


RESEARCH ARTICLE

Persistence and habitat associations of Purple Martin roosts quantified via weather surveillance radar

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Abstract

Context Weather surveillance radars (WSR) have been used to locate roost sites used by Purple Martins (*Progne subis*) for decades. Improvements in radar data processing and accessibility now make it possible to monitor roosts over a broad spatial scale.

Objectives We sought to locate all of the Purple Martin roosts in North America and to use the data to evaluate (1) the land cover types associated with roosts (2) relationships among roost persistence, land cover type, and regional population trends.

Methods We used mosaicked images of radar reflectivity based on the NEXRAD WSR network to locate

234 Purple Martin roosts that were active between 2009 and 2014. Of these roosts, we ground-truthed a subset of 57 with site visits and reports from citizen scientists. We assigned roosts to different classes based on local land cover, and used a variety of statistical and spatial analyses to address the objectives listed above.

Results Roosts were mainly associated with forest, cropland, urban, and water land cover types, with cropland being the most common. There was an apparent preference for urban sites, and urban roosts were associated with the high year-to-year persistence. We found no correlation between roost persistence and regional population trends in data from the North American Breeding Bird Survey (BBS).

Conclusions Although they use a diverse array of roosting habitats, urban roosting areas appear to be increasingly important for Purple Martins. Persistence

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of urban roosts was high, which aligns with the species' unique natural history and its association with human societies.

Keywords Aerial insectivores · Aeroecology · Purple Martin · Radar · Remote sensing · Roost behavior

Introduction

As we enter an era of dramatic environmental change, there is an imperative to determine how natural systems will respond. Collecting data that match the breadth of temporal and spatial scales at which the impacts of climate-change might be evident has become a central challenge for ecologists (e.g., Jetz et al. 2012). The importance of these data sets is evinced by investment in new national observatories aimed at measuring these impacts, such as the National Ecological Observatory Network (Schimel 2011). Even with these new investments, the ability to remotely sense the dynamics of animal populations and how they respond to climate change has remained largely hypothetical (Pettorelli et al. 2011), and proposed applications rely primarily on either extrinsic markers placed on select animals or sensing of primary producers as a proxy for consumer habitats (Tøttrup et al. 2012).

More than 40 years ago, satellite-based remote sensing revolutionized our approach to broad-scale studies of plant communities and primary productivity, but remote-sensing studies of animals have lagged behind. With regard to animal populations, there is little if any research that is comparable to a typical vegetative remote-sensing study in terms of fine spatial scales, high sampling frequency, and continental spatial extent.

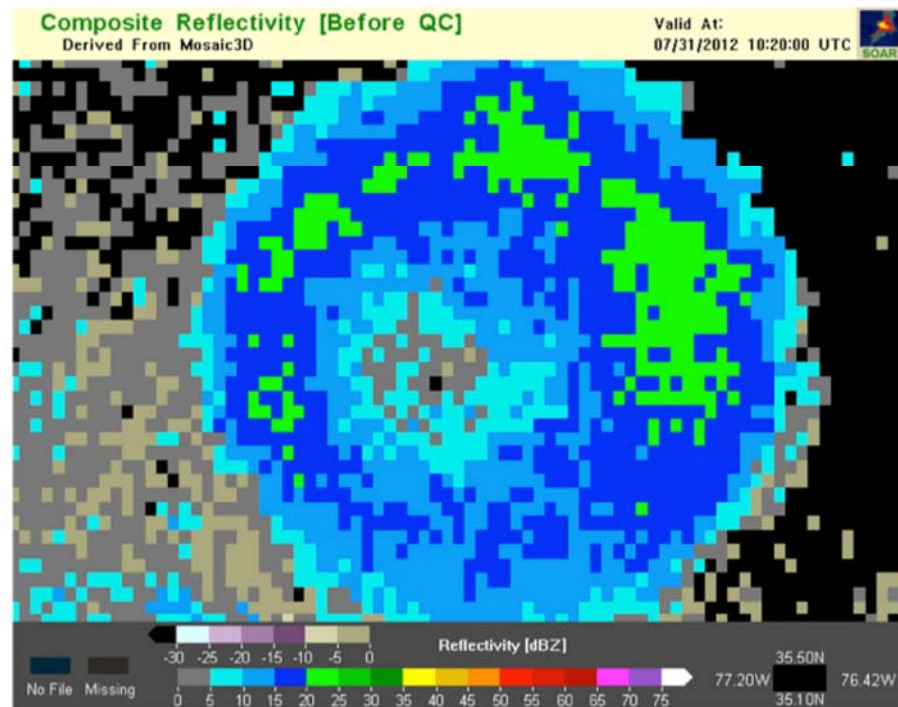
Although satellite-based sensors cannot yet directly monitor animals, there is a land-based remote-sensing system that has been recording animal activities for decades. The NEXRAD network of weather surveillance radars (WSR) has long been recognized as a means of monitoring the movements and densities of airborne animals (Gauthreaux 2006). However, there are difficulties associated with processing data from separate radar installations to generate a sensible and comprehensive biological product as well as limits on

our ability to identify the species detected by the radar. These constraints often limit the use of NEXRAD as a continental-scale remote sensing system for animals. However, the present study overcomes these limitations by employing two key strategies. First, we used recently available mosaics of NEXRAD reflectivity that combine information from all operational NEXRAD radars to provide reflectivity snapshots of the entire continental United States over intervals of 2–10 min. Second, we focused on roosting aggregations of Purple Martins (*Progne subis*), which are usually associated with a characteristic ring-shaped radar reflectivity pattern (Fig. 1). This approach has allowed us to generate what we regard as a complete inventory of all major Purple Martin roosts detectable by NEXRAD in eastern North America from 2009 to 2014.

During the late summer and early fall, Purple Martins roost in large communal aggregations at night. When they depart from these roosts in the hour before dawn they often fly much higher than most other small birds, which allows for long-range detection by radar. This distinctive flight behavior, as well as abundant reports by bird watchers and our own observations (see “Methods” section), give us great confidence in our ability to identify Purple Martin roosting aggregations in radar data. The only other species that create similar radar signatures in North America are the Tree Swallow (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*; see Laughlin et al. 2013; Winkler 2006); however, roost aggregations typically occur later for these species than for Purple Martins.

The recognizable radar signature of Purple Martins has made these birds the subject of previous radar-based studies. Russell and Gauthreaux (1998) demonstrated that radar reflectivity factor (dBZ) measured at a single WSR near a Purple Martin roost was correlated with the number of Purple Martins observed departing that roost. Independent validation of this conclusion came from Chilson et al. (2011), who demonstrated that intensity of radio-wave scatter detected by a WSR and expressed in terms of radar reflectivity factor is directly proportional to radar reflectivity, which can be related to the density of birds in a sampled air volume. Extending previous efforts, Russel and Gauthreaux (1999) and Russell et al. (1998) combined reflectivity-factor data at individual radars to identify 33 martin roosts throughout 13 states in the southeastern U.S. In addition to radar-based studies, the Purple Martin Conservation Association

Fig. 1 Typical roost ring from the SOAR web page, which was used to identify the locations of a Purple Martin roost sites. Each pixel is $0.01^\circ \times 0.01^\circ$. This site is in Beaufort County, NC, 35.35° latitude, -76.85° longitude



(purplemartin.org) has initiated a publicly available database of martin roost locations, many of which were located in 2004 using WSRs. Using the roosts in this database, Kelly et al. (2012) showed that the UNQC CREF data product (i.e. un-quality-controlled composite reflectivity) was an effective way to measure the seasonal phenology of Purple Martin roost formation and dissipation at hundreds of roost sites. These analyses also showed that most of the sites identified in 2004 were active in subsequent years.

As far as we are aware, there has been no national multi-year inventory and monitoring of a continentally distributed consumer using any remote-sensing methodology, and the effort described here is the first to use radar to monitor the dynamics of a wildlife population on a continuous and continental scale. Many potential avenues of research are enabled by this inventory. Here we chose to investigate linkages among three general metrics: (1) year-to-year persistence of roosts, (2) regional trends in Purple Martin populations, and (3) the land cover types associated with roosts. We predicted that the persistence of roosts would reflect the population trends in the surrounding region, with higher roost persistence in areas where Purple Martin populations are increasing. Given the

differences in available habitats across the species range, we also predicted that there would be regional differences in the land cover types selected as roost habitat. Finally, we made the null prediction that there is no relationship between roost persistence and underlying land cover type.

Methods

Study species and roosting behavior

Purple Martins are the largest of the swallows (Family Hirundinidae), and one of five *Progne* swallows in the Americas. They are abundant migrant aerial insectivores that breed in North America each spring (Tarof and Brown 2013). The species is common in the eastern U.S., where they nest communally in human-provided nesting structures. During most of the non-breeding season they spend nights in large communal aggregations (henceforth: roosts). Although reliable counts for the numbers of birds in these roosts are lacking, estimates are often in the tens of thousands, and they vary by an order of magnitude from roost to roost. Roosts begin to assemble as the breeding season

ends (early to late July) and are common in the eastern United States through August (Kelly et al. 2012), at which time Purple Martins begin migrating south to wintering sites in central Brazil (Fraser et al. 2013). Although the same locations often serve as roost sites from year to year, little is known about the processes that govern when and where roosts form or how long they persist. Aside from anecdotal accounts of roosts in groves of trees or under bridges (Tarof and Brown 2013), there has been little quantitative assessment of biogeographic features associated with roost locations.

Compilation of roost data

We began compiling Purple Martin roost locations using coordinates for 365 roost sites identified by the Purple Martin Conservation Association (purple-martin.org; Kelly et al. 2012). For each of these locations, we visually searched the UNQC_CREF radar mosaic product on the Surveillance Of the Atmosphere using weather Radar (SOAR) web page (<http://soar.ou.edu/legacy.html>) [see Zhang et al. (2011) and Kelly et al. (2012) for details]. These radar mosaics are available every 2–10 min with a spatial resolution of 1 km². In August 2013 the National Severe Storms Lab released a new web interface for accessing the UNQC_CREF data that replaced the SOAR web page. We used this Multi-Radar Multi-Sensor System (http://nmq.ou.edu/applications/qvs_2d_maps.html) to search the UNQC_CREF for roosts that occurred from June 1 through September 15 of each year. Searches entailed visually inspecting the UNQC_CREF images associated with sunrises during the late summer and fall to identify reflectivity patterns associated with post-breeding Purple Martin roost sites (Fig. 1).

Roosts typically appeared approximately 30 min before local sunrise, and were evident as a small, circular cluster of pixels with radar-reflectivity-factor values of 15–30 dBZ, which is appreciably larger than the background signal. Over the next hour, the cluster of pixels generally expanded and opened in the center to form the characteristic “roost-ring” reflectivity pattern (Fig. 1), with a maximum diameter of 20–70 km. The spatial extent of the ring was likely determined by both the distance between the roost and the radar and the number of birds occupying the roost. The rings typically expanded and dissipated until they

were no longer visible against background reflectivity, which usually happened approximately 1.5 h after the time of emergence.

When emerging from roost sites, Purple Martins did not always create ring-shaped radar signatures. Often, Martin roost sites located close to WSR stations retained the appearance of a solid circle. This pattern was frequently observed for roosts in both Tulsa, Oklahoma and Oklahoma City, Oklahoma. Another atypical roost signature was a semi-circle formation, presumably generated when a given heading is biased upon emergence. This pattern was observed often at the Garland, Texas roost site, which was one of several roosts that we visited. Because of this variation, a flexible search image was maintained when scanning for Purple Martin roosts, and we required repeated observations across a season to classify a reflectivity pattern as a roost.

At each potential roost location, we examined the radar images that corresponded to one hour before local sunrise until at least 10 min after (approximately 10:00 until 12:00 UTC) for the period from 1 June through 15 September of 2009 through 2014. Radar images were typically refreshed every 5 or 10 min. We included all Purple Martin roosts where (1) emergences persisted for at least 7 days in at least 1 year, and (2) where emergences took the form of roost rings on some mornings. Emergences that occurred less than 7 times and never took the shape of the roost-ring signature were considered to be of uncertain status and not included in further analysis. We were often unable to determine if a roost was present due to saturation of the reflectivity data by precipitation or other anomalous reflectivity. These instances were scored as missing data and did not count toward the minimum of 7 detection days required to identify a roost.

To validate our identification of radar features as Purple Martin roosts, we attempted to visit 17 suspected Purple Martin roost sites in and around Oklahoma during the summers of 2011 and 2012. We confirmed the presence of Purple Martins at 12 of these sites. At the remaining 5 roosts, we were unable to approach the roost sites as they were located on large parcels of private land, and we lacked landowner permission to access the immediate roost sites. There were no cases for which we identified roost rings by radar and later discovered that they were caused by species other than Purple Martins. Additionally, we were able to assemble ground-truth data for an

additional 46 roosts that we detected by radar. All of these were confirmed to be Purple Martin roosts by observers on the ground during years for which we examined the radar data. For these reasons, we are confident that our data set captures virtually all large Purple Martin roosts; however, it is likely that many small transient roosts (i.e., those with relatively few birds) that occurred from 2009 to 2014 are missing from our data set.

Tree Swallows have been reported to comprise a significant minority of individuals at some martin roosts in the eastern U.S. and may even dominate some roosting aggregations (Burney 2002). Tree-Swallow-dominated roosts present a radar signature similar to that of Purple Martin roosts, but Tree Swallows begin roosting later than Purple Martins and their pre-migratory roosts persist through October, well after fall migration for Purple Martins (Laughlin et al. 2013). Roosts dominated by Tree Swallows and perhaps other species are clearly evident in radar data along the Gulf Coast in autumn, after the Purple Martin pre-migratory roosts have dispersed (Laughlin et al. 2013). None of the reflectivity patterns classified as Purple Martin roosts in the present study corresponded with this late roost phenology. We know of one Tree Swallow roost, located in the Montezuma National Wildlife (Seneca Falls, New York), that sometimes begins as early as August. It is possible that this roost and a few others regarded as Purple Martin roosts are mischaracterized in our data set, but given the large number of roosts included in the study, it is unlikely that these misinterpreted radar signatures would have any qualitative effect on the patterns we report.

While searching for Purple Martin emergences at specific roost locations, we concurrently searched all adjacent areas of the radar imagery, such that we identified all roosts that were visible in the UNQC_CREF radar products within the eastern United States, where the vast majority of the population breeds. We recorded latitude, longitude, county, and state of all previously unknown roosts that we discovered. We also archived a time-stamped, UNQC_CREF image of each roost when it most resembled the characteristic roost ring. To assign geographic locations to roost sites we adopted the coordinates reported by the Purple Martin Conservation Association for roosts that had records in their existing database. For roosts that were not in that database we assigned a location based on the earliest

sign of emergence in the radar data on several mornings. The minimum elevation radar scan at each roost depends on the distance from that roost location to the nearest WSR. Consequently, the correspondence between the location where birds were first detected by radar in the air and the location of the roost on the ground is inexact, and the coordinates we report are necessarily an approximation of the locations of the roosts. Based on the roost sites for which we have direct visual observations, nearly all emergence locations estimated from the radar mosaic occurred within 10 km of the actual on-the-ground roost site.

To determine if there was declining detectability of roosts with increasing distance from the nearest WSR installation, we generated 234 random points within the land surface contained in the minimum convex polygon of all detected roost sites. We then compared the distribution of distances between random points and the nearest WSR (i.e., random distances) to the distribution of distances from roost sites to nearest WSR (i.e., roost distances). We predicted that if roost detections declined with increasing distance from WSRs, then distances from random points to WSRs would be greater, on average than the distances from roosts to WSRs.

Land cover assignments

We characterized the dominant land cover type surrounding each roost based on the 2010 North American Land Cover Data (Natural Resources Canada et al. 2010). This dataset had a resolution of 250 m and categorized all of North America into one of 19 land cover types. To aid interpretability we condensed these land cover types into eight categories: forest, shrubland, grassland, wetland, cropland, barren, urban, and water. We had precise locations for 57 roosts by virtue of on-the-ground verification by the authors or by reports from citizen scientists. For these roosts the dominant land cover type was assigned based on the pixel from the North American Land Cover data that corresponded to the roost's coordinates. For the remaining roosts, we obtained a similar categorization for the estimated roost location, but we also tabulated all pixels within a 10×10 km square with the roost at the center. If 75 % or more of the land cover within this 10×10 km plot was of a single type and if that land cover type was the same as the roost's initial land cover assignment, then we regarded the roost as having a

“confirmed” land-cover assignment. These roosts, in addition to those with on-the-ground verification comprised a subset of 115 roosts. For the remaining roosts, we made land cover assignments based on the dominant land cover type within the 10 × 10 km plot surrounding the roost. For convenience, we refer to different “roost types” in accordance with their underlying land cover (e.g. water roosts, crop roosts, etc.); however, we note that characterization of the exact land cover type immediately associated with each roost was unknown among roosts that lacked on-the-ground confirmation. For statistical tests that relied on accurate land cover assignments, we performed separate analyses for the entire dataset and for the subset of confirmed roost types. Finally, we performed a third evaluation of land cover within a 40 × 40 km square surrounding the roost to allow for comparison of the local roost land-cover type to the land cover in the surrounding area. Discrepancies between the roost land-cover type and the dominant land cover in the surrounding area may be indicative of selection for particular roosting habitats.

Initial visual inspection of the distribution of roost types suggested clustering of roosts in association with the dominant land cover in the roost vicinity (e.g. crop roosts, and forest roosts, Fig. 2). To test whether clustering was real or perceived, we used R version 3.1.0 (R Core Team 2014) to perform an Individual Species Area Relationship (ISAR) analysis as described by Wiegand et al. (2007) using R packages *spatstat* (Baddeley and Turner 2005) and *spatialsegregation* (Rajala and Illian 2012). This analysis yielded an index value for each roost type represented by 3 or more roosts indicating the degree to which roosts of the same type tended to cluster together. To test whether the ISAR indices differed from a random spatial distribution of roost types we first calculated ISAR indices for 1000 random Poisson-process point simulations based on the range and sample sizes of the original data set. We then compared the ISAR indices from the real data to the means and 95 % confidence intervals of the simulated ISAR indices, with the expectation that significant clustering would yield ISAR scores less than the lower 95 % confidence interval.

Roost persistence

We quantified roost persistence as the number of years a roost was apparent in the radar data from 2009 to

2014. We used R version 3.1.0 (R Core Team 2014) to test for spatial autocorrelation with regard to roost persistence by performing a Mantel test with the package *ade4* (Dray and Dufour 2007). We then used ANOVA to test the null hypothesis that roost persistence was even across all roost types.

We also tested whether roost persistence was related to regional, long-term population trends for Purple Martins. These trends were assessed using data from the North America Breeding Bird Survey (Sauer et al. 2014). Breeding Bird Survey data consist of species counts for established roadside surveys conducted regularly during summer months by skilled amateur and professional ornithologists. We used data from 66,136 survey routes from 1966 to 2014, which constituted almost all routes for all available years wherein a Purple Martin was detected in at least one year. We excluded 13 surveys that reported 250 martins or more, which likely reflect instances where observers saw large flocks or breeding colonies; these chance occurrences were essentially outliers that could strongly influence trend estimates. We generated a 3-degree grid for the Purple Martin breeding distribution, and we estimated population trends by fitting a zero-inflated poisson linear model to all of the survey data within each grid cell, with year as the independent variable and survey count as the dependent variable. We smoothed the trends for each grid cell using inverse distance weighting with a q of 1.5. We extracted an average population trend value for a circle with a radius of 100 km around each roost. We tested for a relationship between these population trends and roost persistence using linear regression, and we also tested whether perennial roosts (those observed for 4 or more consecutive years) and intermittent roosts differed in accordance to regional population trends.

Results

From 2009 through 2014 we located a total of 234 roost sites used by Purple Martins in 31 U.S. states and Ontario, Canada (Fig. 2). The number of roost sites detected in a single year varied from 124 in 2014 to 144 in 2012. Of the total number of roost sites, 113 (48 %) were active for at least 4 years (hereafter referred to as perennial roost sites), whereas 121 (52 %) were active for 1, 2 or 3 years (hereafter

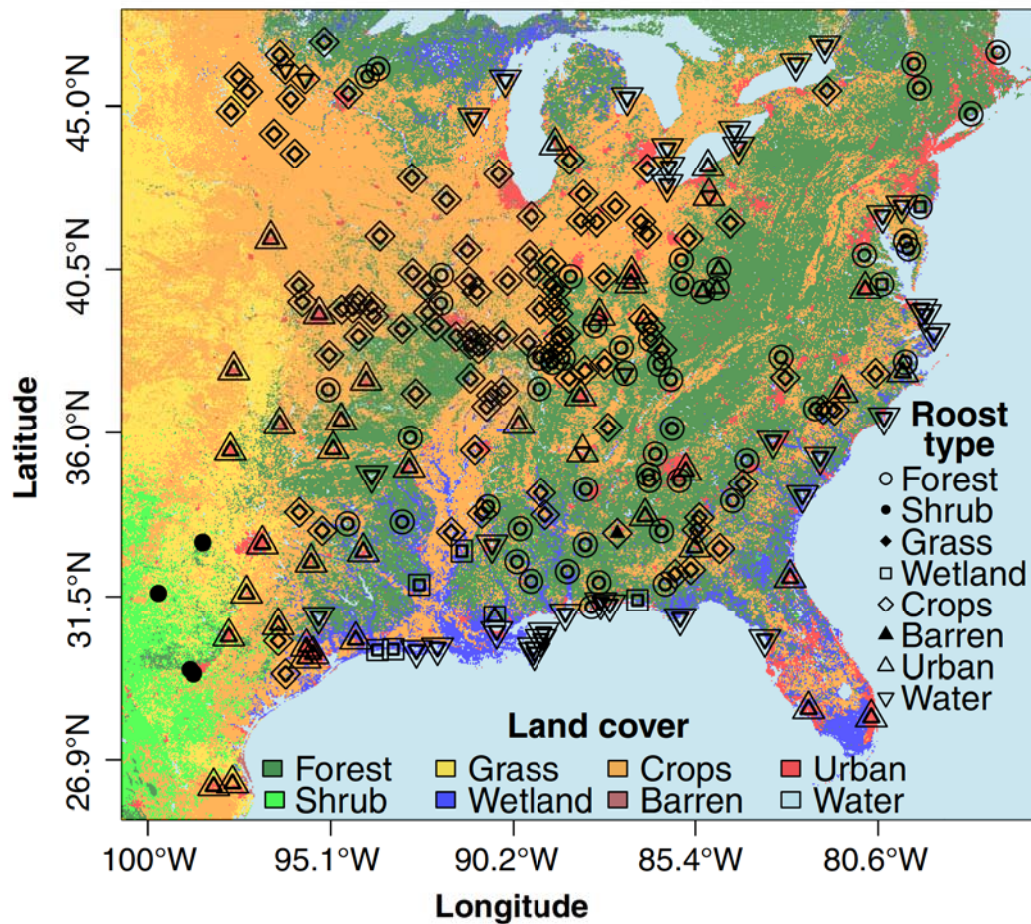


Fig. 2 Locations of 234 Purple Martin roosts identified using weather surveillance radars over 6 years (2009–2014). Map colors correspond to eight different land cover classifications. Symbols denote Purple Martin roost types with regard to the

underlying land cover. For each roost, a smaller symbol representing the land cover type at the estimated roost coordinates is surrounded by a larger symbol that represents the dominant land cover type within a 10×10 km square surrounding the roost

referred to as intermittent roost sites). Of the 234 roost sites that we verified as active, 81 were not in the original database of sites maintained by the Purple Martin Conservation Association (PMCA), and we detected no activity at 211 sites listed in the database. Our failure to detect these 211 roosts is not surprising given that the PMCA database dates back to 2004; hence, the roosts we failed to detect had probably ceased being used by martins prior to 2009.

There were 89 WSRs in the area where we detected roost sites. The average nearest-neighbor distance between WSRs was 169 ± 38 km with a maximum distance of 247 km. Roost sites were located an average of 85 ± 38 km from the nearest WSR with the greatest distance between a roost site and the nearest WSR of 206 km. Hence, we appeared to have

complete radar coverage of the area where we detected Purple Martin roost sites. There was no correlation between the distance from a roost site to the nearest WSR and the number of years a roost site was active ($F_{1,232} = 2.81$, $R^2 = 0.012$, $P = 0.09$), which suggests that our results were not biased by failure to detect roosts that were relatively far from the nearest radar. Moreover, we found no significant difference when comparing the mean nearest-neighbor distance between 234 randomly located points and the WSRs (89.0 ± 39.0 km) to the mean nearest-neighbor distances between the actual roost sites and the WSRs ($F_{1,232} = 0.15$, $P = 0.66$).

Purple Martin roost sites were located predominately in four land-cover types: forest, cropland, water, and urban (Fig. 3). There were only seven roosts in

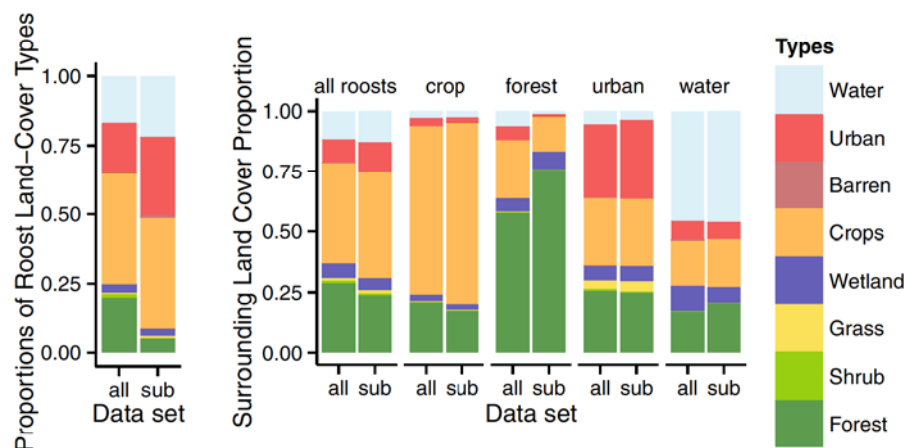


Fig. 3 Proportions of different roost types (*left*) and proportions of land cover within 40×40 km boxes centered on roost locations (*right*). Bars are paired to show results for the entire data set (“all”) and for the subset of confirmed roost types (“sub”). Sets of bars depicting land cover proportions in the

areas surrounding roosts are shown for the four main roost types. Note that surrounding land cover is generally dominated by the same land cover type associated with the roost site, with the exception of urban roosts

wetlands and the remaining land cover types (shrubland, barren, and grass) hosted three or fewer roosts. The most common land cover type for the 115 roosts with confirmed land cover assignments was cropland (40 %), followed by urban (29 %). For all 234 roost sites, crop roosts were again the most common (40 %), while the second most common was forest (24 %). This discrepancy among confirmed roosts is likely due to a bias in validation efforts, with more validations of urban roosts than forest roosts. Given the opportunistic nature of on-the-ground confirmation of roost sites, there is an implicit bias towards validation of urban roosts as they are nearer to more potential observers.

Our examination of ISAR indices indicated that there was significant clustering within different roost types. For the entire data set, four of the five ISAR indices for the real data were below the 95 % confidence interval of the ISAR scores from the random simulations; urban roosts were the exception. We repeated this analysis using only the 115 roosts with confirmed land cover assignments, and the results were similar except that all roosts types, including urban, were below the 95 % confidence intervals of the simulated ISAR values. Hence, almost all roost types showed strong evidence of spatial clustering, which is likely due in large part to regional land cover patterns. Land cover in the 40×40 km square representing the surroundings of each roost was generally dominated by the same land cover type assigned to each roost (Fig. 3). Again, urban roosts

were a notable exception. The larger area surrounding urban roosts was only 31 % urban on average (Fig. 3). Hence, as a group, urban roosts did not occur in urban dominated surroundings. Moreover, Urban land cover within the land surface delineated by the minimum convex polygon containing all roosts, amounted to less than 5 % of the land cover, whereas urban roosts comprised 18 % of the roosts detected. These findings suggest that Purple Martins may be drawn to urban environments during the roosting period, particularly in the western part of their range.

Roost persistence

There was no significant spatial autocorrelation with regard to roost persistence (Mantel test: $r = 0.014$, $P = 0.12$). We could not evaluate roost persistence for shrubland, grassland, and barren roosts, because there were too few of them (≤ 3), so the following analysis applies to the remaining five roost types. An ANOVA of roost persistence versus roost type indicated a difference among the means for the roost types (all roosts: $F_{4,224} = 5.29$, $P < 0.001$; confirmed subset: $F_{4,108} = 5.98$, $P < 0.001$), and Tukey’s post hoc test indicated that the mean persistence of urban and water roosts was significantly higher than that of forest roosts ($P \leq 0.007$ for both data sets; Fig. 4). Persistence of urban roosts was also marginally greater than that of crop roosts (all roosts: $P = 0.077$; confirmed subset: $P = 0.068$), and water roosts were marginally

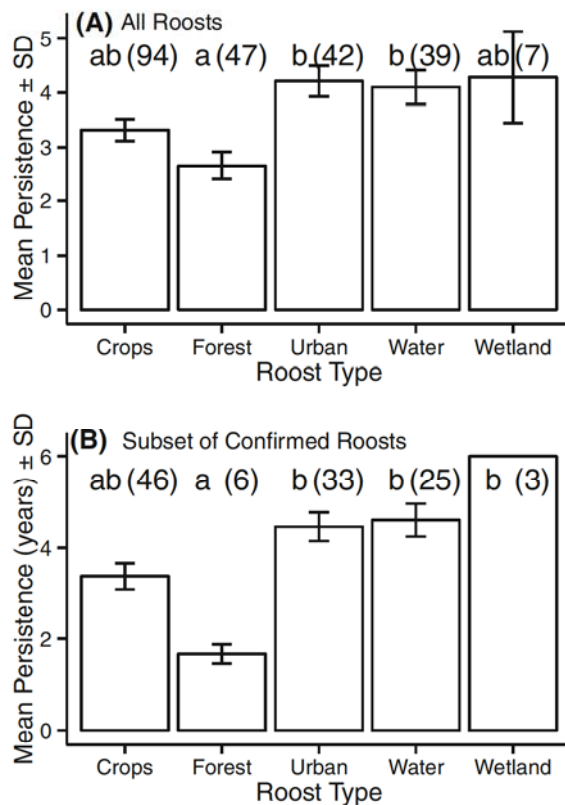


Fig. 4 Roost persistence for five different roost types based on **a** the entire data set and **b** the subset of confirmed roost types. Significant differences ($\alpha = 0.05$) in mean persistence for the different roost types based on Tukey's post hoc test are indicated by lowercase letters along the top of the graph alongside sample sizes in parentheses. Error bars represent standard deviation

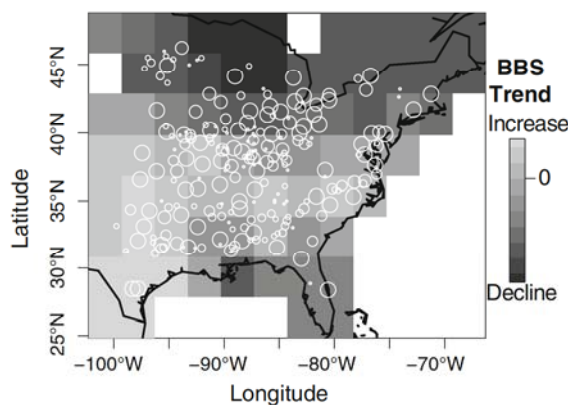


Fig. 5 BBS population trend data interpolated using a zero-inflated Poisson linear model and inverse distance weighing for sets of survey counts within 3° grid cells. Purple Martin roost locations are indicated by circles, with larger circles indicating more persistent roosts

more persistent than crop roosts for confirmed roosts types only (all roosts: $P = 0.18$; confirmed subset: $P = 0.051$). There was general agreement between the analysis based on all roosts and the one for the confirmed roosts; however, forests were poorly represented in the confirmed roosts subset ($n_{\text{subset}} = 6$). Moreover, wetlands were poorly represented in both data sets ($n_{\text{all}} = 7$ and $n_{\text{subset}} = 3$).

The trend map derived from BBS data indicated slight differences in regional population trajectories, with Purple Martins declining in the northern United States while remaining unchanged or increasing in the southern and coastal portions of their range (Fig. 5). This pattern agrees with Tautin's et al. (2009) previous assessment of BBS data for Purple Martins. There was no correlation between roost persistence from 2009 to 2014 ($R^2 < 0.001$, $P = 0.88$, $n = 234$). There was also no difference between the population trends in areas surrounding perennial and intermittent roosts ($F_{1,232} = 0.18$, $P = 0.67$).

Discussion

Purple Martins are unique among wild bird species with regard to their extreme dependence on anthropogenic nesting structures. The history of Purple Martin stewardship in North America extends as far back as the pre-Columbian agricultural practices of Native Americans (Wilson et al. 1831). Prior to this time, Purple Martins likely nested in abandoned woodpecker cavities available in the abundant old-growth forests that preceded European colonization. Dependence on anthropogenic structures and habitats likely occurred in response to degradation of forest habitats via logging and introduction of invasive competitors. Purple Martins have thus demonstrated remarkable flexibility in adapting to changes in the ecological landscape, and a key element in their success has been an ability to exploit the emergence of Purple Martin stewardship in American culture. In recent decades the range of Purple Martins has been expanding westward (Brown 1997; Ray 1995). It is interesting to note here that nearly all of the roosts near the westward edge of the species range occur in urban zones. The only exceptions were the three shrubland roosts—the only roosts of this type in our dataset—all of which were transient. Thus, Purple Martins' attraction to anthropogenic environments both for nesting and roosting as well as their evident

persistence at such sites may be a significant driver of their current range expansion.

As we have shown, Purple Martins' use of the ecological landscape varies both temporally and spatially with respect to land cover. Perhaps our most notable finding is that roost persistence differed according to the land cover type within which it occurred. Persistence was high for urban and water roosts, low for forest roosts, and intermediate for crop roosts. It is possible that this pattern is related to year-to-year variability in these different land cover types. Forests in the eastern US (i.e., 20 ecoregions defined in Omernik and Griffith 2014), experienced a 4.1 % decrease in area from 1973 to 2000; and in the Great Plains (17 ecoregions in Omernik and Griffith 2014), forest declined by 0.4 % (Loveland and Acevedo 2014). The Purple Martin roost range also overlaps with a third ecoregion (Midwest-South Central); however, the regional synthesis for this area is unavailable. Over the same time period, urban and water land cover types in the eastern US saw an increase of 26.5 % and 3.8 % respectively (Drummond and Loveland 2010; Loveland and Acevedo 2014); and in the Great Plains, there were increases of 0.3 and 0.4 %, respectively (Drummond and Auch 2014; Drummond et al. 2012). Although these percentages of actual land cover change (i.e. replacement of one type with another) are small in some cases, they suggest that there is more frequent disturbance and turnover associated with forests, whereas water bodies and urban cover tend to remain stable, or increase, once established. We suggest that greater stability of urban and open-water environments (as distinct from wetlands) helps promote roost persistence. Both of these roost types are less likely to be strongly impacted by weather extremes, like drought, and could provide a consistent and dependable annual roost structure and location. Forests as roost habitats, however, are perhaps less dependable. They are much more sensitive not only to their outright removal and fragmentation via logging, but also to drought, insect infestation, and fire. Cropland habitats, though they were intermediate with respect to persistence, could also be impacted by stochastic phenomena, both ecological and economic.

Our analysis demonstrates that WSRs in the U.S. provide the data necessary for monitoring the locations and dynamics of Purple Martin roosts throughout their breeding range. Moreover, comparison between roost

locations and random locations suggests that it is unlikely that many roosts are too far from radars to be routinely detected. We demonstrate the ability to monitor the temporal dynamics of roosts between years by tracking activity between 2009 and 2014. Somewhat surprisingly, the overall number of roosts used by martins varied relatively little between years (124–144).

Although it may be possible to monitor Purple Martin Roosts using a network of volunteer observers on-the-ground as the PMCA has attempted to do, at present these efforts do not capture the entirety of the Purple Martin roosting range and have a clear bias towards urban zones. Radar remote sensing eliminates this bias and provides an opportunity for interested observers to greatly increase knowledge of the large-scale habitat characteristics at roost sites. A major drawback to our method is the need to visually assess radar reflectivity data to locate roosts. We have attempted to develop automated methods of identifying and monitoring roosts, and have met with limited success so far. The reflectivity patterns of roosts are often quite variable and roosts are often partially obscured by noise in the radar data. Nevertheless, we remain optimistic that more sophisticated detection algorithms and/or crowd-sourcing of the manual search tasks will soon allow for a less labor-intensive path to monitoring Purple Martins and other animals using radar data. We also plan to work with interested citizen scientists to improve the amount of data available on Purple Martin roost locations and the numbers of birds they contain. By combining NEXRAD data and citizen science initiatives, we hope to enable a low-cost, remotely-sensed, continental-scale monitoring program for other animals, including bats, insects, and other migratory birds.

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References

- Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. *J Stat Softw* 12(6):1–42
- Brown CR (1997) Purple Martin (*Progne subis*). In: Poole A (ed), *The birds of North America*. Cornell Lab of

- Ornithology, Ithaca, NY. Available via <http://bna.birds.cornell.edu/bna%29/species/287> doi:10.2173/bna.287
- Burney CW (2002) A study of swallow roosts found in the Eastern United States. Cornell University, Ithaca
- Chilson PB, Frick WF, Kelly JF, Howard KW, Larkin RP, Diehl RH, Westbrook JK, Adam Kelly T, Kunz TH (2011) Partly cloudy with a chance of migration: weather, radars, and aeroecology. *B Am Meteorol Soc* 93(5):669–686
- Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 22(4):1–20
- Drummond MA, Auch R (2014) Land-cover change in the United States Great Plains. Available via <http://landcover.trends.usgs.gov/gp/regionalSummary.html>. Accessed 23 Mar 2015
- Drummond MA, Loveland TR (2010) Land-use pressure and a transition to forest-cover loss in the Eastern United States. *Bioscience* 60(4):286–298
- Drummond MA, Auch RF, Karstensen KA, Sayler KL, Taylor JL, Loveland TR (2012) Land change variability and human-environment dynamics in the United States Great Plains. *Land Use Policy* 29(3):710–723
- Fraser KC, Stutchbury BJM, Kramer P, Silverio C, Barrow J, Newstead D, Mickle N, 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. *Auk* 130:291–296
- Gauthreaux SA Jr (2006) Bird migration: methodologies and major research trajectories (1945–1995). *Condor* 98:442–453
- Jetz W, McPerson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trend Ecol Evol* 27(3):151–159
- Kelly J, Shipley J, Chilson P, Howard K, Frick W, Kunz T (2012) Quantifying animal phenology in the atmosphere at a continental scale using NEXRAD weather radars. *Ecosphere* 3(2):16
- Laughlin AJ, Taylor CM, Bradley DW, Leclair D, Clark RC, Dawson RD, Dunn PO, Norris DR (2013) Integrating Information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *Auk* 130(2):230–239
- Loveland TR, Acevedo W (2014) Land cover change in the Eastern United States. Available via <http://landcover.trends.usgs.gov/east/regionalSummary.html>. Accessed 23 Mar 2015
- Natural Resources Canada, The Canada Centre for Mapping and Earth Observation, United States Geological Survey, Instituto Nacional de Estadística y Geografía (INEGI), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional Forestal (2010) North American land cover at 250 m spatial resolution
- Omerik JM, Griffith GE (2014) Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environ Manage* 54(6):1249–1266
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewski B, Lima M, Kausrud K (2011) The Normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Clim Res* 46:15–27
- R Core Team (2014) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. Accessed 15 Nov 2014
- Rajala T, Illian J (2012) A family of spatial biodiversity measures based on graphs. *Environ Ecol Stat* 19(4):545–572
- Ray JD (1995) Purple Martins in northwest Texas. *Purple Martin Update* 6(3):10–12
- Russell KR, Gauthreaux SA (1998) Use of weather radar to characterize movements of roosting purple martins. *Wildl Soc Bull* 26:5–16
- Russell KR, Gauthreaux SA (1999) Spatial and temporal dynamics of a Purple Martin pre-migratory roost. *Wilson Bull* 111:354–362
- Russell KR, Mizrahi DS, Gauthreaux SA (1998) Large-scale mapping of Purple Martin pre-migratory roosts using WSR-88D weather surveillance radar. *J Field Ornithol* 69(3):509–509
- Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ Jr, Link WA (2014) The North American breeding bird survey, results and analysis 1966–2013. USGS Patuxent Wildlife Research Center, Laurel, MD
- Schimmel D (2011) The era of continental-scale ecology. *Front Ecol Environ* 9(6):311
- Tarof S, Brown CR (2013) Purple Martin (*Progne subis*). In: Poole A (ed) *The birds of North America Online*. Cornell Lab of Ornithology, Ithaca
- Tautin J, Cousens B, Kostka K, Kotska S, Airola DA (2009) Addressing regional declines in Purple Martin populations. In: Rich T. D., Arizmendi C., Demarest D., Thompson C. (eds), *Tundra to tropics: connecting birds, habitats and people*. In: *Proceedings of the fourth international partners in flight conference*. Partners in Flight, McAllen, TX, pp 82–87
- Tøttrup AP, Klaassen RH, Strandberg R, Thorup K, Kristensen MW, Jørgensen PS, Fox J, Afanasyev V, Rahbek C, Alerstam T (2012) The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proc R Soc* 279(1730):1008–1016
- Wiegand T, Gunatilleke CVS, Gunatilleke IAUN, Huth A (2007) How individual species structure diversity in tropical forests. *Proc Natl Acad Sci USA* 104(48):19029–19033
- Wilson A, Bonaparte CL, Jameson R, Ord G, Hetherington WM (1831) *American ornithology; or the natural history of the birds of the United States*. Constable and co., Edinburgh
- Winkler DW (2006) Roosts and migrations of swallows. *Hornero* 21:85–97
- Zhang J, Howard K, Langston C, Vasiloff S, Kaney B, Arthur A, Van Cooten S, Dempsey C (2011) National mosaic and multi-sensor QPE (NMQ) system—description, results and future plans. *Bull Am Meteorol Soc*. doi:10.1175/BAMS-D-11-00047.1