SPRING MIGRATION PHENOLOGY OF FOUR NORTH AMERICAN INSECTIVOROUS BIRD SPECIES IN RELATION TO CLIMATIC VARIABLES

by

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A Thesis
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LIST OF ABBREVIATIONS AND SYMBOLS

Bank Swallow	BANS
Barn Swallow	BARS
Degrees Celcius	°C
Degrees Fahrenheit	°F
First Arrival Date	FAD
North American Bird Phenology Program	NABPP
Northern Atlantic Oscillation Index	NAO
Purple Martin	PUMA
Southern Oscillation Index	SOI
Tree Swallow	TRES

ABSTRACT

SPRING MIGRATION PHENOLOGY OF FOUR NORTH AMERICAN INSECTIVOROUS BIRD SPECIES IN RELATION TO CLIMATIC VARIABLES

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This thesis describes the relationships between the timing of spring migration (phenology) of four bird species and eight environmental variables which could influence migration. Different bird species respond differently to various cues, and research in this area has shown a wide range of results. Some species respond strongly to weather (often shorter distance migrants) while others do not (often longer distance migrants). If environmental conditions continue to change as recently observed, bird species may respond in different ways, potentially leading to ecological mismatches. Historical First Arrival Date observations were obtained from the North American Bird Phenology Program and compared with weather data. Approximately 2,000 total records of First Arrival Date observations from 1899 to 1962 were included in the analyses. Purple Martins (*Progne subis*, April 16 ± 12.6 days) and Tree Swallows (*Tachycineta bicolor*, April 18 ± 14.1) arrived earliest, followed by Barn Swallows (*Hirundo rustica*, April 25

± 9.07) and Bank Swallows (*Riparia riparia*, May 3 ± 10.4). Multiple regression and stepwise regression were conducted to describe relationships between weather and arrival timing. Two species (Bank Swallow and Purple Martin) responded with no significant influence imposed on arrival timing by weather or climate conditions. This follows expectations due to their long distance migration patterns. The two other species studied did not respond as expected. Tree Swallow, despite being the shortest distance migrant examined responded to very few environmental parameters, mainly the Southern Oscillation Index. Barn Swallow, a mid- to long-distance migrant, was unexpectedly the most responsive to weather and climate, responding to all types of weather parameters, including temperature, precipitation, Southern Oscillation Index, and Northern Atlantic Oscillation Index.

INTRODUCTION

Migratory birds have complex and multidimensional lives, living in different locations during portions of year, and undergoing tremendous physiological changes to perform their annual migration (Greenberg and Marra 2005, Gordo 2007, Cox 2010). An estimated 200 bird species migrate between non-breeding grounds in Central and South America to North American breeding grounds each spring, with individual migrating birds numbering in the billions (Gill 1995).

Birds live in a wide range of climates and habitats, making use of a wide variety of food resources. Migration strategies vary in many factors as well, such as distance, duration, rate, and route. Some species such as the redknot (*Calidris canutus*) and bar-tailed godwit (*Limosa lapponica*) are known for impressive migration feats. The *C. canutus rufa* redknot subspecies winters in great numbers in Tierra del Fuego and breeds in northern Canada near the Arctic Circle, essentially migrating from the southern tip of South American to the northern tip of North America (Harrington 2001). The bar-tailed godwit was recently observed migrating between Alaska and New Zealand, a distance of more than 10,000 km, giving this species the distinction of undertaking the longest known non-stop migration (Battley *et al.* 2012). Other species make more modest migrations, such as the Tree Swallow (*Tachycineta bicolor*), which breeds in the

Northern U.S., most of Canada, to Alaska, and winters along the Caribbean coast, through central Mexico, to Baja California (Winkler *et al*. 2011).

Researchers have attempted to understand what environmental factors influence the rate and timing of bird migrations. In general, it is thought that longer-distance migrants use photoperiod and internal physiological rhythms as cues to begin pre-breeding migration, while shorter distance migrants are thought to respond more to local weather conditions, beginning to migrate only after favorable conditions exist (Gill 1995). Other studies have observed a hybrid approach for longer-distance migrants, suggesting that photoperiod is used to initiate migration while birds 'fine tune' their rate of migration based on local temperatures along the route (Tottrup *et al.* 2010, Saunders 1959).

While those generalities exist, research attempting to describe better the relationships between climatic cues and bird migration has mixed results. Studies have made use of different environmental parameters to represent climate (Carey 2009, Gordo 2007, and Lehikoinen *et al.* 2004). Most often authors have used temperature or atmospheric pressure indices as indicators of weather, although other factors such as precipitation, winds, or snowmelt date have also been used (Gordo 2007). Studies making use of pressure-based indices have used the North Atlantic Oscillation Index (NAO) or the Southern Oscillation Index (SOI).

In general, temperature and NAO have demonstrated relationships with the timing of spring migration arrival, although not consistently in most locations and for most species. Numerous studies in Europe have found NAO associations (Forchhammer *et al.*

2002, Ahola *et al.* 2007, Vahatalo *et al.* 2004, Sparks *et al.* 2007, Tottrup *et al.* 2010, among others, but see Cotton 2003) suggesting that NAO is a good predictor for many European breeding birds. The value of NAO is less clear in North America. MacMynowski and Root (2007) found an NAO relationship in the majority of the 11 long distance species studied in Chicago, IL, while Marra *et al.* (2005) found no relationship between NAO and arrival date for 32 species migrating between southwestern Pennsylvania and southern Ontario. Miller-Rushing *et al.* (2008) and Wilson (2007) both found some species which responded to NAO values, but neither study found an NAO correlation in the majority of species studied. Of the North American studies which found NAO to be a factor, most occurred in New England or near the Great Lakes. The size of the North American continent and the general eastward motion of global weather patterns likely limit the influence of NAO to birds in the eastern U.S.

As explained by Gordo (2007), the NAO and other indices are composites of multiple weather variables, thus use of NAO is also an indirect use of the individual factors. Wind speed and direction, for example, may provide an obvious mechanism for earlier arrival date. A strongly positive NAO value typically indicates wind conditions which would assist Europe-bound migrants and allow for shorter migration duration. Thus demonstrating a relationship between NAO and arrival time does not explain the root driver of the relationship, as it could be temperature, wind speed, or any other conditions related to NAO values.

Studies making use of SOI have had mixed findings. Of the three studies known to have analyzed SOI, one North American study (Miller-Rushing *et al*. 2008) found a relationship with arrival dates, and that was strongest for mid-distance migrants. MacMynowski and Root (2007) and Cotton (2003) reported no relationship with SOI in North American and European species, respectively. SOI measures the atmospheric pressure differences in parts of the Pacific Ocean. These differences drive the *El Niño – La Niña* cycles, which are known to influence weather conditions in parts of North America (Latif and Barnett 1994, Ropelewski and Halpert 1986). If birds are influenced by local weather conditions, then it logically follows that there should be some relationship between SOI and migration phenology.

The majority of work on this topic has been conducted in Europe (Carey 2009, Gordo 2007, and Lehikoinen *et al.* 2004), although growing numbers of publications are now coming from North America (Gordo 2007). As already described here, North American results are not always consistent with European results. The reasons for this may be that weather patterns are different in the two hemispheres, or that land mass configuration provides different migration opportunities and limitations.

With results varying not only by species, but also by location, there is clear need for detailed response information in order to understand potential future bird population scenarios. The research conducted to date provides some general guidance on how changing climates may influence bird phenophases; i.e., short distance migrants have the potential to arrive earlier while long distance migrants may not change arrival as much, and that European studies are much more complete than North American. Given the geographic size of North America, it is likely that arrivals in different regions will be influenced by different climate measures rather than a single factor influencing most birds coast to coast. Additionally, most studies published to date have been limited by number of species, geographic extent, and temporal duration. Given these limitations, a more complete picture of migration phenology in North America should be highly informative.

Climate Change and Birds

The question of how bird migration is influenced by weather and climate variation has important implications as global climate patterns are exhibiting changes from historic norms. The Earth's average recorded temperature has increased by approximately 0.74°C in the previous century with greater variation at regional and local scales (IPCC 2007). Such changes in global temperatures are expected to induce significant environmental and biological change. For example, Artic Sea ice extent and thickness are reducing and models predict these trends to continue (Douglas 2010) while sea levels are expected to rise, with differing impacts in different locations (Storlazzi et al. 2013, Sallenger et al. 2012).

In general, the available research indicates that that many populations of birds on different continents are experiencing advances in spring migration timing as temperatures increase. This general observation is based upon numerous studies from Europe (Cotton 2003, Thorup *et al*. 2007, Sparks and Braslavska 2001, Sparks 1999, Sokolov 2006) and North America (Droege *et al*. 2003, Dunn and Winkler 1999, Foster *et al*. 2010, MacMynowski and Root 2007, Swanson and Palmer 2009, and Butler 2003). Lehikoinen *et al*. (2004) analyzed 26 studies and found on average that First Arrival Dates (FAD) are advancing by 0.373 days per year, despite some species which did not advance and others which delayed arrival.

These changes in weather and climate have the potential to influence more than migration phenology as well. Numerous accounts document the changes in breeding times. McCleery and Perrins (1998) describe early egg laying by Great Tits (*Parus major*) after 1970, which they correlate with warmer temperatures. Forchhammer *et al*. (1998) report numerous European birds are advancing breeding phenology with a correlation to NAO. According to Dunn and Winkler (1999), Tree Swallow (*T. bicolor*) egg laying dates advanced by five days between 1951 and 1991. Winkel and Hudde (1997) found three species advanced egg laying dates by 3 to 9 days in correspondence with warmer temperatures. Two additional studies (Both *et al*. 2004 and Crick *et al*. 1997) found similar results, both reporting a relationship between local temperatures and egg laying dates for numerous European species. Brown *et al*. (1999) produced the first North American example of climate change and bird breeding phenology by documenting that Mexican Jays (*Aphelocoma ultramarina*) in Arizona have advanced breeding by more than 10 days.

Although trends for earlier laying dates and relationships between temperature and laying dates have become prominent in the literature, it must also be considered that not all species have changed laying dates with weather conditions (Both *et al*. 2004, Crick *et al*. 1997, and Visser *et al*. 1998).

A small number of studies have addressed ways in which changes in climate may directly or indirectly influence avian populations. Sillett *et al*. (2000) describe a relationship between both adult survival and fecundity SOI for Black-throated Blue Warblers (*Dendroica caerulescens*). In *El Niño* years (years with a strong negative SOI value) the species had lower survival and reproductive success, conversely survival and fecundity were higher in *La Niña* years. Ahola *et al*. (2007) report that changes in migration times have caused temporal overlap and increased competition for nesting sites between Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*), resulting in increased mortality for Flycatchers. A model produced by Beale *et al*. (2006) suggests that declines in the Ring Ouzel (*Turdus torquatus*) in the United Kingdom may be attributed to changes in climate.

There is also evidence that some species' ranges have shifted in recent years. Thomas and Lennon (1999), for example, demonstrated that British birds changed their northern ranges by nearly 19 km over a 20 year period. Visser *et al*. (2009) also reported range changes in 12 species which breed in the Netherlands. Models produced by Huntley *et al*. (2008) predict significant changes in European species by the late 21st century.

Ecological Linkages

As birds are found to respond to changing conditions, so too are other species. Researchers have begun to document how changes in the physical environment influences a range of taxa, including plants, animals, and other organisms (see Walther et al. 2002, Penuelas and Filella 2001, Menzel and Fabian 1999, Bradley et al. 1999, Parmesan and Yohe 2003, Inouye et al. 2000, Kannan and James 2009, Gordo and Sanz 2005).

As different species respond in different ways, scientists and resource managers are considering scenarios where ecologically linked species respond differently to environmental change. Many studies suggest ecological mismatches as an issue (Both *et al.* 2004, Penuelas and Filella 2001) or address it directly through research (Visser *et al.* 1998, Stenseth and Mysterud 2002, Both and Visser 2001, Visser and Both 2005, Strode 2003), while Carey (2009) and Harrington *et al.* (1999) have reviewed the issue. A prime example is given by Visser *et al*. (1998), who report that laying dates for great tits (*Parus major*) have not shifted, yet the caterpillars which they rely on during breeding season are peaking earlier in the spring. One cannot assume that species across trophic levels will respond in step with each other, thus a basic understanding of how bird species respond to environmental change is needed to better predict potential mismatches.

Temperature and Insectivores

Insectivorous birds should be sensitive to local temperatures during spring migration. It is presumed that their foraging ecology will make them highly responsive to temperature, because (1) their prey items will not be active below certain temperature thresholds, and (2) aerial foraging itself is highly energy intensive (Williams 1988). These conditions provide incentive to minimize foraging effort in cooler conditions when nutritional return diminishes.

Environmental conditions have many influences on foraging activity in insectivorous species. Brown (1976) observed foraging efficiency temperature thresholds, reporting that Purple Martins (*Progne subis*) are not able to successfully forage below 6 °C and forage most successfully above 13 °C. Turner (1982) calculated caloric requirements and determined that Barn Swallows (*Hirundo rustica*) and Bank Swallows (*Riparia riparia*) should not able to obtain their required calories below 8.6 °C and 10.3 °C respectively. Lower ambient temperatures were also found to negatively influence fat reserves in pre-migratory Barn Swallows (Pilastro and Magnani 1997), assumed to be due to decreased foraging efficiency.

Other insectivorous species have reportedly adjusted their feeding behaviors under different weather conditions (Lack and Owens 1955, Murphy 1987, and Troy and Baccus 2009). In most of these cases, as temperature decreased, behavior changed from more energy intensive aerial feeding habits, such as hawking, to less intensive ground or substrate based habits, such as gleaning or perch-to-ground sallying. If weather conditions do not allow minimally efficient feeding during migration, any of these shifts would suggest a decrease in the rate of migration until temperatures increase.

OBJECTIVES

This thesis reports on research designed to describe how four species of North American insectivorous birds have historically responded to variations in weather and climate. Historical observations of spring arrival dates were compared to weather and climate conditions for Barn Swallow (*Hirundo rustica*, BARS), Tree Swallow (*Tachycineta bicolor*, TRES), Bank Swallow, (*Riparia riparia*, BANS), and Purple Martin (*Progne subis*, PUMA).

Given the variation in results from other phenological studies, a suite of weather and climate factors were used as possible explanatory variables for arrival dates.

These four species have similar life history traits, particularly similar foraging patterns. All four are aerial insectivores, with some distinct differences and preferences. For example, Barn Swallows tend to forage at lower heights (usually less than 10 meters), while Bank Swallows (less than 33 meters), Tree Swallows (less than 50 meters), and Purple Martins (higher than 50 meters) prefer to forage at higher altitudes. There are also some differences in preferred prey, in either taxa or size (Brown and Brown 1999, Garrison 1999, Winkler *et al*. 2011, and Brown 1997).

All four species breed over large portions of the contiguous United States and parts of Canada, again, with some variation (Winkler *et al.* 2011, Garrison 1999, Brown and Brown 1999, Brown 1997). Tree Swallows and Bank Swallows occur most northward of the four species, with similar breeding ranges extending into much of Alaska and across Canada to the North and not much further south than Tennessee in the East and Utah in the West. Barn Swallows extend north slightly into Alaska, south into Central Mexico, and cover nearly all of the lower 48 states. Purple Martins have the most restrictive range of these species, breeding predominantly in the Eastern U.S., east of approximately -100 degrees longitude and between southern Ontario and the Gulf Coast, with smaller populations breeding in sections of the Southwest and Baja California.

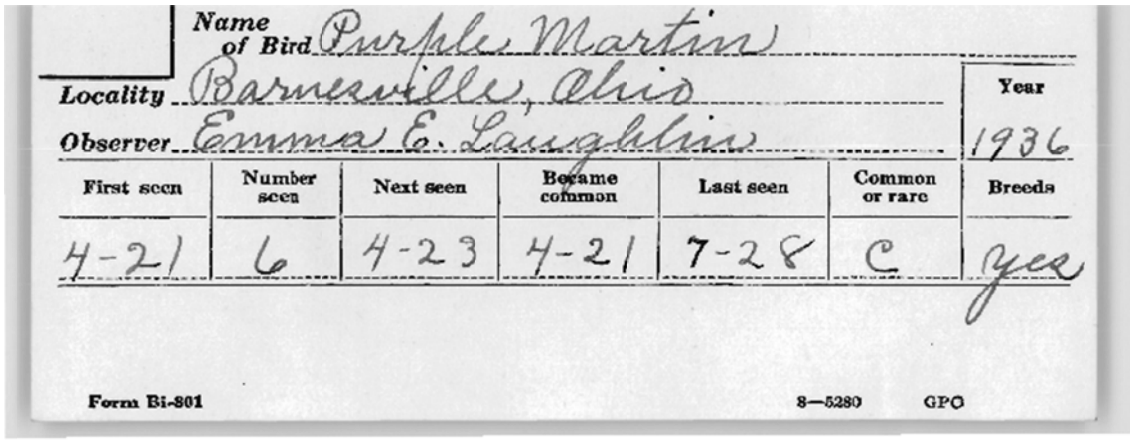
Their non-breeding ranges can be seen as a spectrum from Central America to South America, with Tree Swallows wintering in Central America and Gulf Coast portions of the southern US, Barn Swallows wintering in Central America and most of South America, Bank Swallows wintering in portions of Central America and portions of South America, and Purple Martins wintering only in South America.

DATA AND METHODS

Migration Phenology Data

First Arrival Date (FAD) data were obtained from the U.S. Geological Survey's Patuxent Wildlife Research Center (North American Bird Phenology Program 2011). These newly available data are part of a legacy dataset comprised of an estimated 4 million records of FAD observation from individual birders across the United States from the late 1800s to the early 1970s when the program ceased to collect data. The majority of records are between 1900 and 1940. These records have remained in handwritten format until recently when efforts are being made by the North American Bird Phenology Program (NABPP) to transcribe and digitize these data. Nearly 700,000 records have been digitized to date by numerous volunteers across the country, allowing analysis of these data.

Each record includes at minimum the species name, location (usually a town or county), observer, year, and date first seen (Figure 1). Some records include additional data such as the date the species was first commonly observed, the breeding status of the species in that location, and the date that species was last seen, although this study did not make use of these latter fields, if they existed.



Name of Bird Purple Martin
Locality Barnesville, Ohio
Observer Emma E. Laughlin
Year 1936

First seen	Number seen	Next seen	Became common	Last seen	Common or rare	Breeds
4-21	6	4-23	4-21	7-28	C	yes

Form Bi-801 8—5280 GPO

Figure 1 Example of First Arrival Date Record from the North American Bird Phenology Program

Data were provided by the NABPP as a Microsoft Excel file, after being digitized by volunteers but prior to being quality controlled. All records were reviewed for transcription accuracy and consistency. Original observation cards were referenced when any discrepancies were found. If a review of the original observation card did not resolve a discrepancy, the record was removed from analysis. To standardize the use of dates between leap years and non-leap years, FADs were converted from Day/Month/Year format to Day of Year, using January 1 as day 1, adding one for each sequential day after. Acceptable FAD records were then georeferenced using an online forward-geocoding system (Morse 2006) which provides longitude and latitude values for a specified town or county.

Weather and Climate Data

Monthly weather data were obtained from the National Oceanic and Atmospheric Administration (National Climatic Data Center 2007). This dataset provides weather data for each of approximately 350 geographically defined climate divisions (Figure 2) including monthly mean temperature (°F) and monthly precipitation (inches). The provided values are modeled data, designed to represent the weather conditions within each division through readings taken at a collection of weather stations (National Climatic Data Center 2007).

Monthly North Atlantic Oscillation Index and Southern Oscillation Index values were obtained from the National Center for Atmospheric Research (2013a and 2013b).

Geographic Information System

A Geographic Information System (GIS) was developed to verify the accuracy of the georeferenced coordinates and to associate the observation points with their respective climate divisions. The GIS was created in ESRI ArcMap 10 and freely available base map data for continental and state boundaries (U.S. Census Bureau 2010), Climate Division data (National Climatic Data Center 1991), and the georeferenced First Arrival Date observation points. The GIS was used to verify that all georeferenced locations occurred within the correct state, and a ten percent random sample of all locations was checked further against Google Maps to verify georeferencing accuracy within the state. Records with irresolvable georeferencing issues were discarded.

Each observation point was associated to the appropriate Climate Division (Figure 2) through the GIS. Weather and climate data were linked to each observation point outside of the GIS. Division weather data (precipitation and temperature) were associated with each observation point based on the division in which it resides and the observation year. Values for NAO and SOI were associated with each observation point based on the observation year.

Figure 2 Map of National Climatic Data Center's climate divisions (National Climate Data Center 1991). Data from the six shaded divisions were used in this study.

Data Analysis

Multiple regression and stepwise linear regression were both used to compare FADs with local weather and hemispherical climate conditions as possible explanatory variables. Both approaches were used to cast a broad net, given the wide variety of results other studies have found in different locations.

Observations were limited to those occurring in March, April, and May only, assuming this would measure the full extent of migration period and any observations outside this period would be anomalies.

Observations were used from six climate divisions, North Central Ohio (OH NC), Northeast Ohio (OH NE), Southeastern Pennsylvania (PA), Northern New Jersey (NJ), Central Massachusetts (MA), and Southern New Hampshire (NH) (Figure 2). These divisions were selected for having the highest number of observations available to increase sample size. It so happened that the six divisions are located in three pairs which can be thought of as representing the Great Lakes, Mid-Atlantic, and New England Regions of the United States. Not all NABPP records were transcribed at the time of the research, and it is likely that additional records have since been made available for these and other divisions.

Three types of analyses were conducted: (1) multiple regression for each species in each division; (2) multiple regression for each species collectively including all observations from all six divisions; and (3) stepwise linear regression for each species collectively including all observations from all six divisions. Insufficient observations did not allow for meaningful stepwise regressions at the divisional level. Microsoft Excel 2010 was used for all three tests. An Excel extension package (Pekoz 2009) was used for the stepwise regression.

Each regression analysis compared the FAD (after conversion to Day of Year) against nine possible explanatory variables, two describing local weather conditions, six describing hemispherical-scale climate conditions in the Atlantic and Pacific Oceans, and one for time. March temperature and precipitation values were used as a proxy for local weather conditions during the migration season. NAO and SOI values for January, February, and March were each included to allow for the possibility that conditions in the oceans may not have immediate influence on conditions far away where the migration is occurring.

Sixteen outlier FAD records fell outside 95% and were removed (BANS = 0, BARS = 7, PUMA = 8, TRES = 1). Approximately 2,000 total records spanning the years 1899 to 1962 were included in the final analyses.

RESULTS

Descriptive statistics for each species' arrival dates are shown in Table 1. Purple Martins and Tree Swallows arrived earliest, on the average, with mean FADs of April 16 (+/-12.6 days) and April 18 (+/- 14.1 days) respectively. Barn Swallows tended to arrive later with a mean FAD of April 25 (+/- 9.07 days), and Bank Swallow arrived last with an average of May 3 (+/- 10.4 days). Figure 3 shows the frequency of reported FADs for each species over the migration period.

Table 1 Descriptive statistics of FAD data for all four species.

	BANS	*BARS*	*PUMA*	*TRES*
Mean (as Day of Year)	123.99	114.78	105.65	107.56
Mean (as date)	3-May	25-Apr	16-Apr	18-Apr
Median	124	114	103	106
Standard Deviation	10.36	9.069	12.64	14.12
Minimum (as Day of Year)	92	88	75	64
Minimum (as date)	2-Apr	29-Mar	16-Mar	5-Mar
Maximum (as Day of Year)	151	146	143	146
Maximum (as date)	31-May	26-May	23-May	26-May
Count	229	883	385	499

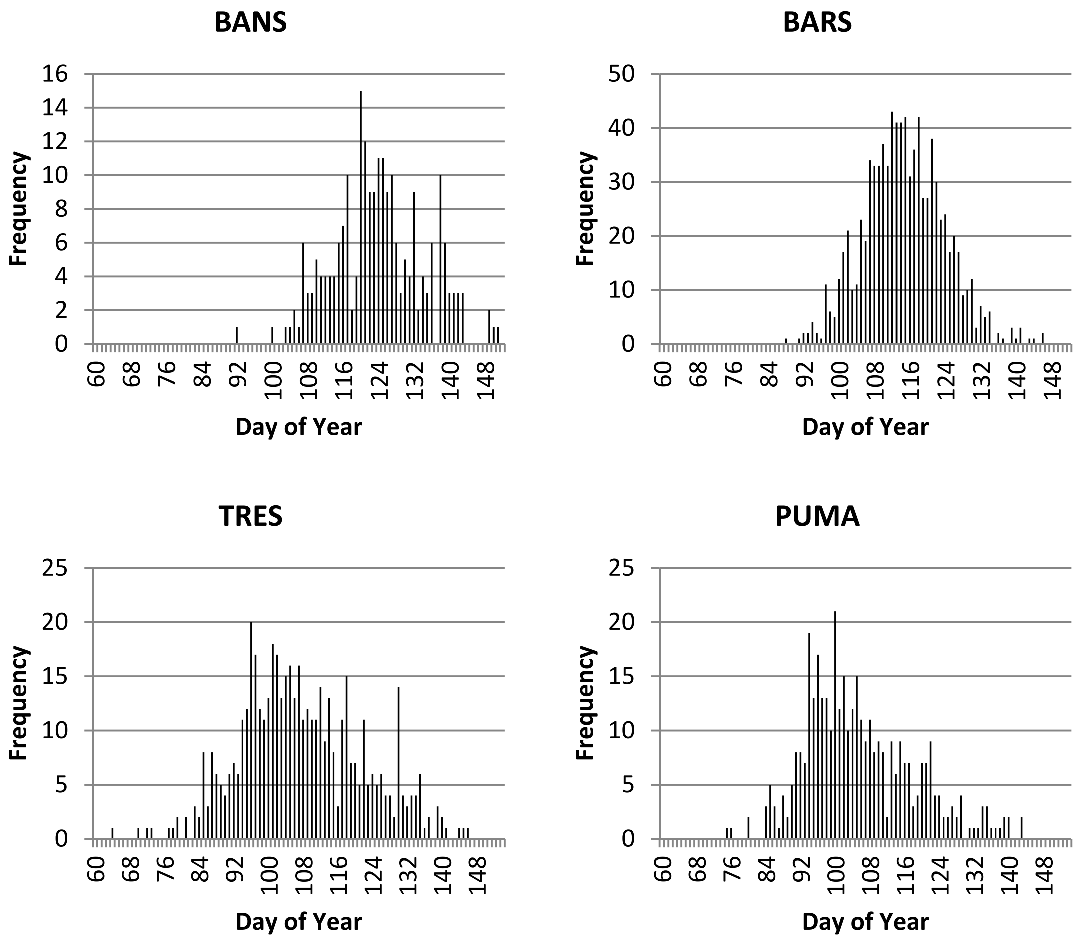


Figure 3 Date of First Observation Histograms for each species

Multiple Regression with Collective Data

The results of analyzing FAD for each species against weather and climate in all locations collectively are shown in Table 2. BARS shows a significant relationship with five variables: Year, March Temperature, March Precipitation, March NAO, March SOI, and January SOI (R-squared = 0.045). PUMA shows a significant relationship with one variable, March SOI (R-squared = 0.020). TRES also shows one significant relationship, with January SOI (R-squared = 0.032). BANS has no significant results. All tests are run using a 0.05 significance level.

Table 2 Results of Multiple Regression Analyses, conducted for each species using all locations collectively. P-values significant at the 0.05 level are highlighted in yellow.

	BANS, N = 229		BARS, N = 883	
	Coefficients	*P-value*	*Coefficients*	*P-value*
Year	-0.033929557	0.574778597	0.117259391	3.79846E-06
Mar.Temp	-0.110443844	0.49825729	-0.384151557	9.84396E-10
Mar.Precip	0.092272688	0.863492147	0.504313447	0.030319831
March.NAO	-1.061668236	0.123654306	0.547527069	0.058951926
Feb.NAO	0.004919956	0.993823767	0.222840362	0.41302628
Jan.NAO	0.103348012	0.852135751	0.279247862	0.254211087
March.SOI	0.928824939	0.120435011	1.048481701	2.14146E-05
Feb.SOI	-0.855344709	0.101673264	-0.123053742	0.586940748
Jan.SOI	-0.242038789	0.681545697	-0.486780341	0.045196662

	PUMA, N = 385		TRES, N = 499	
	Coefficients	*P-value*	*Coefficients*	*P-value*
Year	-0.043935894	0.457061129	-0.073503574	0.175384495
Mar.Temp	-0.114161502	0.471307331	0.107678287	0.435798602
Mar.Precip	0.626251304	0.306093318	0.000962586	0.998386386
March.NAO	-0.36920582	0.579575185	-1.176611038	0.052121357
Feb.NAO	0.660044662	0.261753295	0.172827927	0.766988288
Jan.NAO	-0.052911636	0.922898523	-0.38686026	0.471303582
March.SOI	1.277984125	0.025485209	-0.019979126	0.969453292
Feb.SOI	-0.333058363	0.510682928	0.663064053	0.16301379
Jan.SOI	-0.098375814	0.856974759	-1.51438766	0.003279407

Multiple Regression with Divisional Data

The results of analyzing FAD for each species against weather and climate in each of the six climate divisions are shown in Table 3. Barn Swallow shows significant relationships in nine of the 54 tests run, including March SOI in Massachusetts; Year, March Temperature, and February SOI in New Hampshire; Year, February NAO, March SOI, and February SOI in Ohio NC; and March SOI in Ohio NE.

Bank Swallow data are significant in five of the 54 tests, including: January SOI in New Hampshire; Year in Ohio NC; March NAO and January SOI in Pennsylvania; and January SOI in New Jersey. Tree Swallow has significant results in three of the 54 tests, including March Temperature in New Hampshire, Year in Pennsylvania, and January SOI in New Jersey. Purple Martin data are significant in one of the 36 tests run, year in Ohio NC. Purple Martin observations were insufficient in New Hampshire and non-existent in Massachusetts, thus only four divisions were included.

Table 3 Results of Multiple Regression Analyses, conducted for each species in each climate division. P-values significant at the 0.05 level are highlighted in yellow. Data were insufficient for PUMA in MA and NH divisions.

BANS	*MA, N = 62*		*NH, N = 33*		*OH NC, N = 41*		*OH NE, N = 47*		*PA, N = 22*		*NJ, N = 24*	
	Coeff.	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*
Year	-0.1182	0.2811	0.0281	0.8571	-0.4213	0.0093	0.1436	0.3577	-0.4665	0.0529	-0.2426	0.2908
Mar.Temp	0.3839	0.3275	0.5850	0.2278	0.6881	0.1459	0.2718	0.5259	1.7790	0.1122	0.8375	0.4827
Mar.Precip	-1.5327	0.1200	-0.8875	0.4381	1.1978	0.4933	0.9544	0.6048	0.0893	0.9630	-1.0413	0.7825
March.NAO	-1.2032	0.3937	-2.0484	0.2191	-3.2915	0.0544	-2.7932	0.1020	-11.8627	0.0160	2.3469	0.5221
Feb.NAO	-0.7642	0.5195	0.3353	0.7958	0.7768	0.5540	1.0561	0.4422	5.7678	0.0964	-1.6071	0.7649
Jan.NAO	-0.7570	0.4822	1.3586	0.3189	0.8683	0.5115	0.4346	0.6538	1.5552	0.5571	-0.7631	0.8297
March.SOI	-0.3201	0.7719	1.4251	0.3199	-0.2581	0.8919	1.2079	0.2976	4.5757	0.0917	-1.2374	0.6262
Feb.SOI	-0.3286	0.7456	0.6725	0.5738	-0.7653	0.5113	-1.2332	0.2990	-2.1346	0.3402	-2.0920	0.4245
Jan.SOI	-0.9072	0.4561	-3.3124	0.0262	1.4357	0.3453	-0.0498	0.9692	-7.7287	0.0471	4.3839	0.0346

BARS	*MA, N = 141*		*NH, N = 164*		*OH NC, N = 110*		*OH NE, N = 105*		*PA, N = 195*		*NJ, N = 175*	
	Coeff.	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*
Year	-0.0416	0.5551	0.1479	0.0061	0.1890	0.0102	-0.0093	0.9059	-0.0105	0.8263	0.0804	0.1716
Mar.Temp	0.0630	0.7490	-0.4041	0.0194	-0.0896	0.6813	-0.2374	0.2089	-0.0573	0.7431	-0.0528	0.7950
Mar.Precip	-0.5989	0.2310	0.4454	0.2470	0.8216	0.3716	0.1506	0.8740	0.2818	0.5979	0.0263	0.9665
March.NAO	0.2970	0.6697	0.2687	0.6543	0.0261	0.9767	0.4244	0.5769	-0.0321	0.9606	0.3935	0.5840
Feb.NAO	-0.5283	0.4225	-0.0700	0.8971	1.6071	0.0245	0.6739	0.3072	-0.0462	0.9351	-0.2987	0.6655
Jan.NAO	0.5420	0.3295	0.2019	0.6629	-1.2730	0.0793	0.3970	0.4432	1.0040	0.0553	-0.0176	0.9775
March.SOI	1.2632	0.0278	0.5311	0.2697	1.6133	0.0335	1.4178	0.0157	0.3429	0.5000	1.0748	0.0761
Feb.SOI	-0.1220	0.8250	-0.9235	0.0477	1.4981	0.0188	-0.0164	0.9773	-0.1610	0.7249	-0.1615	0.7569
Jan.SOI	-0.2045	0.7489	-0.3519	0.4672	-1.3382	0.0550	-0.4019	0.5125	-0.1611	0.7446	-0.6539	0.2391

PUMA	*MA, N = 0*		*NH, N = 3*		*OH NC, N = 107*		*OH NE, N = 107*		*PA, N = 132*		*NJ, N = 44*	
	Coeff.	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*
Year					-0.2318	0.0066	0.0574	0.6603	-0.0185	0.8732	-0.4191	0.2524
Mar.Temp					0.1709	0.5079	-0.2184	0.5239	-0.2355	0.5249	-0.5625	0.4744
Mar.Precip					0.4704	0.6568	0.4605	0.7746	0.1192	0.9109	-0.2442	0.9278
March.NAO					-1.8154	0.0971	-0.4100	0.7732	0.1569	0.9141	2.7041	0.3223
Feb.NAO					0.9457	0.2958	0.8245	0.4385	0.7465	0.5140	-2.8681	0.4037
Jan.NAO					-0.4011	0.6349	-0.2046	0.8350	0.3373	0.7357	-2.5662	0.3497
March.SOI					0.6908	0.4322	1.2423	0.2472	1.9475	0.0809	1.3974	0.5400
Feb.SOI					0.2734	0.7227	-0.3927	0.7218	-0.3077	0.7511	-2.3351	0.2212
Jan.SOI					-0.2601	0.7531	-0.1576	0.8861	0.1521	0.8858	-0.8500	0.7233

TRES	*MA, N = 128*		*NH, N = 127*		*OH NC, N = 67*		*OH NE, N = 57*		*PA, N = 45*		*NJ, N = 76*	
	Coeff.	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*	*Coeff.*	*P-value*
Year	0.0427	0.7264	0.1018	0.2845	0.0462	0.7999	-0.0326	0.9099	-0.3870	0.0086	-0.2342	0.0916
Mar.Temp	-0.2430	0.5372	-0.6336	0.0469	-0.4532	0.3752	-0.5461	0.3585	0.5484	0.3788	-0.3692	0.4475
Mar.Precip	-0.3735	0.7003	0.7421	0.3095	1.7579	0.3918	1.9362	0.5270	2.1335	0.2183	-0.2863	0.8665
March.NAO	-1.1493	0.3872	-1.1519	0.2661	-1.9895	0.3413	0.2871	0.9162	-4.1284	0.0585	1.2064	0.4943
Feb.NAO	0.8665	0.5004	0.0524	0.9563	2.3530	0.2141	-0.7615	0.7038	0.8250	0.6438	-0.4051	0.8216
Jan.NAO	0.3327	0.7823	-0.7986	0.3674	-2.9929	0.0789	-0.4999	0.7375	1.8217	0.3325	-1.2390	0.4476
March.SOI	-0.7099	0.5298	-0.3390	0.6926	0.0872	0.9574	0.9193	0.6639	0.7580	0.6484	1.0698	0.4722
Feb.SOI	-0.7627	0.4661	-0.2890	0.7308	1.7119	0.2276	2.3962	0.1884	2.5054	0.0545	1.7368	0.1968
Jan.SOI	-0.4133	0.7164	-1.2999	0.1624	-1.6656	0.3183	-1.8220	0.3762	-2.9301	0.0565	-2.8798	0.0376

Stepwise Regression with Collective Data

The Barn Swallow stepwise regression models included the most explanatory variables, including March Temperature, March Precipitation, March NAO, March SOI, and January SOI with March Temperature as the best single predictor (N = 883, R-squared = 0.079). The Tree Swallow stepwise model included two variables, February SOI and January SOI with January as the best single predictor (N = 499, R-squared = 0.021). The Bank Swallow model resulted in a single significant variable, March NAO (N = 229, R-squared = 0.017). Stepwise regression did not result in a meaningful model for the Purple Martin data.

DISCUSSION

The analyses produced a mix of expected and unexpected results. As shown in many other studies, long-distance migrants were expected to be less influenced by weather and climate, while shorter-distance migrants were expected to be more influenced.

Bank Swallow and Purple Martin responded to none of the weather variables in any of three analyses completed, and to climatic variables in only a few cases. This follows expectations, as they are long distance migrants and likely use photoperiod to time their migration than environmental conditions in their breeding grounds. If they use local weather conditions to fine tune their arrival time, it was not strong enough to show in these tests. They may respond to local weather on the non-breeding grounds or along the migratory route, but these factors were not examined here.

The results for Barn Swallow and Tree Swallow are not as expected and require further discussion. Tree Swallows migrate the shortest distance of the four species, therefore this species was expected to be the most responsive to weather and climate conditions. The results, however, showed significant relationships in only a few cases. January or February SOI was significant in each of the three tests types, but only significant in one of the locations in the divisional multiple regression. Temperature was significant in only one location (New Hampshire) in divisional multiple regression. The response to both SOI and Temperature may be showing the same phenomenon, as high SOI conditions typically result in higher temperatures in the southeastern US where some Tree Swallows winter. It appears that Tree Swallows are influenced by SOI, but the divisional multiple regression produces an inconsistent conclusion.

Conversely, Barn Swallow is a medium to long distance migrant which appears to respond more like a shorter distance migrant, with the greatest number of significant variables. The collective data for all locations show relationships with both Temperature and Precipitation, as well as with March and January SOI. The Temperature coefficient is negative (-0.38) indicating the species is arriving earlier in warmer conditions, consistent with most other species that have responded to increasing temperatures. The results for the divisional regressions show a mix, responding to Temperature only in New Hampshire, and to SOI in four of the six locations, but with no significant relationships for any of the tested explanatory variables in either Pennsylvania or New Jersey.

Of the four species considered, two (BANS and PUMA) responded as expected based on their migration strategies. The other two (BARS and TRES) responded in an opposite fashion. These species were selected in part due to an expectation that their insectivorous feeding habits would render them sensitive to local temperature conditions. Very little sensitivity was found here. These results echo a statement in Carey's (2009) review paper on climate change and avian biology, that "different investigators working on different populations at different places have found different results". This reflects the reality that birds can travel great distances and be influenced by any number of conditions along their path.

Further Considerations

It is not clear whether the inconsistent results of this study are due to the true behavior of the birds or due to the data use and study design. There are some factors that may have limited the clarity of study results, including data quality, sample size, geographic considerations, detectability issues, and selection of climate variables.

The FAD dataset used here was obtained from a historical, citizen science effort spanning nearly 100 years. While the author assumes that observers were given and adhered to strict protocols, it is possible that this was not the case. While reviewing observation records some obviously 'bad' records were encountered. For example, there were instances of double reporting, where a single observer submitted two different FAD dates for the same species in the same location and the same year. Efforts were made to locate these records and remove them, although it is possible all record keeping problems were not all found. It has been assumed for the sake of this study that these problems are not significant enough to be an issue.

There could also be an issue of statistical power given the study design. The NABPP includes approximately 4 million records. However the number of records available at the time of analysis for a species in a given location can be small. When conducting the regression analyses at the climate division level, the largest sample size was 195 (BARS in PA), and 11 of the 22 division tests run had fewer than 100 observations. Given the number of possible explanatory variables included, this test may be limited in meaning. It may be worth revisiting this test when more NABPP records have been transcribed.

The six geographic locations included were selected based primarily on the number of observations available. Given how different the results are among locations, both here and in cited studies, it's probable that populations are influenced differently in different locations. Combining the data from all six divisions into one test may have watered down the unique conditions and responses in each location. This again would be helped with availability of additional NABPP records.

Detectability is a potential issue for three reasons. First, there is no record of observer effort, so there are potential accuracy issues with the FADs that have been provided. An observer who visits the field frequently will have a much higher probability of documenting the true arrival of a species than an observer who only makes occasional visits. Second, and related, is the probability for a weekend bias in the data. As shown by Courter *et al*. (2012), citizen science observations tend to be made more often on weekend days than weekdays. This likely is not an issue here, as the same bias should be exhibited each year, thus should not significantly influence results. Third, FAD detectibly can be an issue with species that are declining in population (Miller-Rushing *et al*. 2008). It is certainly possible that any of the four species included here experienced declines during the observation period, in any or all locations. If so, the FADs may not be as accurate as hoped. The same paper suggests that median arrival date is a more accurate measure of phenology for a species as a whole. This measure, however, is not available through the NABPP data.

Lastly, but perhaps most importantly, is the consideration of which weather and climate data to include. Temperature, NAO, or SOI are common among the literature and were easy to consider for this study. Reality may be completely different, however, and weather conditions on the wintering grounds or along the migration route may be just as important is not more important than conditions are the observation location.

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CURRICULUM VITAE

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