

UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MACROSCALE POPULATION ESTIMATES FOR A MIGRANT SONGBIRD  
USING WEATHER RADAR

A THESIS

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

Degree of

MASTER OF SCIENCE

By

KYLE R. BROADFOOT  
Norman, Oklahoma  
2017

MACROSCALE POPULATION ESTIMATES FOR A MIGRANT SONGBIRD  
USING WEATHER RADAR

A THESIS APPROVED FOR THE  
DEPARTMENT OF BIOLOGY

BY

---

Dr. Jeff Kelly, Chair

---

Dr. Eli Bridge

---

Dr. Phil Chilson

© Copyright by KYLE R. BROADFOOT 2017  
All Rights Reserved.

## **Dedication**

I dedicate this work to my mother, Luan Broadfoot, without whose love and support I would be neither who, nor where, I am today.

## Acknowledgements

I would like to thank my adviser, Dr. Jeff Kelly. Through your patient guidance and support I have achieved more than I ever thought possible. The opportunities that you've provided me over the past few years are humbling, and have allowed me to grow in ways seldom afforded to most. Your persistence and expansive thinking is a model for scientists in any field, and an example I hope to follow in all of my future endeavors.

I would like to thank my committee member Dr. Eli Bridge, whose door was always open, no matter what half-baked question I may have come to pose to him. You're generosity, guidance, and encouragement for student research is truly admirable.

I would like to thank my other committee member, Dr. Phil Chilson. Through your instruction, a field biologist came to understand radar, and realize at least some of its potential. I also wish to thank Sandra Pletcher, without whose painstaking work over the last several years I would not have had such a rich data set to build upon. To all my lab mates, past and present, I thank you for the always-interesting discussions and for your open-ears and constructive ideas all throughout my journey: Dr. Andrea Contina, Dr. Jeremy Ross, Kayleigh Anaya, Paula Cimprich, and Jonathan Kruk.

Finally, I thank my colleague and lab mate, Dr. Kyle Horton, who has been instrumental in my ability to code and work confidently with radar data; who taught me to care about nice, clean figures and who showed me how to make them. You have been the perfect role model of a dedicated, engaged, and productive graduate student, and not least of all, a great friend.

## Table of Contents

|                                     |      |
|-------------------------------------|------|
| Acknowledgements .....              | iv   |
| List of Tables .....                | vii  |
| List of Figures .....               | viii |
| Abstract.....                       | ix   |
| Introduction.....                   | 1    |
| Background .....                    | 1    |
| Motivation .....                    | 2    |
| Study Species .....                 | 3    |
| Phenomenon of Interest .....        | 4    |
| Justification .....                 | 5    |
| Conceptual Approach .....           | 7    |
| Methods .....                       | 10   |
| Radar Network and Data Sources..... | 10   |
| Data Sampling and Processing .....  | 11   |
| Quantitative Estimates .....        | 12   |
| Phenology.....                      | 13   |
| Habitat.....                        | 14   |
| Results. ....                       | 15   |
| Roost Populations .....             | 15   |
| Seasonal Phenology .....            | 15   |
| Habitat.....                        | 16   |
| Spatial Biases .....                | 16   |

|                 |    |
|-----------------|----|
| Discussion..... | 18 |
| References..... | 32 |

## **List of Tables**

|   |    |
|---|----|
| Table 1. Timeline of major publications examining avian roosts with radar ..... | 24 |
|---|----|



## List of Figures

|                |    |
|----------------|----|
| Figure 1 ..... | 25 |
| Figure 2.....  | 26 |
| Figure 3.....  | 27 |
| Figure 4.....  | 28 |
| Figure 5.....  | 29 |
| Figure 6.....  | 30 |
| Figure 7.....  | 31 |

## **Abstract**

Changes in migratory bird populations can signal environmental change occurring on the wintering grounds, the breeding grounds, or along the migratory route between them. Aerial insectivores (swifts, swallows, etc.) additionally serve as an indicator of the abundance of airborne arthropods across these domains. The Purple Martin (*Progne subis*) is one such species and aspects of its life history make it ideal for remote, large-scale population studies.

During the summer months, Purple Martins form dense roosting colonies across eastern North America. As they leave these sites on diurnal foraging trips in the lower atmosphere, their exodus is routinely captured by NEXRAD weather radar facilities across the country. Data collected by these facilities are publicly available through the National Weather Service and represent a free, large-scale archive of ecological and behavioral information.

I present a method of translating radar reflectivity into a biological density product to generate raw and modeled estimates of Martin populations to examine abundance, phenology, and habitat use across the eastern U.S. Results suggest that while radar-derived estimates are variable within individual sites, aggregate population measures across roosts illustrate trends in abundance, phenology, and habitat use at continental spatial scales, and decadal temporal scales. These data can help inform and validate other citizen science efforts (e.g. Breeding Bird Survey, eBird, etc.), lay the groundwork for large-scale, long-term remote monitoring of these populations, and have broad applicability to other colonially roosting bird and bat species.

## **Introduction**

### *Background*

A long-term goal of ornithologists and conservation biologists is to monitor the size of migrant bird populations as a basis for conservation planning. A primary limitation in achieving this goal is the availability of quantitative population estimates at spatial extents relevant to understand range-wide population dynamics. Through decades of citizen science efforts such as the Breeding Bird Survey (hereafter, “BBS”, Sauer et al. 2015) and eBird (Kelling et al. 2014), ornithologists have gained invaluable information about population trends of migrant bird species at large spatial extents and decadal temporal scales. However, nearly all of these estimates are restricted to the breeding period of the annual cycle. There are few quantitative estimates of population size for any migrant passerine from periods of the annual cycle outside of the breeding season. Obtaining non-breeding season estimates of population size could be used to validate citizen science population estimates and provide new insights into the dynamics of the annual cycle of migrant populations.

While robust abundance estimates are critical to understanding migrant bird populations, conservation planning is guided by knowing how abundance changes in both space and time (Faaborg et al. 2010). Migrant bird populations are particularly susceptible to shifts in productivity between wintering and breeding ground brought on by climate change (Bowlin et al. 2010.) Understanding changes in the timing of key life history events can enable ornithologists to identify and predict these events, and better plan conservation strategies around them. Similarly, the spatial patterns of habitat use are critical for conservation because the interactions between phenology and habitat drive changes in abundance. Habitats used by migrants in the breeding range represent

critical resources in a key stage of their annual cycle. Changes in abundance associated with habitat are indicative of the needs of the species as expressed through habitat selection, but also of the overall health of their ecosystems.

The ideal means of realizing such a monitoring program would sample continuously across a species range, creating an archive of population data that could be used to assess trends in abundance and behavior. The closest approximation to this monitoring platform is the national network of WSR-88D weather radars, or NEXRAD.

Weather surveillance radar has emerged in recent decades as a useful tool for ornithologists (Gauthreaux and Belser 2003, Chilson et al. 2012). Weather radar data have been employed by a broadening number of users for diverse applications in recent years (Stepanian et al. 2016). These data hold promise for shedding light on macroscale phenology (Kelly et al. 2012, 2016), movement (Shamoun-Baranes et al. 2016), behavior (Horton et al. 2016) and habitat use (Buler et al. 2012) of animals in the atmosphere. Here we test the possibility of using weather radar as a sensor for monitoring the population of a migrant bird species at unprecedented scale and frequency.

### *Motivation*

Nebel et al. (2010) examined trends in BBS data and found that across North America, aerial insectivores have been declining. However, more recent and detailed analyses suggest that patterns of decline vary substantially by region and species (Michel et al. 2015). Collectively, there is concern about the conservation of migratory aerial insectivores and additional population data would be helpful in guiding

conservation planning. We explore the possibility of using the weather radar network in the U.S. to provide these estimates.

Together with their prey, aerial insectivores (birds and bats) constitute the majority of non-meteorological radar scatter, or so-called bioscatter, detected by the network of U.S. weather radars (Chilson et al. 2012). Many previous radar studies have examined a handful of aerial insectivores including the Brazilian Free-tailed bat (*Tadarida brasiliensis*, Horn and Kunz 2008, Frick et al. 2012), the Tree swallow (*Tachycineta bicolor*, Laughlin et al. 2014), and most notably the Purple Martin (*Progne subis*, Russell and Gauthreaux 1998). The Purple Martin is an ideal candidate for a macroscale radar analysis, given its tendency to form large aggregations at discrete locations throughout the Eastern U.S. that are routinely observed on weather radar (Fig 1.)

### *Study Species*

The Purple Martin (*P. subis*) is a large charismatic swallow species that breeds in much of eastern North American and parts of the West. Overwintering in the Brazilian Amazon (Fraser et al. 2012), Martins arrive in south Florida by late February into early March to breed. In the last century Martins have become increasingly reliant on human-provided nesting structures, often erected and maintained by a dedicated number of Martin “Landlords.”(Tarof and Brown 2013) A secondary cavity nester, the trend of Martins towards this synanthropic life history is thought to be attributable to the loss of old-growth forest across the eastern U.S., with the practice of anthropogenic nest box provision dating to pre-Colombian Native Americans (Wilson et al. 1831). Western Martins still nest in natural cavities, as with *P. s. hesperia* in the desert Southwest, or a

mixture of natural and artificial cavities in the Pacific Northwest in the case of *P. s. arboricola*.

After fledging young from breeding colonies, eastern Purple Martins (*P. s. subis*) typically form large aggregations at discrete roosting locations as a prelude to fall migration (Brown et al. 2013). Western Martins do not seem to engage in this roosting behavior. Eastern roosts may host from several thousand to many hundreds of thousands of individuals (Russell and Gauthreaux 1998). During the roosting period, Martins depart from roosts *en masse* each morning in the hour before local sunrise to spend the day foraging aloft. While the morning flights are regularly large and high enough to be observed and recorded by local weather surveillance radar, evening return flights are composed of sporadic flocks descending upon the roost site below radar coverage (Russell and Gauthreaux 1998). Summer roosts typically begin to form in June, with a peak in activity near early August, and most roosts having been vacated by late September (Kelly et al. 2012).

#### *Phenomenon of Interest*

The emergence of Martins from nocturnal roosting colonies often form diagnostic radar signatures called “roost rings”—expanding, circular patterns of radar reflectivity that increase in size and density as Martins take wing, and then dissipate as individuals disperse over foraging grounds. Purple Martin roost ring echoes are typically detected in the hour before local sunrise. Weather radar coverage at altitudes needed to detect Martin foraging flights is nearly continuous within their roost range in the eastern U.S. (Crum and Albery 1993.) Radar data from the U.S. network is publicly available through the National Oceanic and Atmospheric Administration (NOAA) and

represents an archive spanning over 25 years that contains valuable ecological information about Martins and other airborne organisms.

### *Justification*

Much of radar ornithology has focused primarily on understanding nocturnal bird migration (e.g., Able 1970, Gauthreaux 1970, Buler et al. 2014, Horton et al 2016). However, of secondary interest is the use of radar to locate and monitor communal roosts of volant organisms. Previous authors have applied radar data towards: (1) locating roosts (Russell et al 1998, Burney 2002, Tautin et al. 2005); (2) validating the correspondence of abundance indices of observers on-the-ground with radar reflectivity (Russell and Gauthreaux 1998); and (3) examining ecological correlates of emergence times (Eastwood et al 1962, Frick et al 2012) among others. Several authors have examined roosts of swallow species other than Purple Martins. Robinson et al (2009) provide a series of radar images from Oregon in September of 2008 attributed to Barn Swallows. Laughlin et al (2013 and 2014) conducted extensive monitoring of Tree Swallow roosts in Louisiana and found that the earliest roosts were initiated on 11 October and the latest roosts dissipated on 20 April. There have similarly been numerous observations of aerial flight and roosting behavior of Common Swifts (*Apus apus*) in Europe using tracking (rather than surveillance) radars (Backman and Alerstam 2001, Leichti et al 2013).

Attribution of species identity that form roosts detected by radar depends, ultimately on ground-truthed observations. However, certain life history traits of the Purple Martin make it possible to attribute roost rings to Martins with exceptionally high confidence. Martin roosts are typically active from June through September, and

are generally only observed emerging at sunrise. The diurnal nature of roost rings preclude the possibility of being attributable to bats, and the seasonal differences between Martin and Tree Swallow (Laughlin et al 2013) point strongly against their co-occurrence outside of New York and New England where some summer Tree Swallow roosts have been reported (e.g. Burney 2002, Kelly unpublished data). Table 1 summarizes nearly 60 years of radar studies of roost research and indicates the near total absence of any indication that roosts of passerine birds other than Purple Martins have ever observed in June, July, or August in North America. Ligda (1957) is the exception. He observed a roost ring near Texarkana, TX and attributed the signature to Red-winged Blackbirds (*Agelaius phoeniceus*) but did not confirm the identity visually. Given the time of observation, the surrounding habitat, and the proximity to a current, known Martin roost, it is highly likely the roost ring was indeed Purple Martins.

The use of radar to study roosting populations of Purple Martins holds the potential to address several major challenges in conservation biology. If radar can be used to quantify individuals at roost sites, it could be used as a tool to monitor populations across nearly the entire eastern range of the species, which contains the vast majority of the individuals of the species. This kind of species-level estimations at the spatial and temporal extent available with weather surveillance radar could also be useful in understanding population dynamics, especially with regard to shifts in phenology and landscape patterns that may result from climate change. Additionally, ground studies of roosts at this scale are not feasible for myriad reasons. Russell et al (1998) point out the logistical difficulty of visiting more than 100 locations across eastern North America within the window that they might be active. The fact that roosts



may occur on private lands or with remote accessibility exacerbates this challenge. While the need for ground verification of observations is critical, use of radar as a viable remote sensing technology for this and other species should be tested.

### *Conceptual Approach*

In this study, we present an application of the method developed by Chilson et al (2012) for converting radar reflectivity factor (dBZ) into raw and modeled estimates of the number of birds aloft within a radar sample volume. We apply this method to estimating the number of Purple Martins aloft above known roost locations throughout the Eastern U.S. We then examine these estimates across seasons and inter-annually as a test of the feasibility of using the NEXRAD network as a remote sensing platform for studying populations of these aerial insectivores. Finally we use the generated estimates to explore regional trends in both Martin phenology and population sizes at roost sites with respect to habitat.

Our overall hypothesis is that martin roosts represent local catchments or gathering locations for the breeding populations from surrounding locations rather than stopover locations of en route migrants. While there has been disagreement about this topic in the literature (Tarof and Brown 2013), recent tracking data indicate that en route migrants do not stopover at roost locations (Fraser et al 2013). From this hypothesis we derive several predictions. Our first prediction is that annual variation in population estimates within a roost will be smaller than that variation among roosts. Cross-regional population trends have been demonstrated to vary considerably (Nebel et al. 2010, Fraser et al. 2013, Michel et al. 2016). This suggests that because roosts are

aggregation points for local, post-breeding birds, Martins occupying the same roost should be subject to similar environmental pressures. Therefore the variation in radar-estimates within a roost (i.e. population) ought to be smaller than the variation among roosts. This outcome would also increase the likelihood that the radar method would be more reliable as a quantitative monitoring platform as such.

Our second prediction about the seasonal variation in phenology of roost populations is derived from a previous study (Kelly et al. 2012). This work examined reflectivity directly above roost sites versus control sites and found a unimodal seasonal peak in radar reflectivity across active roost sites. However, the approach used in this study only provided an index of activity rather than a quantitative estimate of the magnitude of that activity. Here, we test whether radar-derived population estimates correspond to the unimodal seasonal phenology of the local breeding populations as suggested by Kelly et al. (2012).

In summary our two predictions are: (1) Variation in population estimates across years for a roost will be smaller than variation among roosts; and that (2) seasonal phenology of population estimates will be unimodal and a lagged reflection of the regional breeding season with a peak between the start and end dates of roost detection period (Kelly et al. 2012). The alternative outcome is that the roost dynamics are not tied to the local seasonality, but rather to migration stopover dynamics at a continental scale in which case the phenology patterns would not be predictably unimodal through the season.

We further apply this quantitative method to explore trends in roost populations with respect to habitat associations presented by a previous study (Bridge et al. 2016)

that examined annual persistence of roosts with respect to predominant land cover. For eastern populations of Martins, breeding habitat is limited by the availability of human-provided nest boxes. Therefore, the breeding Martin distribution likely reflects human settlement and provisioning behaviors; however this represents a small portion of the annual cycle (~ 2 months). Roosts occur in many different habitat types (Bridge et al. 2016) and could reflect selection based on resources other than proximity to breeding locations. In a series of annually persistent roosts, we relate radar-derived population estimates as a way to quantitatively examine patterns in habitats as evinced by land cover.

To our knowledge, this effort is the first attempt to estimate populations for a migratory vertebrate species at the continental scale using an existing remote sensing framework. If successful, these methods have the potential to be applied to other colonially roosting species of birds and bats, and also to be the groundwork for a largely automated monitoring program for this and other ecologically important aerial species.

## Methods

### *Radar Network and Data Sources*

The National Weather Service (NWS) operates a network of 159 NEXRAD (WSR-88D) weather radar observation sites in the continental U.S. (Crum and Alberty 1993). These stations have operated continuously since the NEXRAD update was completed. Radar scans are collected in a circular fashion, with each sweep at successively higher tilt, or elevation angles. Within a single sweep, each radar sample volume can be spatially identified by the elevation of the radar antenna, the ordinal direction (azimuth), and the distance from the antenna, from which the radar pulse was returned. Radar reflectivity, given in dBZ, is a measure of how much of the radio pulse is returned, after being reflected back from an object aloft. Several other data products are available, however only reflectivity was used for this study. Samples are collected round-the-clock in approximately 10 minute intervals while the station is operating in Clear-Air Mode (i.e. free of significant meteorological activity.) These files are then archived and made publicly available through the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information data portal.

The Oklahoma Biological Survey maintains an updated database of roost rings of Purple Martins (Kelly et al. 2012, Bridge et al. 2016, Kelly unpublished data) detected by weather radar. It contains observations from 2009 to the present. From this database we obtained the on-the-ground point locations of roost emergences and the start and end dates of radar-observed roost activity.

In order to maximize the detection of among-year trends, and the accuracy of our estimates, we selected only those persistent roosts that had been active for five consecutive years in the period between 2009 and 2015 (n=66). We removed roosts for

which the radar data archive was incomplete (n=2) and those for which ground-truth data suggested the roosts were predominantly Tree Swallows (*Tachycineta bicolor*), Barn Swallows (*Hirundo rustica*), or Bank Swallows (*Riparia riparia*) (n=3). Roosts that were removed due to species composition were localized to the northeastern U.S. We can be relatively certain about the identity of the species at remaining roosts given the record of on-the-ground validation (Bridge et al. 2016, Kelly unpublished data), as well as the combination of the season of interest and the phenology of other potential species (Table 1, Kelly et al. 2012). Our sample for this study was 61 unique roost sites—36 of which have been validated on-the-ground—out of 234 total roosts detected intermittently across the study years. 11 roosts were analyzed for the 5 consecutive years, 50 roosts were analyzed for 6.

#### *Data Sampling and Processing*

Archived level II weather radar data were collected and processed through Amazon Web Services. In partnership with the NOAA, AWS hosts this archive for the contiguous U.S. weather radar network dating back to 1991. Using Amazon Machine Images—cloneable virtual computers—we distributed computing requirements, which reduced time needed for the analyses. We downloaded and interrogated radar data for the hours that encompassed local sunrise (generally 0900 – 1300 UTC) at the roost sites, for every day within the date range that each roost was known to be active (mean = 45.5 days).

To set the sampling domains around roosts we visually inspected radar images at each roost using a web-based, mosaicked composite ([http://mrms.ou.edu/metop/nco\\_v11\\_maps.php](http://mrms.ou.edu/metop/nco_v11_maps.php)). We made three measurements of the

diameter of a roost emergence at each site to arrive at an average radius. For each roost these radii reflect the maximum radius for that roost in that year. That is, radii were taken from days when the roost ring was particularly apparent and large. We used images from these mornings to quantify the radius around the roost site where Martins are detected by radar (e.g. Fig. 1, panel 3). Mosaicked radar images were not available for all years so radii were measured annually for each roost between 2013 and 2015. For the period from 2010 to 2012 we used the average of the 2013 -2015 measurements (year-to-year SD = 54.5 km).

### *Quantitative Estimates*

We used these radii as the roost sample extent and converted radar reflectivity (dBZ) for each radar sample volume into the biologically relevant metric  $\eta$  ( $\text{cm}^2/\text{km}^3$ ) as suggested by Chilson et al. (2012). This value may be approximately considered to be the surface area of targets detected by the radar receiver. Because in this case we can be relatively certain that the scatterers were Martins, we incorporated an approximate Radar Cross Section (RCS,  $\alpha$ ) of a Martin in order to estimate the number of Martins required to produce a given echo. In lieu of a modeled RCS of a live Purple Martin, we approximated this value based on Eastwood's (1967) calculation of  $13 \text{ cm}^2$  for the similarly-sized Common Swift (*Apus apus*). Making this assumption about the reflectivity of single Martin allowed us to estimate the number of Martins potentially occupying each radar sample volume. This value was summed for the each roost domain, within individual radar sweeps. We then added these estimates for the two lowest elevation angle sweeps (generally  $0.5^\circ$  and  $1.5^\circ$ , Fig 2A).

Summed estimates from each defined roost domain were filtered to minimize the effect of weather contamination. Estimates taken from radar files that indicated a radar sampling pattern outside of clear-air operation (i.e. elevation angles higher than 1.5°) were omitted as they likely contained significant meteorological activity. Following this summation, we censored the top 10% of the estimates as a method for removing anomalously large values that could not be due primarily to purple Martins; we retained the remaining 90 percent of the data for each year-site combination. To account for the background (non-Martin) level of reflectivity retrieved by the radar we subtracted an estimated background value from the Martin estimate (Stepanian et al 2014). For each daily emergence we calculated the maximum daily estimate as the difference between the highest and lowest (background) estimated value of Martins aloft between an hour before, and one-half hour after local sunrise.

To test whether within-site variation was less than that among sites, we calculated the coefficient of variation for each roost site and compared them to among roost coefficient of variation using a one-tailed, one-sample t-test.

### *Phenology*

We made these daily estimates of Martins aloft for each day during a period between a start and end date of roost activity. This was done for each of 61 roosts across a period of 5-6 consecutive years. To describe roost phenology we fitted Generalized Additive Models (GAMs) to each site-year combination (Fig. 3). We visually inspected the form of these models to evaluate the fraction of roosts that produced results of the expected unimodal seasonal phenology (*sensu* Kelly et al. 2012). To examine

phenology at the continental scale, we created GAMs for cumulative roost abundance (i.e. across years) for each study year.

### *Habitat*

Bridge et al (2016) found that annual persistence of Purple Martin roosts differed significantly between predominant land cover types found within 5 and 10 km of the roost location. Here, we examine this relationship further by comparing radar-derived population estimates across the land cover types identified as most abundant within 10 km of each roost. Land cover data used is from NLCD2011, and is here simplified into 4 classes: agriculture, forest, urban, and water.

Additionally, we look for spatial biases in sampling that could affect roost population estimates. Namely we examine the effect on population estimates of the distance from the roost to the nearest radar station, and the size of the radius used for sampling. Finally we combined all radar estimates taken across roost sites and years to illustrate the continental phenology of total Martin abundance at these 61 roosts. Values are reported as means plus/minus standard deviations unless otherwise noted.



## Results

### *Roost Populations*

Across 61 roost locations, average mean daily population was  $27,533 \pm 23,476$ . Maximum total roost population averaged approximately  $101,000 \pm 91,000$  Martins (Fig 5). Variation within sites was significantly lower than variation between sites ( $t = -27.928$ ,  $df = 60$ ,  $p < 0.001$ ), which is consistent with our first prediction.

We calculated net population change across the study years for each roost as the year-to-year difference in means. Average net population change across sites was  $-2,695 \pm 13,984$  ( $n = 61$ ). Approximately 56% of roosts showed a net decrease in maximum roost population across the 6 study years, while 44% showed net increases.

The modeled annual maximum cumulative roost population (Fig 6.) across all years is approximately  $1.164$  million  $\pm 79,105$  Martins ( $n = 6$ ). Cross-roost, within year mean population estimates were significantly different (Fig 7,  $F_{5,60}=6.01$ ,  $p < 0.001$ )

### *Seasonal Phenology*

Of the 355 roost-seasons that we examined (61 roosts x 5 or 6 years), 57% of GAM curve fits ( $n=202$ ) showed no evidence of a seasonal peak and instead described an overall increase or decrease across the season. Another 5% ( $n=18$ ) of these GAM fits showed an inverted, trough shaped curve that might describe high roost abundance early and late in the season with low abundance mid-season, which was contrary to our predictions of roost growth and dispersal. The final 38% ( $n=135$ ) of GAM fits displayed at least one clear peak in Martin abundance. Of these, 6 (1.6%) predicted two distinct seasonal peaks. These patterns suggest that the roosting phenology of a minority of roosts is primarily driven by local breeding dynamics whereas the phenology of a

majority of roosts is strongly influenced by regional or continental scale movements of birds among roosts.

When we examined total Martin abundance estimated on each day by aggregating data across sites and within years, the phenological curves produced by the GAM are much more consistent between years and with our expectations about the seasonal phenology of Martin roosts (Fig. 6.). This pattern suggests that the dynamics of roosts are governed by larger scale regional or continental environmental factors and bird movements. Overall peak martin roost populations occurred within an approximately 8 day range across all six years (mean = 2 Aug,  $\pm$  2.9 days). Many sites, and especially the continental abundance estimates, predict 2012 as having a peak earlier than other years (Figs 4., 5.).

#### *Habitat*

The roosts included in this study fell into 4 habitat types as described by Bridge et al. (2016) which classified them according to dominant land cover class within 10 km from the roost location: agriculture (n = 25), forest (n = 5), urban (n = 15), and water (n = 16)(Fig 5). Mean population estimates for roosts differed significantly by habitat type (Fig 8,  $F_{df=3}=3.11$ ,  $p=0.026$ ) between the 4 predominant classes with water-dominated roosts differing from forest-dominated roosts. Net population change across years and within classes were not significantly different ( $F_{3,57}=0.868$ ,  $p = 0.46$ ).

#### *Spatial Biases*

Because roost locations are widespread and distributed throughout the range covered by NEXRAD installations, and distances between roost sites and radar facilities are non-uniform—especially in the eastern and Midwestern U.S.—we explored

potential sources of sampling bias. The 61 target roosts averaged  $75.2 \pm 36.8$  km from radar sites. Distance between roosts and radar generally increased with latitude but was not significant (Adj.  $r^2=0.043$ ,  $p>0.05$ ).

Using the MRMS mosaic, we were able to make 189 unique measures of roost radii that defined the active roost domain used for daily estimates ( $34.1 \pm 10.1$  km). On average we made 3 individual measures per roost and these measures were generally for the years 2013-2015. For 8 sites, multi-year measurements were not available, so a single, static radius was used to define the roost domain. Because radii were used to define the roost domain, which in turn defined which radar sample volumes would contribute to each sample's estimate, the size of the radius was significantly and positively correlated with estimated mean daily roost population (Adj.  $r^2 = 0.42$ ,  $p<0.0001$ ).

## Discussion

The results of our population estimates confirm that weather radars are a useful tool for measuring the broad-scale patterns of phenology and abundance of Purple Martins. Variation in population estimates was greater among sites than within, suggesting that radar sampling does record distinct roost population differences. However, at the individual roost level, we observed the expected phenological trend of roost formation and dissipation from modeled radar estimates in only 135 of 355 cases. At the continental scale—all roosts taken together—the overall pattern more clearly matched our expectations (Fig. 5).

Local variation in roost populations (i.e. within roost) was lower than variation among roosts. This supports our first prediction and indicates that radar stations are sampling discrete roost populations, and that differences between roost estimates are potentially meaningful. The results from the phenological modeling do not support our second prediction, that seasonal curves should be a unimodal, lagged reflection of local breeding patterns. Some models (38%) do show this expected trend, however, the majority (62%) suggest that many roost population dynamics are more stochastic and are not necessarily driven by local breeding patterns.

Calculated coefficient of variation in estimated roost populations was significantly correlated with the percent of GAM curves that matched our predictions at each site (Adj.  $R^2=0.12$ ,  $p=0.002$ ). For each roost site, the higher the fraction of annual models that matched our predicted phenology, the lower that roost's coefficient of variation was, which also reflects the seemingly more stochastic roost populations at the majority of sites. Our data are not consistent with local breeding populations being the primary driver of Martin abundance at the majority of roost sites. One explanation is

that these populations reflect either higher levels of meteorological contamination, or that some populations could be driven by between roost, or migratory movements. However, the fraction of models matching our prediction was not significantly related to latitude (Adj.  $R^2=0.01$ ,  $p=0.195$ ), indicating that the above pattern is not likely a result of northern Martins using southern roosts as stop-over sites.

While our overall seasonal results confirm the unimodal pattern reported in Kelly et al (2012) in only 38% of cases, the sampling approach we use and that used by Kelly et al. (2012) are markedly different. For our analyses, we used larger, whole roost domains, as defined by roost radii encompassing many thousands of radar sample volumes, whereas Kelly et al. (2012) used nine pixels directly above and adjacent to roost locations as seen through the MRMS mosaic. Worth noting too, is that dates used to temporally constrain radar evaluation (i.e. start and end dates) were taken as the first and last days on which a definite morning emergence was visible through the MRMS mosaic data; meaning that if post-breeding roost assemblage and/or Fall migratory departure was relatively sudden, we may not have been able to observe the expected growth and decay of roost populations.

Martin roosts are widespread throughout the eastern half of the U.S. However, the landscape context with respect to habitat type fall across a limited spectrum of land cover classes (Fig 5.) In general roosts dominated by agriculture, water, and urban areas in the vicinity tend to be larger than those dominated by forests (Fig 8.) This compares well with findings from Bridge et al. (2016) who found that these habitats tended to host more persistent roosts. However, forest roosts in our study also had the smallest sample size ( $n=5$ ) than other classes. This may indicate that these other three habitats are more

stable from year-to-year, especially given the fact that all roosts included in this study had high persistence (i.e. 5-6 years, Bridge et al. 2016.)

For this study we used the habitat classifications delineated by Bridge et al. (2016) as the predominant land cover class within 10 km<sup>2</sup> around the radar-derived roost location. In measuring the radii of roost ring echoes we found that emergence flights are of sufficient density to retain the distinct shape out to between 18 and 67 km away from the roost center (mean = 34.1 ± 10.1 km). Russell and Gauthreaux (1998) observed this density even further away. This suggests that Martins are likely foraging at distances much greater than 10 km and are thus experiencing different foraging habitat than that present nearer the roost site. One possible explanation for the persistence of the roosts in this study from year-to-year is that the stability of the roost site structure (e.g. island, barn, bridge, etc.) is more critical than minimizing the distance to suitable foraging habitats.

In lieu of on-the-ground visual surveys of roost populations, which are costly, time-consuming, and logistically impossible at this scale, we offer estimates derived from radar remote sensing. Across sites, maximum roost populations averaged approximately 101,000 ± 91,000 Martins. Modeled cumulative roost abundance within years suggests that there are a maximum of 1.164 million Martins across the study roost sites (Fig. 5). While ground validation of these numbers is infeasible, it is instructive to compare radar derived estimates with historical visual surveys.

Russell and Gauthreaux (1998) estimated that a persistent Martin roost on Lunch Island in Lake Murray, SC contained upwards of 700,000 individuals during one morning exodus. Using our method, we estimate a maximum population, at the same

site, of approximately 32,800 birds. Again, the sampling area is considerably different: whereas Russell and Gauthreaux (1998) visually counted Martins passing over a limited section of the sky and then extrapolating, we made our calculations based on the radius-delimited roost domain.

Rich et al. (2004) estimate a global abundance of Purple Martins at 10 million  $\pm$  5 million birds. Over the years studied here there was an average of 131 roosts detected on radar for at least 7 consecutive days in any given year. This indicates that on average there were approximately 70 active roosts in each year for which we did not estimate populations. GAM-fitted estimates predict continental abundance of 1.164 million  $\pm$  79,105 Martins across the 61 roost sites of interest. If these sites may be taken as representative of the other sites in those years, this would indicate that there may be approximately 1.339 million Martins at the remaining sites. This would lead to a global estimate of 2.503 million Martins, well below that put forward by Rich et al. (2004). Alternatively, extrapolating from the average mean population estimate across roosts of 27,533  $\pm$  23,476 Martins for the 131 average annual sites yields an estimate within the eastern range (*P. s. subis*) of approximately 3.6 million birds. Finally, we could extrapolate from average maximum roost population of approximately 101,000, to arrive at a theoretical range-wide estimate of 13.23 million Martins. There are clearly several ways of extracting range-wide and species-level population estimates, and an expanded analysis could increase our confidence in one or the other method.

We chose to estimate daily abundance of Martins at each roost by taking the difference between the minimum and maximum estimates of Martins aloft within radar samples around local sunrise. This gave us a single value of the total contribution of

Purple Martins above the background radar reflectivity on each day. Because Martins are generally flying up and away from the roost location, they are necessarily flying in and out of individual radar sample volumes, meaning that each 10-minute sample may have a new set of Martins in each sample volume, with later birds replacing earlier birds. This leads to the current approach being somewhat conservative. A possible improvement on this design is to incorporate Martin airspeeds in order to model cumulative Martin emergence and better estimate the flow of whole roost emergences through the radar beam.

Recent advances in electromagnetic modeling have been able to illustrate the detailed reflective characteristics of Brazillian Free-tailed Bats (*Tardarida braziliensis*, Mirkovic et al. 2016) to more accurately predict the RCS. To date, no such model has been created for the Purple Martin, however, it would allow for more precise estimates due to the flying Martin's dynamic orientation in flight. We have here used a static RCS value borrowed from one calculated for a similarly-sized bird and have assumed them to be an isotropic scatterer. Provided with a measured RCS of a Martin, we could incorporate other, dual-polarimetric, radar products for more accurate estimates, more detailed weather discrimination, and perhaps for more precise delineation of the roost emergence, without using static roost radii.

Improvements such as those mentioned above will help increase the accuracy and generalizability of remotely-sensed population estimates for aerial insectivores. However, one advantage to our current approach is that it utilizes a publicly available data repository to acquire species-level population information without the need for difficult or logistically infeasible ground surveys (Eastwood 1967, Caccamise et

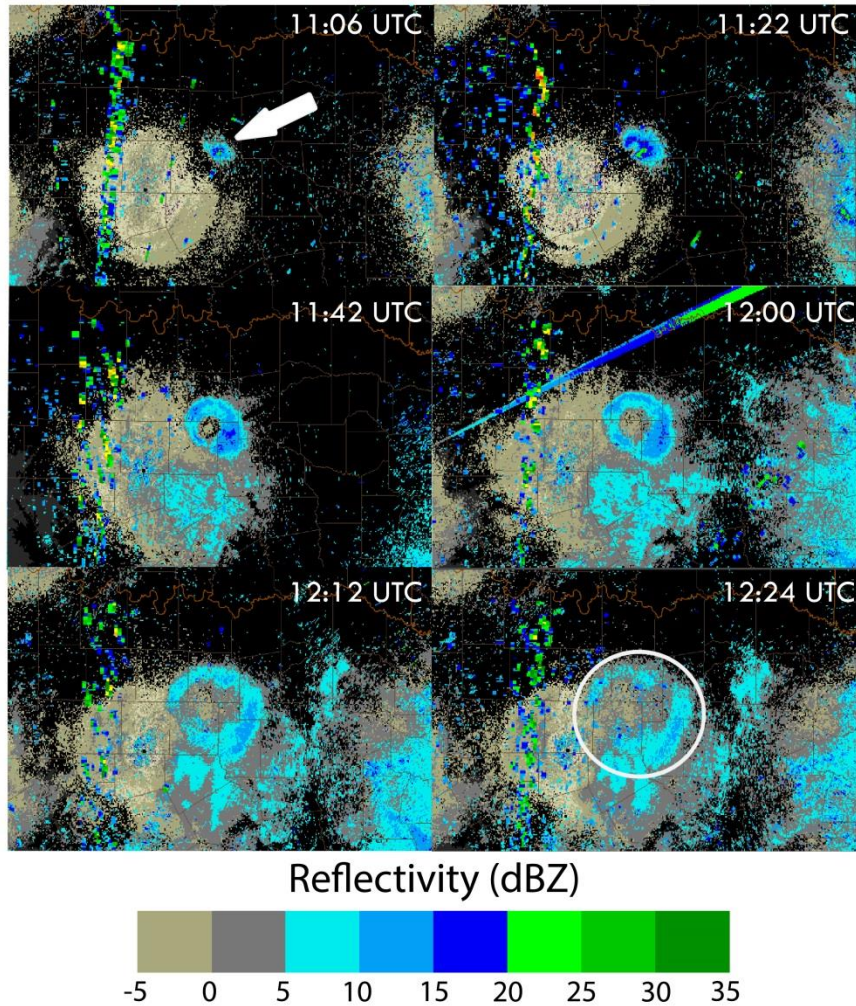


al.1983). The method we present here is also largely automated, save for several key inputs. As such, it could very easily be applied to other species of colonially roosting organisms. Other swallow species like Tree Swallows and Barn Swallows as well as Mexican Free-tailed Bat or other roosting bat species could be estimated provided with a point location, a defined spatial domain, and Radar Cross Section.

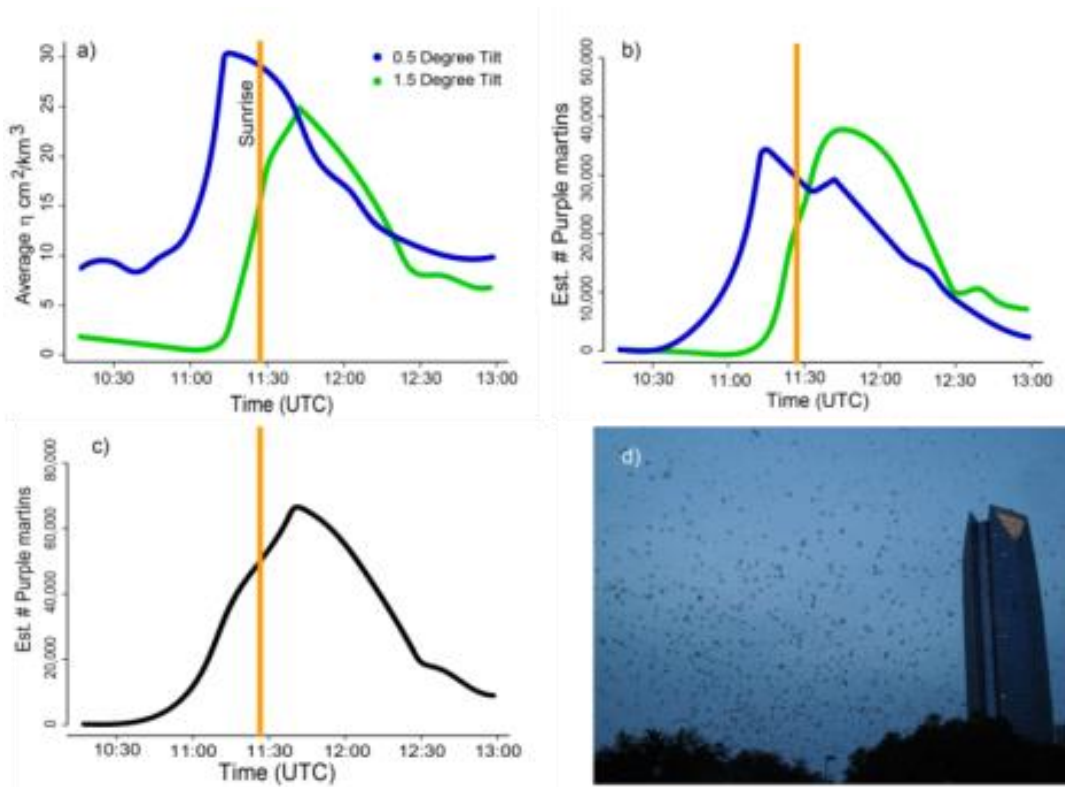
Using our current approach as a framework to build upon, we envision numerous applications in the near- and long-term. Future directions should include expanding an analysis across the full radar archive at known historic and recent sites in order to generate multi-decadal patterns of roost occupancy, if not an index of abundance. Analyses could also begin by processing radar data in near real-time to add to population trends moving forward. This would be useful also to both validate citizen science reports and to direct citizen science efforts towards on-the-ground verification of roosts. As a conservation planning tool, it would be invaluable to use archived population estimates derived from radar across a spectrum of roost persistence rates according to habitat types. Because in this study we analyzed only persistent roosts, we were not able to identify the relationships between annual persistence and population that such an analysis could. Finally, Martin breeding colonies depend greatly upon the continuity of human provisioning and maintenance of breeding boxes. The human population of Purple Martin Landlords is aging (Jervis, pers. comm.), and changes the demographics of Landlords can have significant repercussions for Martin breeding biology. It is our hope that large-scale studies of this kind may help generate public interest in observation of Martin roosts as well as conservation and thereby in establishing or maintaining breeding colonies.

**Table 1.** Timeline of major publications examining avian roosts with radar

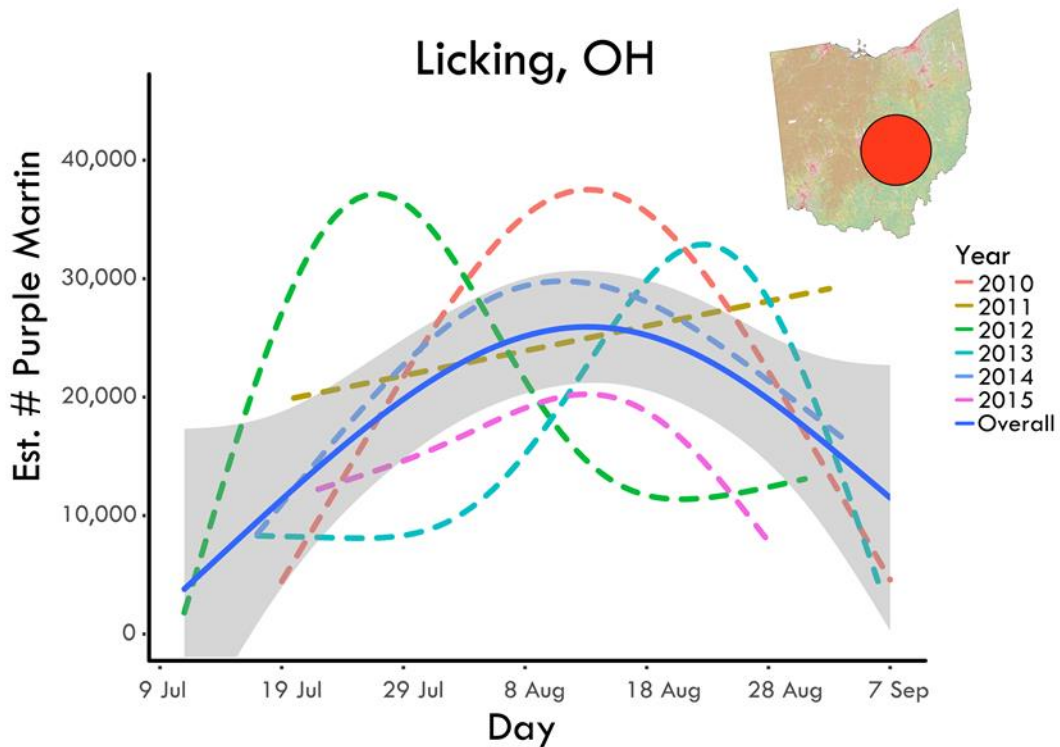
| Year          | Author(s)                 | Species                                | Area                         | Time           | Ground Confirmed | Radar Type                         |
|---------------|---------------------------|--|------------------------------|----------------|------------------|------------------------------------|
| 1957          | Ligda                     | Red Wing Blackbird                     | Texas,<br>U.S.A.             | July-Aug       | No               | Air<br>Defense<br>Command<br>Radar |
| 1959          | Harper                    | European Starlings,<br>Rooks, Jackdaws | UK                           | Winter-Spring  | Yes              | S-band                             |
| 1960          | Lack                      | European Starlings,<br>Rooks, Jackdaws | UK                           | March-April    |                  | S-band                             |
| 1960,<br>1962 | Eastwood                  | European Starlings,<br>Rooks, Jackdaws | UK                           | Year-round     | Yes              | S-band                             |
| 1998          | Russell and<br>Gauthreaux | Purple Martins                         | South<br>Carolina,<br>U.S.A. | June-Aug       | Yes              | S-band                             |
| 1998          | Russell et al.            | Purple Martins                         | S.E., U.S.A.                 | July-Aug       | No               | S-band                             |
| 2002          | Burney et al.             | Purple Martins, Tree<br>Swallow        | New York,<br>U.S.A.          | July-March     | Yes              | S-band                             |
| 2005          | Tautin et al.             | Purple Martins                         | Eastern<br>U.S.A.            | July-September | Partial          | S-band                             |
| 2009          | Robinson et<br>al.        | Barn Swallows                          | Oregon,<br>U.S.A.            | September      | Uncertain        | S-band                             |
| 2012          | Kelly et al.              | Purple Martins                         | Eastern<br>U.S.A.            | June-Sept      | No               | S-band                             |
| 2013          | Van den<br>Broeke         | Purple Martins                         | Alabama,<br>U.S.A.           | July           | No               | S-band                             |
| 2013          | Dokter et al.             | Common Swift                           | Netherlands                  | May-Aug        | Yes              | C-band                             |
| 2013,<br>2014 | Laughlin et al.           | Tree Swallows                          | Louisiana,<br>U.S.A.         | Oct-December   | Yes              | S-band                             |



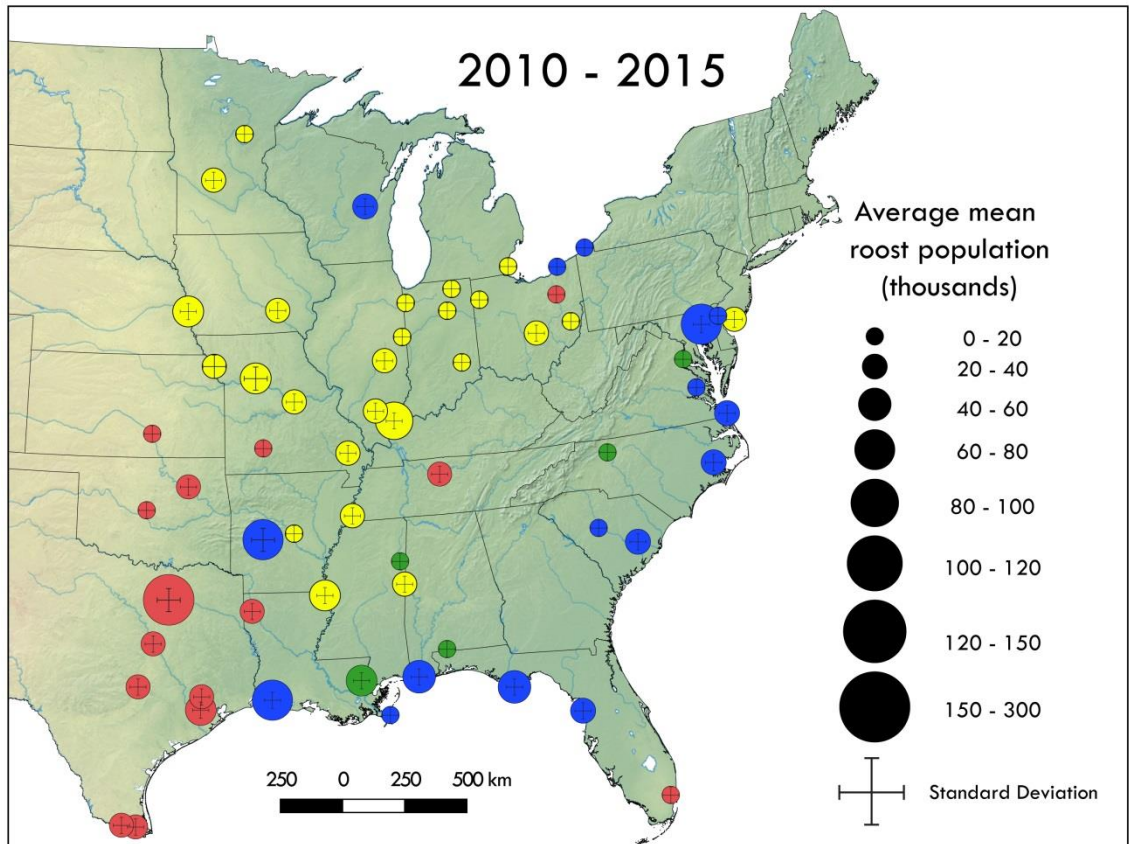
**Figure 1** Mosaicked radar images before quality control taken from nmq.ou.edu centered on Dallas, TX (KFWS). This time series 11:06-1224 UTC) shows the characteristic pre-dawn emergence and dissipation of a Purple Martin roost ring in Garland, TX. Note that the strong diagonal band of reflectivity at 12:00 UTC is a “sun spur” caused when solar radiation strikes a radar installation; in this case it is an adjacent installation to the West.



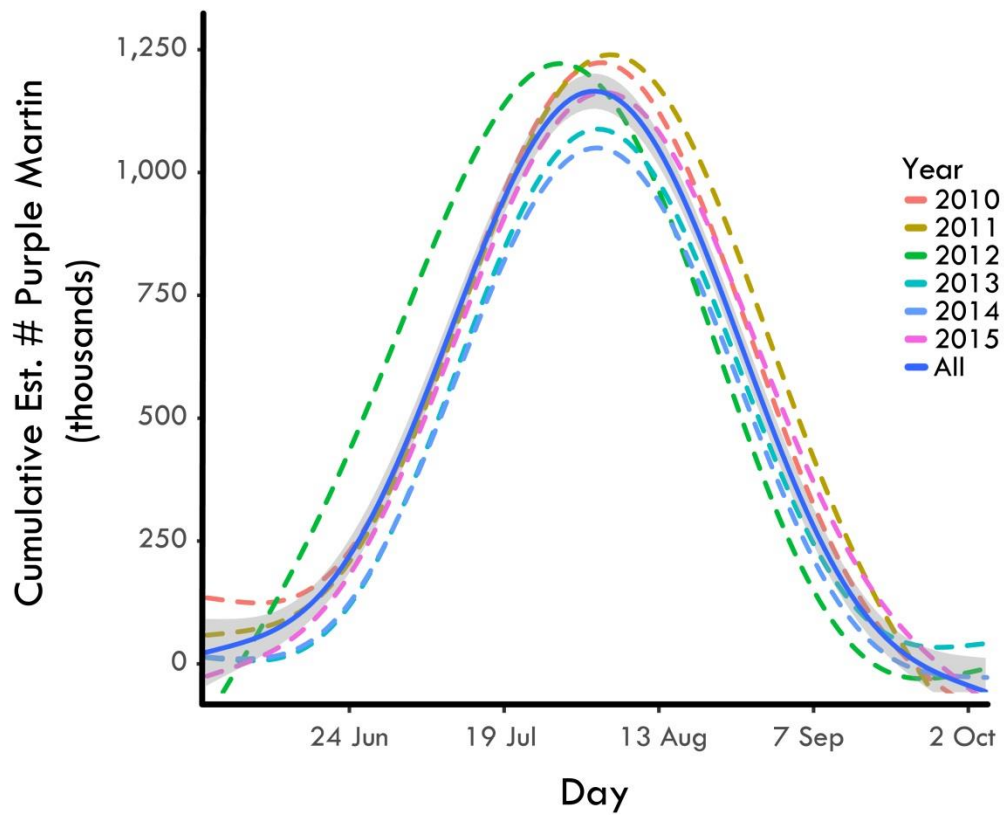
**Figure 2** Populations of Purple Martins aloft from NEXRAD radar products from KFWs station near Garland, Texas on July 13, 2014. a) Averaged values of  $\eta$  per radar sample volume for the two lowest elevation angles (blue = 0.5° and green = 1.5°) for each timestamp from 1 hour before and 1.5 hours after sunrise. Orange bar indicates time of local sunrise (11:29 UTC). b) Number of Martins aloft in two elevation angle sweeps estimated by dividing cumulative  $\eta$  by a radar cross section of 13 cm<sup>2</sup> for each elevation angle separately. Note that a background filter has been applied by subtracting a noise-floor of the minimum background reflectivity. c) Estimated population of Martins aloft at the Garland roost site taken by combining the two lowest elevation angle radar sweeps. d) Purple Martins filling the sky as they return to a roost in Oklahoma City, OK (photo: Jeff Kelly).



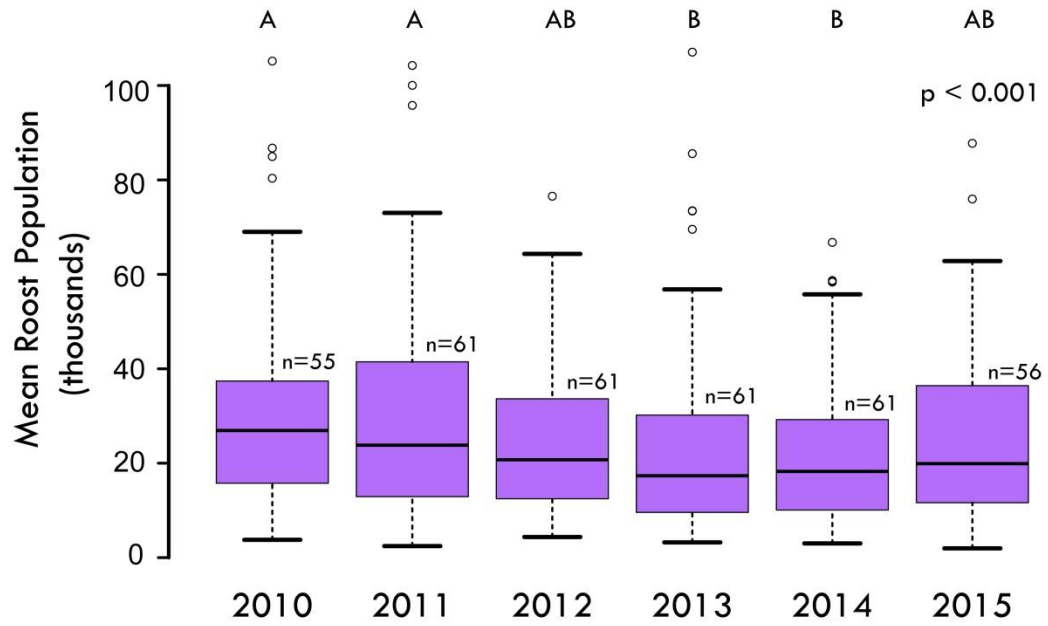
**Figure 3** Generalized Additive Model fitted estimates of Martin population at a roost in Licking, Ohio in the years 2010-2015. Peak estimates from year-to-year vary by date and population maximum. At this site, several models predict seasonal phenology of abundance, while 2011 predicts a gradual increase. As with the cumulative site models (Fig 5) 2012 is predicted to be an earlier year for peak abundance. Overall model suggests approximately 27,000 Martins attend this site across years, which is very near the between site average.



**Figure 4.** Average mean roost population estimate derived from radar according to land cover context with standard deviation. Colors indicate the dominant land cover type out to 10 km (NLCD2011, Bridge et al. 2016) in the same color scheme as Fig 7.

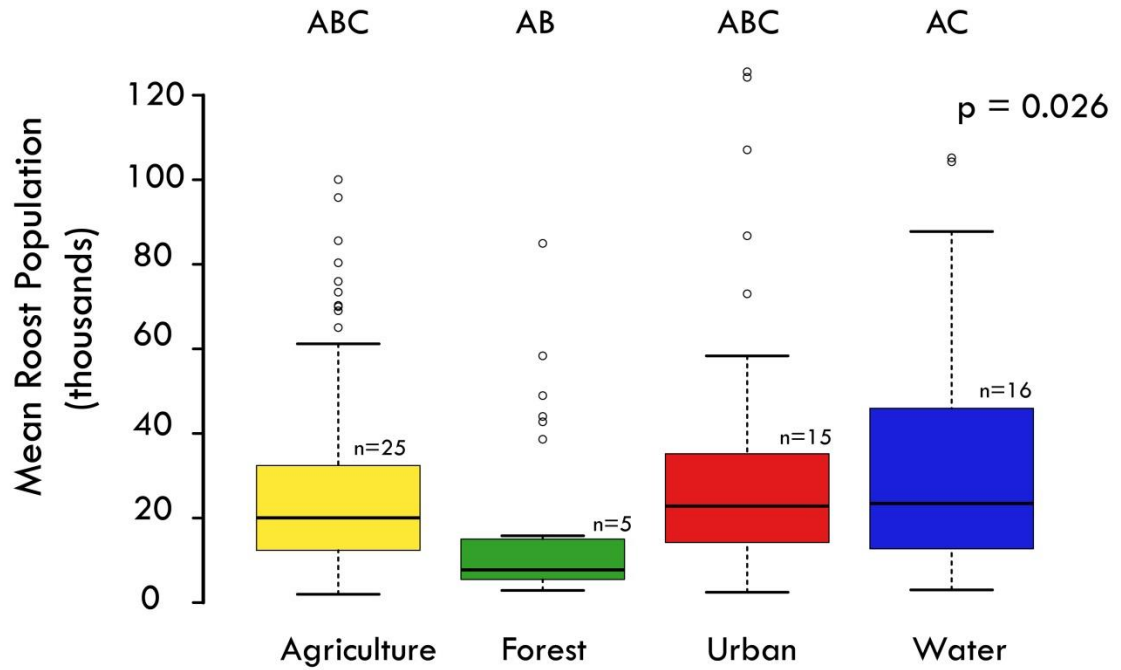


**Figure 5** GAM-fitted cumulative population of Purple Martins across 61 roost sites in eastern U.S. over a six year period. The year 2012 is predicted to be have a slightly earlier peak in abundance than other years. Overall abundance is predicted to be 1.164 million  $\pm$  79,105 Martins.



**Figure 6** Mean annual average populations for across all roosts, within years. Overall, populations differed significantly across years. Letters denote results of Tukey's Multiple Comparisons test with years 2010 and 2011 being greater somewhat greater than years 2013 and 2014.





**Figure 7.** Mean annual average populations across all roosts, within habitat classifications. Overall, populations differed significantly across classes. Letters denote results of Tukey’s Multiple Comparisons test which indicate that water roosts were significantly higher than forest roosts.

## References

Bowlin, M.S., Bisson, I.A., Shamoun-Baranes, J., Reichard, J.D., Sapir, N., Marra, P.P., Kunz, T.H., Wilcove, D.S., Hedenström, A., Guglielmo, C.G. and Åkesson, S., 2010. Grand challenges in migration biology. *Integrative and comparative biology*, 50(3), pp.261-279.

Brown, CR and Tarof S. 2013. Purple Martin (*Progne subis*), *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/purmar> DOI: 10.2173/bna.287

Bridge ES, Pletschet SM, Fagin T, Chilson PB, Horton KG, Broadfoot KR, Kelly JF. 2016. Persistence and habitat associations of Purple Martin roosts quantified via weather surveillance radar. *Landscape Ecology*, DOI 10.1007/s10980-015-0279-0

Buler JJ, Randall LA, Fleskes JP, Barrow WC Jr., Bogart T, Kluver, D. 2012. Mapping Wintering Waterfowl Distributions Using Weather Surveillance Radar. *PLoS ONE* 7(7): e41571. doi:10.1371/journal.pone.0041571

Chilson PB, Frick WF, Kelly JF, Howard KW, Larkin RP, Diehl RH, Westbrook JK, Kelly TA, and Kunz TH. 2012. Partly cloudy with a chance of migration: weather, radars, and aeroecology." *Bulletin of the American Meteorological Society* 93(5): 669-686.

Chilson PB, Kelly JF, Frick W, Stepanian PM, Shipley JR, Kunz TH. 2012. Estimating animal densities in the aerosphere using weather radar: to Z or not to Z? *Ecosphere* 3(8).

Chilson, PB, Frick WF, Kelly JF, Howard KW, Larkin RP, Diehl RH, Westbrook JK, Kelly TA, and Kunz TH. 2012. Partly cloudy with a chance of migration: weather, radars, and aeroecology. *Bulletin of the American Meteorological Society* 93(5):669-686.

Crum, TD, and Alberty RL. 1993. The WSR-88D and the WSR-88D operational support facility. *Bulletin of the American Meteorological Society*, 74(9), 1669-1687.

Diehl TH, Larkin RP, Black JE. 2003. Radar observations of bird migration over the Great Lakes. *The Auk*, 20(2), 278-290.

Eastwood E, 1967: *Radar Ornithology*. Methuen, 278 pp.

Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, Gauthreaux SA, Heglund P, Hobson KA, Jahn AE, Johnson DH and Latta SC. 2010. Conserving migratory land birds in the New World: do we know enough?. *Ecological applications*, 20(2), pp.398-418.

- Finlay JC. 1971. Breeding Biology of Purple Martins at the Northern Limit of their Range. *The Wilson Bulletin*, 83(3):255-269.
- Fraser KC, Stutchbury BJM, Kramer P, Silverio C, Barrow J, Newstead D, Mickle N, Shaheen T, Mammenga P, Applegate K, Bridge E, Tautin J. 2013. Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*) despite different migration routes at the Gulf of Mexico. *The Auk* 130(2): 291-296.
- Frick WF, Stephanian PM, Kelly JF, Howard KW, Kuster CM, Kunz TH, Chilson PB. 2012. Climate and Weather Impact Timing of Emergence of Bats. *PlosOne* 7(8):e42737
- Gauthreaux Jr. SA, Belser CG. 1998. Displays of Bird Movements on the WSR-88D: Patterns and Quantification. *American Meteorological Society*, 13:453-464.
- Gauthreaux Jr SA, Belser CG. 2003. Radar ornithology and biological conservation. *The Auk* 120(2): 266-277.
- Horton KG, Van Doren BM, Stepanian PM, Farnsworth A, Kelly JF. 2016. Seasonal differences in landbird migration strategies. *The Auk*, 133(4): 761-769 doi: 10.1642/AUK-16-105.1
- Jones T, Cresswell W. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology* 79: 98-108.
- Kelly JF, Bridge ES, Frick WF, Chilson PB. 2013. Ecological Energetics of an Abundant Aerial Insectivore, the Purple Martin. *PLoS ONE* 8(9)
- Kelly JF, Horton KG, Stepanian PM, de Beurs KM, Fagin F, Bridge ES, and Chilson PB. 2016. Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere* 7(8).
- Kelly JF, Shipley JR, Chilson PB, Howard KW, Frick WF, Kunz TH. 2012. Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars. *Ecosphere*, 3(2):2-9.
- Laughlin AJ, Sheldon DR, Winkler DW, Taylor CM. 2014. Behavioral drivers of communal roosting in a songbird: a combined theoretical and empirical approach. *Behavioral Ecology*. 1-10. doi:10.1093/beheco/aru044
- Michel NL, Smith AC, Clark RG, Morrissey CA, and Hobson KA. 2015. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. *Ecography*, 39: 774–786.
- Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conservation and Ecology*. 5(2):1

Russel KR, Gauthreaux Jr. SA. 1998. Use of weather radar to characterize movements of roosting Purple Martins. *Wildlife Society Bulletin*, 26(1) 5-16.

Rich TD, Beardmore CJ, Berlanga H, Blancher PJ, Bradstreet MSW et al. 2004. Partners in Flight North American Landbird Conservation Plan. NY: Cornell Lab of Ornithology Ithaca Partners in Flight website [http://wwwpartnersinflightorg/cont\\_plan/](http://wwwpartnersinflightorg/cont_plan/)(March: VERSION 2005).

Shamoun-Baranes J, Farnsworth A, Aelterman B, Alves JA, Azijn K, Bernstein G, et al. 2016 Innovative Visualizations Shed Light on Avian Nocturnal Migration. *PLoS ONE* 11(8): e0160106. doi:10.1371/journal.pone.0160106

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski Jr. DJ, and Link WA. 2014. The North American Breeding Bird Survey, Results and Analysis 1966 - 2013. Version 01.30.2015

Mirkovic D, Stepanian PM, Kelly JF, Chilson PB. 2016. Electromagnetic model reliably predicts radar scattering characteristics of airborne organisms. *Scientific Reports*, 6:35637, DOI: 10.1038/srep35637

Stepanian PM, Chilson PB, Kelly JF. 2014. An introduction to radar image processing in ecology. *Methods in Ecology and Evolution*, 5(8), 730-738.

Stepanian PM, Horton KG, Melnikov VM, Zrnić DS, Gauthreaux Jr. SA. 2016. Dual-polarization radar products for biological applications. *Ecosphere*, 7(11).

Tarof S, and Brown CR. 2013 Purple martin (*Progne subis*). *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.