Papers in the Earth and Atmospheric Sciences   Earth and Atmospheric Sciences, Department of

2019

Radar quantification, temporal analysis and influence of atmospheric conditions on a roost of American Robins (*Turdus migratorius*) in Oklahoma

Matthew S. Van Den Broeke

University of Nebraska-Lincoln, mvandenbroeke2@unl.edu

ORIGINAL RESEARCH

Radar quantification, temporal analysis and influence of atmospheric conditions on a roost of American Robins (*Turdus migratorius*) in Oklahoma

Matthew S. Van Den Broeke [iD]

Department of Earth and Atmospheric Sciences, University of Nebraska-Lincoln, 306 Bessey Hall, Lincoln Nebraska, 68588

Abstract

Radar observations present a way to monitor large, mobile populations across long temporal scales, and are especially valuable when individual scatterers are challenging to count visually. The focus of this study is a large and relatively homogeneous wintertime roost of American Robins (*Turdus migratorius*) in central Oklahoma. Radar observations are used to estimate the roost population through winter 2010–2011, and the population time series is related to weather variables and radar beam propagation. Radar-estimated roost population gradually increased to an estimated peak of 1.5–2 million individuals from November 2010 to January 2011, and then decreased in a more stepwise manner through the spring until roost dispersal in early March. Weather conditions did not definitively explain these population decreases leading toward roost dispersal. Birds from the roost were often observed to travel >50 km away during the daytime. About 25–30% of the variability in the radar-derived roost population estimate could be explained by atmospheric variables. This work provides an example of how radar methods may be used to estimate populations and monitor their temporal trends, which may be valuable to conservation efforts by facilitating estimates of population change through time.

Introduction

American Robins (*Turdus migratorius*) are one of the most common short-distance migrants in North America, often forming large, nearly homogeneous wintertime roosts in the southern USA (e.g. Black 1932). This behavior facilitates monitoring their phenology, which can be accomplished for volant species over long time periods using radar remote sensing methods (e.g. Gauthreaux and Belser 1998; Diehl et al. 2003; Bonter et al. 2009; Buler and Dawson 2014; Horton et al. 2016a,b; Stepanian and Wainwright

2018). Their repeatable behavior and nearly homogenous roosts also facilitate the development of radar-based monitoring methods which can be applied more broadly, and the exploration of factors such as weather which may alter the radar beam path (e.g. Doviak and Zrnić 1993) and therefore influence the proportion of a population that is observed. Operational weather radars, such as the Weather Surveillance Radar-1988 Doppler (WSR-88D) network in the USA, provide broad coverage and can be used in combination with ground-based survey methods (e.g. Farnsworth et al. 2004; O'Neal et al. 2010; Horton et al. 2015).

One variable produced by this network, radar reflectivity factor (Z_{HH}), has long been used to monitor birds (e.g. Gauthreaux and Belser 1998; Diehl et al. 2003) and to estimate the total number of scatterers (e.g. individual birds or bats) if those scatterers are nearly homogeneous (e.g. Black and Donaldson 1999; Chilson et al. 2012a; Stepanian and Wainwright 2018). A radar-based approach has been used to answer questions in biology such as birds' choices of stopover locations during migration (e.g. Bonter et al. 2009; Buler and Diehl 2009; Buler and Dawson 2014), has value to address how populations have changed over many years (e.g. Kelly et al. 2012; Stepanian and Wainwright 2018), and may be beneficial as conservation strategies are developed for the future (e.g. Kelly and Horton 2016).

Weather has been linked to avian migration behavior in a large body of literature. For instance, weather reanalysis datasets have been used to understand migratory behavior of Turkey Vultures (Mandel et al. 2011). Climate change has been linked to varying avian phenology, including changing migration dates (e.g. Gordo 2007). Weather data have been used in combination with operational radar data to understand, for example, the behavior of migrating birds (e.g. Horton et al. 2016a,b). Meteorological datasets have a large potential to contribute to our understanding of biological questions, and several calls have been made to better link the two disciplines (e.g. Chilson et al. 2012b).

Avian roosting has also been studied prior using weather radar. Most such studies focus on Purple Martins (*Progne subis*), which are known to form large late-summer roosts with well-defined morning dispersal behavior. Purple Martin roosts were a relatively early focus of radar-based avian research (e.g. Russell and Gauthreaux 1998; Russell et al. 1998). Radar methods have since been used to describe their roost behavior in more detail (e.g. Kelly et al. 2012), and to relate roost sites to land cover (Bridge et al. 2016). Many additional species are known to form roosts, and a few have been studied using radar. For instance, Tree Swallow (*Tachycineta bicolor*) roost site selection has been studied using weather radar data (Laughlin et al. 2014). Some other species, such as the American Robin, may form large wintertime roosts. While American Robins may form late-summer roosts near breeding areas (Eiserer 1980; Diuk-Wasser et al. 2010), individuals migrate equatorward in the non-breeding season (approximately October-February) and are known to form roosts exceeding 250 000 individuals over a square mile (e.g. Black 1932). Reports indicate that during the day, birds in such roosts may feed close to the roost site, or possibly more than 19 km from it (Black 1932). American Robin roost sites are often characterized by dense vegetation (Walsberg and King 1980), but in Arkansas have been associated with secondary forest with dense undergrowth (Black 1932).

In this paper, weather radar data are used to document characteristics of a roost of American Robins in central Oklahoma during winter 2010–2011. The roost is larger than any described in the literature of which the author is aware. Changes in the roost population are shown through the winter, and an attempt is made to relate day-to-day variability in the morning radar-derived roost population estimate to surface weather variables and radar beam propagation. This work aims to increase our understanding of wintertime American Robin communal behavior, and provide an example of how radar methods may be used to monitor populations through time.

Materials and Methods

Roost location, radar site and analysis of radar data

The roost location was identified precisely (35.20117°N, −97.45776°W) by a survey conducted on foot by the author during the early part of winter 2010–2011 (Fig. 1). It was located along a creek flowing through a residential neighborhood in Norman, Oklahoma, and was characterized by numerous tall trees and scattered dense underbrush. Observers have noted that a large roost may or may not be present in the region during any particular year, and that location of a roost may change between years. This winter season was used because the roost was

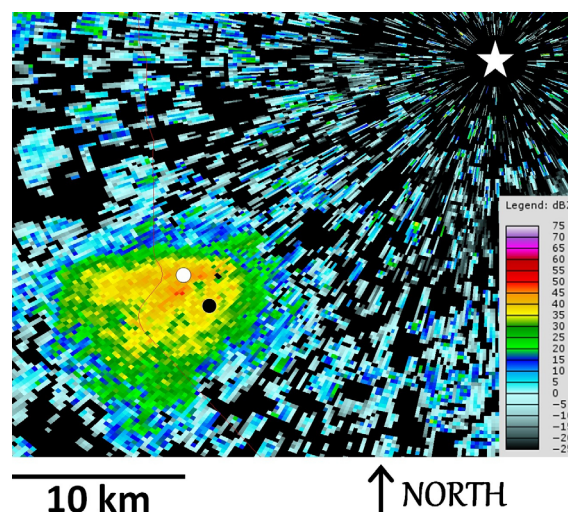**Figure 1.** Location of the Oklahoma City, Oklahoma, radar (KTLX; white star), roost as determined by ground survey (white circle), and sounding location (black circle). Radar reflectivity from 1331 UTC on 4 January 2011, when the radar-derived morning population estimate was 1 791 700 ± 258 005 American Robins. Large area of reflectivity >20 dBZ in the southwest portion of the image represents morning roost dispersal.

relatively close to the radar and meteorological data station, facilitating high-quality population estimates and comparison with weather variables. Two ground-based surveys sampled the roost and estimated its population in December 2010. The methods and results of these surveys are described below, and the ground survey population estimates were compared with radar-derived population estimates as a means of calibrating them.

Data from the Oklahoma City, Oklahoma, WSR-88D (KTLX; ~21.9 km northeast of the roost, Fig. 1) were gathered when the roost was active. Although KTLX currently collects polarimetric data, which allows the ability to differentiate biological scatterers from precipitation (e.g. Zrnić and Ryzhkov 1999; Van Den Broeke 2013; Stepanian et al. 2016), the radar had not yet been upgraded when the roost was active. Thus, in this study identification of biological scatterers is limited to known signatures (e.g. divergence of Z_{HH} from a known roost in the morning, convergence of Z_{HH} toward a known roost in the evening, expanding Z_{HH} around the radar site through the evening). The signature associated with the American Robin roost was most pronounced in base scan (lowest elevation angle; 0.5°) data (e.g. Fig. 1) and never more pronounced in the next-highest radar scan (elevation angle of 0.9°). Thus, solely base scan data were analyzed to estimate the roost population. Going away from a radar site, the radar beam spreads out both horizontally and vertically. At the location of the roost, vertical centerline of the base scan radar beam was ~0.21 km above the surface assuming standard beam propagation (what would be observed under 'typical' atmospheric conditions; e.g. Doviak and Zrnić 1993). During daily roost dispersal and formation many individuals were closer to or farther from the radar site than the roost location, so the radar beam centerline may be slightly higher or lower than this value across the area where roost-associated birds were detected. If a substantial number of birds are flying at lower altitude than beam centerline, the radar-derived population is underestimated.

Derivation of radar-derived roost population estimates

For each day, a radar-derived roost population estimate was created for the morning (roost dispersal) and evening (roost formation). To identify the analysis time for each morning and evening period, several base scans were collected during which the roost was active, and a population estimate was derived for each. The single base scan which yielded the largest population estimate was selected as the analysis time (as by Stepanian and Wainwright 2018). This methodology could contribute to a population underestimate if not all individuals were sampled

simultaneously. Data were manually examined to remove potential analysis times with data quality problems and/or precipitation. Times were also eliminated during which environmental conditions caused the radar beam to bend downward more than usual and interact with the ground (superrefraction), leading to unusually high Z_{HH} values domain-wide (e.g. Hubbert et al. 2009). For each analysis period, population was estimated following a procedure established in prior work (e.g. Chilson et al. 2012a; Stepanian and Wainwright 2018). Spatial subsetting was manually performed on each radar scan to encompass pixels associated with the roost and minimize other area. For each pixel in the subset area, the raw value of Z_{HH} was converted from units of dBZ to units of dB, using

$$\eta = Z + 10 \log_{10} \left(\frac{1000 \pi^5 K_m^2}{\lambda^4} \right) \quad (1)$$

In this equation, η = reflectivity [dB], Z = the raw radar reflectivity value [dBZ], and λ = the radar wavelength [cm]. K_m^2 is the complex dielectric constant, which is assigned given the assumed properties of scatterers. Biological scatterers are assumed to be liquid, in which case, the value of K_m^2 is set at 0.93 (e.g. Doviak and Zrnić 1993; Chilson et al. 2012a). The resulting value was converted to linear units, which provides better biological interpretation (e.g. Dokter et al. 2011; Chilson et al. 2012a):

$$\eta_{lin}[cm^2 km^{-3}] = 10^{\eta/10} \quad (2)$$

Next, volume of the radar sample volume and cross-section of the scatterers being observed are needed to estimate a total number of scatterers present:

$$Num = \frac{\eta_{lin} * Vol}{\sigma_b} \quad (3)$$

where Num = the total number of birds estimated from a pixel, Vol = the volume of a radar sample volume represented by that pixel [km³], and σ_b = the backscatter cross-section of an individual bird [cm²]. Then, the values from all subset pixels are summed to yield a total population estimate. Volume of a radar sample volume is calculated using a standard equation:

$$Vol = \pi \left(\frac{c\tau}{2} \right) \left(\frac{r\theta}{2} \right)^2 (1^{-9}) \quad (4)$$

where c = the speed of light [m s⁻¹], τ = the radar pulse length [s], r = range to the pixel of interest [m], and θ = the beam width [radians]. Backscatter cross-section for a biological scatterer (σ_b) varies by species (e.g. Eastwood 1967) and radar wavelength (e.g. Wilson et al. 1994). For this analysis, a radar cross-section of 21.2 cm²

was used for an American Robin as estimated by Kyle Horton (K. Horton pers. comm.). This estimate assumes a 10-cm radar wavelength and uses regression to predict radar cross-section given the average mass of an American Robin in comparison to the known masses and cross-sections of other species from the literature, and has an uncertainty of ~25%.

One morning and one evening ground survey during December 2010 represent the best available ground truth estimates of the roost population given their careful methods (described below). Thus, these ground survey population estimates were used to calibrate the radar-derived estimates. Multiplying the radar-derived estimate by a constant correction factor of 8.5 was found to yield close agreement to the ground survey values (±4.4%). Error in the ground survey values was estimated at 10%, which means that the optimal value of the correction factor could range from 7.65 to 9.35. This multiplicative factor accounts for a large number of individuals flying below the radar beam and for uncertainty in the assumed radar cross-section of an American Robin. The same correction factor was used throughout the winter given similar observed behavior, but may introduce error if flight altitude changed substantially through time. Note that Stepanian and Wainwright (2018) did not apply a correction factor to their radar-derived population estimates. They were studying bats which forage for insects at high altitude; thus, it is likely that the whole population is sampled by the radar beam. In this study, Robins do not forage at high altitude but rather approach and leave a roost site at relatively low altitude, decreasing the proportion of the total population within the radar beam. Utilizing a situation-specific correction factor informed by ground truth population estimates limits potential error in the radar-derived population estimate. The same methodology can be used to derive a correction factor for any situation, including any geographic region or target species. If the goal of research is to estimate the number of individuals present, a situation-specific correction factor must be derived if there is doubt about the radar cross-section and/or flight altitude of the target species relative to the radar beam. For example, substantial movement of a roost site toward or away from the radar location would necessitate the derivation of a new correction factor since a different proportion of the population is likely sampled. If the goal of research is to track the relative number of individuals across seasons or years, no correction factor is needed and the resulting population estimate can be thought of as a population density estimate.

For statistical analysis, the seasonal trend of the roost population was approximated as a third-order polynomial (e.g. Fig. 2) and removed. Detrending the data allows a more robust characterization of how various factors influence the radar-derived population estimate.

Radar beam refraction calculations

A radar beam generally curves downward as it propagates away from the radar site, but the Earth curves at a faster rate, resulting in the radar beam becoming farther from the Earth's surface with distance. This 'typical' situation may not be the case, however, nonstandard vertical gradients of temperature and/or moisture can result in subrefraction, when the beam bends downward less than usual and thus ends up at higher altitude than expected, or in superrefraction, when the beam bends strongly downward and ends up at lower altitude than expected (Doviak and Zrnić 1993). The latter may occur when temperature increases with height and/or when there is strong drying with height (Doviak and Zrnić 1993). If birds fly toward and away from a roost at a preferred altitude, altitude of the radar beam (e.g. degree of subrefraction or superrefraction) could mean the difference between detecting few birds (with subrefraction) or many birds (with superrefraction). Degree of beam bending with height can be quantitated using the vertical gradient of refractivity, so it was examined as a possible contributor to variations in the radar-derived roost population estimate. Such a contribution is meteorological in that it results from vertical distributions of meteorological variables, but their effect is not necessarily due to meteorological conditions influencing birds' behavior, but rather to the physics of radar beam propagation. Refractivity was approximated using:

$$N = \left(\frac{77.6p}{T}\right) + \left(\frac{373000e}{T^2}\right) \tag{5}$$

where N = refractivity [N-units], p = pressure [mb], e = vapor pressure [mb; a measure of moisture content], and T = temperature [K] (Doviak and Zrnić 1993). The mean refractivity gradient was calculated over the five lowest data levels in the sounding, as a simple refractivity difference divided by the altitude difference. It was important to consider whether the resulting refractivity gradient value was representative, since it could be calculated using a layer which ranged in depth from 250 to 600 m above the surface. The depth of this layer did not predict variability in values obtained ($r^2 = 0.047$; not shown), so the resulting refractivity gradient values were thought to well represent lower atmospheric conditions. Data for the refractivity calculations were taken from 1200 UTC (morning) and 0000 UTC (evening) Norman, Oklahoma (KOUN) soundings, launched from a site ~2.8 km southeast of the roost (Fig. 1). Given the near spatial collocation of the KOUN sounding observations with the roost and the small temporal offset between the sounding times and radar roost observations, surface weather observations reported from each
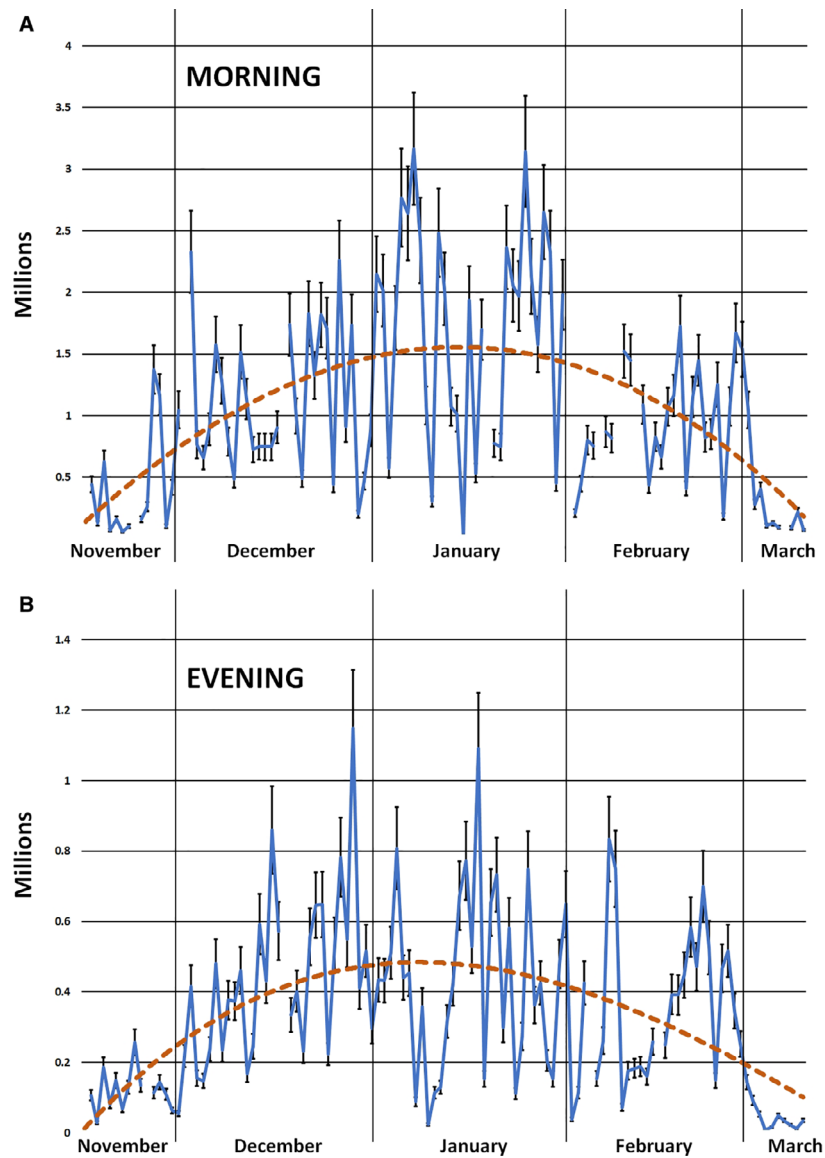
Figure 2. (A) Morning and (B) evening population estimates of American Robin roost from mid-November 2010 to mid-March 2011 (blue line), where *y*-axis is in millions of individuals. Standard uncertainty indicated as dark gray bars for each estimate. Orange dashed line indicates third-order polynomial best fit line. Breaks in the lines indicate times when data were excluded.

sounding were taken as representative of those experienced at the roost. Weather variables collected include pressure, temperature, dewpoint, relative humidity, mixing ratio, wind speed and direction, and potential temperature.

Predictive models for radar-derived roost population

Once data were gathered for each morning/evening period, predictive models were developed for radar-derived roost population as a function of weather and refractivity. The goal of this analysis was to estimate the upper limit of predictability of the radar-derived population estimate when accounting for these factors. To derive an upper limit of predictability, linear and quadratic models were constructed, and the most predictive model (e.g. model with the highest adjusted r^2 value) was selected. Predictive equations were checked for overfitting using Belsley collinearity diagnostics with a maximum allowable condition index value of 30 (Belsley et al. 2013).

Results

Ground survey population estimates

A surface observer-based roost population estimate was needed to calibrate the radar results. With two such surface-based estimates, confidence was increased that the radar-derived estimates were reasonable. Roost population estimates were derived by two independent observers on 30 December 2010. The observers did not know that multiple attempts were being made to estimate the roost size, in other words, the estimates were completely independent. The first observer noted American Robins leaving the roost during the morning of 30 December 2010. Birds were leaving the roost in all directions about equally, according to radar observations. The observer estimated they could see a swath of birds leaving the roost that extended ~60° (one-sixth of the total area), and that they could see ~250 individuals in the air at one time while looking toward the roost. The observer estimated that these individuals were replaced on average each 12 s, and that this level of activity continued for, conservatively, 60 min, or 300 replacement periods (J. Grzybowski pers. comm.). Thus, the observer's conservative estimate was that the roost contained (300 periods*250 individuals*6 to represent the full area) ~450 000 American Robins. The radar-derived estimate for this time was 466 800 individuals with the correction factor applied (within 3.7% of the ground survey value). Given the methods used to arrive at this estimate, it is taken as the most representative ground truth estimate of the roost population at a known time. On the following evening (30 December 2010), the author walked to near the location of the roost and used similar methodology to obtain a population estimate of (300 replacement periods*550 individuals*3 to represent the full area) ~ 495 000 individuals. The radar-derived estimate for this time was 516 550 individuals with the correction factor applied (within 4.4% of the ground survey value). An upper limit on error of the ground survey estimates is approximated at 10%, or ±45 000–50 000 individuals. More informal observations suggest that behavior of birds near the roost, including the time it took for birds to exit the roost in the morning and return in the evening, remained reasonably similar through the time the roost was active.

Radar-derived morning population estimates

The population estimate is plotted from mid-November 2010 to mid-March 2011, separately for the morning (Fig. 2a) and evening (Fig. 2b). Across the dataset, Pearson's correlation between the estimates from one evening and the next morning was 0.257. Error of these estimates, indicated in Figure 2, may be as high as 14.4% (10% error in population surveys +4.4% error in the correction factor). A third-order polynomial best fit line is added to the population estimate plots in Figure 2 to give an approximate sense of how the roost population changed through the analysis period. The morning population, estimated on 107 days, started at <500 000 ± 72 000 individuals in mid-November, exceeded ~1 million ±144 000 birds by early December, peaked in mid-January at ~1.5 million ±216 000 individuals, and then decreased until roost dispersal in mid-March (Fig. 2a). Estimates of >2 million ±288 000 individuals were recorded from about the end of December through the end of January ($n = 16$; 15% of all days), though such high values could be a result of changing flight altitude (e.g. the multiplicative correction factor is too large). Fall and spring population changes are dissimilar—through the fall (November and December); the roost population appears to have gradually and steadily increased, while in the spring there were two events when the roost appears to have undergone a large reduction in population. These reductions occurred at approximately 31 January and 2 March 2011.

Time of maximum population estimate relative to sunrise and sunset

Morning roost dispersal and evening roost formation followed generally similar temporal patterns from day to day. In the morning, roost dispersal generally occurred such that the maximum radar-estimated population was ~5 min prior to sunrise (Fig. 3a). During the day, birds from the roost were routinely observed to travel >50 km away, presumably to forage (e.g. Black 1932). In contrast, evening roost formation time varied from day to day. On some days, large numbers of individuals came to the roost starting an hour before sunset, while on other days a similar rate of movement did not occur until around the time of sunset (Fig. 3b). On average, the maximum radar-derived evening population estimate occurred 20–30 min prior to sunset.

Morning population estimate variability related to weather variables

Although a gradual change in the radar-derived roost population estimate was clear through the winter, the population estimate was not stable from day to day. Here, the potential contribution of weather conditions to this variability is explored. In the morning, only wind speed explained >10% of the variability in the radar-derived roost population estimate ($r^2 = 0.109$; Fig. 4; Table 1). The same was observed for the evening ($r^2 = 0.139$; not
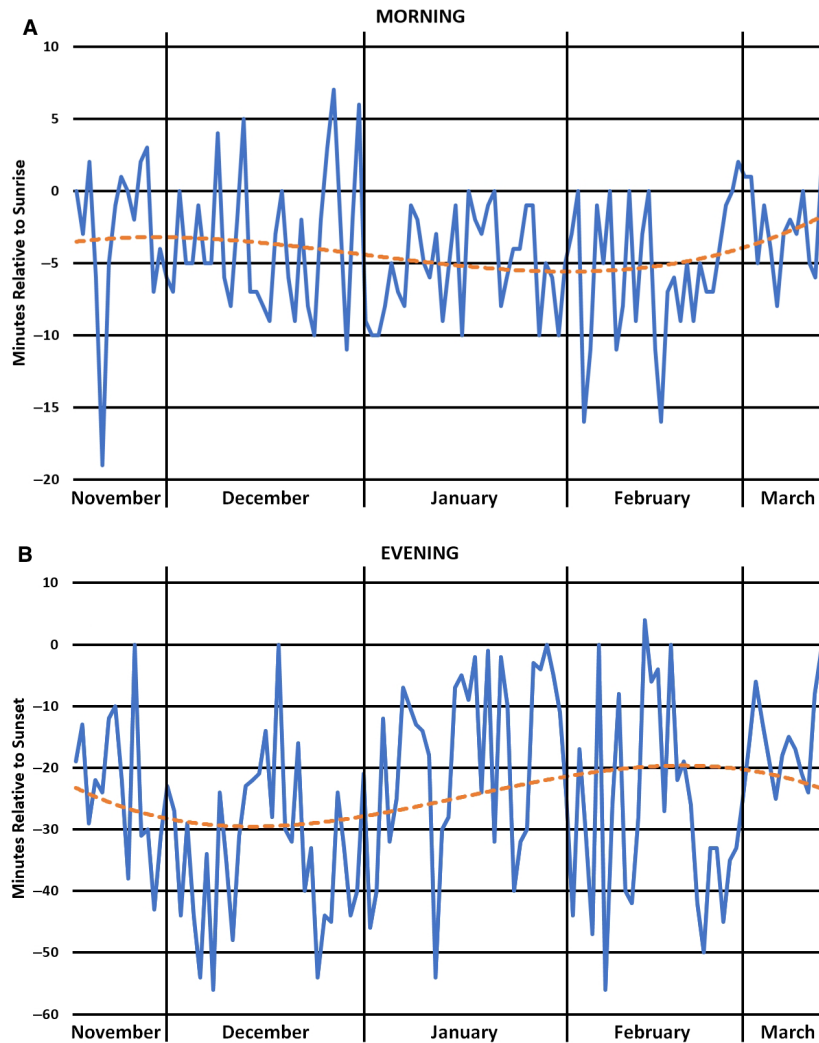
Figure 3. Time of maximum radar-derived population estimate relative to (A) sunrise and (B) sunset (blue line). Negative values represent a maximum population estimate (A) before sunrise and (B) before sunset. Orange-dashed line indicates third-order polynomial best fit line.

shown). Several models were tested to predict the morning radar-derived population estimate using weather variables as predictors. Surface potential temperature and pressure were successively removed during Belsley multicollinearity analysis, resulting in a set of predictor variables with a maximum condition index of 14.50. Since this is <30, the set of predictor variables is sufficiently independent to avoid model overfitting (Belsley et al. 2013). With the remaining predictors, a stepwise regression model with an intercept, linear terms, and squared terms was best ($r^2 = 0.320$; adjusted $r^2 = 0.257$; Fig. 5). This indicates that the set of predictors included in this analysis can reasonably be expected to predict 25–30% of the variability in the morning radar-derived population estimate. Predictability of the evening population estimate was similar.

Sunrise- and sunset-relative timing of the maximum radar-derived population estimate did not depend strongly on weather variables, though inclusion of additional variables such as cloud cover may yield better predictability.

Population estimate variability related to radar beam propagation effects

Variability in the vertical refractive index gradient was examined as a function of weather variables and month to see if any systematic patterns emerged. Morning and evening were examined separately since the vertical temperature and moisture characteristics vary substantially from morning to evening because of daytime mixing (Stull 1988). Mean morning and evening values are
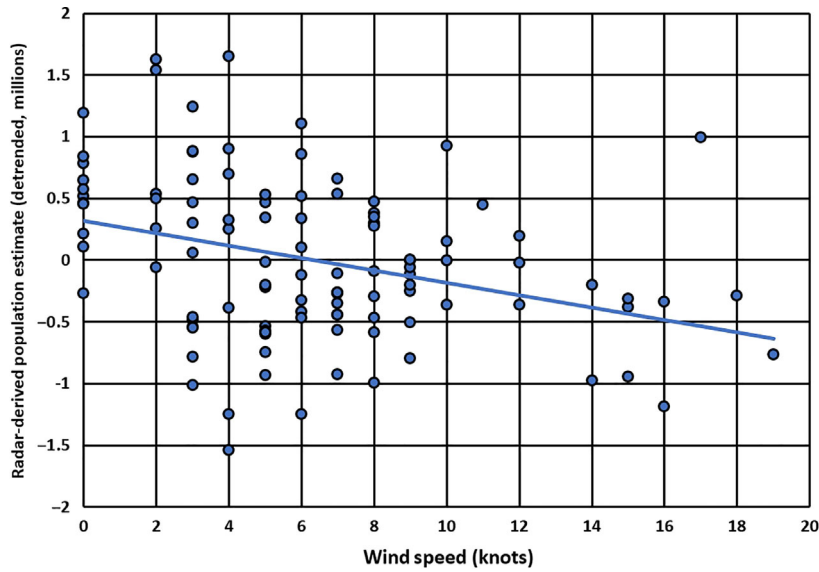
Figure 4. Morning variation in the detrended radar-derived roost population (y-axis, millions) versus surface wind speed from the corresponding sounding at Norman, Oklahoma (x-axis, knots). Stronger winds are associated with lower population estimates (Pearson's correlation = −0.330). Blue line is a linear trend fit to the data.
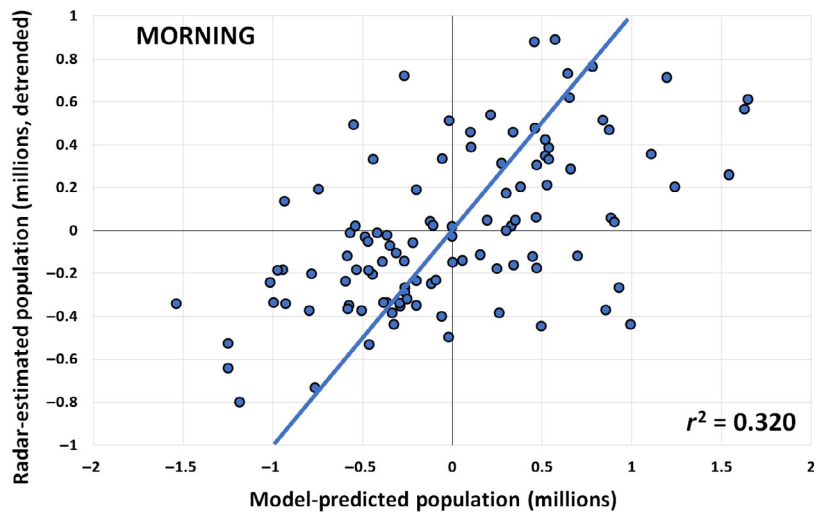

Figure 5. Morning radar-estimated roost population (y-axis, millions, detrended data) versus best model prediction (x-axis, millions) using weather and refractivity variables. Blue line indicates a perfect model prediction.

Table 1. Pearson's correlation (first row) and associated P-values calculated with significance level 0.05 (second row) between detrended radar-derived population estimates and select surface weather variables: p = pressure [mb], T = temperature [°C], T_d = dewpoint [°C], RH = relative humidity [%], w = mixing ratio [g kg^{-1}], Direction = wind direction (deg), Speed = wind speed [kt], and Theta = potential temperature [K].

Time of day		p	T	T_d	RH	w	Direction	Speed	Theta
Morning		0.106	−0.079	−0.104	−0.110	−0.127	−0.140	−0.330	−0.084
	p	0.277	0.419	0.286	0.259	0.192	0.150	5.18E − 4	0.390
Evening		−0.181	0.182	0.285	0.100	0.245	−0.172	−0.373	0.187
	p	0.057	0.056	2.43E − 3	0.296	9.55E − 3	0.071	5.50E − 5	0.049

Table 2. Mean values of the low-level refractive index gradient (N-units m^{-1}) by month.

Time of day	November	December	January	February	March
Morning	−0.0509	−0.0414	−0.0463	−0.0436	−0.0441
Evening	−0.0356	−0.0322	−0.0310	−0.0353	−0.0361

shown in Table 2. Evening (00 UTC) values are smaller than morning (12 UTC) values, indicating less stable conditions in the evening. Mean morning and evening values are also reasonably similar through the winter. Stable mornings (and consequently beam superrefraction) were, however, produced by different weather conditions than stable evenings (Table 3). Stable mornings occur when the surface pressure is high, temperature and moisture are low, and wind speed is low—this describes nights when strong surface cooling is likely to establish a low-level radiation inversion. In contrast, stable evenings are associated with low surface pressure and high temperature/moisture—more descriptive of times when clouds are likely present, leading to reduced surface heating and relatively stable conditions.

Neither morning nor evening radar-derived population estimates were strongly related to the low-level mean refractivity value (Fig. 6). Morning refractivity was more variable (Fig. 6a), though weakly predictive of the radar-derived population estimate (Pearson's correlation = −0.176). Evening refractivity values (Fig. 6b) tended to cluster around −0.03 N-units m^{-1}, with little predictive value (Pearson's correlation = −0.059). Likewise, the time of the maximum radar-derived population estimate relative to sunrise and sunset was not well-correlated with mean low-level refractivity (Pearson's correlation = 0.089 [morning] and −0.145 [evening]; not shown).

Discussion

According to radar observations, in 2010 the roost first became active in mid-November and peaked around 1.5 million birds in mid-January 2011. It dispersed through the spring, primarily in two episodes centered on the end of January and the beginning of March. This temporal evolution is consistent with new migrants arriving at the roost through the fall, with more punctuated events in which large numbers of individuals left the roost in the spring.

The evening population, estimated on 111 days, was thought to under represent the actual roost population, and was lower than the corresponding morning estimate by an average factor of 2.19. Greater evening atmospheric instability likely caused the radar beam to under sample birds at low levels. Birds also likely approached the roost at lower altitude in the evening (as observed by Russell and Gauthreaux 1998), leading to a smaller population estimate. In their study, results of morning radar and ground-based population estimates were highly correlated, though there was little correlation between the two methods in the evening. In this study, birds were observed to arrive at the roost over a relatively long period of time after foraging up to 50 km away; this longer period over which the roost population was arriving would also lead to undersampling at any one radar analysis time. The evening population estimate showed the same general trends as the morning estimate (Fig. 2b). For birds that depart a roost at higher altitude in the morning than they approach it at in the evening, the results presented here lead to the recommendation that the morning population estimate be used as most representative. Evening population estimates may be used and appear to show similar long-term temporal trends but may substantially underestimate the population being sampled.

Weather variables were somewhat correlated with the radar-derived population estimate, and clearly more correlated with it than the value of the low-level refractivity gradient. This may indicate that weather variables affecting the behavior of individuals in the roost is more important to the radar-derived population estimate than the low-level refractivity gradient, which primarily produces an effect on radar beam propagation. Windy days were associated with smaller radar-derived population estimates, possibly indicating that birds fly at lower altitude on windy days and/or that fewer birds leave the roost to forage on windy days. Atmospheric conditions

Table 3. Pearson's correlation (first row) and associated *P*-values calculated with significance level 0.05 (second row) between mean low-level refractive index gradient and surface weather variables: p = pressure [mb], T = temperature [°C], T_d = dewpoint [°C], RH = relative humidity [%], w = mixing ratio [g kg^{-1}], Direction = wind direction [deg], Speed = wind speed [kt], and Theta = potential temperature [K].

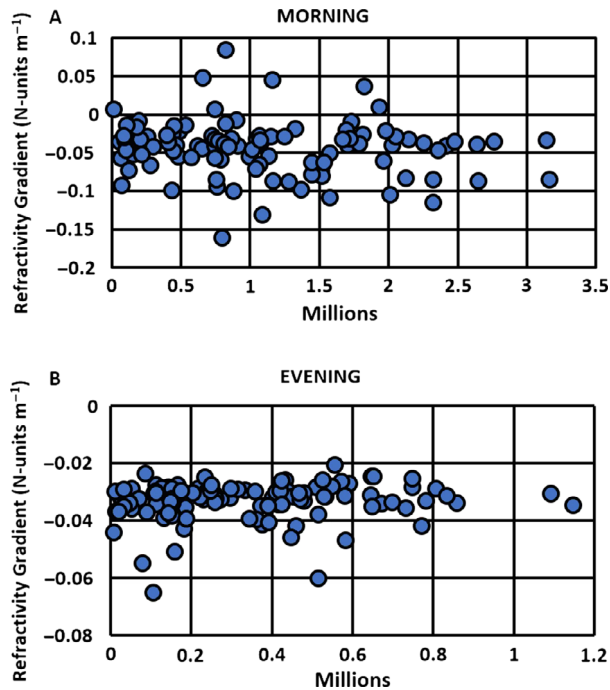| Time of day		p	T	T_d	RH	w	Direction	Speed	Theta
Morning		−0.184	0.260	0.264	0.087	0.232	0.128	0.385	0.259
	p	0.058	6.84E − 3	6.00E − 3	0.373	0.016	0.189	4.20E − 5	7.07E − 3
Evening		0.278	−0.338	−0.336	−0.042	−0.291	−0.041	0.019	−0.343
	p	3.14E − 3	2.85E − 4	3.12E − 4	0.662	1.95E − 3	0.669	0.843	2.28E − 4

Figure 6. (A) Morning and (B) evening radar-derived maximum population estimate (x-axes, millions) versus mean low-level refractivity (y-axes, N-units m^{-1}).

explained ~25–30% of the variability in the detrended morning and evening roost population estimates. Predictor variables included temperature, dewpoint, mixing ratio, relative humidity, wind direction and speed, temperature squared, relative humidity squared and wind direction squared. While the effect of wind speed has been hypothesized above, effects of the other predictor variables on roosting populations are unknown—this would be a good topic for future work. These results indicate that weather variables should not need to be extensively controlled for when using radar to derive a population estimate, though on windy days the resulting population estimate may be biased low. It is recommended to consider weather variables and lower atmospheric refractivity when using radar to estimate populations: weather may influence population behavior, and abnormal radar beam refraction may influence what proportion of a flock is observable by the radar. For species with similar roosting behavior as American Robins (e.g. Purple Martins [*Progne subis*], several other swallow species, several blackbird species, European Starling [*Sturnus vulgaris*]), to obtain the best population estimate it is recommended to use a morning observation on a day with average weather conditions and a normal to stable boundary layer. It remains unclear what proportion of day-to-day population estimate variability may be due to genuine population fluctuations. Once a semi-permanent

feature such as a large roost is established, behavioral changes seem more likely to influence changes in the day-to-day radar-derived population estimate.

Large morning population estimate decreases occurred on approximately 31 January and 2 March (Fig. 2a). This may be consistent with males leaving first to arrive on their breeding grounds early, with females following (e.g. Howe 1898; Howell 1942). It was hypothesized that large roost dispersal events should be related to weather conditions leading up to and during the dates on which the dispersals were indicated, but this hypothesis was not conclusively supported. Several cold fronts passed through Oklahoma through January 2011 with attendant north winds, likely inhibiting northward movement from the roost. A lee cyclone developed over southwest Kansas on 29 January, with the warmest southwest winds that Oklahoma had yet seen. Many birds may have left the roost during this time of favorable winds, but this is inconclusive. Super-refractive conditions on the morning of 1 February in cold north winds precluded a morning population estimate. Conditions across Oklahoma were bitterly cold during several periods over the first 2 weeks of February, followed by a general warming trend with occasional periods of moderate to strong southerly flow. No exceptional conditions were noted around 2 March, when the second radar-derived roost population reduction was indicated. Thus, while weather may be an initiator of migratory behavior, this is not a conclusive result and warrants additional research.

Herein, weather radar has been shown to be a useful tool for estimating populations of known biological scatterers through time. Such a high-resolution population record can be compared with other factors such as weather to gain new insight about population dynamics and their controls. In addition, the long-term population records possible using similar methods could be applied to many problems in conservation biology, such as how populations respond to changing land cover (e.g. urbanization, cropland development), and how populations adapt to climate variability. Similar methods can be used with historic radar data, allowing construction of long population time series which could be used to retrospectively address many ecological questions.

Acknowledgments

Data Accessibility

Radar data is freely available from the National Centers for Environmental Information (https://www.ncdc.noaa.gov/has/HAS.FileAppRouter?datasetname=6500&subqueryby=STATION&applname=&outdest=FILE) or from Amazon Web Services (https://s3.amazonaws.com/noaa-nexrad-level2/index.html). Upper air data are available at many archives, such as the University of Wyoming's sounding archive (http://weather.uwyo.edu/upperair/sounding.html).

References

Belsley, D. A., E. Kuh, and R. E. Welsch. 2013. *Regression diagnostics: identifying influential data and sources of collinearity*. Wiley-Interscience, Hoboken, New Jersey.

Black, J. D. 1932. A winter Robin roost in Arkansas. *Wilson Bulletin* **44**, 13–19.

Black, J. E., and N. R. Donaldson. 1999. Comments on "Display of bird movements on the WSR-88D: patterns and quantification". *Weather and Forecasting* **14**, 1039–1040.

Bonter, D. N., S. A. Gauthreaux, and T. M. Donovan. 2009. Characteristics of important stopover locations for migrating birds: remote sensing with radar in the Great Lakes basin. *Conserv. Biol.* **23**, 440–448.

Bridge, E. S., S. M. Pletschet, T. Fagin, P. B. Chilson, K. G. Horton, K. R. Broadfoot, et al. 2016. Persistence and habitat associations of Purple Martin roosts quantified via weather surveillance radar. *Landscape Ecol.* **31**, 43–53.

Buler, J. J., and D. K. Dawson. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. *The Condor* **116**, 357–370.

Buler, J. J., and R. H. Diehl. 2009. Quantifying bird density during migratory stopover using weather surveillance radar. *IEEE Trans. Geosci. Remote Sens.* **47**, 2741–2751.

Chilson, P. B., W. F. Frick, P. M. Stepanian, J. R. Shipley, T. H. Kunz, and J. F. Kelly. 2012a. Estimating animal densities in the aerosphere using weather radar: to Z or not to Z? *Ecosphere* **3**, 1–19.

Chilson, P. B., W. F. Frick, J. F. Kelly, K. W. Howard, R. P. Larkin, R. H. Diehl, et al. 2012b. Partly cloudy with a chance of migration: weather, radars, and aeroecology. *Bull. Am. Meteor. Soc.* **93**, 669–686.

Diehl, R. H., R. P. Larkin, and J. E. Black. 2003. Radar observations of bird migration over the Great Lakes. *Auk* **120**, 278–290.

Diuk-Wasser, M. A., G. Molaei, J. E. Simpson, C. M. Folsom-O'Keefe, P. M. Armstrong, and T. G. Andreadis. 2010. Avian communal roosts as amplification foci for West Nile Virus in urban areas in northeastern United States. *Am. J. Trop. Med. Hyg.* **82**:337–343.

Dokter, A. M., F. Liechti, H. Stark, L. Delobbe, P. Tabary, and I. Holleman. 2011. Bird migration flight altitudes studied by a network of operational weather radars. *J. R. Soc. Interface* **8**, 30–43.

Doviak, R. J., and D. S. Zrnić. 1993. *Doppler radar and weather observations*, 2nd ed. Dover Publications Inc, Mineola, New York.

Eastwood, E. 1967. *Radar ornithology*, 1st ed. Methuen Young Books, London.

Eiserer, L. A. 1980. Roosting behavior of the American Robin. *Passenger Pigeon* **42**, 96–101.

Farnsworth, A., S. A. Gauthreaux, and D. van Blaricom. 2004. A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. *J. Avian Biol.* **35**, 365–369.

Gauthreaux, S. A., and C. G. Belser. 1998. Displays of bird movements on the WSR-88D: patterns and quantification. *Weather and Forecasting* **13**, 453–464.

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migration phenology. *Clim. Res.* **35**, 37–58.

Horton, K. G., W. G. Shriver, and J. J. Buler. 2015. A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording. *Ecol. Appl.* **25**, 390–401.

Horton, K. G., B. M. Van Doren, P. M. Stepanian, W. M. Hochachka, A. Farnsworth, and J. F. Kelly. 2016a. Nocturnally migrating songbirds drift when the can and compensate when they must. Scientific Reports 6:article number 21249.

Horton, K. G., B. M. Van Doren, P. M. Stepanian, A. Farnsworth, and J. F. Kelly. 2016b. Seasonal differences in landbird migration strategies. *Auk* **133**, 761–769.

Howe, R. H. 1898. Breeding habits of the American Robin (Merula Migratoria) in eastern Massachusetts. *Auk* **15**, 162–167.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius* L.). *Am. Midl. Nat.* **28**, 529–603.

Hubbert, J. C., M. Dixon, S. M. Ellis, and G. Meymaris. 2009. Weather radar ground clutter. Part I: identification, modeling, and simulation. *J. Atmos. Ocean Tech.* **26**, 1165–1180.

Kelly, J. F., and K. G. Horton. 2016. Toward a predictive macrosystems framework for migration ecology. *Glob. Ecol. Biogeogr.* **25**, 1159–1165.

Kelly, J. F., J. R. Shipley, P. B. Chilson, K. W. Howard, W. F. Frick, and T. H. Kunz. 2012. Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars. *Ecosphere* **3**, 1–9.

Laughlin, A. J., D. R. Sheldon, D. W. Winkler, and C. M. Taylor. 2014. Behavioral drivers of communal roosting in a songbird: a combined theoretical and empirical approach. *Behav. Ecol.* **25**, 734–743.

Mandel, J. T., G. Bohrer, D. W. Winkler, D. R. Barber, C. S. Houston, and K. L. Bildstein. 2011. Migration path annotation:

cross-continental study of migration-flight response to environmental conditions. *Ecol. Appl.* **21**, 2258–2268.

O'Neal, B. J., J. D. Stafford, and R. P. Larkin. 2010. Waterfowl on weather radar: applying ground-truth to classify and quantify bird movements. *J. Field Ornithol.* **81**, 71–82.

Russell, K. R., and S. A. Gauthreaux. 1998. Use of weather radar to characterize movements of roosting Purple Martins. *Wildl. Soc. Bull.* **26**, 5–16.

Russell, K. R., D. S. Mizrahi, and S. A. Gauthreaux. 1998. Large-scale mapping of Purple Martin pre-migratory roosts using WSR-88D weather surveillance radar. *J. Field Ornithol.* **69**, 316–325.

Stepanian, P. M., and C. E. Wainwright. 2018. Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Glob. Change Biol.* **24**, 3266–3275. https://doi.org/10.1111/gcb.14051.

Stepanian, P. M., K. G. Horton, V. M. Melnikov, D. S. Zrnić, and S. A. Gauthreaux. 2016. Dual-polarization radar products for biological applications. *Ecosphere* **7**, 1–27. Article e01539. https://doi.org/10.1002/ecs2.1539

Stull, R. 1988. *An Introduction to Boundary Layer Meteorology*. Springer, Dordrecht, Netherlands.

Van Den Broeke, M. S. 2013. Polarimetric radar observations of biological scatterers in Hurricanes Irene (2011) and Sandy (2012). *J. Atmos. Ocean Tech.* **30**, 2754–2767.

Walsberg, G. E., and J. R. King. 1980. The thermoregulatory significance of the winter roost-sites selected by Robins in eastern Washington. *Wilson Bulletin* **92**, 33–39.

Wilson, J. W., T. M. Weckwerth, J. Vivekanandan, R. M. Wakimoto, and R. W. Russell. 1994. Boundary layer clear-air radar echoes: origin of echoes and accuracy of derived winds. *J. Atmos. Ocean Tech.* **11**, 1184–1206.

Zrnić, D. S., and A. V. Ryzhkov. 1999. Polarimetry for weather surveillance radars. *Bull. Am. Meteor. Soc.* **80**, 389–406.