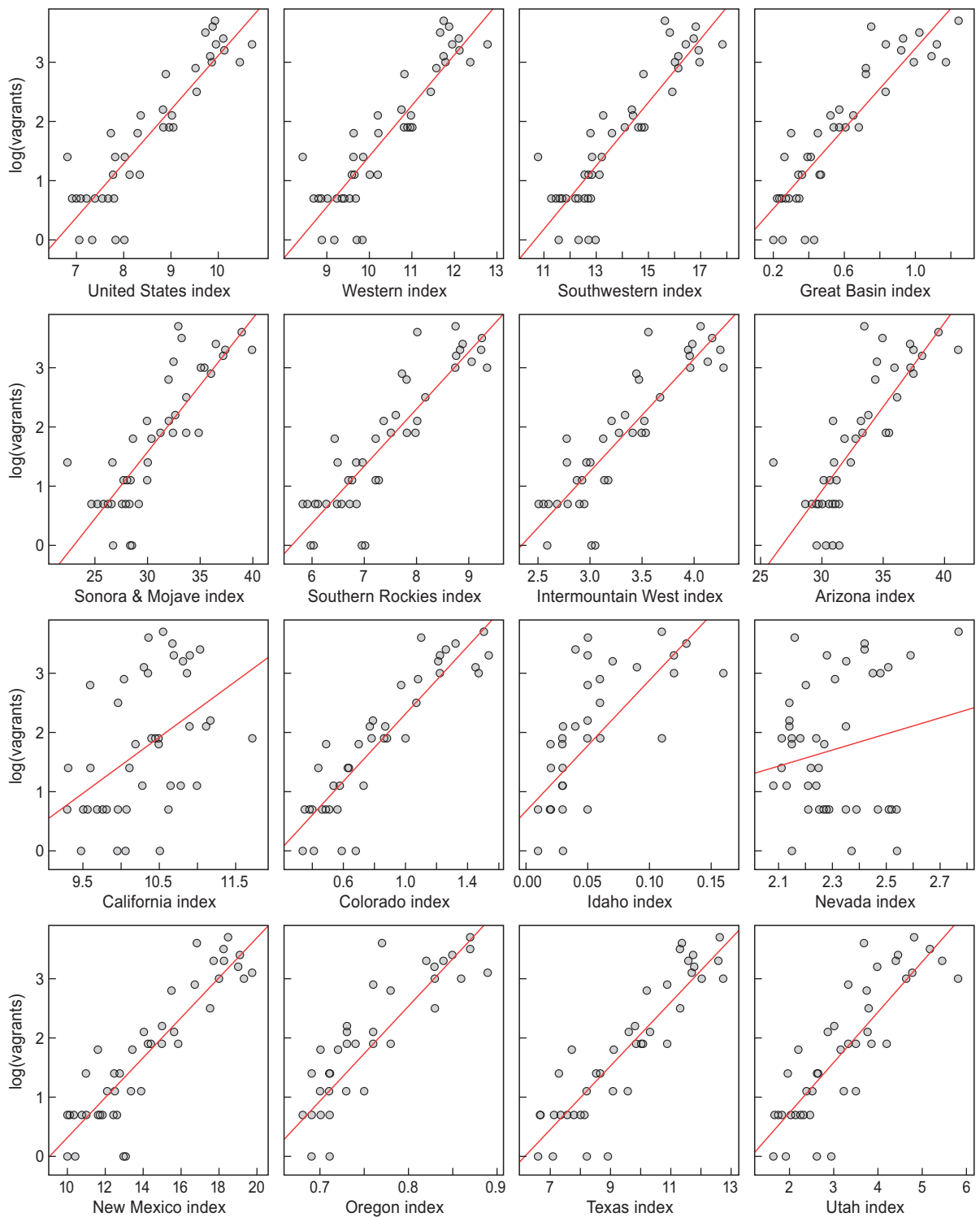


Figure 7. Linear relationships between BBS Index in year $t + 1$ and number of vagrants to the East Coast were analysed for the 16 study regions outlined in Figure 6, in 1968–2012. A significant relationship between the log-transformed number of vagrants in year t and the annual index of birds in year t was present for each study region (with the exception of Nevada, $P = 0.214$; see Table 1), indicating the importance of the growing population in its western core range in explaining the incidence of vagrants in the east.

state (Table 2, 3). Arizona is the abundance centroid of the entire breeding population (Figure 1), and has a relatively high abundance of Ash-throated Flycatchers compared to other southwestern states within the breeding range (Figure 7). It seems reasonable then that a substantial fraction of vagrant flycatchers is produced in Arizona, rather than in areas in the breeding range with lower levels of population growth (i.e. Texas and other surrounding states). Birds from Arizona are possibly emigrating to the surrounding areas, explaining the strong correlation found between BBS Index and vagrancy for the other study regions (Table 1), but not between Fledge Rate and vagrancy.

The limited support for prevailing winds in explaining vagrancy indicated by our models is consistent with the lack of support of wind-driven vagrancy found by Thorup (1998) for *Phylloscopus* warblers in Western Europe, and, more directly, with results of Van Impe & Derasse (1994) that show that inter-annual variability in westwards displacement of Yellow-browed Warblers *P. inornatus* and Pallas' Warblers *P. proregulus* to Europe is not correlated with predominant easterly airflow. Although weather events have been proposed to have displaced birds (McLaren 1981, Brinkley 1999, Mlodinow *et al.* 1999, McNair & Post 2001, McLaren *et al.* 2000, 2006, Newton 2008, Kosciuch *et al.* 2006, Hameed *et al.* 2009), our analysis shows that south-westerly airflow is of secondary importance after population growth. Furthermore, if displacement of Ash-throated Flycatchers to the East Coast was primarily driven by patterns of wind circulation, then these birds would have appeared off and on throughout the 20th century, rather than as a major incursion coincident with their population growth and range expansion beginning in the 1960s (Table S1). Nevertheless, atmospheric circulation is complex, and more spatially explicit modelling of vagrant trajectories might be able to explain more variation.

One puzzling aspect of vagrancy by Ash-throated Flycatchers to the U.S. East Coast is that peak occurrence is during mid-November, at least three months after they normally finish breeding. The species moults its flight feathers after leaving the breeding grounds and completes this moult by early November, the timing of which corresponds to peak appearance on the East Coast (Butler *et al.* 2006).

Vagrants, on average, produce more offspring than non-vagrants under certain conditions as suggested by Baker (1978) and supported by Veit & Lewis (1996), Phillips *et al.* (2008) and Barbraud *et al.* (2003), and is amply demonstrated by the spread of invading species (Hengeveld 1989). Range expansions have resulted

from these vagrant events (Veit & Lewis 1996, Lovette *et al.* 1999, Boertmann 2008, Phillips 2000, Buckley *et al.* 2009, Nisbet *et al.* 2013, Veit *et al.* 2016). This process is the basic means by which birds expand their ranges, and how oceanic islands are colonized, as Diamond's 'supertramps' (Diamond 1974) are essentially vagrants (Veit & Lewis 1996, Veit *et al.* 2016).

Our analysis of vagrancy of the Ash-throated Flycatcher highlights the potential for using these data to understand population dynamics of birds, and supports the notion that population growth strongly affects vagrancy and consequent exploration, in the sense of Baker (1978). Molecular studies (Joseph *et al.* 2004) and recent observations (Veit *et al.* 2016) support the role of vagrancy in the colonization of Caribbean islands, including colonization and consequent speciation by *Myiarchus* flycatchers. These processes are likely to become increasingly important as the earth's climate changes. Incorporation of vagrant data into future studies on bird populations will allow for a better understanding of long-distance dispersal in birds.

Our current analysis was constrained by the data available, and did not allow us to account for variables that would have required information on individual tracks of birds. Very little is known about the flight speed, number of stopovers or directness of flight of any Ash-throated Flycatcher travelling from its breeding range in southwestern North America to the East Coast. Thus, our model relied on a series of assumptions: (1) detection date was arrival date, (2) continuous flight without stopovers, and (3) a single point of origin for all vagrants. Though we could not definitively disentangle effects of wind on vagrant individuals (i.e. we cannot relate individual flight directly to airflow), our model allowed us to test the hypothesis that eastward movement of Ash-throated Flycatchers results from the occurrence of south-westerly winds during the 72 hours over which these weather conditions persist, with the justification that numerous past authors have postulated that weather conditions immediately preceding the arrival of vagrants on the east coast have been responsible for bringing the birds there (Bagg 1970, Able 1972, 1974, Heil 1981, Brinkley & Lehman 2003, Sullivan & Wood 2005, Farnsworth & Iliff 2012). In other words, our models relied on the approximation from theoretical support (Bagg *et al.*) that these birds are entrained in broadscale south-westerly airflow across the continent, and, by implication, make the trip in 3–4 days, or less.

Our models suggest that eastwards-moving Ash-throated Flycatchers can get entrained by south-westerly winds, and this entrainment is reflected by the

inclusion of three wind variables within our best models for Arizona and the breeding range (Total; Table 2, 3). Nevertheless, the impacts of long-term population growth (BBS Index) is consistently larger, and reproduction (Fledge Rate and BBS Difference) have effect sizes that are similar, and in some cases even larger (cf. models Arizona region). The recent (since 1990) increase of Ash-throated Flycatchers to the East Coast is driven primarily by both long-term and short-term population growth, and this eastwards movement is enhanced through occurrence of south-westerly winds. Understanding the link between vagrancy and population growth is important to the consideration of how habitats can be most appropriately preserved, taking into consideration the proclivity of birds to travel as vagrants and the adaptive value of vagrancy (Jiguet & Barbet-Massin 2013).

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SAMENVATTING

Het begrijpen van de oorzaken van zwervende vogels onder trekvogelsoorten is van toenemend belang nu klimaatverandering de overleving van sommige soorten onder druk zet. Zwerven kan er voor zorgen dat populaties beschermd zijn tegen veranderingen in de omgeving door uitbreiding van hun geografische verspreiding. Om onderliggende oorzaken van dit zwerven te onderzoeken, analyseerden we gegevens over het voorkomen van dwaalgasten van de Grijskeeltiran *Myiarchus cinerascens* aan de oostkust van Noord-Amerika en populatiegroei binnen hun broedgebied, om te testen in welke mate zwerven wordt aangestuurd door populatiegroei en de productie van jongen die een sterkere inclinatie hebben om nieuwe plekken te verkennen. We hebben ook getest in welke mate zwerven gerelateerd is aan drift door heersende windrichtingen, door analyse van synoptische weerkaarten van Noord-Amerika. Onze analyses probeerden te kwantificeren welke factoren het meest van invloed zijn op de variatie in het aantal Grijskeeltirannen die de oostkust van Noord-Amerika bereiken. We hebben waarnemingen verkregen van zwervers uit 'North American Birds', populatiegegevens van de North American Breeding Bird Survey (BBS), reproductief succes van Monitoring Avian Productivity en Survivorship (MAPS) databases en synoptische weerkaarten van de NOAA NCEP North-American Regional Reanalysis database. We ontdekten dat zwerven voornamelijk werd verklaard door de groeiende broedpopulatie zoals geïndexeerd door BBS-gegevens. Bovendien vonden we significante effecten van de jaarlijkse productie van jongen binnen het broedareaal, evenals drie maten van luchtcirculatie in Noord-Amerika. Onze modellen wezen op een belangrijke rol van de populatiegroei, met bijkomende effecten van reproductief succes en overheersende luchtstroming die het voorkomen van zwerven beïnvloedt. Jaren met hoog reproductief succes brengen grotere aantallen Grijskeeltirannen naar het oosten, en dit aantal wordt versterkt onder bepaalde gunstige weersomstandigheden.

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SUPPLEMENTARY MATERIAL

Table S1. All records of vagrant Ash-throated Flycatchers *Myiarchus cinerascens* extracted from ‘North American Birds’, between Newfoundland and Florida from August to January, 1956 to 2014¹.

Year	Date	State	Location	Number	Evidence	Annual total
1956	Oct 21	FL	Pensacola	1	Specimen	1
1957	Nov 22	MD	Monkton	1		
1957	Dec 26	VA	Virginia Beach	1		2
1960	Sep 15	RI	Block Island	1	Specimen	1
1962	Dec 04	MD	Emmitsburg	1		1
1969	Dec 13	VA	Chincoteague	1		1
1970	Nov 22	NY	Larchmont	1	Photographed ²	1
1971	Sep 17	ME	Appledore Island	1	Photographed	1
1972	Nov 25	MA	Gloucester	1	Photographed	1
1973	Dec 05	NY	Ridge	1	Specimen	1
1975	Oct 20	FL	Santa Rosa County	1		
1975	Nov 21	ME	Bar Harbor	1		
1975	Nov 22	MA	Orleans	1		3
1976	Sep 25	RI	Block Island	1		1
1977	Oct 10	Quebec	Franquelin	1		1
1978	Dec 27	VA	Cheriton	1	Photographed	1
1979	Jan 20	FL	Miami Beach	1		
1979	Nov 12	RI	East Providence	1	Photographed	
1979	Dec 01	MA	Cambridge	1	Photographed	
1979	Dec 09	VA	Haymarket	1		
1979	Dec 30	VA	Kiptopeke	1	Photographed	5
1980	Nov 10	MA	Wellesley	1		1
1981	Sep 04	NC	Cape Hatteras	1		1
1982	Nov 14	Nova Scotia	Brier Island	1		
1982	Dec 27	MA	Magnolia	1		2
1983	Oct 05	VA	Dismal Swamp	1		1
1984	Nov 21	NY	Jones Beach	1	Photographed	
1984	Dec 09	NJ	Assunpink	1	Photographed	2
1985	Nov 10	New Brunswick	Grand Manan Island	1		
1985	Nov 24	NJ	Cape May	1	Photographed	2
1986	Sep 13	VA	Chincoteague	1		
1986	Dec 12	FL	Jacksonville	1	Photographed	
1987	Oct 31	NJ	Brigantine	1		
1987	Dec 19	VA	Onancock	1	Photographed	3
1989	Jan 19	FL	Delay Beach	1	Photographed	
1989	Nov 05	MA	Martha's Vineyard	1	Photographed	
1989	Nov 11	NJ	Cape May	1		
1989	Nov 17	NJ	Cape May	1		
1989	Dec 17	VA	Williamsburg	1	Photographed	5
1990	Dec 29	FL	Lake Jessup	2	Specimen (1)	2
1991	Nov 04	ME	Somerville	1		
1991	Nov 15	MA	Wellfleet	1		2
1992	Oct 24	NY	Fort Tilden	1		
1992	Nov 09	NJ	Cape May	1		
1992	Nov 14	New Brunswick	Alma	1	Photographed	
1992	Nov 28	NJ	Cape May	1	Photographed	
1992	Dec 04	VA	Blackwater	1	Photographed	
1992	Dec 20	CT	Stamford	1	Photographed	
1992	Dec 27	VA	Cape Charles	1		7
1993	Early Jan	FL	Honeymoon Island	2	Photographed	
1993	Nov 02	NY	Jones Beach	1	Photographed	

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
1993	Nov 07	MA	Arlington	1	Photographed	6
1993	Dec 13	NJ	Cape May	1		
1993	Dec 19	FL	Jacksonville	1		
1994	Sep 24	NC	Pea Island	1	Photographed	8
1994	Oct 23	NY	Jones Beach	1		
1994	Nov 07	VA	Eastern Shore	1		
1994	Nov 08	MA	Sandwich	1		8
1994	Nov 08	NY	Robert Moses State Park	1	Photographed	
1994	Dec 02	FL	Turkey Creek	1	Photographed	
1994	Dec 06	FL	Paynes Prairie	1	Photographed	6
1994	Dec 31	FL	Seminole	1		
1995	Oct 13	FL	Turkey Creek	1		
1995	Oct 23	RI	Barrington	1	Photographed	6
1995	Oct 25	NJ	Cape May	1	Photographed	
1995	Nov 23	FL	St. Marks	1		
1995	Nov 28	NJ	Cape May	1		6
1995	Nov 28	FL	Tomoka	1		
1996	Nov 10	NY	Long Island	1	Photographed	
1996	Nov 10	NY	Long Island	1	Photographed	6
1996	Nov 10	NY	Long Island	1	Photographed	
1996	Nov 17	FL	Gainesville	1		
1996	Nov 30	CT	Old Lyme	1		6
1997	Early Jan	NJ	Long Branch	1		
1997	Sep 14	MA	Monomoy	1	Photographed	
1997	Nov 12	NJ	Cape May	1	Photographed	Photographed, Videotaped
1997	Nov 23	MA	South Darmouth	1		
1997	Nov 24	PA	Northhampton	1		
1997	Nov 26	NJ	Cape May	1		7
1997	Dec 26	NJ	Palmyra	1		
1998	Nov 13	NJ	Cape May	1		
1998	Nov 28	MA	Cambridge	1		6
1998	Late Nov	NH	Lyme	1		
1998	Dec 10	MA	Edgartown	1		
1998	Dec 12	ME	Westbrook	1		6
1998	Dec 20	MA	Sandwich	1		
1999	Jan 02	FL	Bald Point	1		
1999	Nov 05	MA	Westport	1		1
1999	Nov 07	NC	Bodie Island Lighthouse	1		
1999	Nov 10	FL	Tallahassee	1		
1999	Nov 20	NY	Fort Tilden	1		15
1999	Nov	NJ	Cape May	1		
1999	Nov	NJ	Cape May	1		
1999	Nov	NJ	Cape May	1		Photographed
1999	Dec 12	NC	Pea Island	1		
1999	Dec 26	FL	Brooker Creek	1		
1999	Dec	FL	Lake Apopka	5	Photographed	15
2000	Jan 03	FL	Palm Beach	1		
2000	Jan 08	GA	Quitman	1	Photographed	
2000	Jan 19	FL	Ocklawaha Prairie	1		4
2000	autumn	DE	Coastal Hudson-DE	4		
2000	Sep 05	NY	Jamaica Bay Wildlife Refuge	1		
2000	Oct 31	FL	Indian River	1		1
2000	Nov 25	FL	Lake Jackson	1		

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
2000	Dec 03	FL	Paines Prairie	1		
2000	Dec 16	GA	St. Catherine's Island	1		
2000	Dec 28	PA	Lancaster	1		
2000	Winter	FL	Lake Apopka	4		18
2001	Aug 30	MA	Belmont	1		
2001	Sep 29	MD	Assateague Island	1	Photographed	
2001	Oct 06	NH	Concord	1	Photographed	
2001	Oct 26	RI	Middletown	1	Photographed	
2001	Oct 27	NJ	Cape May	1		
2001	Oct 30	NJ	Sandy Hook	1		
2001	Nov 01	FL	Lake Apopka	5		
2001	Nov 02	NJ	Cape May	1		
2001	Nov 04	D.C.	Little Island City Park	1	Banded	
2001	Nov 11	D.C.	Kenilworth Park	1	Photographed	
2001	Nov 15	MA	Gloucester	1	Photographed	
2001	Nov 18	NJ	Brigantine	1		
2001	Nov 22	NY	Queens	1		
2001	Nov 24	MA	Cohasset	1		
2001	Nov 25	New Brunswick	Jemseg	1		
2001	Nov 26	NJ	Bedminster	1	Photographed	
2001	Dec 01	NY	Fort Tilden	1		
2001	Dec 02	New Brunswick	Westfield	1		
2001	Dec 02	New Brunswick	Alma	1		
2001	Dec 04	NY	Northville	1		
2001	Dec 15	ME	Bath	1		
2001	Dec 16	NC	Alligator River	1	Photographed	
2001	Dec 20	New Brunswick	Sackville	1		
2001	Dec 21	New Brunswick	Lower Jemseg	1		
2001	Dec 22	MA	Martha's Vineyard	1		
2001	Dec 22	NY	Central Suffolk CBC	1		
2001	Dec	FL	Alachua	1		
2001	Dec	FL	Seminole	1	Specimen	
2001	Dec	FL	Hendry	1		
2001	Dec	FL	Lake	2		
2001	Dec	FL	Lake Apopka	4 more*		39
2002	Nov 16	NJ	Cape May	1		
2002	Nov 21	NY	Jones Beach	1		
2002	Nov 23	NJ	Cape May	1		
2002	Nov 25	NY	Breezy Point	1		
2002	Dec	FL	Leon	1		
2002	Dec	FL	Alachua	4		
2002	Dec	FL	Lake Apopka	2		11
2003	Oct 11	New Brunswick	Pointe Verte	1		
2003	Oct 19	FL	Bald Point	1		
2003	Nov 05	FL	Lake Apopka	1		
2003	Nov 05	FL	Paynes Prairie	2		
2003	Nov 07	MA	Stoneham	1		
2003	Nov 08	NC	Pea Island	1		
2003	Nov 10	NJ	Cape May	1		
2003	Nov 10	FL	San Felasco Hammock	1		
2003	Nov 11	MA	Melrose	1		
2003	Nov 18	New Brunswick	New River Beach	1		
2003	Nov 18	MA	Martha's Vineyard	1		
2003	Nov 22	Nova Scotia	St. Pierre et Miquelon	1	Videotaped	

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
2003	Nov 27	FL	Emeralda Marsh	1		
2003	Nov 30	NC	North River	1		
2003	Dec 03	MD	Baltimore	1		
2003	Dec 04	FL	Guana River	1		
2003	Dec	FL	Lake Apopka	9		26
2004	Nov 01	NJ	Cape May	1		
2004	Nov 06	VA	Eastern Shore	1	Photographed	
2004	Nov 14	FL	Lake Apopka	1		
2004	Nov 17	NJ	Cape May	1		
2004	Nov 20	VA	Craney	1		
2004	Nov 20	Quebec	Bois-Deliessee	1	Photographed	
2004	Nov 21	FL	Paynes Prairie	1		
2004	Nov 23	VA	Chesapeake Bay Bridge Tunnel	1	Photographed	
2004	Nov 23	NY	Prospect Park	1		
2004	Nov 26	MA	Halibut Point	1	Photographed	
2004	Nov 29	NJ	Cape May	1		
2004	Dec 03	NY	Hamlin Beach	1	Photographed	
2004	Dec 05	NY	Prospect Park	1		
2004	Dec 05	NC	North River Farms	1		
2004	Dec 19	NC	Fort Macon	1		
2004	Dec	FL	Lake Apopka	3		
2004	Dec	FL	Alachua	2		
2004	Dec	FL	Brecard	2		
2004	Dec	FL	Pinellas	1		24
2005	Jan 07	VA	Richmond	1	Photographed	
2005	Jan 10	VA	Dutchcap	1	Photographed	
2005	Jan 28	NC	Pocosin Lake	1		
2005	Oct 12	FL	Lake Apopka	1		
2005	Oct 25	FL	Tavernier	1		
2005	Nov 02	FL	Fort Walton Beach	1		
2005	Nov 06	MA	Plum Island	1	Photographed	
2005	Nov 12	NJ	Assunpink	1		
2005	Nov 13	NJ	Cape May	1		
2005	Nov 19	NJ	Verona	1		
2005	Nov 19	VA	Kiptopeke	1		
2005	Nov 20	New Brunswick	Cape Jourimain	1		
2005	Nov 25	FL	Merritt	1		
2005	Nov 29	NJ	Cape May	1		
2005	Dec 23	FL	Lake Apopka	12		
2005	Dec 27	NC	Cape Hatteras	1	Photographed	
2005	Dec	FL	Seminole	1		
2005	Dec	FL	Santa Rosa	1		
2005	Dec	FL	Okaloosa	1		30
2006	Jan 01	NC	Alligator River	1		
2006	Jan 07	NC	North River Farms	1		
2006	Oct 18	FL	Lake Apopka	1		
2006	Oct 25	NJ	Cape May	1		
2006	Oct 31	FL	St. Marks	1		
2006	Nov 01	FL	Cedar Key	1		
2006	Nov 23	FL	Lantana Landing	1		
2006	Nov 27	FL	Paynes Prairie	1		
2006	Nov 28	ME	Saco	1	Photographed	
2006	Dec 02	NJ	Marlton	1		
2006	Dec 04	NY	Central Park	1		

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
2006	Dec 09	MA	Annisquam	1	Photographed	
2006	Dec 16	GA	Newton	1		
2006	Dec 17	CT	Stamford	1	Photographed	
2006	Dec 17	NC	Newport	1		
2006	Dec 17	NC	Nassawaddox	1	Photographed	
2006	Dec 17	FL	Lake Apopka	1		
2006	Dec 19	MA	East Orleans	1		
2006	Dec 30	NJ	Stockton	1	Photographed	19
2007	Feb 16	GA	Baker	1	Photographed	
2007	Nov 01	FL	Fort Walton Beach	1		
2007	Nov 07	FL	Lake Apopka	1		
2007	Nov 08	MA	Carlisle	1	Photographed	
2007	Nov 09	FL	Paynes Prairie	1		
2007	Nov 13	NC	Brunswick	1		
2007	Nov 17	FL	Lake City	1		
2007	Nov 21	MD	Pig Point	1		
2007	Dec 05	FL	Tallahassee	1		
2007	Dec 08	FL	Osteen	1		
2007	Dec 16	FL	Paynes Prairie	2		
2007	Dec 29	DE	Rehoboth	1	Photographed	
2007	Dec	DE	Hudson-DE	5		
2007	Dec	FL	Lake Apopka	15		33
2008	Jan 07	VA	Montgomery	1		
2008	Nov 09	FL	Bald Point	1	Photographed	
2008	Nov 11	NC	Lake Mattamuskeet	1		
2008	Nov 15	MD	Ocean City	1	Photographed	
2008	Nov 23	FL	Lake Apopka	4		
2008	Nov 28	FL	Pelican Island	1	Photographed	
2008	Nov 29	NJ	Cape May	1		
2008	Nov 29	NJ	Thompson Park	1		
2008	Dec 03	DE	Rehoboth	1		
2008	Dec 03	VA	Occoquan	1		
2008	Dec 05	FL	Merritt Island	1		
2008	Dec 14	FL	Paynes Prairie	1		
2008	Dec 15	FL	Lake	1		
2008	Dec 15	NC	New Bern	1		
2008	Dec 22	NJ	West Cape May	1		
2008	Dec 28	MD	Worcester	1		
2008	Dec 30	NC	Alligator River	1		22
2008	Dec	FL	Lake Apopka	2		
2009	Jan 03	FL	Paynes Prairie	2		
2009	Jan 29	FL	River Lakes	1	Photographed	
2009	Feb 26	FL	Delray Beach	1		
2009	Oct 19	GA	Tattnall	1	Photographed	
2009	Oct 29	FL	Gulf Breeze	1		
2009	Nov 01	VA	Kiptopeke	1		
2009	Nov 01	NC	Carteret	1		
2009	Nov 01	FL	Fort Pickens	1		
2009	Nov 14	DE	Prime Hook	1		
2009	Nov 14	NY	Ozone Park	1		
2009	Nov 14	Newfoundland	Ferryland	1	Photographed	
2009	Dec 06	FL	Lake Mattamuskeet	1	Photographed	
2009	Dec 09	NJ	Sandy Hook	1		
2009	Dec 13	FL	Gulf Breeze	1		

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
2009	Dec 13	FL	Lake	1		
2009	Dec 17	FL	Hamilton	1		
2009	Dec 20	FL	Lakeland	1		
2009	Dec 21	FL	Merritt Island	1		
2009	Dec 27	GA	Okefenokee	1	Photographed	
2009	Dec 31	VA	Virginia Beach	2	Photographed	
2009	Dec	FL	Lake Apopka	4		26
2010	Jan 15	GA	Savannah Spoil Site	1		
2010	Jan 19	FL	Viera Wetlands	1		
2010	Oct 21	FL	Fort Pickens	1		
2010	Oct 23	FL	Fort Walton Beach	1		
2010	Oct 29	NJ	Cape May	1		
2010	Oct 29	FL	St. George Island	1		
2010	Nov 06	FL	Boyd Hill	1		
2010	Nov 09	NJ	Cape May	1		
2010	Nov 13	Nova Scotia	Canso	1	Photographed	
2010	Nov 14	FL	Lake Apopka	2		
2010	Nov 18	Nova Scotia	Antigonish	1	Photographed	
2010	Nov 18	VA	Kiptopeke	1		
2010	Nov 19	FL	Paynes Prairie	1		
2010	Nov 25	NJ	Cape May	1		
2010	Nov 25	NY	Jones Beach	1		
2010	Nov 26	NC	Winston-Salem	1		
2010	Nov 27	VA	Assateague	1		
2010	Dec 25	NC	Alligator River	1		
2010	Dec 29	FL	Escambia	1		20
2011	Sep–Nov	FL	Florida	14		
2011	Sep 27	MA	Plum Island	1		
2011	Oct 08	MA	Plum Island	1	Banded	
2011	Oct 14	NC	Wrightsville	1		
2011	Oct 23	ME	Monhegan	1		
2011	Oct	MA	Massachusetts	3		
2011	Nov 09	MD	Queen Anne's	1	Banded	
2011	Nov 11	MA	Eastham	1	Photographed	
2011	Nov 11	NC	Alligator River	1		
2011	Nov 13–30	DE	Hudson-DE	6		
2011	Nov 24	ME	Waldo	1	Taken to Rehab Center	
2011	Nov 25	MA	Nantucket	1	Photographed	
2011	Nov 30	MD	Queen Anne's	1	Banded	
2011	Nov	RI	Newport	1		
2011	Dec 08	NJ	Cape May	1		
2011	Dec 08	NJ	Monmouth	1		
2011	Dec 14	NC	Lake Phelps	1		
2011	Dec 20	NJ	Thompson Park	1		38
2012	Jan 19	NC	Mattamuskeet	1		
2012	Oct 11	FL	Florida	11		
2012	Oct 30	Newfoundland	Bonavista	1		
2012	Nov 03	MA	Squantum	1		
2012	Nov 04	NC	Pender	1		
2012	Nov 07	NC	Alligator River	1		
2012	Nov 12	CT	Lighthouse Point	1		
2012	Nov 24	NJ	Cape May	1		
2012	Nov 27	NC	Craven	1		

Table S1. Continued.

Year	Date	State	Location	Number	Evidence	Annual total
2012	Dec 02	NJ	Burlington	1		
2012	Dec 02	NC	Carteret	1		
2012	Dec 08	VA	Hopewell	1	Photographed	
2012	Dec 16	MA	Gloucester	1		
2012	Dec 27	NC	Washington	1		
2012	Dec 29	GA	Charlton	1	Photographed	
2012	Dec	FL	Florida	9		34
2013	Jan 03	FL	Lake	1		
2013	Jan 04	FL	Volusia	1		
2013	Jan 18	FL	Citrus	1		
2013	Jan 19	FL	Brevard	1		
2013	Feb 01	FL	St. Lucie	1		
2013	Oct 21	ME	Monhegan	1	Photographed	
2013	Nov 04	GA	Kiowah	1	Photographed	
2013	Nov 15	VA	Kiptopeke	1		
2013	Nov 16	NY	Jones Beach	1		
2013	Nov	FL	Florida	7		
2013	Dec 03	FL	Pasco	1		
2013	Dec 15	NC	Ogden	1		
2013	Dec 15	FL	Paynes Prairie	1		
2013	Dec 22	NC	Alligator River	2		
2013	Dec 31	NJ	Cape May	1		
2013	Dec	FL	Lape Apopka	9		31
2014	Jan 09	NC	Washington	1		
2014	Jan 11	VA	Hopewell	1		
2014	Jan 18	GA	Turner	1		
2014	Jan	VA	Mitchell	2		
2014	Oct 15	FL	Fort Pickens	1		
2014	Nov 01	VA	Roanoke	1		
2014	Nov 01	FL	Fort Walton Beach	1		
2014	Nov 02	FL	St. George Island	1		
2014	Nov 05	RI	Sachuest Point NWR	1		
2014	Nov 08	MA	Harwich	1		
2014	Nov 08	FL	Brevard	1		
2014	Nov 10	FL	Gulf Breeze	1		
2014	Nov 11	FL	Pasco	1		
2014	Nov 22	MA	Plymouth	1		
2014	Nov 24	MA	Milton	1		
2014	Nov 29	GA	Miller	1		
2014	Dec 14	Nova Scotia	Dartmouth	1		
2014	Dec	GA	Okefenokee	1		
2014	Dec	FL	Florida	13		32
				Total		509

¹All these records are filtered through North American Birds editors who use all available information to identify separate individuals, including distance between sightings.

²Some records in this table are not listed as having evidence. However, rarities committees hold additional photos, and others are accessible via eBird.

*Of the birds seen in Lake Apopka that year, four more birds were recorded for the total autumn record.

Table S2. Model selection for eight breeding regions of the Ash-throated Flycatcher in the United States in 1989–2011. Wind directions were obtained from the 1000 mb level. Models were built from the form Vagrants = Reproduction (MAPS; Fledge Rate) + Reproduction (BBS Difference) + Population Size (BBS Index) + Airflow + Average Wind Direction 1 + Average Wind Direction 2 + Average Wind Direction 3 + Error. ns indicates not significant. AIC shows the value for the best model for the region.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-pseudo- <i>R</i> ² (best model only)
AZ	Neg. Binomial	Fledge Rate (<i>P</i> < 0.001)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.01)	Wind 1 (ns)	Wind 2 (ns, <i>P</i> < 0.1)	Wind 3 (ns)	152.59	1.97	-68.29	0.20
		Fledge Rate (<i>P</i> < 0.001)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.01)	Wind 1 (ns)	Wind 2 (ns, <i>P</i> < 0.1)		150.62	0.00	-68.31	0.20
	Poisson	Fledge Rate (<i>P</i> < 0.001)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.05)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (ns)	159.18	8.56	-71.59	0.50
		Fledge Rate (<i>P</i> < 0.001)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.05)	Wind 2 (<i>P</i> < 0.05)		157.31	6.69	-71.65	0.50
CA	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (ns, <i>P</i> < 0.1)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	181.09	7.03	-82.55	0.04
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.05)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)		179.16	5.10	-82.58	0.04
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (ns, <i>P</i> < 0.1)	Air Flow (ns)	Wind 2 (ns)			177.49	3.43	-82.75	0.04
		BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.05)	Air Flow (ns)	Wind 2 (ns)				175.77	1.71	-82.88	0.03
	Poisson	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.05)	Wind 2 (ns)					174.29	0.23	-83.15	0.03
		BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.05)	BBS Index (ns, <i>P</i> < 0.1)					174.06	0.00	-84.03	0.02
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns, <i>P</i> < 0.1)	263.04	88.98	-123.52	0.14
NM	Neg. Binomial	Fledge Rate (ns)	BBS Index (<i>P</i> < 0.001)	BBS Diff (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 2 (ns, <i>P</i> < 0.1)	Wind 3 (ns)		261.31	86.98	-123.65	0.14
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	149.90	8.35	-66.95	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)		147.90	6.65	-66.95	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)			145.92	4.67	-66.96	0.22

Table S2. Continued.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo- <i>R</i> ² (best model only)
OR	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)				143.95	2.70	-66.98	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)					142.22	0.97	-67.11	0.22
		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						141.25	0.00	-67.43	0.21
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	155.38	14.13	-69.69	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 3 (ns)		153.38	12.13	-69.69	0.52
		Fledge Rate (ns)	BBS Diff BBS Index (<i>P</i> < 0.001)	Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 3 (ns)			151.42	10.17	-69.71	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 3 (ns)				149.50	8.25	-69.75	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)					147.68	6.43	-69.84	0.52
		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						147.65	6.40	-70.82	0.51
Poisson	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	157.28	6.90	-70.64	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)		155.30	4.92	-70.65	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)	Wind 3 (ns)			153.31	2.93	-70.66	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)				151.44	1.06	-70.72	0.17
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)					150.66	0.28	-71.33	0.17
		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						150.38	0.00	-72.19	0.16
		Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	170.32	19.94	-77.16	0.46

Table S2. Continued.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo- <i>R</i> ² (best model only)
TX	Neg. Binomial	Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)		168.32	17.94	-77.16	0.46
		Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)			166.32	15.94	-77.16	0.46
		Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)				164.36	13.98	-77.18	0.46
		Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)				163.72	13.34	-77.86	0.46
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)								
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	154.86	6.50	-66.43	0.19
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)		152.90	4.54	-66.45	0.19
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)	Wind 3 (ns)			150.95	2.59	-66.48	0.19
		BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)	Wind 3 (ns)				149.12	0.76	-69.56	0.19
		BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)					148.36	0.00	-70.18	0.18
	Poisson	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (<i>P</i> < 0.05)	168.61	20.25	-76.31	0.47
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (<i>P</i> < 0.05)		166.61	18.25	-76.31	0.47
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns, <i>P</i> < 0.1)	Wind 3 (<i>P</i> < 0.05)			165.11	16.75	-76.56	0.47
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (<i>P</i> < 0.05)				163.40	15.04	-76.70	0.47
UT	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	170.88	5.72	-77.44	0.10
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)		168.90	3.74	-77.45	0.10
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)	Wind 3 (ns)			167.19	2.03	-77.59	0.09
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 2 (ns)	Wind 3 (ns)						

Table S2. Continued.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo- <i>R</i> ² (best model only)
Poisson	BBS Diff (<i>ns</i> , <i>P</i> < 0.1)		BBS Index (<i>P</i> < 0.001)	Wind 2 (<i>ns</i>)	Wind 3 (<i>ns</i>)				166.32	1.16	-78.16	0.09
	BBS Diff (<i>ns</i> , <i>P</i> < 0.1)		BBS Index (<i>P</i> < 0.001)	Wind 3 (<i>ns</i>)					165.50	0.34	-78.75	0.08
	BBS Diff (<i>ns</i>)		BBS Index (<i>P</i> < 0.001)						165.16	0.00	-79.58	0.07
	Fledge Rate (<i>P</i> < 0.5)		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>ns</i>)	Wind 1 (<i>ns</i>)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (<i>P</i> < 0.01)	211.95	46.79	-97.98	0.32
	Fledge Rate (<i>P</i> < 0.05)		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (<i>ns</i>)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (<i>P</i> < 0.01)		210.76	45.60	-98.38	0.32
Total	Neg. Binomial	Fledge Rate (<i>ns</i>)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 1 (<i>ns</i> , <i>P</i> < 0.1)	Wind 2 (<i>ns</i> , <i>P</i> < 0.1)	Wind 3 (<i>ns</i>)	146.12	1.75	-65.06	0.24
		Fledge Rate (<i>ns</i> , <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 1 (<i>ns</i> , <i>P</i> < 0.1)	Wind 2 (<i>ns</i> , <i>P</i> < 0.1)		144.37	0.00	-65.18	0.24
	Poisson	Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.05)	Wind 2 (<i>P</i> < 0.05)	Wind 3 (<i>ns</i>)	149.65	5.28	-66.83	0.54
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.05)	Wind 2 (<i>P</i> < 0.05)		148.07	3.70	-67.04	0.53

Table S3. Continued.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo- <i>R</i> ² (best model only)
NM	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	149.55	8.30	-66.78	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)		147.56	6.31	-66.78	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)			145.62	4.37	-66.81	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				143.70	2.45	-66.85	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)					142.22	0.97	-67.11	0.22
	Poisson	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						141.25	0.00	-67.1	0.21
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	154.52	13.27	-69.26	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)		152.52	11.27	-69.26	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)			150.69	9.44	-69.35	0.52
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				148.9	7.65	-69.45	0.52
OR	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				147.68	6.43	-69.84	0.52
		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						147.65	6.40	-70.82	0.51
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	157.00	6.62	-70.50	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 3 (ns)		155.00	4.62	-70.50	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)			153.05	2.67	-70.52	0.18
	Poisson	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				151.16	0.78	-70.58	0.18
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)								
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)								
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)								
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)								

Table S3. Continued.

Region	Distribution	Predictor 1 (<i>P</i>)	Predictor 2 (<i>P</i>)	Predictor 3 (<i>P</i>)	Predictor 4 (<i>P</i>)	Predictor 5 (<i>P</i>)	Predictor 6 (<i>P</i>)	Predictor 7 (<i>P</i>)	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo- <i>R</i> ² (best model only)
TX	Neg. Binomial	Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.001)	BBS Index (ns)					150.66	0.28	-76.39	0.11
		BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)						150.38	0.00	-72.19	0.16
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	168.28	17.90	-76.14	0.47
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)		166.58	16.20	-76.29	0.47
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 3 (ns)			164.84	14.46	-76.42	0.47
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				163.64	13.26	-76.82	0.47
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	156.99	8.00	-70.49	0.18
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)		154.99	6.00	-70.49	0.18
		BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 2 (ns)	Wind 3 (ns)			153.05	4.06	-70.52	0.18
		BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (ns)				151.13	2.14	-70.57	0.18
TX	Poisson	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)					149.84	0.85	-70.92	0.17
		BBS Diff (ns)	BBS Index (<i>P</i> < 0.001)						148.99	0.00	-71.50	0.17
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns, <i>P</i> < 0.1)	173.66	24.67	-78.83	0.45
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (<i>P</i> < 0.05)		171.68	22.69	-78.84	0.45
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (ns)	Wind 3 (<i>P</i> < 0.05)			169.92	20.93	-78.96	0.45
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (<i>P</i> < 0.05)				168.30	19.31	-79.15	0.45
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (<i>P</i> < 0.05)				167.66	18.67	-79.83	0.45
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (<i>P</i> < 0.05)							
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (<i>P</i> < 0.05)							
		BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 3 (<i>P</i> < 0.05)							

Table S3. Continued.

Region	Distribution	Predictor 1 <i>(P)</i>	Predictor 2 <i>(P)</i>	Predictor 3 <i>(P)</i>	Predictor 4 <i>(P)</i>	Predictor 5 <i>(P)</i>	Predictor 6 <i>(P)</i>	Predictor 7 <i>(P)</i>	AIC	ΔAIC	Log-likelihood	Maximum-likelihood pseudo-R ² (best model only)
UT	Neg. Binomial	Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind (ns)	Wind 2 (ns)	Wind 3 (ns)	171.06	5.90	-77.53	0.10
		Fledge Rate (ns)	BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)		169.07	3.91	-77.53	0.10
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)	Wind 3 (ns)			167.44	2.28	-77.82	0.09
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)				165.88	0.72	-77.94	0.09
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns, <i>P</i> < 0.1)				165.03	0.14	-78.65	0.08
		BBS Diff (ns, <i>P</i> < 0.1)	BBS Index (<i>P</i> < 0.001)	Wind 1 (ns)					165.16	0.00	-79.58	0.07
		BBS Diff (ns)	BBS Index (<i>P</i> < 0.001)									
		BBS Diff (ns)	BBS Index (<i>P</i> < 0.001)									
Poisson		Fledge Rate (<i>P</i> < 0.01)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (<i>P</i> < 0.01)	Wind 2 (ns)	Wind 3 (ns)	215.17	50.01	-99.59	0.31
		Fledge Rate (<i>P</i> < 0.01)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns)	Wind 1 (<i>P</i> < 0.01)	Wind 3 (ns)		213.79	48.63	-99.90	0.31
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.01)	Wind 3 (ns)			213	47.84	-100.50	0.30
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Wind 1 (<i>P</i> < 0.01)				211.82	46.66	-100.91	0.30
		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns, <i>P</i> < 0.1)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	147.45	3.32	-65.72	0.23
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 2 (ns)	Wind 3 (ns)		146.16	2.03	-66.08	0.23
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 2 (ns)			145.37	1.24	-66.69	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)				144.13	0.00	-67.06	0.22
Total	Neg. Binomial	Fledge Rate (ns, <i>P</i> < 0.1)	BBS Diff (<i>P</i> < 0.01)	BBS Index (<i>P</i> < 0.001)	Air Flow (ns, <i>P</i> < 0.1)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (ns)	147.45	3.32	-65.72	0.23
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 2 (ns)	Wind 3 (ns)		146.16	2.03	-66.08	0.23
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)	Wind 2 (ns)			145.37	1.24	-66.69	0.22
		Fledge Rate (ns)	BBS Diff (<i>P</i> < 0.05)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.05)				144.13	0.00	-67.06	0.22
Poisson		Fledge Rate (<i>P</i> < 0.05)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.01)	Wind 1 (ns)	Wind 2 (ns)	Wind 3 (<i>P</i> < 0.05)	150.58	6.45	-67.29	0.53
		Fledge Rate (<i>P</i> < 0.01)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.01)	Wind 1 (ns, <i>P</i> < 0.1)	Wind 3 (<i>P</i> < 0.05)		149.68	5.55	-67.84	0.53
		Fledge Rate (<i>P</i> < 0.01)	BBS Diff (<i>P</i> < 0.001)	BBS Index (<i>P</i> < 0.001)	Air Flow (<i>P</i> < 0.01)							

Table S4. List of papers that address which factors influence the interannual variation in number of vagrants occurring in any particular area. No paper to date includes both weather and population variables in their analysis. The only other studies to statistically address the influence of wind on vagrancy are Nisbet (1962) and Van Impe & Derasse (1994).

Source	Time span	Species	Weather Data	Population Size or Growth Data
Nisbet 1962. British Birds 55: 74–86.	1950–1959	Eurasian passerines	Germany (origin of migration)	No
DeBenedictis 1971. California Birds 2: 111–128.	1962–1970	Wood warblers and vireos	No	Yes, of source population
Baker 1977. Bird Study 24: 233–242.	1968–1975	Siberian passerines	Central USSR (origin of migration); qualitative analysis	No
Elkins 1979. British Birds 72: 417–433.	1967–1976	Nearctic passerines and non-passerines	Atlantic weather patterns; qualitative analysis	No
Robbins 1980. British Birds 73: 448–457.	1947–1976	Nearctic landbirds	No	Yes, but not annual
DeSante 1983. Auk 100: 826–852.	1968–1978	Western North American passerines	No	No
Van Impe & Derasse 1994. Oriolus 60: 3–17.	1961–1990	<i>Phylloscopus</i> warblers	Siberia (origin of migration)	No
Patten & Marantz 1996. Auk 113: 911–923.	1972–1994	South-eastern warblers and vireos	No	No
Veit 1997. Ardea 85: 135–143.	1966–1988	Yellow-headed Blackbird <i>Xanthocephalus xanthocephalus</i>	No	Yes, Breeding Bird Survey (BBS)
Patten & Burger 1998. Can. J. Zool. 76: 433–439.	1972–1994	Eastern North American wood warblers	No	Yes, spruce budworm population
Veit 2000. Auk 117: 242–246.	1966–1988	Western North American passerines	No	Yes, Breeding Bird Survey (BBS)
Thorup 2004. Bird Study 51: 228–238.	1958–1992	Eurasian passerines	No	Yes, but not annual
McLaren <i>et al.</i> 2006. Ibis 148: 707–726.	1955–1980 and 1998	Nearctic landbirds	No	Yes, but not annual
Pfeifer <i>et al.</i> 2007. J. Ornithology 148: 379–385.	Not specified	Eurasian passerines	No	Yes, but not annual
Hameed <i>et al.</i> 2009. Earth Interactions 13: 1–22.	1980–2000	Asiatic birds	Yes, summarized in climate indices	No
Farnsworth <i>et al.</i> 2015. Wilson Bulletin 127: 582–592.	1957–2014	American Purple Gallinule <i>Porphyrio martinicus</i>	Yes, drought and temperature data	No

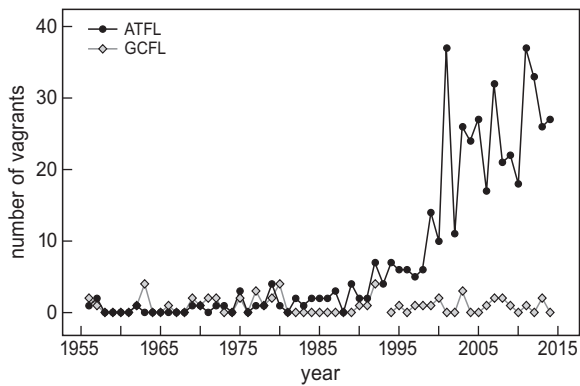


Figure S1. Records of Ash-throated Flycatchers (ATFL) and Great Crested Flycatchers (GCFL) from 'North American Birds' (NAB) from 1 October to 31 December in eastern coastal North America (Newfoundland to Florida) in 1956–2014. Late autumn records of ATFL and GCFL are not significantly correlated ($r = 0.02$, $P = 0.86$). Note NAB is missing records for GCFL for 1993.

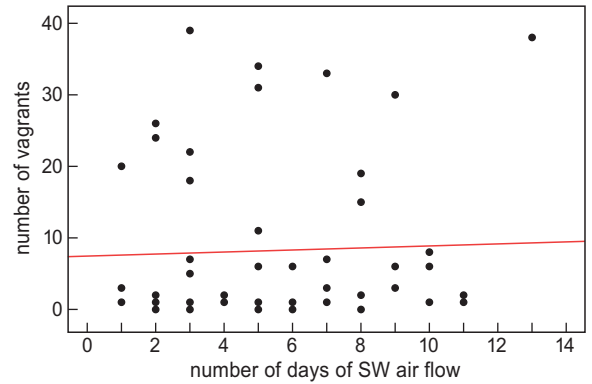


Figure S3. Influence of south-westerly airflow on occurrence of vagrants ($P = 0.79$).

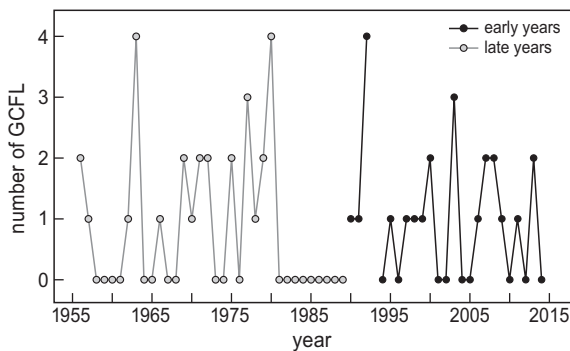


Figure S2. Records of Great Crested Flycatchers (GCFL) from 'North American Birds' (NAB) from 1 October to 31 December in eastern coastal North America (Newfoundland to Florida) in 1956–2014. Late autumn records of GCFL are not significantly different across years ($P = 0.980$); there is no relationship between the year and the number of GCFL.