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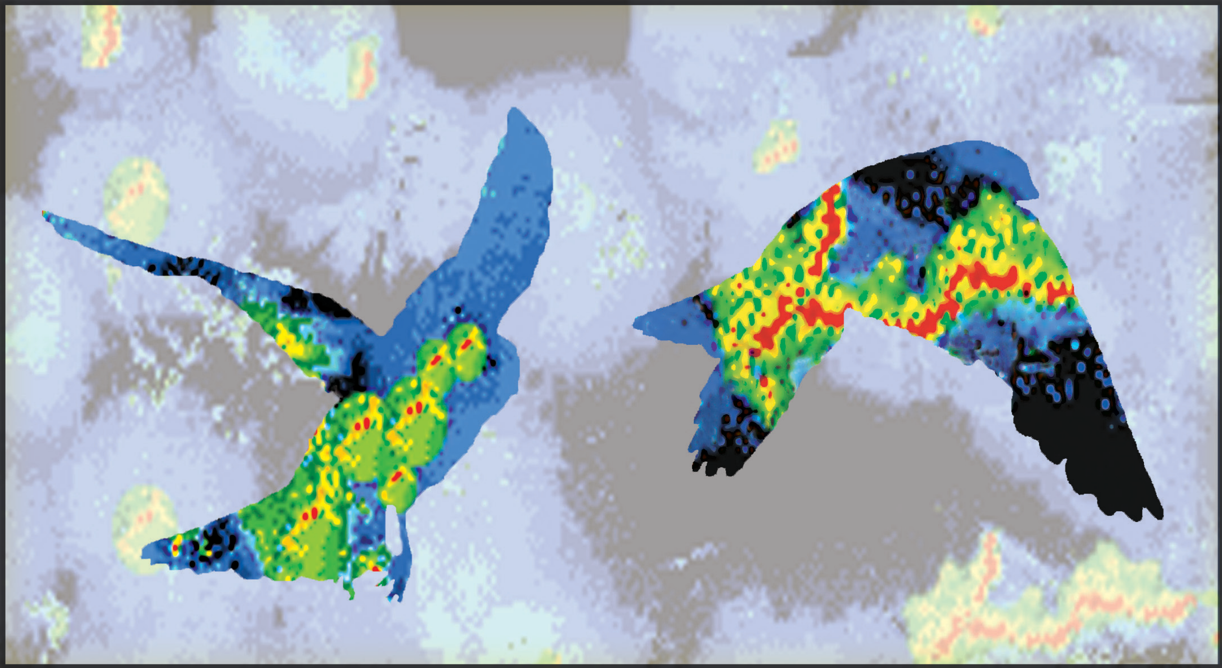
Bird Migration Patterns in the Arid Southwest—Final Report

By Janet M. Ruth, Rodney K. Felix, Jr., and Robert H. Diehl



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Executive Summary

Twice each year millions of North American landbirds migrate thousands of kilometers between their breeding and wintering grounds. In spring and fall migrants must cope with natural and anthropogenic challenges to a successful migration. As recognition grows concerning the need for full life cycle conservation, so does the call for research and monitoring geared toward understanding the behavior of migratory birds en route and for conservation and management plans aimed at protecting habitats, including migration aerohabitats, that support their successful migration.

There is a particular need to understand bird migration patterns in the desert Southwest where western migrants cross potentially inhospitable, arid landscapes between breeding and wintering grounds, and anthropogenic pressures are imposed on already limited habitat for birds during migration. It is known that migrants use riparian habitats (one of the most threatened habitats in the region) for refueling during migration (Hutto, 1985; Skagen and others, 1998). We know less about how broad patterns of migrant density or abundance vary across the Southwest and how use of riparian habitats compares with use of grassland, desert, shrubland, mesquite bosque, or montane habitats during migratory stopover. Furthermore, biologists lack information on migrant altitude distributions, speed and direction of travel, and how all these patterns vary seasonally and annually.

This project uses data from weather radar to study the behavior and ecology of migratory birds. Considerable discussion in this final report is devoted to a full account of methodologies used. Extensive preprocessing of radar echoes in preparation for statistical analysis is required to remove unwanted ground clutter, remove or reduce sources of bias, and improve target discrimination capabilities.

Using data collected by weather surveillance radars in the U.S. Southwest in spring and fall 2005 and spring 2006, we identified targets likely dominated by nocturnally migrating birds and determined their flight altitudes, flight speeds, directions over ground, and variations in abundance. Using these radar data and satellite land cover imagery collected in 2001, we determined the landscape-level habitats with which they are associated during migration stopover. Migrating or foraging bats likely are present across the region in some of these data, particularly in central Texas. Advanced methods are being developed to improve biologists' ability to distinguish and quantify bird- and bat-dominated movements.

We found that migrants flew at significantly lower altitudes and significantly higher speeds in spring than in fall. In all seasons migrants maintained seasonally appropriate directions of movement. We detected significant differences in vertical structure of migrant densities that varied both geographically within seasons and seasonally within sites.

During the spring, the highest densities of migrants passed through the eastern sites (Brownsville and Del Rio, Tex.); in the fall the highest densities were seen in the central sites (Albuquerque, N. Mex. and El Paso, and Midland, Tex.). Such patterns are consistent with the presence of at least two migration systems through western North America and the possibility of elliptical migration routes for some western migrants.

For two sites (Flagstaff and Tucson, Ariz.) there were significant differences in bird densities among habitat types in all seasons, whereas in three sites (El Paso, Midland, and Brownsville), and possibly a fourth (Albuquerque), there were significant differences in bird densities among habitat types only in fall. Upland forest habitat around Flagstaff, Tucson, and Albuquerque supported high migrant densities, especially in fall. Developed habitat around human population centers with little upland forest habitat (El Paso, Midland, and Brownsville) supported high densities of migrants. Forested/shrub wetland habitat (within which riparian forest is classified) was not a major habitat type at any of our sites, and yet supported intermediate migrant densities at three sites (Albuquerque, El Paso and Midland). Scrub/shrub habitat was the most represented habitat by area at all sites except Brownsville, and grassland habitat was abundant around Albuquerque and Midland. Although these two habitat types supported low to intermediate densities of migrants, they cover large spatial extents in the borderlands region and may in actuality be at least as important in supporting large numbers of migrants as smaller habitats like riparian corridors that concentrate migrants. This may be especially true for shrubland and grassland specialists that do not use forested habitats during migration.

There remain limitations and potentially confounding factors associated with these analyses related to: (1) difficulty in distinguishing birds from bats; (2) temporal and spatial differences among radar, wind speed, and land cover data; (3) radar beam occultation; (4) migrant displacement away from stopover habitat during initiation of migration; and (5) radar scale and resolution issues. Further research is needed to improve our ability to use radar data and to ground-truth the results of radar analyses using other methodologies.

In summary, based on our results it is overly simplistic and paints an incomplete picture to: (1) consider the arid west as a largely inhospitable landscape in which there only are relatively small oases of habitat that provide the resources needed by all migrants; (2) think of western riparian and upland forest habitat as the preferred habitat for all migrants; or (3) consider a particular habitat type unimportant migrant stopover habitat based solely on migrant densities. In reality western landscapes are a complex mosaic of habitats through which a complex assemblage of migrants passes twice a year, stopping to refuel in the specific habitats that meet their needs.

Introduction

The bird conservation community increasingly recognizes the need to understand more about migration ecology and the value of stopover sites and resources to en route migratory birds (Moore and others, 1995; Hutto, 1998; Moore, 2000; Heglund and Skagen, 2005; Carlisle and others, 2009). Migration is arguably the most hazardous period of a migratory bird's annual life cycle; Sillett and Holmes (2002) and Paxton and others (2007a) have shown that a disproportionate amount of mortality occurs in the relatively short migration periods of the life cycle. Birds must overcome multiple natural challenges including high energy demands, competition, predation, severe weather, large geographic barriers (such as large bodies of water, mountain ranges, and deserts), and the need to find suitable foraging and resting habitat in unfamiliar terrain. But, we do not yet know whether the high migration mortality is occurring during stopover, or during migratory flights, or both. Discussions of migration ecology regularly consider anthropogenic effects on the physical, biological and environmental components of migrating birds' terrestrial and aquatic stopover habitats, including en route habitat loss or degradation, and effects of global climate change on habitat and migration phenology (Moore and others, 1995; Root and others, 2003; MacMynowski and others, 2007). However, it is less common to consider the physical atmosphere as habitat (Kunz and others, 2008). Flying migratory wildlife requires what could be called aerohabitat. Migratory birds, bats, and insects are uniquely susceptible to atmospheric disturbances and human use of the air space. Tall anthropogenic structures such as communication towers and wind turbines (Manville, 2001; Cooper and others, 2004; Kuvlesky and others, 2007), and meteorological and climatic phenomena (for example, storms, adverse wind speeds and directions) represent threats to migratory birds in their aerohabitat. Conversely, migrating birds themselves present risks to humans through bird-aircraft collisions. Much remains unknown about patterns in bird flight altitude, speed, direction of travel, density, and stopover habitat use, as well as the seasonal and annual variation in these migration characteristics, all occurring at regional and continental scales. Understanding broad migratory patterns en route and aloft is important to any avian conservation plan that addresses natural and anthropogenic factors affecting migrants across all phases of their life cycles (Ruth and others, 2005; Berlanga and others, 2010).

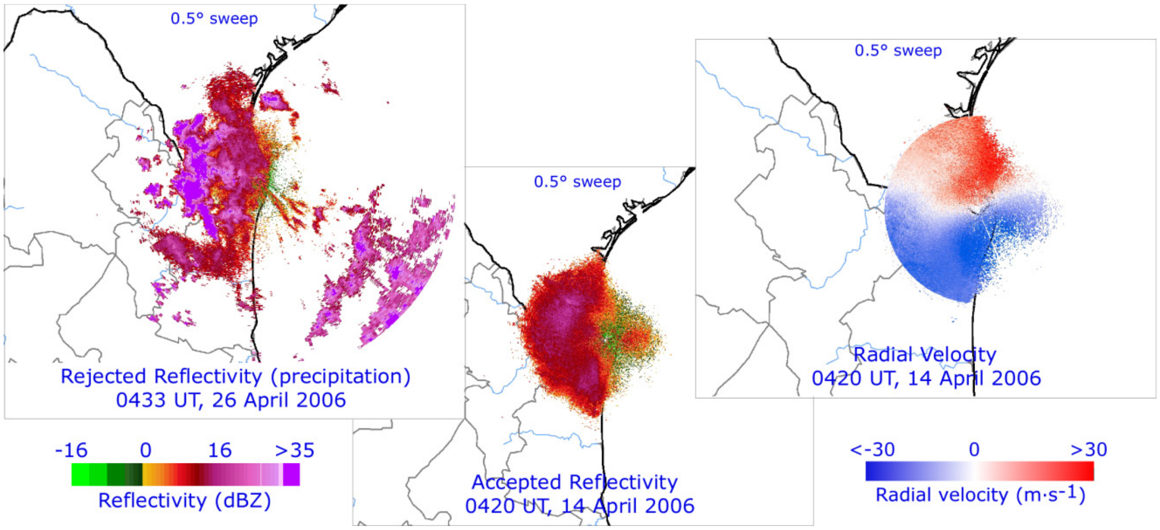
Much of what we know about passerine migration in North America is based on research conducted east of the Mississippi River. In eastern North America, research at local, small scales has evaluated migrant responses to weather (Richardson, 1978), predators (Lindström, 1990; Moore, 1994), and stopover habitat quality (Kuenzi and others, 1991; Moore and Aborn, 2000; Petit, 2000), as well as the physiological condition (Parrish, 2000) and foraging behavior of migrants (Moore and Simm, 1986). However, many factors potentially affecting western migrants are unique to the western landscape or at least are manifested in a different way and affect our ability to understand western migration dynamics. Western migratory systems may be unique in being largely overland (Kelly and Hutto, 2005), in comparison to migration systems studied in the eastern U.S. and western Europe where migrants undertake major overwater flights. Nevertheless, western migrants face other physical obstacles such as the Rocky Mountains and vast arid ecosystems that dominate the landscapes they must cross or circumnavigate. Our knowledge about western migration ecology has increased substantially during the past 10-15 years, as summarized by Carlisle and others (2009). It remains the case that much migration research has been conducted at stopover sites on the ground. The relatively unpopulated expanses of the West also present logistical challenges to the field-based studies and monitoring efforts that characterize most bird migration research. Methodologies that allow for remote collection of migration data across large landscapes, such as the use of weather surveillance radars, overcome some of these logistical obstacles, improve our understanding of migratory biology at broad spatial scales, and offer a context to guide future research.

The Sonoran and Chihuahuan Deserts, the Sierra Madre Occidental, and the Tamaulipan brushlands of the U.S.-Mexico borderlands region typify the potentially inhospitable landscapes that western birds must traverse during migration. The great majority of western migratory landbirds funnel through this area; thus, conservation of migration/stopover habitats – aerial and terrestrial – in this region is crucial. Our knowledge of migration patterns and ecology in the borderlands region is extremely limited, and much of what we know comes from site-specific banding station data focused on documenting the critical importance of riparian stopover habitats to migrants (Kelly and others, 1999; Finch and Yong, 2000; Skagen and others, 2005; Paxton and others, 2007b). We know much less about migrant use of other habitat types or about larger-scale migrant distributions and behavior aloft in this region.

Radar Applications

The U.S. network of more than 150 WSR-88D weather radars (**W**eather **S**urveillance **R**adar, 19**88** design year, **D**oppler capable) administered by the National Oceanic and Atmospheric Administration (NOAA) offers widespread coverage of U.S. airspace (14 WSR-88Ds operate in the U.S. Southwest from San Diego, CA to Brownsville, Tex.) and has been shown to detect migrating birds (Gauthreaux and Belser, 1998; Diehl and Larkin, 2005). A WSR-88D radar emits electromagnetic pulses that intercept targets; portions of the pulses are reflected back to the WSR-88D antenna, where they are received and interpreted. Properties of these pulses and the ability to measure the moving targets' Doppler shifts (Diehl and Larkin, 2005) contribute to three data categories (products): *reflectivity*, the overall size/density/abundance of targets; *radial velocity*, the target's speed relative to the radar; and *spectrum width*, variation in velocity among targets (Crum and others, 1993). Reflectivity and radial velocity are the products most frequently used in studying bird movement patterns (Fig. 1b and 1c). The three products are constituents of so-called "Level II" and "Level III" WSR-88D data sets that are archived by NOAA at the National Climatic Data Center (NCDC) and are available by free download (Del Greco and Hall, 2003). WSR-88D can provide information about bird movement patterns at broad spatial and temporal scales and is well suited to studying bird distributions and movements aloft. Where the radars provide effective coverage and there are no beam obstructions, it is also useful in identifying migrant stopover sites. However, target identification, especially distinguishing among various biological target types, remains a challenge. Other flying wildlife, notably bats and arthropods, can be locally common to widespread in the atmosphere, especially at lower altitudes. In addition, obstruction of radar beams by topographic relief (mountains) and anthropogenic structures can be problematic.

We provide a final report here on the results of a study examining migratory bird behavior, movement patterns, and stopover habitat use in the U.S. portion of the 1,500-kilometer (km) U.S.-Mexico borderlands region. Part I – Movement Patterns - Using data collected by weather surveillance radars, we identified biological targets likely to be migratory birds. We determined the speed, direction, vertical structure, and density of birds during nocturnal migration and explored how these measures varied seasonally and among sites in the borderlands region. Most of the results of Part I, with the exception of information about patterns in migrant density, and some revised results related to vertical structure in migration, have been published in Felix and others (2008). Part II – Stopover Habitat Use - By using WSR-88D to quantify migrant densities at the onset of migration and overlaying these densities on land cover data that describes habitat with which they are associated at the time of takeoff, we describe migrants' habitat use during stopover. Understanding migratory behavior, movement patterns, and stopover habitat use will allow resource managers, regulators, and conservationists to make



(a) **(b)** **(c)**

Figure 1. (a) WSR-88D reflectivity data rejected because of the presence of precipitation, (b) reflectivity data accepted for further analyses, and (c) the radial velocity of the middle radar sweep to be used in target identification and analysis.

decisions and prioritize conservation efforts in the borderlands region that will protect migratory birds and the airspace and habitat on which they depend and mitigate any negative effects of various anthropogenic activities (Ruth and others, 2005; Ruth, 2007). In addition, results will provide information to further explore migration systems and pathways in North America (Cooke, 1915; Kelly and Hutto, 2005) and baseline data that could be useful in modeling migrant responses to anthropogenic factors such as wind turbines (Cooper and others, 2004) and global climate change.

Methods

Initial Data Selection

Radar Data Selection

We downloaded Level II radar data from the NCDC archive for 13 WSR-88D sites across the Southwest (Table 1), although only seven were ultimately used in analyses (see below). For analysis, we selected radar data from these sites for days during spring migration (March 20 to May 20) in 2005 and 2006, and fall migration (August 10 to October 20) in 2005 (for ease of reference we will refer to these day-site combinations simply as “day-sites”). We visually examined reflectivity data at the 0.5º elevation for all of these day-sites at local civil twilight plus three hours and eliminated any day-sites at each radar site that were dominated by nonbiological echoes caused by precipitation or ground clutter (for example, tall buildings, bridge overpasses, or relief in terrain). We then visually reexamined the remaining reflectivity data for the time period from local civil twilight--when the sun is between 0° and 6° below the horizon--until four hours later and eliminated any additional day-sites that were dominated by nonbiological echoes. We screened radar sweeps (one full 360° radar scan) at the lowest beam elevation (0.5º) available for each day-site, a conservative approach to data screening. Day-sites that were dominated by echoes caused by precipitation (Fig. 1a), ground clutter (a common feature of low elevation sweeps), or other unwanted sources were not considered for further analysis. Day-sites that passed this initial visual screening were considered dominated by biological targets; all radar products (reflectivity and velocity data at multiple beam elevations) from these day-sites were retained and subjected to further target discrimination and other analyses.

A variety of data types from radars and other sources are used in the analyses described below. Radar reflectivity and velocity data from various radar beam elevations are used, along with radiosonde wind speed data, and satellite-based land cover data. Table 2 shows which types of data are used for which analyses.

Table 1. Thirteen WSR-88D sites initially considered in studying bird migration patterns in the arid Southwest, east to west. Boldface indicates locations for which wind velocity data are available, and where we were able to identify likely migrant landbird targets.

WSR-88D Site	City	Latitude North (degrees)	Longitude West (degrees)
BRO	**Brownsville, Tex.**	**25.92**	**-97.42**
EWX	Austin, Tex.	29.70	-98.03
DFX	**Del Rio, Tex.**	**29.27**	**-100.28**
SJT	San Angelo, Tex.	31.37	-100.49
MAF	**Midland, Tex.**	**31.94**	**-102.19**
FDX	Cannon AFB, N. Mex.	34.64	-103.63
HDX	Holloman AFB, N. Mex.	33.08	-106.12
EPZ	**El Paso, Tex.**	**31.87**	**-106.70**
ABX	**Albuquerque, N. Mex.**	**35.15**	**-106.82**
EMX	**Tucson, Ariz.**	**31.89**	**-110.63**
FSX	**Flagstaff, Ariz.**	**34.57**	**-111.20**
IWA	Phoenix, Ariz.	33.29	-111.67
YUX	Yuma, Ariz.	32.50	-114.66

Table 2. Types of data used to generate different metrics used in this project.

Metric	Data	Beam elevation (degrees)
Occultation	Reflectivity	0.5
Distinguishing Biological from Non-Biological Targets	Reflectivity	0.5
Distinguishing Vertebrate from Invertebrate Targets	Radial Velocity, Radiosonde	3.5
Target Velocity (speed and direction)	Radial Velocity	3.5
Vertical migration structure	Reflectivity	0.5 - 4.5
Intensity of migration	Reflectivity	0.5 - 4.5
Migrant-habitat associations	Reflectivity, Land Use and Land Cover	0.5

Occultation

WSR-88D beam propagation is affected by the medium in which it travels, so when describing biological targets, special consideration must be given to atmospheric conditions and relief in terrain surrounding the radar. Radar beams are blocked, both fully and partially, by structures and terrain that intrude into the path along which the beam propagates. This complete or partial beam blockage is referred to as occultation. A significant number of WSR-88D sites in the western U.S. are located where relief in terrain (for example, mountains) interferes with detection of low altitude biological targets. As a radar beam propagates, its cross-sectional area increases. It follows that if there is little relief in terrain or if a terrain feature is far from the radar, it is more likely that not all of the radar beam is blocked; that is, portions of the beam pass unobstructed. (More of the propagating beam will pass above obstructing terrain because of the curvature of the earth, as the earth's surface curves down and away from the propagating beam with increasing distance from the radar.) To more conservatively account for occultation effects, we chose not to rely solely on existing occultation maps that were produced from mapping beam geometry and its intersection with terrain relief (defined by Digital Elevation Models; National Oceanic and Atmospheric Agency, 2006). Using radar reflectivity data from the lowest beam elevation (0.5º), we created occultation maps (Fig. 2) and geospatial filters based on boundaries defined by those existing maps, but only after reviewing radar data to determine where likely partial beam blockage or other apparent terrain effects affected target echoes. As a result, these more conservative filters excluded areas showing both full- and partial-beam obstruction from subsequent analyses, thus further reducing the area of habitats analyzed. Occultation at the lowest elevation of the radar beam had the greatest effect on our analyses of stopover habitat use by migrants (see Part II below), and the geospatial filters were used there. The effects of occultation because of terrain decreases as beam elevation increases and were nonexistent at beam elevations used for vertebrate target identification and analyses of migrant movement patterns during middle of the night migration (Part I) in this study.

Radiosonde Wind Data

Radiosondes provide wind velocity data that were required to distinguish vertebrate targets (birds and bats) from invertebrate targets (see below). Unfortunately, radiosonde launch stations coincide with only seven WSR-88D stations in the study area, limiting the study to use of data from only these radars. Radiosondes are balloon-launched meteorological instrument packages programmed to collect data at certain atmospheric pressures (Office of the Federal Coordinator for Meteorology, 1997). These atmospheric pressures correspond to altitudes (meters) above sea level (ASL). An additional limitation imposed by the use of radiosonde data is related to the temporal separation between the time when radiosondes sample wind velocity and the time when radar is sampling bird targets during night migration. Balloons typically are launched twice daily, at 0000 Coordinated Universal Time (UTC; 1700 H MST the previous calendar day) and 1200 H UTC (0500 H MST). The 0000 UTC launch time is closest to the time of peak nocturnal migration across most of the borderlands region. However, this means that wind velocity and target ground velocity data used in target identity (see below) are still separated by four or five hours, depending on time zone. Unfortunately, other potential sources of winds aloft information either did not improve spatial and temporal coverage or were not sufficiently accurate (see Estimating Wind Velocity shaded box). Therefore, we were limited to analyzing radar data only at the seven WSR-88D sites where radiosonde wind velocity data were available (Fig. 3). We retrieved vertical profiles of wind velocity (speed and direction) data gathered using these radiosondes for the day-sites dominated by biological targets as described above.

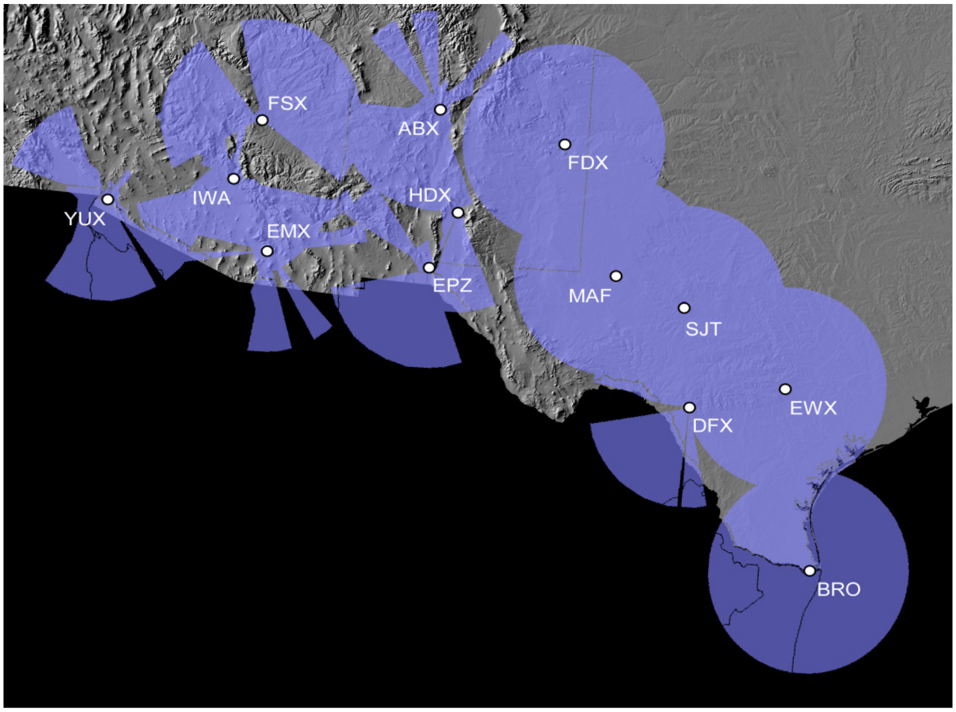


Figure 2. Occultation of the lowest beam elevations (~0.5º) of 13 radars across a shaded relief map of the southwest. White dots indicate radar locations, and light blue regions around each radar (230 kilometer radius) indicate where data is not obscured.

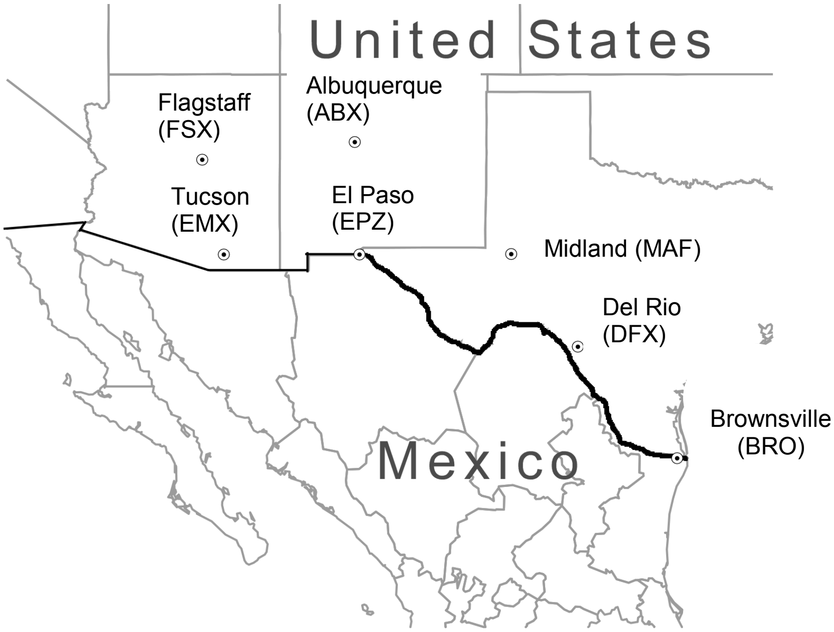


Figure 3. Locations of the seven WSR-88D radars used in this study.

Estimating Wind Velocity—Other Meteorological Models

Interpolated wind vectors are available for other radars in the U.S./Mexico borderlands region through synoptic models generated by NOAA using the National Operational Model Archive and Distribution System (NOMADS) (Rutledge and others, 2006). We briefly explored the accuracy of wind vectors from three such models: the Rapid Update Cycle (RUC-2) (Benjamin and others, 2004); the North American Mesoscale model (NAM) (Black, 1994); and the North American Regional Re-analysis model (NARR) (Mesinger and others, 2006). All three models generate gridded meteorological data over the entire continental United States (including winds aloft vectors) with 20- to 40-square kilometer (km^2) horizontal resolution, up to 50 millibars (mb) atmospheric pressure height resolution, and 1- and 3-hour temporal resolution. If accurate, the RUC-2, with its 20-km^2 horizontal and 50-mb vertical spatial resolution and hourly temporal resolution, could dramatically narrow the temporal gaps in our winds aloft data at the WSR-88D sites in question. It could also increase the spatial coverage of the study by allowing us to re-introduce data from the remaining 6 WSR-88D sites in the study region.

In determining the efficacy of the models for incorporation in our analyses, first we compared output from each model with a pair of contemporaneous radiosonde soundings at each of the seven WSR-88D sites; these comparisons yielded mean ± SD differences in wind speed of 1.3 ± 1.2 $m \cdot s^{-1}$ (NARR), 1.4 ± 1.1 $m \cdot s^{-1}$ (NAM), and 1.7 ± 1.2 $m \cdot s^{-1}$ (RUC-2). We then compared contemporaneous RUC-2 and radiosonde data from Tucson (EMX), Ariz., and Lincoln (ILX), Ill., a site where the landscape is free of substantial relief in terrain. From precipitation-free spring days, at Tucson (N = 10) we found that the RUC-2 model and radiosonde-measured wind speeds differed by 1.1 ± 0.8 $m \cdot s^{-1}$(mean ± SD), and at Lincoln (N = 5) they differed by 1.7 ± 1.8 $m \cdot s^{-1}$.

As an alternative to the models, we also compared contemporaneous WSR-88D radial velocity data to 0000 UTC radiosonde data for all of spring 2005 at Tucson, Ariz. and Brownsville (BRO), Tex. These radiosonde data and corresponding WSR-88D data are collected about 90 minutes before the onset of migration--times when fewer bird targets are believed to be in the atmosphere and when radial velocities from targets that ride the air currents (for example, small insects, dust) might approximate synoptic wind velocities. (If this method proved accurate, we would have explored the potential of using radial velocity data immediately before the onset of migration to narrow the time gap that currently exists between radiosonde data and when we identify targets.) The differences between radiosonde and WSR-88D radial velocity data at Tucson (N = 41 days) were 2.2 ± 2.4 $m \cdot s^{-1}$ (mean ± SD difference) and at Brownsville (N = 26 days) were 1.9 ± 1.4 $m \cdot s^{-1}$. From a meteorological perspective, differences of 2 $m \cdot s^{-1}$ may be negligible; however, given the need to use wind velocity data in calculating and distinguishing between invertebrate and bird target air speeds, with a cut off at 6 $m \cdot s^{-1}$ (see below), such a difference was unacceptable. We concluded that neither modeled winds aloft data nor winds approximated by radar data were sufficiently accurate alternatives to radiosonde data for purposes of target identification, especially because model errors were large relative to the threshold airspeed used to distinguish bird- from insect-dominated migrations (see below).

Vertebrate Target Identity, Vertical Structure, Movement Patterns (Part I)

Having identified day-sites dominated by biological targets with a conservative approach using the data from 0.5º radar beam elevations, most of the remaining analyses in Part I use radar data from higher beam elevations to distinguish vertebrate from invertebrate targets during night migration and to analyze movement patterns during that time.

Estimating Target Ground Velocity

In order to distinguish vertebrate targets (birds and bats) from invertebrate targets during migration in the middle of the night, target ground velocity data were required. A target's ground velocity is its speed and direction relative to a stationary point on the ground. The Doppler capability of WSR-88D radars enabled ground velocity estimates of biological targets. WSR-88D radar measures the frequency or Doppler shift of returned radar pulses caused by a target's motion relative to the radar. The magnitude of this motion is displayed in the WSR-88D radial velocity product. The display of radial velocity data indicates speed and direction of targets (Fig. 4). Two distinct colors of varying intensity represent movement toward the radar (blue) and movement away (red); the display of radial velocity data gives an immediate impression of the overall speed and direction of movement. Velocities with the highest magnitudes are measured when the targets are moving directly toward or away from the radar, and those with the lowest magnitudes (or zero) are measured when the targets are moving perfectly tangential to the radar (the whitish area in Fig. 4, referred to as the Doppler null; it can be helpful in illustrating the direction of movement).

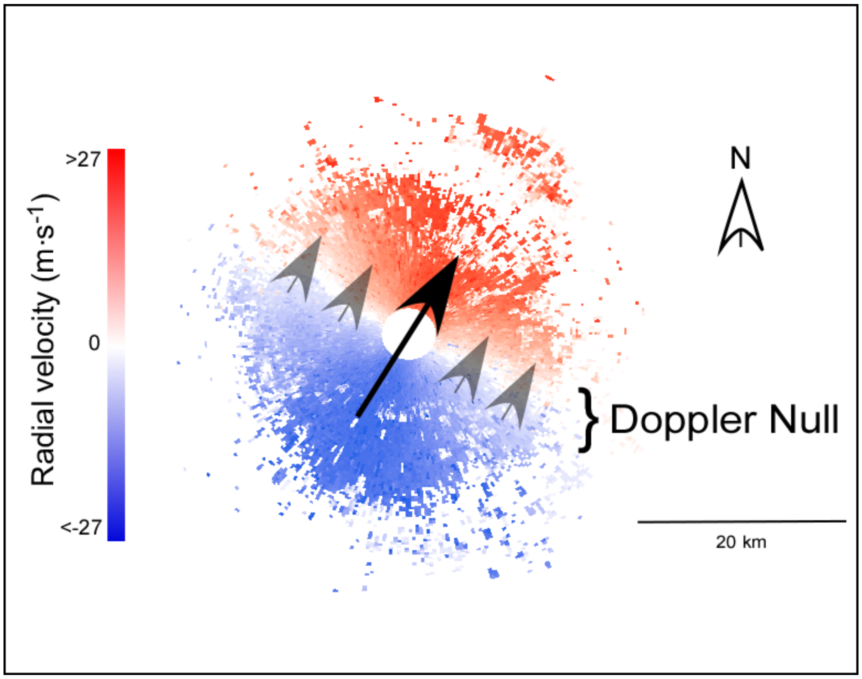


Figure 4. The radial velocity data (in this case from Del Rio,Tex., April 04, 2005, 0515 Coordinated Universal Time [UTC]) indicate targets moving with a generally even ground velocity: blue is negative velocity (toward the radar) and red is positive velocity (away from the radar). Radial velocities indicate a general north-northeast ground velocity (moving from blue to red), perpendicular to the Doppler null.

Using radar radial velocity data from the 3.5º beam elevation for the day-sites dominated by biological targets, we determined ground speed and direction using an approach which incorporates radial velocities from all azimuthal directions around the radar (Browning and Wexler, 1968). By a process of least-squares minimization, the kinematic properties of target motion captured by these radial velocity data are modeled as

$$(1)\quad v_r = u\cos\theta\sin\phi + v\cos\theta\sin\phi + w\sin\theta$$

Following meteorological conventions, v_r is the predicted radial velocity in $\mathrm{m{\cdot}s^{-1}}$, u and v are the northward and eastward horizontal components of movement respectively in $\mathrm{m{\cdot}s^{-1}}$, w is the vertical component of movement, θ is the beam's angle of elevation above the horizon, and Φ is the azimuth. Least-squares converges on an optimal fit of equation (1) to radial velocity data, generating a set of parameter values for u, v, and w.

Target horizontal ground speed is then determined using the Pythagorean theorem on u and v components, after adjusting them for small bias due to beam elevation angle. Target direction is determined from the tangent of the ratio of adjusted u and v.

This method is applied to narrow range rings of radial velocity data in the following manner. The geometry of a propagating radar beam is such that an increase in range from the radar coincides with an increase in altitude. Our algorithm for quantifying speed and direction is first applied to a narrow range band close to the radar. Using data from a narrow band of ranges prevents underestimating ground speed as a result of wind shear which often is present in radial velocity data. The range (and thus altitude) of this band is then increased slightly and speed and direction recalculated. This process is repeated out to the maximum range for which sufficient velocity data is available. The result is an altitude-specific profile of migrant ground speeds and directions. This approach to determining speed and direction is robust assuming targets are widespread and relatively uniform in their movements across the area under consideration. Although equation 1 was developed for meteorological purposes, it is particularly well suited for many biological applications because this assumption of uniformity in radial velocity is more readily met with widely distributed biological targets. In cases where large regions of data are missing, seemingly critical velocity information used in target discrimination (for example, peak velocities) may be absent. In these cases, the converged model can effectively interpolate missing values and yield estimates of speed and direction.

All analyses of radial velocities were based on radar data gathered from the 3.5° beam elevation. There were several reasons for this. First, the 3.5° elevation data generate more accurate height-specific measures of target speed and direction compared to data at the lowest elevations. Second, using the 3.5° data avoids the effects of occultation - the radar beam at this elevation generally is not obstructed by relief in terrain. Third, a higher elevation beam passes through the migratory layer at relatively short distances from the radar where targets are quantified into higher resolution volumes of space. At lower beam elevations (for example, 0.5°) targets are quantified into larger volumes of airspace at increased distances from the radar. This becomes problematic since larger volumes are more likely to contain nonbird targets that could bias radial velocity. Also, larger volumes are more likely to include targets moving in many different directions when wind direction shear (variation in the speed or direction of wind with altitude) is present, further confounding analysis of radial velocities. Using velocity data from higher beam elevations reduces these sources of bias. This process of determining target ground speed and direction results in a data set of target ground velocities that vary with height for each day-site dominated by biological targets.

Distinguishing Vertebrate from Invertebrate Biological Targets

We distinguished migratory birds from other biological echoes (insects) by target air speed, which is its speed and direction relative to the air mass in which it is traveling. We calculated target air speed by subtracting wind velocity vectors (obtained from radiosonde data) from ground velocity vectors of targets at the same altitudes (as calculated above) (Gauthreaux and Belser, 1998). We visually examined the radar reflectivity data for the day-sites dominated by biological targets to identify the altitude at which peak reflectivity strata associated with biological targets were found. Based on flight characteristics of birds and arthropods, targets exhibiting air speeds >6 $m \cdot s^{-1}$ were considered dominated by birds (Schaefer, 1976; Larkin, 1991; Gauthreaux and Belser, 1998). Biological targets moving at air speeds ≤6 $m \cdot s^{-1}$ were considered dominated by arthropods. Day-sites for which the strata with peak reflectivity corresponded with target air speeds >6 $m \cdot s^{-1}$ were considered to be dominated by birds and retained for further movement pattern and habitat association analyses (example in Table 3). Again, methods used in these analyses cannot distinguish bats occupying the same airspace from migrating birds. While bats may be locally abundant in some circumstances, we assume birds represent the majority of targets in most instances (Able, 1977).

Table 3. Wind velocities, target ground velocities, and target air velocities at increasing altitudes at Tucson, Ariz. (EMX) on April 13, 2006 at 0515 Coordinated Universal Time (UTC), showing stratified bird-like velocities. Bird-like target air speeds (boldface) appear at ~3048 meters above sea level (2,320 meters above ground level).

Altitude above sea level (meters)	Wind speed ($m \cdot s^{-1}$)	Wind direction from (degrees)	Target ground speed ($m \cdot s^{-1}$)	Target ground direction from (degrees)	Target air speed ($m \cdot s^{-1}$)	Target air direction toward (degrees)
1,829.0	7.2	290.0	-5.1	310.4	3.0	-57.4
2,134.0	6.7	275.0	-4.1	283.6	2.7	-21.7
2,438.0	6.2	260.0	-3.7	284.9	3.2	-53.2
2,743.0	6.7	245.0	-2.3	248.2	4.4	-4.8
3,048.0	7.2	245.0	-7.0	141.5	**11.1**	39.0
3,185.0	6.2	245.0	-10.5	134.8	**13.9**	24.6
3,658.0	3.6	200.0	-17.8	137.0	**16.4**	11.3
3,962.0	5.7	160.0	-19.7	143.2	**14.4**	6.5
4,267.0	9.3	150.0	-21.6	147.3	**12.3**	2.0
4,503.0	9.3	152.0	-20.6	149.0	**11.3**	2.4
4,583.0	8.7	153.0	-20.7	149.3	**12.0**	2.7
4,650.0	8.7	153.0	-20.3	148.9	**11.6**	3.1
4,877.0	8.7	155.0	-16.3	145.7	**7.8**	10.5

Defining Vertical Structure and Seasonal Intensity in Migration

Calculations for vertical structure and migration intensity use z values from radar reflectivity data. z is a unit of reflectivity, used here as a surrogate for bird density (Rinehart, 1997). Initially we estimated vertical structure in migration (migrant altitude) using reflectivity data from the 3.5° beam elevation and a process similar to that described for ground velocity estimation above, minus application of the Browning and Wexler (1968) algorithm, to generate height-specific estimates of reflectivity data as a measure of migrant altitude (Felix and others, 2008). However, during the course of the project, an alternate approach to examining vertical structure became available (Buler and Diehl, 2009). The approach takes advantage of reflectivity data from the lowest five elevation sweeps to build more precise vertical profiles of reflectivity (VPR). We chose to use this new method and present those results here. We measured vertical variation in migration intensity at each site using VPRs to quantify migration. Mean and median VPRs were generated for each day-site combination for altitudes ranging from 150 m to 2750 m above ground level (AGL) at 10 m intervals. Day-site values were then combined into single VPRs for each site for each season for the analyses below.

To examine geographic variation in the intensity of migration (this can be thought of as relative migrant density) among sites and seasons, we summed mean z values for each height interval into a single measure of reflectivity for each day-site and then combined these values into a single value for each site for each season to be used in the analyses below (Part II).

Statistical Approach

We examined differences in ground speed, ground direction, and vertical structure across geographic location (that is, across seven radar sites) and three migration seasons. Analyses of vertical structure were based on VPRs computed using the methods described in Buler and Diehl (2009). These vertical structure results are presented descriptively. Non-parametric statistics were used throughout because data often failed to meet assumptions of normality and homoscedasticity, in some cases even after data transformation. Pooling data across sites, we used Kruskal-Wallis analysis of variance by ranks to test for overall differences between the seasons for ground speeds. We used the same Kruskal-Wallis approach to test for differences in ground speed between sites within seasons, and within sites between seasons. Where overall differences in ground speeds were significant among seasons across sites, among sites within seasons, or within sites among seasons, non-parametric Tukey-type multiple comparison of ranks tests (Q statistic) were used to identify among which seasons or sites they occurred (Zar, 1999). Alpha levels were adjusted for comparisonwise error rates.

Median directions of travel relative to the ground (with 25 percent and 75 percent quartiles) were determined using circular statistics (Zar, 1999). Pooling data across sites, we used Mardia-Watson-Wheeler tests (W statistic) to look for differences in ground direction within seasons. Where significant differences were found, Tukey-type multiple comparison tests of circular ranks (Q statistic) were used to identify differences among specific sites.

Migrant Stopover Habitat Use (Part II)

Descriptions of migrant abundances and their stopover habitat associations are possible using weather surveillance radar data and remotely sensed satellite data; they require a measure of the quantity of targets (density, provided by WSR-88D reflectivity data) along with a georeferenced measure of habitat type (landscape composition and configuration, provided by satellite-derived land use and land cover data). Making these bird-habitat associations is limited in numerous ways by the data, assumptions, and available analysis methods as discussed below.

Radar data from the lowest WSR-88D beam elevation (0.5º) around evening civil twilight are used to capture the departure of landbirds, which migrate at night, from stopover habitat. At low beam elevations landbird migrants are detected relatively close to the habitats from which they departed; it might be several seconds before a migrant rises high enough to enter the radar-scanned airspace. As a radar sweeps through these low-altitude airspaces at the onset of migration, migrants will be entering or have entered the airspace approximately over their stopover habitats. During this time, stronger radar echoes (reflectivity z values) identify habitats in which migrants had concentrated during stopover.

We use the day-sites dominated by bird targets that were identified in Part I using 3.5º beam elevations, assuming that these day-sites are dominated by bird targets at lower elevations as well. We visually examined the data around civil twilight and selected a representative sweep for each day-site for inclusion in analyses of stopover habitat use. At the same time, we examined the representative sweeps one more time, eliminating any additional day-sites dominated by nonbiological echoes.

Satellite-based Land Use and Land Cover (LULC) data from the National Map Seamless Server administered by the U.S. Geological Survey (U.S. Geological Survey, 2008) were used for habitat analyses. These most recent LULC data were derived from multispectral Landsat satellite imagery collected in 2001, and provide classification of land use and land cover at a 30-m resolution. We downloaded the LULC data for the regions surrounding the seven radars used in this study. We derived our land cover types from the National Land Cover Data 2001 Class II definitions (Multi-Resolution Land Characteristics Consortium, 2001), *http://www.epa.gov/mrlc/classification.html#one*. We reclassified these cover types into eight classes (Table 4), merging similar cover types into categories that were most likely to represent biologically important habitat types for migrants (Brownsville contained an additional no-data cover type that we omitted from analyses).

The area around each radar that could be used to make bird-habitat associations was limited by a number of factors. We chose to restrict analysis of land cover and migrant reflectivity within a band extending from 35 km to 50 km away from each radar site to limit the effect of range bias. At greater distances (>50 km from the radar) determining habitat associations is less reliable because the radar beam passes further above the earth's surface and therefore migrants displace widely from stopover habitats in the time it takes for them to fly up into the beam (Diehl and Larkin, 2005; Larkin, 2005). At shorter distances (< 35 km from the radar) low altitude radar data are more likely to be affected by clutter caused by relief in terrain or anthropogenic structures (Diehl and Larkin, 2005). Range adjustment techniques described in Buler and Diehl (2009) allow use of a much wider band of ranges (allow use of more of the radar data), but attempts to apply these adjustments to our analyses often resulted in overcorrection. (We hope to apply these methods to these data in the future once the techniques have been perfected.) We also excluded additional land cover and radar data within the 35 km-50 km band from analysis (Fig. 5) if they lay within the filtered regions of full or partial beam occultation identified in the Occultation section above. Finally, we were not able to get comparable land cover data for Mexico where radar coverage extended into Mexico, nor did we use the portion of radar coverage at Brownsville that extended over the Gulf of Mexico.

Within a Geographic Information System (GIS) we verified that all radar reflectivity data and land cover data were accurately geolocated (datum WGS 1984, among zones 12N, 13N, and 14N). Using a model constructed within GIS, for each site we processed each migration-onset radar reflectivity data sweep in relation to the underlying land cover data. For each sweep we determined zonal (areal) means and standard deviations of migrant density associated with each of eight major land cover types, statistics that were calculated by dividing the total z value associated with a habitat type by the total area of that habitat type. This procedure is akin to dropping birds in the airspace over different habitat types (measured in units of z) and calculating a surface (2D) density for that habitat type as z per unit area.

Table 4. Land-cover classifications derived from the National Land Cover Data (NLCD) (Multi-Resolution Land Characteristics Consortium, 2001). These categories are used in this study to characterize study sites and analyze migrant-habitat associations.

Classification	Description
Scrub/Shrub	Dominated by shrubs < 5 meters tall with shrub canopy typically > 20 percent of total vegetation (NLCD category 52)
Grassland/Herbaceous	Dominated by grammanoid or herbaceous vegetation, generally > 80 percent of total vegetation (NLCD category 71)
Upland Forest	Dominated by trees > 5 meters tall; generally > 20 percent of total vegetation; includes deciduous, evergreen, and mixed forest (NLCD categories 41, 42, 43)
Open Water/Wetlands	Combination of open water with < 25 percent cover of vegetation or soil, and palustrine and estuarine emergent wetlands and aquatic beds (NLCD categories 11, 96, 97, 98, 99)
Forested/Shrub Wetlands	Areas where forest or shrubland vegetation accounts for > 20 percent of vegetative cover, and substrate is periodically saturated or covered with water (NLCD categories 91, 92, 93, 94)
Agriculture	Herbaceous vegetation planted or intensively managed for production of food, feed, or fiber accounts for 75-100 percent of cover; includes pasture/hay and cultivated crops (NLCD categories 81, 82)
Developed	Developed area accounts for ≥ 30 percent of land cover; includes low, medium, high intensity development and open space (NLCD categories 21, 22, 23, 24)
Barren	Barren areas including bedrock, gravel pits, strip mines, sand dunes, and unconsolidated shore (NLCD categories 31, 32)

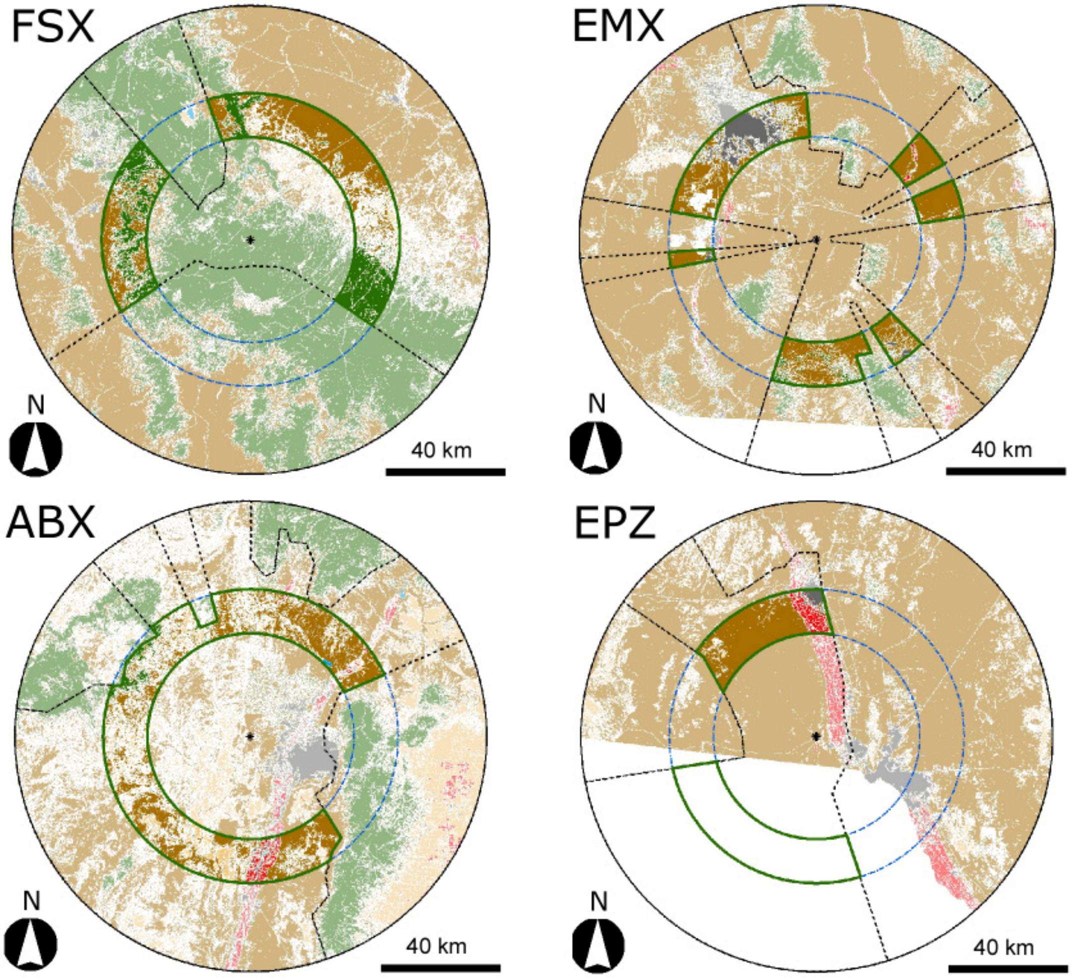
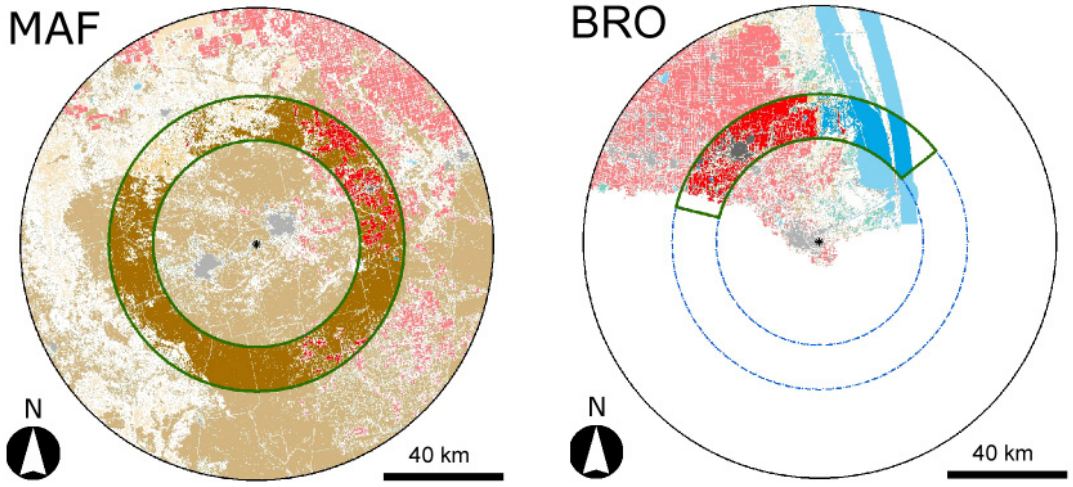


Figure 5. Land cover surrounding the six radars where data were analyzed for bird-habitat associations, showing radar beam occultation masks (Fig. 2) and the band extending from 35 km to 50 km away from the radar within which analyses were conducted. The eight color schemes represent the eight land cover types used in the analyses (see legend); the darker shade of each color indicates areas where migrant reflectivity and land cover were analyzed.



* Radar

⬚ 35 – 50 km Range

🟦 Open Water

⬜ Barren; No Data

Combines: Barren Land; Perennial Ice/Snow; No Data

🟫 Scrub/Shrub

Combines: Scrub/Shrub; Dwarf Scrub

🟩 Forested/Shrub Wetlands

Combines: Woody Wetlands; Palustrine Forested Wetland; Palustrine Scrub/Shrub; Estuarine Forested Wetland; Estuarine Scrub/Shrub; Emergent Herbaceous Wetland; Palustrine Emergent Wetland (Persistent); Palustrine Emergent Wetland; Palustrine Aquatic Bed; Estuarine Aquatic Bed

🟥 Agriculture

Combines: Pasture/Hay; Cultivated Crops

⬚ Occultation Boundary

▭ Analyzed Habitat Boundary

⬛ Developed

Combines: Developed, Open Space; Developed, Low Intensity; Developed, Medium Intensity; Developed, High Intensity

🟩 Upland Forest

Combines: Deciduous Forest; Evergreen Forest; Mixed Forest

🟨 Grassland/Herbaceous

Combines: Grassland/Herbaceous; Sedge Herbaceous; Lichens; Moss

Note: Dark color shades are associated with analyzed habitat; light color shades = outside analyzed habitat. Eight land cover types (large typeface) used in analyses were synthesized from 28 Anderson Level I land cover classes (smaller, indented typeface) from 2001 National Land Cover Dataset.

Figure 5. Land cover surrounding the six radars where data were analyzed for bird-habitat associations, showing radar beam occultation masks (Fig. 2) and the band extending from 35 km to 50 km away from the radar within which analyses were conducted. The eight color schemes represent the eight land cover types used in the analyses (see legend); the darker shade of each color indicates areas where migrant reflectivity and land cover were analyzed. —Continued

Statistical Approach

Daily mean target densities (daily mean *z* values) for given habitats failed to meet assumptions of normality and homoscedasticity, even when transformed. Again we relied on non-parametric Kruskal-Wallis analysis of variance by ranks to test for differences in daily mean target density among habitat types or among seasons within each site, and Tukey-type multiple comparison of ranks where those differences were significant. We analyzed each site separately for these tests (we did not use radar site as a block/factor) because the landscapes at each radar site are inherently different.

Results and Discussion

From 434 representative sweeps evaluated for each spring season (20 March–20 May, across seven WSR-88D sites), those dominated by migrants were retained for further flight behavior analysis - 235 in 2005 (56 percent) and 180 in 2006 (43 percent). Of the 504 sweeps evaluated in fall 2005 (10 August–20 October), 214 (45 percent) were retained for flight behavior analysis (Part I). The number of sweeps each season used for habitat-association analyses (Part II) was further reduced - 105 and 78 for spring 2005 and spring 2006, respectively, and 77 for fall 2005. The number of migrant-dominated evenings at an individual radar site during a season varied from a low of 17 at Brownsville, in spring 2006 to a high of 40, also at Brownsville, in spring 2005. Most rejected sweeps were excluded from analysis because of the presence of precipitation (Table 5). They were also rejected when ground clutter or other anomalous echoes were present, when Level II data were corrupt, when radiosonde reports were missing, or when dominated by insect-like targets, that is, target airspeeds fell below 6 $m \cdot s^{-1}$.

In general for this study we considered migrating and foraging bats to be indistinguishable from birds; like Able (1977), we assume that bats are rare relative to birds in most geographical locations (but see the shaded box – Birds, Bats, and Insects - for a more extensive discussion of this subject, which is crucial to understanding the results and interpretations of our analyses).

Table 5. Number of radar sweeps per season considered and retained for analysis and criteria for their rejection.

	Spring 2005	Fall 2005	Spring 2006
Total sweeps	434	504	434
Sweeps rejected for:			
Precipitation dominant	134	230	175
Unavailable/corrupt radar data	20	31	12
Unavailable radiosonde data	10	3	12
High variability in target velocity	22	9	12
Low target airspeeds	13	17	43
Sweeps retained for target analysis	235	214	180
Sweeps retained for habitat analysis	105	77	78

Birds, Bats, and Insects

Although we assume that bats are rare relative to birds in most geographical locations, the relative abundances of bats and migrating birds remain poorly understood and likely vary geographically and seasonally. In addition, target identification (particularly the ability to distinguish birds from bats and insects) remains an ongoing challenge in radar analyses (for example, bat flight is similar enough to that of birds that these two kinds of targets are indistinguishable at times using airspeed-based techniques). Despite efforts to retain data only from bird-dominated movements, it is possible that bats or insects, or both could be present locally in large numbers in some of these data.

Invertebrate pest species such as corn earworm (*Helicoverpa zea*) and black cutworm (*Agrostis ipsilon*) migrate through Texas (north in spring and south in fall; Wolf and others, 1990; Showers and others, 1993) and possibly other parts of the borderlands region, and their movements are readily detected by weather radar (Wolf and others, 1990). Arthropod abundance is known to increase toward the end of the warmer months (Cleveland and others, 2006), and insect migration through central Texas generally occurs below 1,000 m (Beerwinkle and others, 1994). It is possible that some migrating insects may exhibit velocities high enough that they are not excluded by airspeed-based techniques (Larkin, 1991).

Cryan (2003), in a study of seasonal distribution of migratory tree bats, documents the presence of migratory hoary bats (*Lasiurus cinereus*), eastern and western red bats (*L. borealis and L. blossevillii*), and silver-haired bats (*Lasionycteris noctivagans*) in the region during our spring and fall bird migration sampling periods. In addition, the Southwest supports the highest diversity of bats in the U.S., with >76 percent of U.S. species found in Arizona, New Mexico, and/or Texas (Bat Conservation International, *http://www.batcon.org*). Bats typically emerge from their colonies before sunset to begin foraging (Lee and McCracken, 2001; B. French, personal commun., 2008), where they could be distributed evenly (along with their prey) in low-altitude airspace (Best and Geluso, 2003). Therefore, it is likely that bats occur locally in extremely high densities, such as in central Texas (Horn and Kunz, 2008), but also are broadly present at lower densities across much of the arid Southwest; in both cases this could cause or obscure geographical patterns associated with birds. As an example from our study, in reflectivity data we observed patterns typical of biological targets entering the radar beam from point locations (Russell and Gauthreaux, 1998; Horn and Kunz, 2008) in south and central Texas (Fig. 6). These patterns were observed shortly before and after local civil twilight and were closely associated geographically with several known colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) in central Texas, especially in the Del Rio, Tex. area (B. French, personal commun., 2008). However, these patterns dissipated, and appeared to resemble ambient reflectivity before the times when sweep data were collected for target identification.

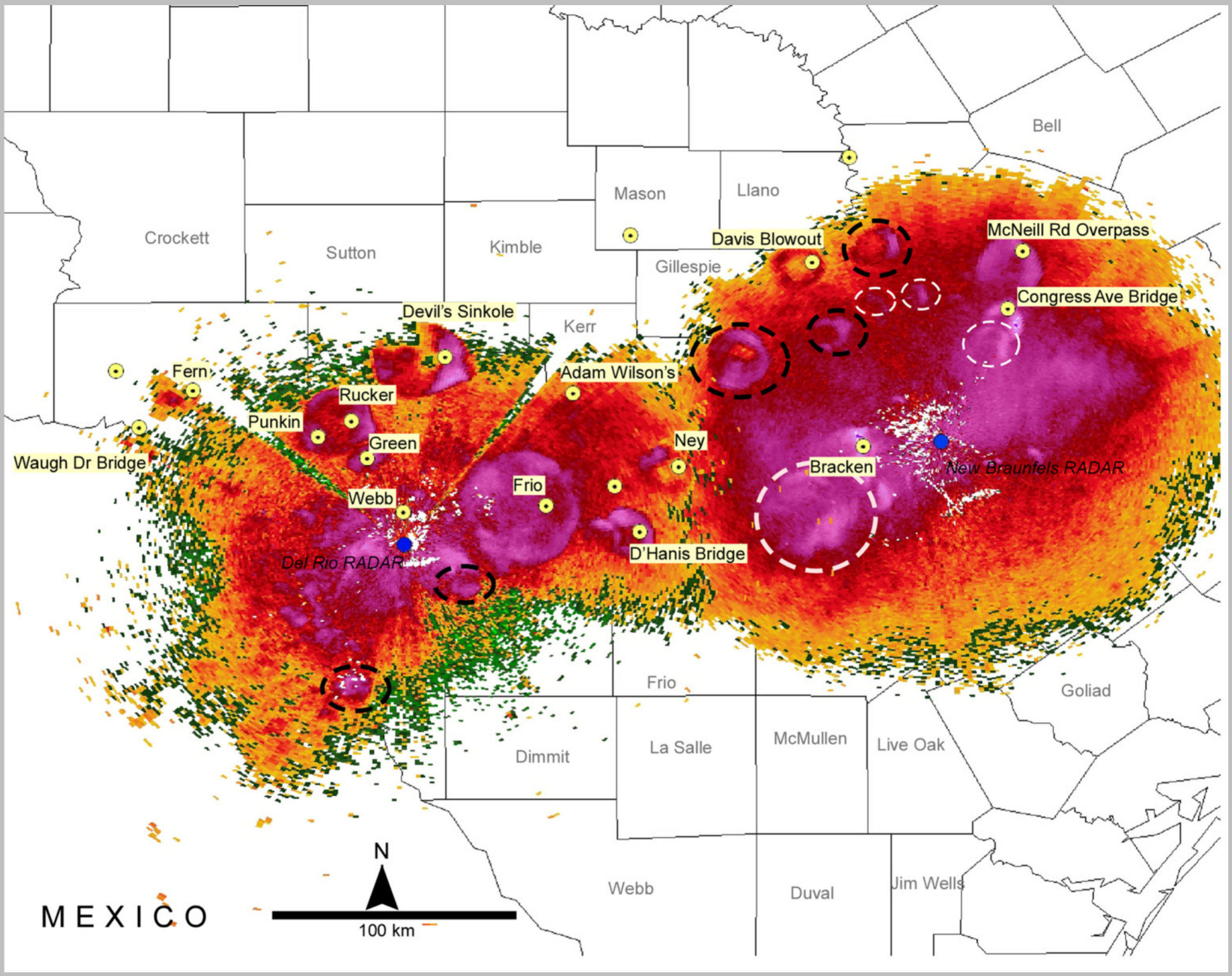


Figure 6. Reflectivity data from Del Rio and New Braunfels, Tex., from around 1900 CST October 14, 2005. According to a Bat Conservation International source, yellow points are documented Mexican free-tailed bat roosting colony sites. Black dashed circles highlight what appear to be echoes of emerging bats that have not been identified for this project.

Therefore, for Part I, which deals with movement patterns during migration in the middle of the night, we included data from all seven radar sites, despite the possibility that bats may be locally abundant at certain locations at certain times. In contrast, Part II addresses bird-habitat associations as birds initiate migration at twilight. The highest concentrations of bats occur as they leave their roosts at approximately the same time as departing migratory birds. Because of the frequency with which bats are likely present in the reflectivity data immediately before and after sunset around Del Rio, we chose to omit this site from habitat association analyses in Part II, limiting our analyses to the remaining six radar sites.

Shear

Upon further visual review of radial velocity data used in target identification, we observed that directional shear was prevalent across the study region. Directional shear occurs when targets move in different directions along an altitude gradient, that is, targets at different altitudes are moving in different directions. In the case of these analyses, directional shear occurred frequently across the central part of the region and appears in WSR-88D radial velocity data as an S-shaped or “yin/yang” pattern in the Doppler null (Fig. 7). Figure 7 also aptly shows how consistent the shear pattern can be at a single WSR-88D site in a season, in this case Del Rio, Tex. We will address the implications of such prevalence below.

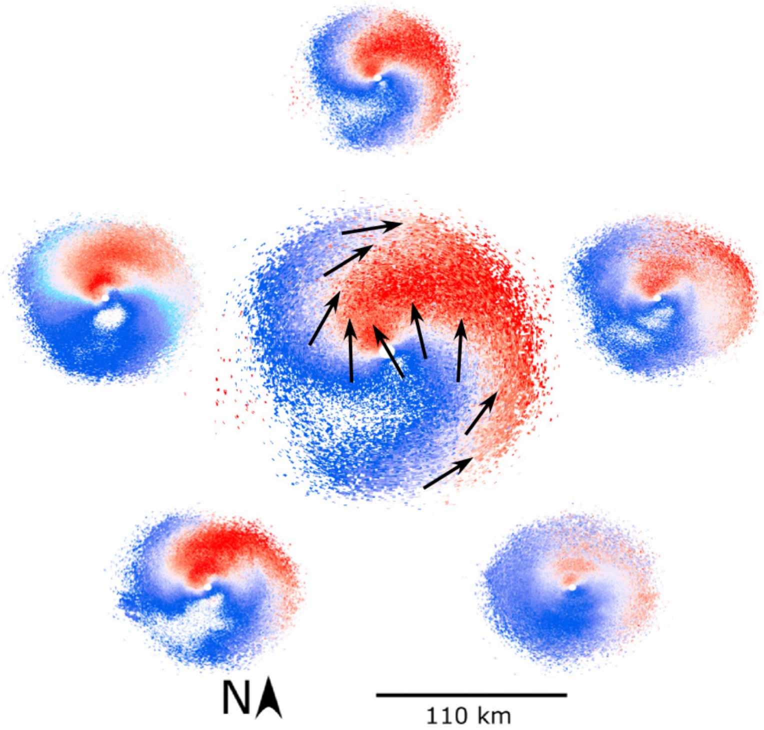


Figure 7. Wind direction shear throughout a season as illustrated by 3.5° beam elevation radial velocity data from Del Rio (DFX), Tex. Clockwise from top are daily sweeps closest to 0500 UTC on March 21, April 5, April 13, May 7, and May 10, 2005 showing a similar shear pattern: speeds vary according to color intensity, yet the radar-relative directions are similar. In the middle is the March 21 sweep enlarged, with arrows indicating target direction.

Part I – Migrant Movement Patterns – Results and Discussion

Vertical Variation in Migrant Densities - Results

Birds showed different patterns and considerable variation in their vertical distributions between seasons at individual radar sites and among radar sites in general (Fig. 8). Measures of both mean and median reflectivity are presented in Figure 8. Median reflectivity at a given height AGL often was considerably less than the corresponding mean reflectivity. The median is a better measure of central tendency than the mean. For this reason, differences between mean and median at any given height AGL are indicative of positively skewed distributions of reflectivity at that height. The magnitude of the skew is evident from magnitude of difference between mean and median reflectivity at a given height. Median observations are not sensitive to extreme migration events, or rare large movements, whereas mean observations are highly affected by rare events. In other words, mean values are a better representation of what all the birds are doing, whereas median values represent the typical situation.

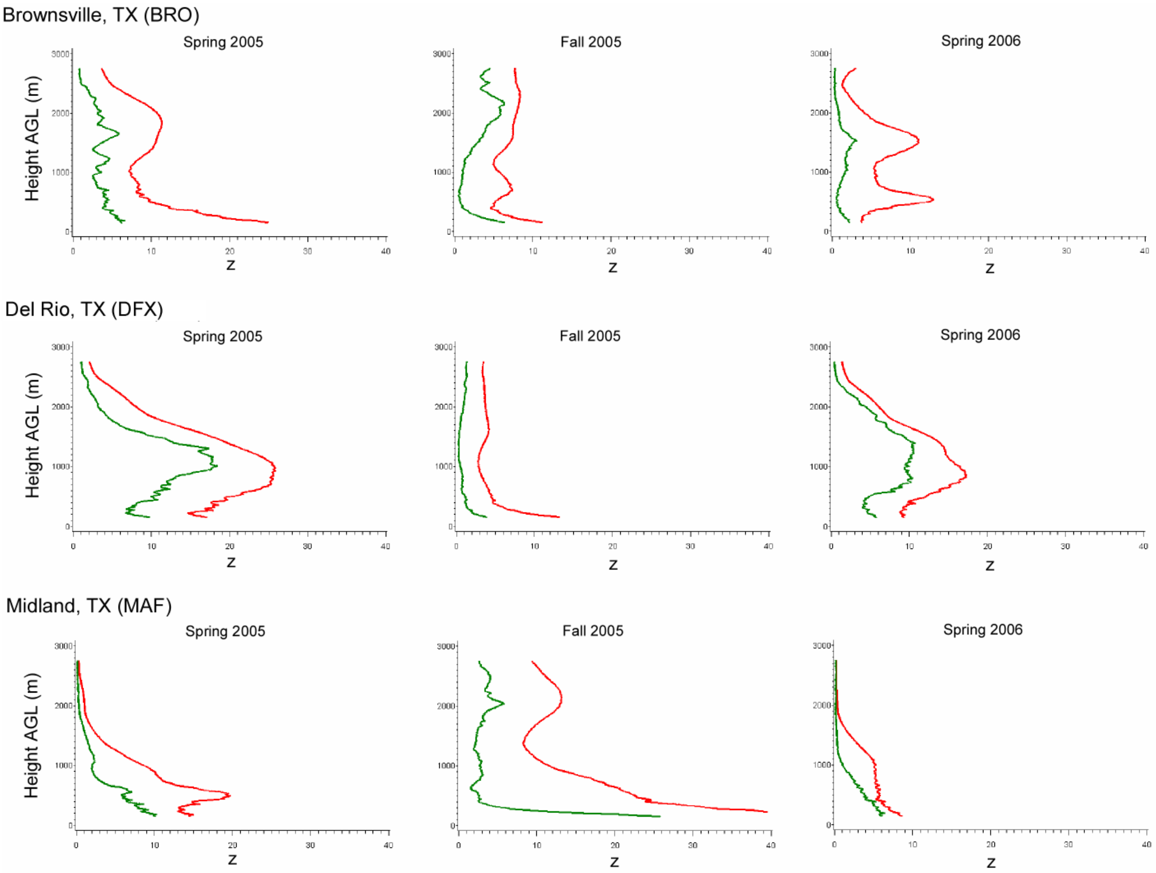


Figure 8. Median (green) and mean (red) vertical profiles of reflectivity for spring 2005, fall 2005, and spring 2006 for each of seven radar sites ordered from east to west.

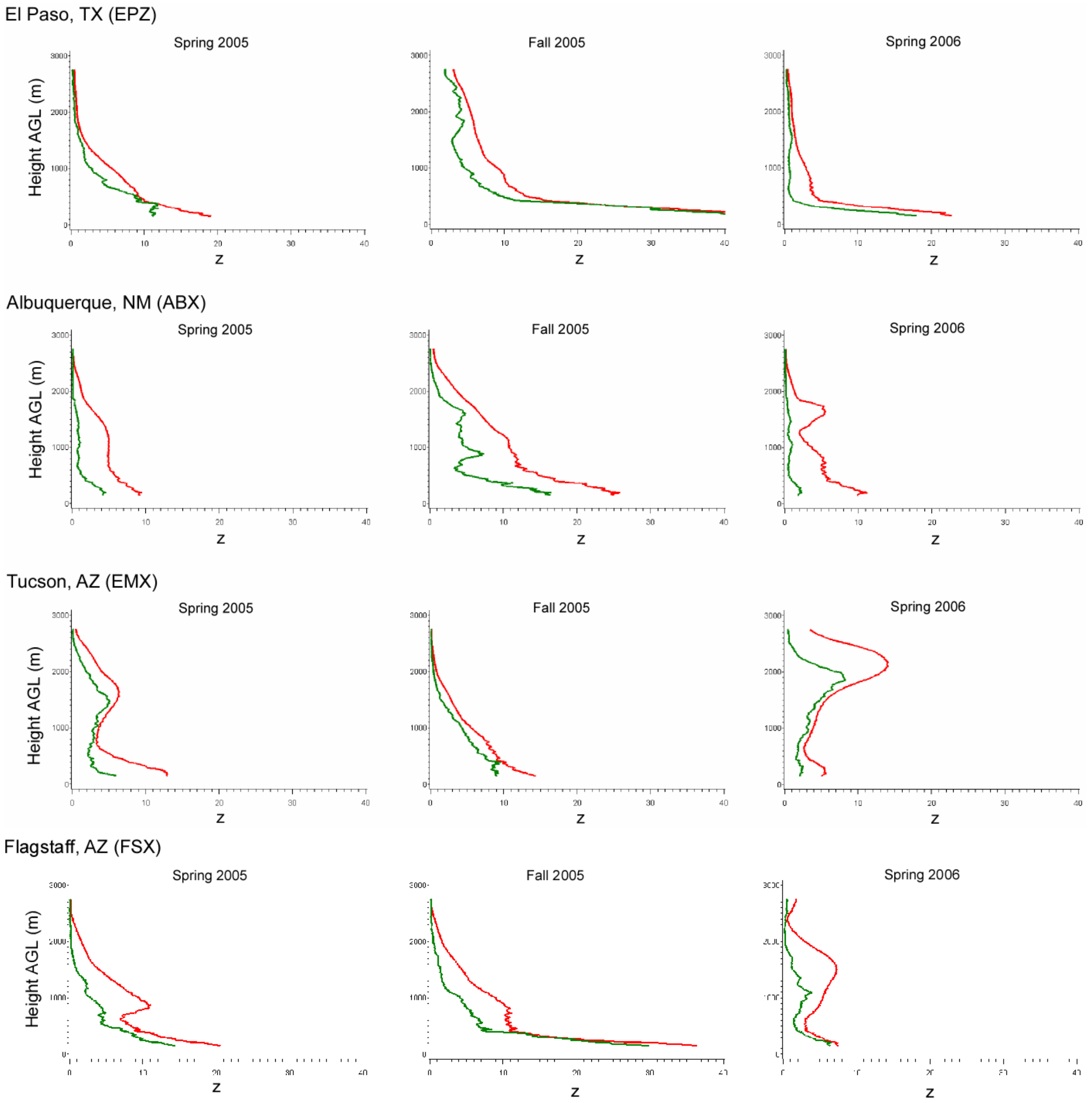


Figure 8. Median (green) and mean (red) vertical profiles of reflectivity for spring 2005, fall 2005, and spring 2006 for each of seven radar sites ordered from east to west. —Continued

Occasionally birds (or bats) consistently occupied discrete layers in the atmosphere across the season; good examples are seen at Tucson, Ariz. spring 2005 and 2006, and Del Rio spring 2005 and 2006 (Fig. 8, median values). Two of the more striking examples of birds occupying discrete layers during specific events (dates) appear in data from spring 2006 at Brownsville (Fig. 8, mean values). Two major migration movements on specific dates are responsible for this overall seasonal pattern; one is presented in greater detail in Figure 9. The large differences at these heights between means and medians indicate that peaks in the mean distribution are the result of rare but strong migration events (Fig. 8, Brownsville). Spring movements at Del Rio showed particularly consistent vertical structure with targets concentrating in a wide band centered on 1,000 m AGL. In many instances, birds were more abundant at low altitudes; good examples are seen at Flagstaff, Ariz. spring and fall 2005, El Paso, Tex. all seasons, Albuquerque, N. Mex. fall 2005, and Midland, Tex. spring 2005 (Fig. 8).

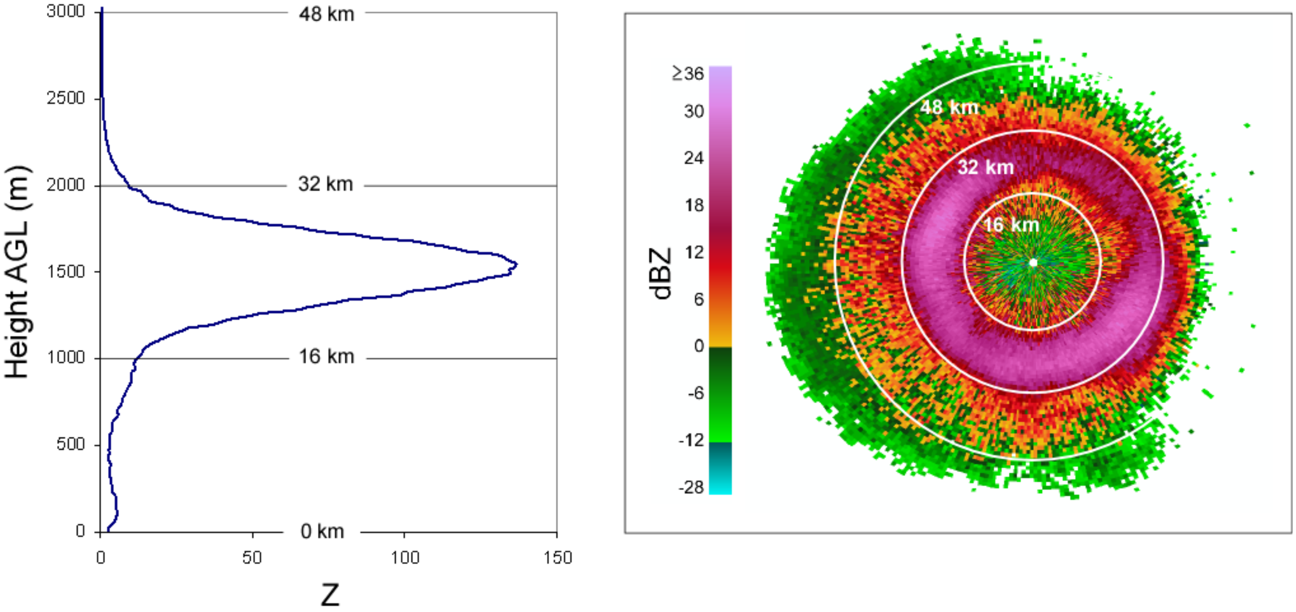


Figure 9. Layered bird migration near Brownsville, Tex. on May13, 2006, 2330 CST. The vertical profile of reflectivity (left) shows birds concentrated in an 800 m layer centered on 1,500 m AGL. This profile was constructed in part from reflectivity data (right) showing a ring of strong echo that appears when the 3.5° elevation beam passes through the migratory layer.

Some sites show substantially different vertical density patterns between spring and fall; good examples are seen at Midland, Del Rio, and Tucson (Fig. 8). At Del Rio and Tucson, spring migrants occupy discrete layers in the atmosphere, while no clear pattern of layers occurs in fall. El Paso showed no clear differences in the vertical density patterns between seasons; targets consistently concentrate below 1,000 m AGL.

It is important to reiterate cautionary notes regarding the limitations of WSR-88D for evaluating patterns of migrants concentrated near the ground. Although the data in this section provide information about vertical structure in bird migration, it should not be assumed that birds are not found at the lowest altitudes (< 500 m); WSR-88D is poorly suited for detecting birds near the ground because of ground clutter, beam height, and spatial resolution of the data.

Migrant Ground Speed - Results

Migrants' ground speeds were significantly different among seasons when pooled across all sites ($\chi^2 = 67.48$, $P < 0.0001$, df = 2; Fig. 10); migrants flew significantly faster in spring than in fall (Table 6a). However, most of this seasonal difference can be attributed to variation at three of the seven sites, Midland, Del Rio, and Brownsville (Tables 6a, 7). Midland ($\chi^2 = 11.34$, $P = 0.003$, df = 2), Del Rio ($\chi^2 = 38.13$, $P < 0.0001$, df = 2), and Brownsville ($\chi^2 = 18.02$, $P < 0.0001$, df = 2) were the only sites with significant differences in ground speed among seasons.

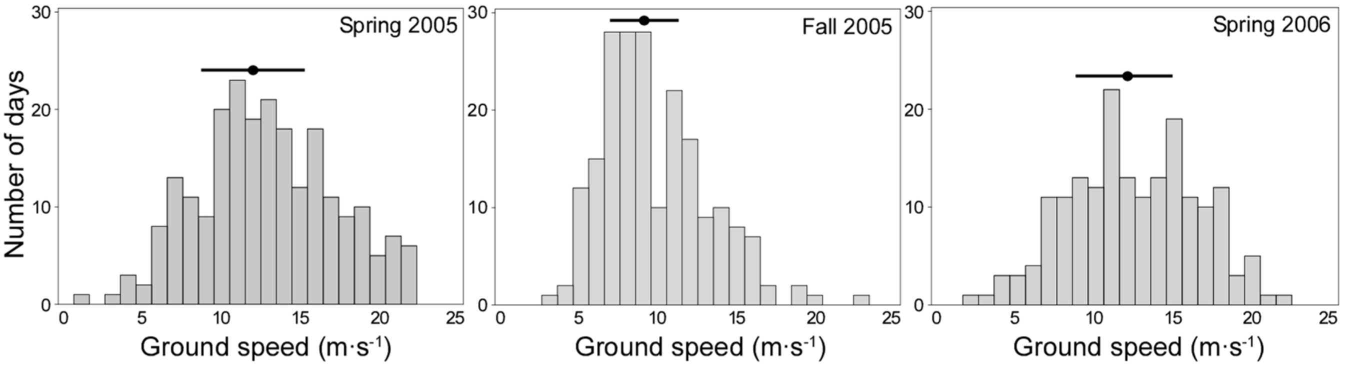


Figure 10. Histogram of ground speed estimates during spring 2005, fall 2005, and spring 2006 where each observation represents one ground speed estimate per day. Error bars represent season median ground speeds + one quartile.

Table 6. Summary of statistics for daily migrant (a) ground speed, and (b) ground direction of travel at each radar site for each season. Radar site acronyms defined in Table 1.

	FSX	EMX	ABX	EPZ	MAF	DFX	BRO	All sites
(a) Flight ground speed (m·s-1)								
Spring 2005								
Median	11.64	11.64	12.52	12.44	13.09	13.40	14.17	12.44
First quartile	9.63	9.01	9.87	8.63	9.77	10.19	10.45	9.74
Third quartile	15.74	13.04	15.43	15.44	18.76	16.44	17.71	15.86
MC[a]	not significantly different across sites within season							
Fall 2005								
Median	9.33	8.55	11.25	9.66	9.96	7.95	9.21	9.27
First quartile	7.90	7.14	8.39	7.45	7.60	5.76	6.77	7.38
Third quartile	11.44	10.83	14.85	11.90	12.33	10.48	11.87	11.86
MC[a]	not significantly different across sites within season							
Spring 2006								
Median	11.10	11.24	12.30	9.59	14.88	15.94	13.06	12.19
First quartile	7.97	9.55	9.32	7.01	10.13	11.92	10.06	9.27
Third quartile	12.73	13.67	15.58	12.42	17.50	17.95	14.49	15.39
MC[a]	BC	BC	ABC	C	AB	A	ABC	
(b) Flight direction (degrees)								
Spring 2005								
Median	359.03	335.42	42.90	73.30	23.68	7.52	22.97	
First quartile	329.04	322.70	2.00	331.91	358.30	355.95	13.13	
Third quartile	37.88	350.78	86.08	90.06	51.87	28.44	32.53	
MC[a]	AB	A	B	B	B	B	B	
Fall 2005								
Median	157.02	173.36	161.92	160.95	187.31	196.54	175.27	
First quartile	113.08	154.12	140.14	126.04	160.08	169.14	169.22	
Third quartile	182.30	182.36	179.28	228.22	211.18	212.70	189.30	
MC[a]	AB	AB	B	AB	AB	A	B	
Spring 2006								
Median	322.52	335.83	6.49	18.16	3.42	9.02	22.49	
First quartile	308.88	329.35	352.87	339.26	345.54	3.07	11.20	
Third quartile	349.04	1.59	86.53	67.87	16.00	19.65	34.76	
MC[a]	A	AB	C	C	BC	C	C	

[a] MC shows where multiple comparisons of ranks identify statistical differences (different letters) within-season across sites in ground speed, and ground direction.

Table 7. Comparisons of migrant ground speeds at those sites that showed significant seasonal differences within sites using non-parametric multiple comparisons of ranks tests (Q). Radar site acronyms defined in Table 1.

Radar site	MAF[a]	DFX[a]	BRO[a]
Flight ground speed			
Spring 2005	A	A	A
Fall 2005	B	B	B
Spring 2006	A	A	AB

[a] Different letters indicate significant differences within sites among seasons (vertical comparisons). Significant differences are those comparisons with Q values $>Q_{(0.017),\,3} = 2.827$, the estimated critical value adjusted for comparisonwise error rates (Table B.15 in Zar (1999), indicates critical $Q_{(0.02),\,3} = 2.713$ and $Q_{(0.01),\,3} = 2.936$).

We found no significant differences in ground speeds within season among sites during spring 2005 ($\chi^2 = 9.24$, P = 0.16, df = 6) or fall 2005 ($\chi^2 = 12.07$, P = 0.06, df = 6), although general patterns could be observed. In spring 2005 median daily ground speed was highest at the easternmost sites (Brownsville, Del Rio, and Midland), and lowest at the westernmost sites (Flagstaff and Tucson) (Table 6a). Fall 2005 median ground speed was highest at the central sites in New Mexico and west Texas (Albuquerque, El Paso and Midland), and lowest at Del Rio (Table 6a).

Migrants' median daily ground speed across all seven sites in spring 2006 was slightly lower than the previous spring (Table 6a). Comparisons of ranked mean daily ground speeds in spring 2006 showed significant differences among sites ($\chi^2 = 34.07$, P < 0.0001, df = 6), yet multiple comparison of ranks for that season showed much overlap in ground speeds (Table 6a).

Vertical Variation in Migrant Densities and Migrant Ground Speed - Discussion

Our initial results showed that spring migrants flew lower and faster than did fall migrants (Felix and others, 2008). Improvements in methodology and subsequent analyses also indicate that migrants showed substantial variation in vertical distributions among sites and between seasons. In both spring and fall, perhaps more so in fall, many sites showed high densities of birds at low altitudes (below 1,000 m AGL) (Fig. 8). In some circumstances in spring, some sites also showed birds occupying discrete layers, usually higher in the atmosphere. The differences between mean and median reflectivity at given heights AGL (with median often less than mean reflectivity) at various sites are indicative of positively skewed distributions of reflectivity. These patterns can occur when weak to moderate migratory movements are common and heavy migrations are few with birds present across a wide range of heights. Alternatively, when heavy migrations are more common but concentrate in different altitudinal layers, any one altitudinal strata may experience strong migration infrequently leading to positive skew at any one altitude seasonally.

Higher spring migrant ground speed is consistent with hypotheses concerning selective pressures for Neotropical and Nearctic migrants to travel faster and arrive earlier on breeding grounds in the spring (Kokko, 1999); a factor that has been positively associated with reproductive success (Smith and Moore, 2005). However, a number of additional factors may affect seasonal and intersite differences in migrant ground speeds, or altitudes, or both: the presence of hatch-year birds during fall migration; bird response to synoptic wind patterns; the possible presence of arthropods, or bats, or both remaining in the data; and our methods for calculating migrant speed.

Hatch-year birds in fall have been found to fly at slower speeds than adults (Hildén and Saurola (1982) or show more variable orientations (Ralph, 1981; Woodrey, 2000). As a consequence of the way speed is measured using large Doppler radars, greater variability in fall migrant directions of travel within a sweep results in lower measured ground speeds. At their highest resolution, these radars quantify the Doppler velocity of all targets within relatively large volumes of airspace; for our sweeps these volumes typically were $3.0 \cdot 10^7$ m^3–$4.7 \cdot 10^7$ m^3 or more. When targets within those volumes travel in approximately the same direction, measured Doppler velocity is higher than when targets' directions vary, even if the actual speeds of individual targets within the volume were identical in both cases. Either of these behaviors in hatch-year birds (slower speeds or variable orientations) could result in calculations of faster migrant ground speeds in spring compared to fall.

Birds are known to concentrate at altitudes where local atmospheric conditions are favorable for migration, typically following winds in the direction of migration (Gauthreaux, 1999; Richardson, 1978). Birds may select altitudinal strata where favorable conditions exist, or avoid strata where unfavorable conditions exist. Selection of altitudes with favorable winds would also enable migrants to increase their speed. In this region, it is possible that birds experience less favorable winds in fall overall that could result in reduced speed and variations in flight altitude and orientation in comparison to spring. Synoptic winds may be structured across the borderlands region such that birds migrating through south Texas in fall encounter unfavorable winds. Caution must be exercised in evaluating this hypothesis with the winds aloft data available in this study. The combined spatial and temporal separation of winds aloft data (provided by radiosondes) from the representative sweeps we analyzed for migrants was as much as 50 km and 5 hr (Midland). Such separation in place and time makes it difficult to be sure what winds aloft are favorable or unfavorable using our methods. Proceeding with caution, however, we can say, based on comparison of winds at Midland and Del Rio (as measured by radiosondes) with migrant directions of travel from our results, that spring winds were more favorable for migration (moving in the same direction as the migrants) than fall winds. Migrant altitude and winds aloft data at Midland and Del Rio suggest that in spring birds were selecting altitudes with consistently favorable winds and in the fall birds faced primarily unfavorable winds. During both springs at Midland and Del Rio migrants appeared to experience favorable and less variable winds, because of relatively consistent directional wind shear (Fig.7). Favorable southerly winds (from the south) occurred at lower altitudes, which is where migrants tended to concentrate, whereas wind directions above 2 km AGL were from the west. In comparison, winds generally were unfavorable for fall migration at all altitudes at Midland and Del Rio. Wind patterns in south and southwest Texas are consistent with Gauthreaux's (1999) observations for the Gulf of Mexico with spring winds aloft being conducive to migration and fall weather patterns generally less favorable to migration. In summary, birds likely are responding to conditions aloft during migratory flight, and variation in vertical distributions likely reflects overall variation in the structure of winds aloft.

To more accurately or comprehensively interpret wind effects at these or any sites would require comparisons of prevailing winds at every altitude and migrants' possible responses therein on a day-by-day basis. In addition, it would require closer spatial and temporal association between radar and winds aloft data than is currently available. Such a full analysis was beyond the scope of this study, but would be useful in further understanding the patterns observed here.

Despite efforts to retain data only from bird-dominated movements, it is possible that bats, or insects, or both could still be present in sufficient numbers in our data to affect our target speed and vertical structure calculations. Either the slower velocities of arthropods or the highly variable velocities of foraging bats could result in reduced target speed estimates (as previously explained for hatch-year migrant behavior) and could distort vertical structure estimates.

Radar data suggest that the majority of both spring and fall migrants were detected flying at low altitudes below 1,000 m (AGL). However, WSR-88D radars in general are ill-suited for studies of very low flying targets because of their scale of operation and low spatial resolution. These constraints, together with those imposed by radiosonde data (which has a relatively low vertical resolution), yielded minimum altitude observations of around 250 m AGL. Therefore, while this work shows that considerable migration can occur above 500 m AGL, particularly in spring, we were not able to detect very low altitude movements.

Migrant Flight Direction - Results

Median directions of travel at all sites in spring 2005 were seasonally appropriate (that is, in a generally northward direction), however there were significant differences among sites ($W = 109.63$, $P < 0.001$, critical W at $\chi^2_{0.05,\ 12} = 21.03$). Travel was slightly east of north at all sites except Flagstaff and Tucson (Fig. 11; Table 6b). Migrants moving through the central part of the region, Albuquerque and El Paso, showed the highest variation in direction (range of circular dispersion between 25% and 75% quartiles); smallest variations in direction occurred at easternmost sites Del Rio and Brownsville (Fig. 11; Table 6b).

Median directions of travel in fall 2005 were significantly different among sites ($W = 52.54$, $P < 0.001$, critical W at $\chi^2_{0.05,\ 12} = 21.03$), yet they remained seasonally appropriate (that is, in a generally southward direction) and varied about due south, with migrants through westernmost sites tending to move somewhat to the east of south. Migrants at Flagstaff showed the largest departure from due south, deviating almost 23° east of south. Circular dispersions in the direction of travel of migrants varied across the borderlands region but without any geographic pattern. The smallest ranges in circular dispersion occurred at Tucson and Brownsville, and the largest at Flagstaff and El Paso (Fig. 11, Table 6b).

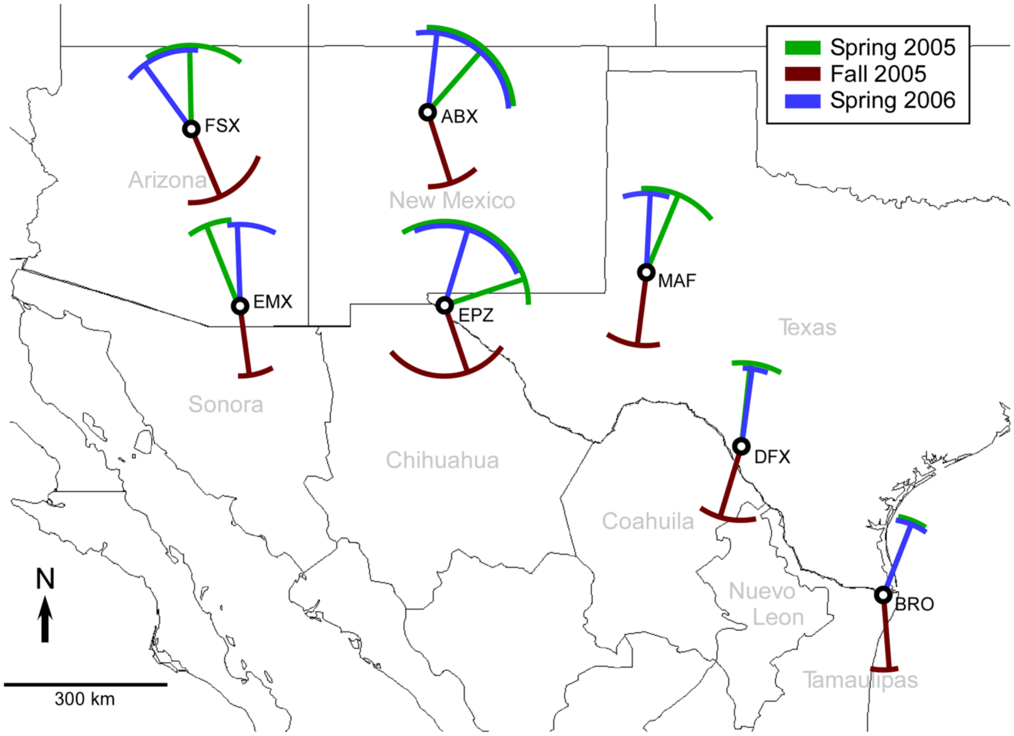


Figure 11. Directions of migration for spring and fall 2005 and spring 2006 at seven radar sites in the southwestern U.S. Green, brown, and blue flags indicate seasonal median migrant directions (with 25 percent and 75 percent quartile whiskers) traveling away from the radar site.

Migrants' directions of travel were again seasonally appropriate in spring 2006, and again directions among sites were significantly different (W = 58.72, $P < 0.001$, critical W at $\chi^2_{0.05,\,12} = 21.03$). Travel was slightly east of north, with the exception of Flagstaff and Tucson, where travel was west of north (Fig. 11; Table 6b). First and third quartiles of ground direction overlapped at all sites with those of spring in the previous year, with the largest difference in median direction at El Paso (Fig. 11; Table 6b). Fifty-five degrees separated the median directions of travel at El Paso between spring 2005 and spring 2006.

Migrant Flight Direction - Discussion

The seasonally appropriate flight directions that we documented for the three time periods of this study are consistent with a 5-day period in spring 2000 when data from the same radar locations showed the directions of travel of migrating birds in four overlapping altitude classes (Gauthreaux and others, 2003). Observed flight directions (Fig. 11) also are consistent with the presence of two major overland migratory systems suggested for western North American wood warblers (Kelly and Hutto, 2005), an important component of the nocturnal migrants measured in this study. Direction of movement patterns for our westernmost sites (Flagstaff and Tucson) in Arizona which were north to west of north in spring and east of south in fall suggest dominance by species that migrate between the Sierra Madre Occidental or Baja California and the Pacific coast (Kelly and Hutto, 2005; Cooke, 1915). Directions of travel in the easternmost sites in Del Rio and Brownsville, which were north to east of north in spring and centered around south in fall suggest that most of these migrants breed in midwestern or eastern North America. High variation in flight directions in the central sites in New Mexico (Albuquerque) and west Texas (El Paso and Midland) suggests that these areas include a combination of migrants from the intermountain west and central-eastern North America (Yong and Finch, 2002; Paxton and others, 2007b), funneling those birds that circumnavigate rather than crossing the Gulf of Mexico between much of North America and points south over the narrower overland route through Mexico.

Geographic Variation in Migrant Densities - Results

We present information about several aspects of geographic variation in migrant densities from our results. The first is to compare density values along an east to west continuum by season (Fig. 12). In spring 2005 geographic variation in the strength of migration as measured by mean density showed the strongest movements through Brownsville and Del Rio, and spring 2006 showed the strongest movements through Del Rio. Fall saw the strongest movements occurring in Midland, El Paso, and Albuquerque. In summary this suggests greater passage through the eastern part of our study region (central and west Texas) in spring and greater passage through the midlongitude part of our study region in fall. However, if bats strongly affect density measures during the middle of the night, especially at Del Rio, then there may be relatively little geographic variation in spring migrant density.

A second approach is to compare spring and fall densities at individual sites. Flagstaff, Tucson, and Brownsville show unremarkable differences between spring and fall migrant densities, while Albuquerque, El Paso, and Midland show markedly stronger migrations in fall than in spring. Del Rio shows markedly stronger movements in spring than in fall (Fig. 12).

A third approach is to compare densities at two sites that are tied in some way through migration. Flagstaff-Tucson and Albuquerque-El Paso represent pairs of sites that are due north and south of each other. In both instances, there is general agreement in the strengths of both spring and fall migration between the pairs.

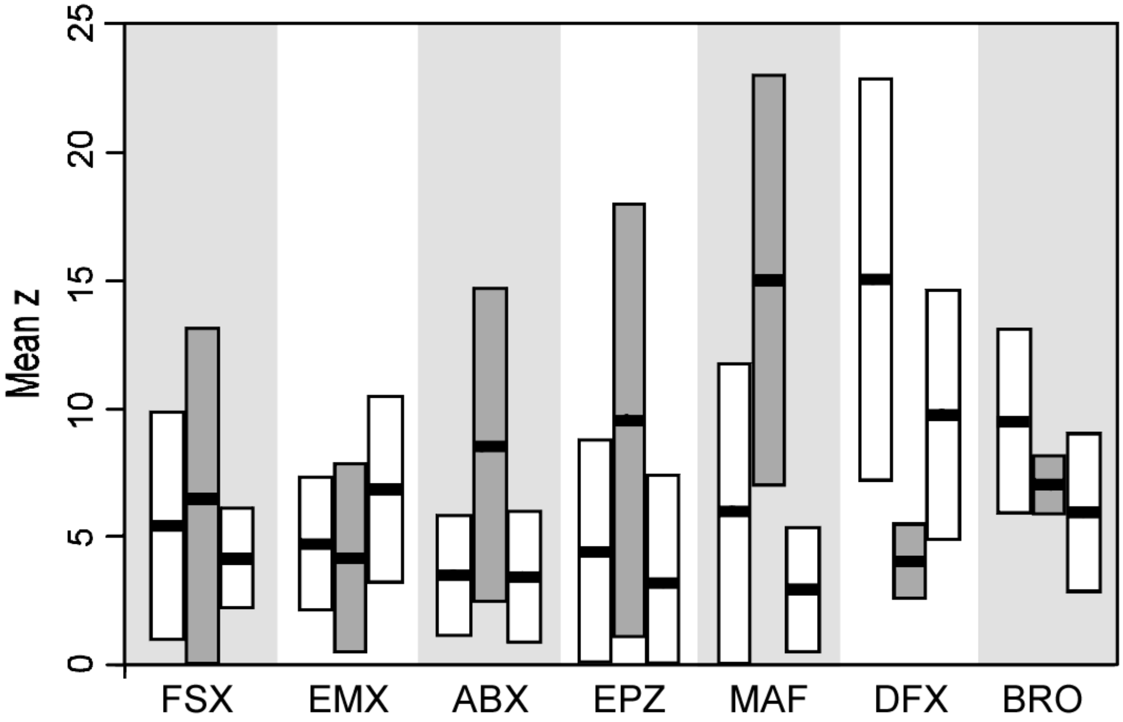
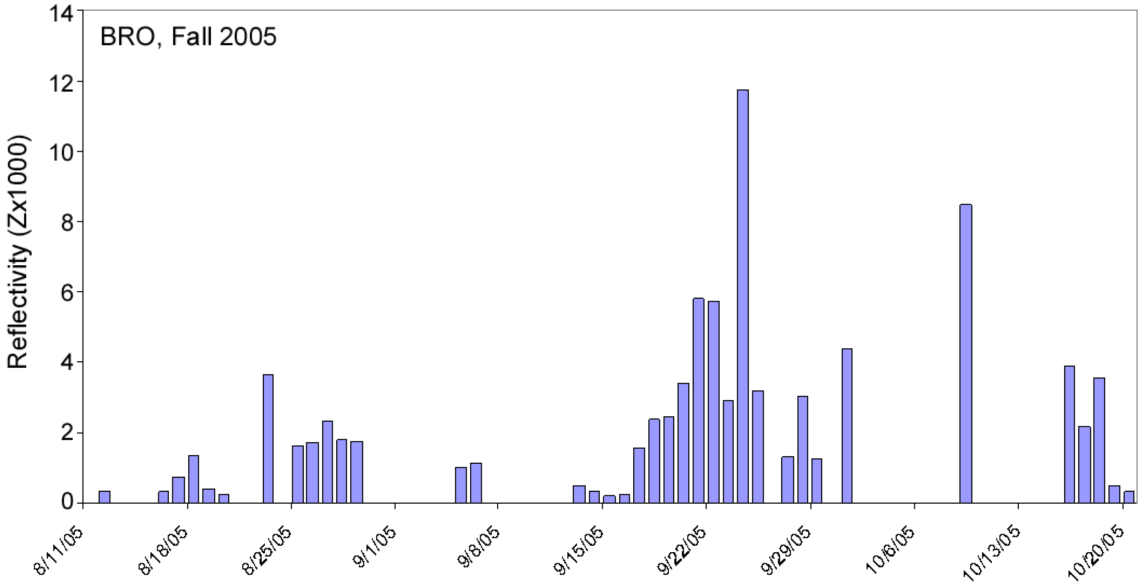


Figure 12. Variation in the strength of migration (mean z±SD, a surrogate for bird density) within and between radar sites across the Southwest. Sites appear from left to right in order of occurrence from west to east. Within a site, bars from left to right represent spring 2005, fall 2005, and spring 2006. Radar site acronyms are defined in Table 1.

Finally, it is useful to assess variability in migrant densities across a season, which can be seen in the standard deviations of the mean in Fig. 12. Large variations indicate that there were substantial differences in migrant densities throughout that season. By comparison, low variation indicates relatively similar densities throughout the season. In both cases, there also may be pulses of migrants passing through on some days and little activity on others. Highest variation in spring 2005 reflectivity was in Midland and Del Rio and lowest variation was in Tucson and Albuquerque. In spring 2006 the highest variation in reflectivity was in Del Rio and the lowest was Flagstaff, Albuquerque, and Midland. Fall saw the greatest variability occurring in the central and western sites, Midland, El Paso, Albuquerque, and Flagstaff. Conversely, extremely low variation occurred at Brownsville and Del Rio in fall. Although the scope of this project did not include documenting daily bird densities across a season, it can help to understand the variation shown in Fig. 12. For example, in Fig. 12 one can see the significant differences in both density and variability of migrants at Brownsville (BRO) and Midland (MAF) in fall 2005. Figure 13 demonstrates these differences in more detail, showing the effect of two large movements (on September 24 and 27) at Midland on both the mean and variation in Fig. 12. It also documents the presence of pulses of migration at both sites.



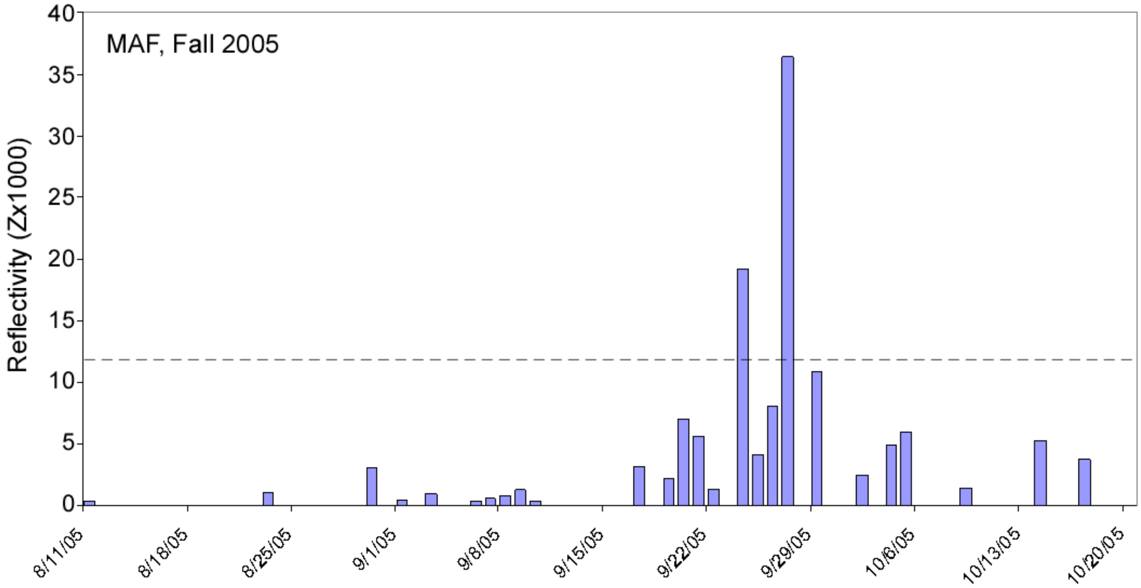


Figure 13. Daily reflectivity caused by biological targets at Brownsville (BRO, above) and Midland (MAF, below), Tex. during Fall 2005. Days marked by zero reflectivity usually indicate either absence of biological targets or removal of that day from analysis because of the presence of nonbiological targets. Note that the reflectivity axes differ between the two charts. The dashed line on the Midland graph below indicates the highest reflectivity measured at Brownsville above.

Geographical and Seasonal Distribution of Migrant Density - Discussion

Migration in eastern and central North America generally is considered to show higher densities than that occurring in the west (Gauthreaux and others, 2003; see also Lowery and Newman, 1966). Although our study focused only on the borderlands region, it would seem to be a good indicator of migration densities throughout the west, as most western overland migrants pass through this region in spring and fall. Although it is beyond the scope of this study to directly compare migrant densities in the western and eastern halves of the United States, using our flight direction and migrant density results, we can make some suggestions regarding the patterns of migrant density across the borderlands region.

In spring, the highest densities of migrants were found at the two easternmost Texas sites. The highest variation in densities within a season are also found in the eastern part of the region, suggesting that there are heavy migration events interspersed among more moderate migration levels or nonmigration periods. In contrast, fall migrant densities in the eastern two sites fall at the lower end of density values for the borderlands region. If, as we have suggested, the eastern sites contain a large proportion of eastern migrants, then perhaps the most likely reason for a pattern of higher densities at Brownsville and Del Rio in spring than fall is that it represents the circular migration pattern described by Rappole and Ramos (1994) in which many eastern migrants that follow a trans-Gulf of Mexico migration route in the fall (passing far east of our study sites and south over the Gulf of Mexico) follow a much more westward trans- and circum-Gulf of Mexico migration route in the spring (coming north overland through Mexico into Texas or crossing the western part of the Gulf of Mexico and making landfall in south Texas). Rappole and Ramos (1994) propose that this circular pattern is caused at least partly by the seasonal weather patterns over the Gulf and their effects on migrants. This circular pattern may even affect migrants in the central part of the borderlands region. Yong and Finch (2002) found that 21 species, mostly eastern breeding Parulinae warblers in small numbers, were only captured in their Middle Rio Grande Valley, N. Mex. sites (Bernalillo and Socorro counties) in spring.

Spring migrant densities throughout the central and western part of the borderlands are relatively lower and less variable than in the eastern part of the borderlands. There also do not appear to be substantial differences between spring and fall densities in the western (Arizona) sites. However, the highest densities and greatest variation in density of fall migrants were found in the central part of the borderlands (New Mexico and west Texas); substantially larger numbers of migrants pass through the central sites in the fall compared to the spring. This is consistent with Yong and Finch's (2002) findings from the Rio Grande Valley in New Mexico. These larger densities could be composed of a larger number of hatch-year birds, although one might expect that pattern to be found regionwide if hatch-year birds follow the migration patterns of conspecific adults. The central pattern is consistent with the higher percentages of hatch-year birds (59 percent) compared to adults (32 percent) found at New Mexican sites in fall by Yong and Finch (2002). It is also possible that the larger numbers of fall migrants in the central sites represent birds that use an elliptical migration path to and from their breeding sites. Phillips (1975) has documented such elliptical migration routes for Allen's Hummingbird (*Selasphorus sasin*) and several other western hummingbird species; in spring they migrate northwest from west Mexico and up the Pacific coast and in the fall they migrate through the Intermountain West and west Texas. Different northbound and southbound migration routes may be relatively common in western species (Kelly and Hutto, 2005; Carlisle and others, 2009) where so much remains to be learned about this subject.

Part II – Stopover Habitat Use – Results and Discussion

Stopover Habitat Use - Results

Table 8 and Figure 5 provide information about the area sampled for each habitat at each site, to be used in our bird-habitat association analyses. Scrub/shrub was the most represented habitat type by area sampled at five of the six sites (all but Brownsville); grassland/herbaceous also occurred in abundance at Albuquerque and Midland. Agriculture was most abundant around Brownsville which also was characterized by a more even representation of land cover types than areas sampled around other sites. Forest occurred in abundance only around Flagstaff. In spite of the ecological importance of forested riparian corridors in the Southwest (incorporated into the forested/shrub wetland category), it was not one of the major habitat types for any of our sites. This category represents a small percentage of the landscape and is marginally visible to satellite. This difficulty in detecting small habitat patches also explains why no upland forest habitat was sampled at El Paso.

Table 9 and Figure 14 provide information about which sites showed significant differences in bird densities among different habitat types. For two sites–Flagstaff and Tucson–there are significant differences in bird densities among habitats within a season for both springs and fall and

Table 8. Mean habitat area (m^2) analyzed across seasons determining habitat-associated migrant densities (±1 SD). Radar site acronyms defined in Table 1.

	Radar site					
Habitat type	**FSX**	**EMX**	**ABX**	**EPZ**	**MAF**	**BRO**
Scrub/Shrub	$6.00*10^{8}$ $(3.18*10^{8})$	$1.00*10^{9}$ $(1.42*10^{8})$	$1.00*10^{9}$ $(4.30*10^{8})$	$5.00*10^{8}$ $(5.94*10^{7})$	$2.00*10^{9}$ $(6.44*10^{8})$	$6.00*10^{7}$ $(5.29*10^{6})$
Grassland/Herbaceous	$1.00*10^{8}$ $(5.74*10^{7})$	$1.00*10^{7}$ $(2.18*10^{6})$	$5.00*10^{8}$ $(1.84*10^{8})$	$1.00*10^{7}$ $(1.99*10^{6})$	$4.00*10^{8}$ $(1.03*10^{8})$	$3.00*10^{7}$ $(3.37*10^{6})$
Upland Forest	$5.00*10^{8}$ $(2.04*10^{8})$	$5.00*10^{7}$ $(7.66*10^{6})$	$8.00*10^{7}$ $(2.79*10^{7})$	0 (0)	$7.75*10^{5}$ $(1.76*10^{5})$	$3.32*10^{6}$ $(2.19*10^{5})$
Open Water/Wetlands	$1.28*10^{6}$ $(3.90*10^{5})$	$2.61*10^{5}$ $(6.95*10^{4})$	$8.43*10^{6}$ $(2.44*10^{6})$	$1.36*10^{6}$ $(1.72*10^{5})$	$1.00*10^{7}$ $(2.66*10^{6})$	$3.00*10^{8}$ $(8.24*10^{7})$
Forested/Shrub Wetlands	$2.69*10^{6}$ $(1.56*10^{6})$	$2.43*10^{6}$ $(3.26*10^{5})$	$6.87*10^{6}$ $(2.39*10^{6})$	$2.56*10^{5}$ $(1.24*10^{4})$	$1.58*10^{6}$ $(2.47*10^{5})$	$1.00*10^{7}$ $(1.62*10^{6})$
Agriculture	$3.11*10^{5}$ $(2.54*10^{5})$	$1.00*10^{7}$ $(1.66*10^{6})$	$7.00*10^{7}$ $(2.75*10^{7})$	$8.00*10^{7}$ $(4.13*10^{6})$	$3.00*10^{8}$ $(8.56*10^{7})$	$5.00*10^{8}$ $(6.22*10^{7})$
Developed	$9.00*10^{6}$ $(3.74*10^{6})$	$2.00*10^{8}$ $(7.75*10^{7})$	$4.00*10^{7}$ $(1.37*10^{7})$	$5.00*10^{7}$ $(3.52*10^{6})$	$6.00*10^{7}$ $(1.31*10^{7})$	$1.00*10^{8}$ $(6.33*10^{6})$
Barren	$1.13*10^{6}$ $(6.61*10^{5})$	$5.00*10^{7}$ $(1.44*10^{7})$	$1.00*10^{7}$ $(4.74*10^{6})$	$2.00*10^{5}$ $(4.04*10^{4})$	$3.00*10^{7}$ $(1.03*10^{7})$	$7.00*10^{7}$ $(9.40*10^{6})$

Table 9. Comparisons of stopover migrant densities (differences in daily mean z) among eight cover types within site by season. Radar site acronyms defined in Table 1.

Radar site	Season	X^2	p
FSX	Spring 2005	45.51	< 0.001
	Fall 2005	30.29	< 0.001
	Spring 2006	18.77	< 0.01
EMX	Spring 2005	105.14	< 0.001
	Fall 2005	45.45	< 0.001
	Spring 2006	29.24	< 0.001
ABX	Spring 2005	0.67	= 1.00
	Fall 2005	10.57	= 0.16
	Spring 2006	5.58	= 0.59
EPZ	Spring 2005	10.48	= 0.11
	Fall 2005	20.84	< 0.01
	Spring 2006	22.37	< 0.01
MAF	Spring 2005	1.59	= 0.98
	Fall 2005	18.82	< 0.01
	Spring 2006	1.88	= 0.97
BRO	Spring 2005	8.25	= 0.31
	Fall 2005	33.61	< 0.001
	Spring 2006	6.26	= 0.51

those habitat- use patterns are relatively consistent across seasons. Around Flagstaff migrant densities are highest in open water/wetland, developed, and upland forest habitats in both springs and fall (Fig. 14). Conversely, some of the lowest densities of birds were found in agricultural habitat. In Tucson, the highest migrant densities were found in upland forest habitat, with no clear pattern among the other habitat types, all with lower densities around this radar.

For three sites–El Paso, Midland, and Brownsville–there were significant differences in bird densities among habitats in fall 2005 (Table 9). In all three sites the highest migrant densities were found in developed habitats. In El Paso and Midland the second highest densities were in forested/shrub wetlands, and in Brownsville the next highest densities were in upland forest and scrub/shrub habitats.

For one site–Albuquerque–there are no significant differences in bird densities among habitats for either spring or fall. However, there is a relatively strong pattern in the bird densities among habitats in fall 2005 that is not quite statistically significant (Table 9; Figure 14), suggesting that Albuquerque may be similar to the three previous sites discussed. The highest fall migrant densities appear to occur in upland forest, open water/wetland, and forested/shrub wetland habitats.

There also are some notable seasonal migrant density patterns (Fig. 14). When comparing general patterns between spring 2005 and 2006, two sites–Flagstaff and Albuquerque–have overall higher migrant densities in spring 2005 than in 2006. There are no clear differences in spring densities between years in El Paso, and at Tucson, Midland, and Brownsville there is a mixed pattern by habitats, with some habitat types supporting higher densities in spring 2005 and others supporting higher densities in spring 2006. When comparing general patterns in fall 2005 with patterns in spring (2005 and 2006), three sites–Albuquerque, El Paso, and Midland–have overall higher migrant densities in fall than in either spring. There are no clear differences between spring and fall for any of the other sites.

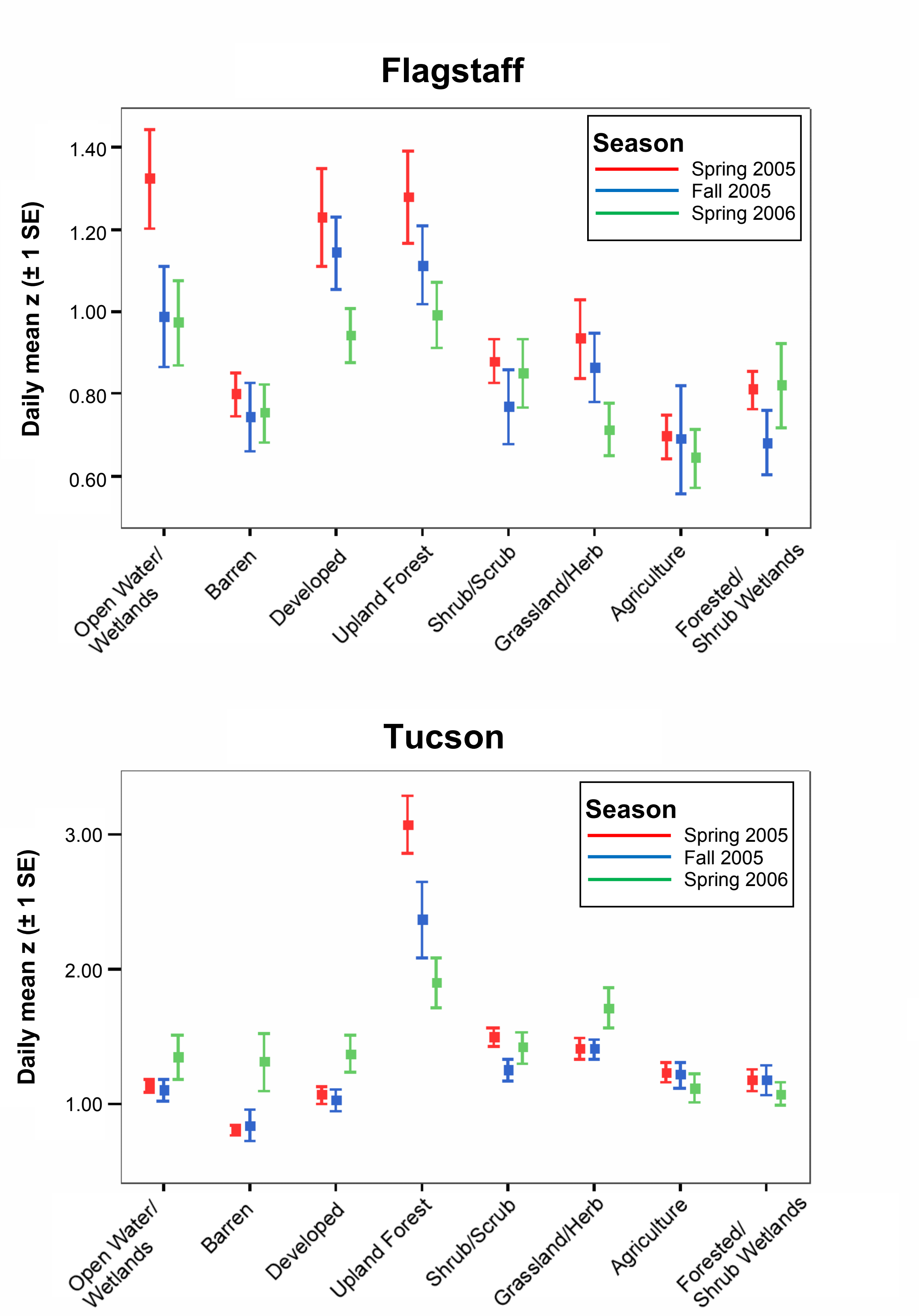


Figure 14. Migrant densities as they are associated with major habitat types at each radar site among seasons (daily mean z ± 1 SE). Note vertical scales for daily mean z are different for each site. Habitat types are defined in Table 4.

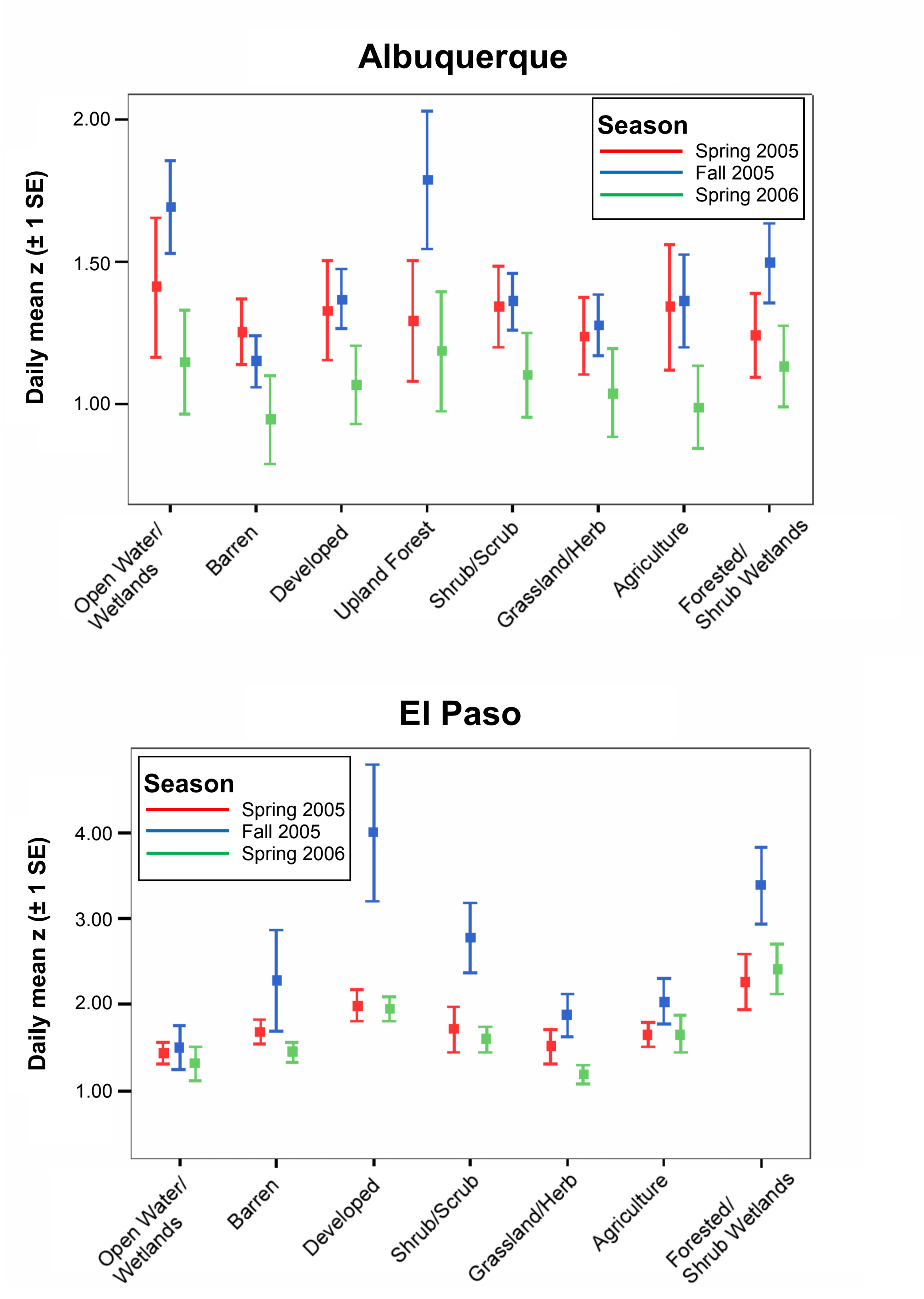
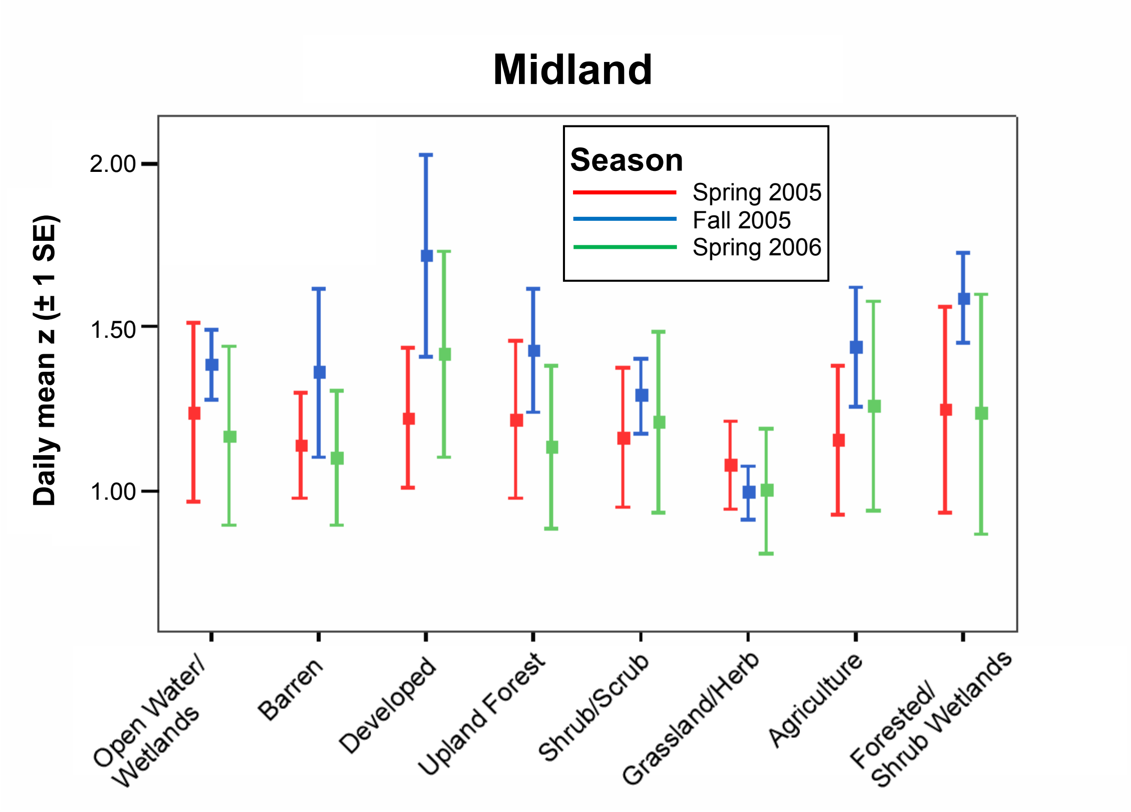


Figure 14. Migrant densities as they are associated with major habitat types at each radar site among seasons (daily mean z ± 1 SE). Note vertical scales for daily mean z are different for each site. Habitat types are defined in Table 4. —Continued



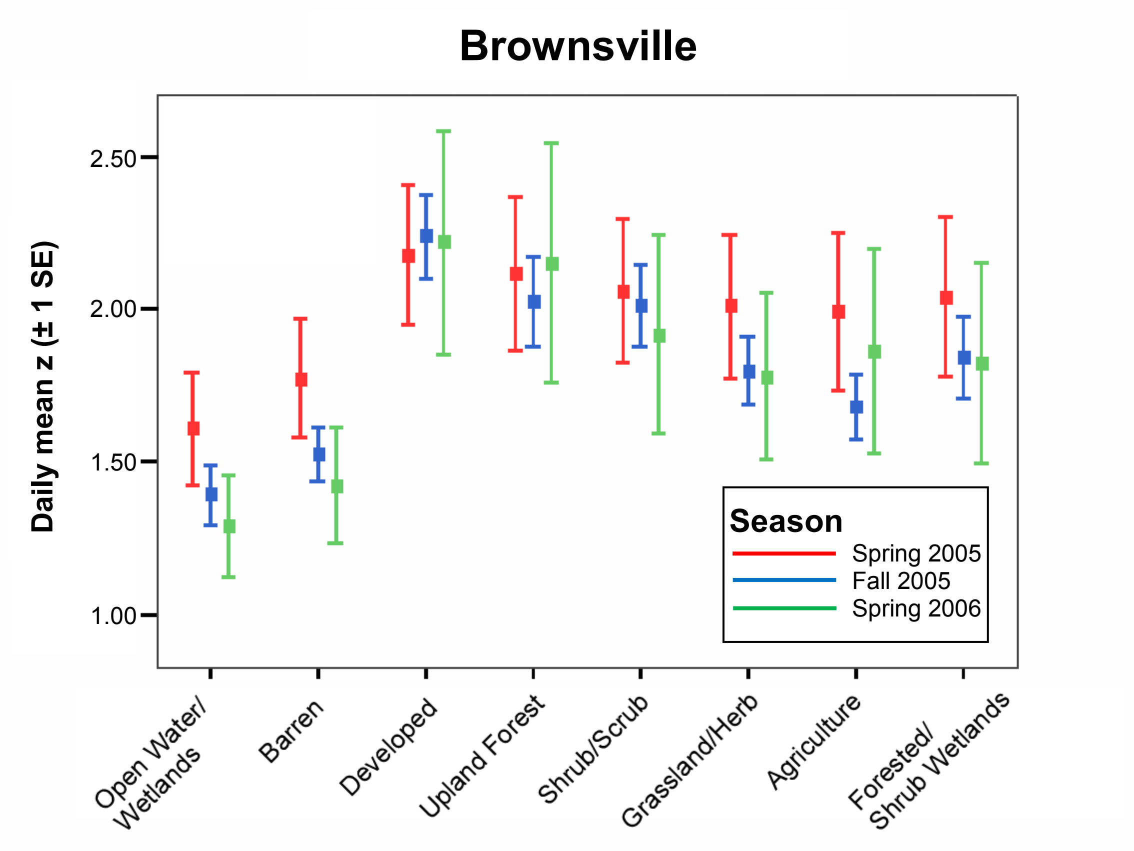


Figure 14. Migrant densities as they are associated with major habitat types at each radar site among seasons (daily mean z ± 1 SE). Note vertical scales for daily mean z are different for each site. Habitat types are defined in Table 4. —Continued

Stopover Habitat Use - Discussion

As mentioned above, the migrant density measures used in evaluating stopover habitat use were taken as birds initiated migration at civil twilight, as compared to density measures taken on birds in full migration mode in the middle of the night in Part I.

We were quite conservative in our bird-habitat association evaluations, excluding areas within our occultation filters and further limiting our analyses to the band of bird and land cover data between 35 and 50 km from the radar that was outside the occultation filters (Fig. 5). It is possible that in a few cases the relative amounts of habitat types sampled were not correlated with the relative amounts of habitats available in the region around the radar. This would affect some of our observations about habitat associations in the context of available habitat. New methods are being developed to address some of the limitations we faced (Buler and Diehl, 2009), which will enable the use of more of the available data for analyses in the future.

Only two sites–Flagstaff and Tucson–show evidence of habitat selection by migrants in both spring and fall and those habitat preference patterns are similar in both seasons. For the remaining four sites there is evidence of habitat selection by migrants only in the fall but no clear pattern in the spring. These different patterns may be a result of migrants' responses to particular available stopover habitats at different sites, as discussed below, or, as mentioned above, it may be a result of seasonal variation in the remaining presence of nonbird targets in the data.

The importance of riparian habitats as migrant stopover habitat in arid landscapes has long been recognized; migrant use of riparian habitats is disproportionate relative to the small area covered by these habitats in the West (summarized in Carlisle and others, 2009). Although our results are generally consistent with this observation, they do not provide strong evidence for the high densities suggested in the literature (but see discussion below). For all sites, forested/shrub wetlands (the category in which forested riparian corridors fall) are among the smallest available habitats; the same applies for open water/wetlands except in Brownsville, where the Gulf of Mexico dominates. Yet forested/shrub wetlands support the second or third highest migrant densities in Albuquerque, El Paso, and Midland, indicating their value as stopover habitat.

A number of recent studies have documented the importance of higher-elevation habitats, especially montane deciduous and coniferous forests, for fall migrants (Hutto, 1985; Carlisle and others, 2005; DeLong and others, 2005; Carlisle and others, 2009). For the three sites–Flagstaff, Tucson, and Albuquerque–with large areas of upland forest habitat, these montane forests supported high densities of stopover migrants in fall, as well as in spring in Flagstaff and Tucson. In fact, because of the areas we were able to analyze at these three sites (Fig. 5), if anything, upland forest is underrepresented in our analyses and forest accounts for a greater abundance of migrants during stopover than our sampled areas suggest. Our results are consistent with on-the-ground migration studies in the Manzano Mountains southeast of Albuquerque (DeLong and others, 2005) and in the Santa Rita, Huachuca, and Santa Catalina Mountains surrounding Tucson (J.L. Kellermann, personal commun., 2010). These studies found that montane forested habitats supported substantial numbers of migrants; some of these species (for example Hermit Warbler, Townsend's Warbler, Olive-sided Flycatcher, Ruby-crowned Kinglet) were found primarily, or in higher numbers, in montane forested habitats than in lower elevation habitat types. A number of studies have suggested that these high elevation habitats may provide cooler microclimates and higher food availability than lowlands, especially during fall migration (summarized in Carlisle and others, 2009) and in particular very arid regions such as Tucson and Albuquerque.

With the exception of Midland, our sites are located near substantial human population centers. For four sites–Flagstaff in one spring and fall, and El Paso, Midland, and Brownsville in fall–developed areas supported high densities of stopover migrants; in contrast there is no such evidence for Tucson or

Albuquerque. Although often considered inhospitable habitats that negatively affect biodiversity (Hansen and others, 2005), developed habitats (urban and exurban) have been found to support some breeding native bird species in the arid Southwest (Germaine and others, 1998; Bock and others, 2008), although in both cases some native grassland (Bock and others, 2008) and native desert (Germaine and others, 1998) species were negatively associated with the exurban habitat characteristics. Developed habitats also have been associated with concentrations of migrants (Bonter and others, 2009), which may be able to use a broader range of habitats during migration than during breeding. The lusher vegetation, ornamental and especially native plantings, landscaping, and free water available in urban and exurban areas can provide food, resources, and shelter for native bird species in arid landscapes (Germaine and others, 1998; Bock and others, 2008), including stopover migrants. In arid landscapes with little or no upland forest habitat available to migrants (El Paso, Midland, and Brownsville), especially in the fall (Carlisle and others, 2009), these developed sites may provide valuable refuges.

Agricultural habitat was the largest habitat type at Brownsville and the second largest in El Paso and the smallest habitat type at Flagstaff. At no sites did agricultural habitat support high migrant densities, although at most sites the low to intermediate densities it supported were relatively similar to the densities in a number of "natural" habitat types (Fig. 14).

Scrub/shrub habitat is arguably one of the most widely distributed habitat types in the borderland region. It was the largest habitat cover type at all sites except Brownsville. At no site did it support high migrant densities, although at many sites it supported low to intermediate densities similar to a number of other habitats. Puschock (1998) also found that spring and fall migrants (including flycatchers and warblers) through New Mexico used both riparian habitat and various scrub/shrub habitat types (mesquite, mountain mahogany, pinyon-juniper, and xeric arroyo scrub). Maximum capture rates for flycatchers always occurred in the scrub/shrub habitats when compared to the riparian habitats, and although warbler capture rates tended to be greater across all the riparian habitats compared to all scrub/shrub habitats, maximum capture rates occurred at the xeric arroyo scrub site in one fall and one spring season. Habitats that support lower migrant densities but cover broad spatial extents, may in actuality be at least as important in supporting the large numbers of migrants moving through the region (DeLong and others, 2005) as smaller habitats (for example, riparian) that concentrate migrants in higher densities. Similarly, grassland/herbaceous is the second-largest habitat cover type at two sites–Albuquerque and Midland–and occurs at intermediate coverage levels at all other sites. Grassland/herbaceous habitats also do not support high migrant densities at any site, but as with scrub/shrub habitat, may support large numbers because of large spatial extent. As an example of the broad spatial extents covered by these two habitat types, based on our analyses (Table 8), in the area around the Albuquerque radar there is about 145 times as much scrub/shrub habitat as forested/shrub wetland habitat, and about 73 times as much grassland/herbaceous habitat.

Grassland/herbaceous and scrub/shrub also may be important stopover habitats, in spite of supporting relatively low migrant densities, because of the migrant species for which they provide stopover habitat. Not all migrants traversing the borderlands region have the same needs or habitat associations. This is most obvious when comparing forest-dwelling, wetland-dependent, grassland, and shrubland migrants, all of which may be components of the stopover migrant takeoffs documented by radar at a particular site. Many short-distance migrant species are a component of the nocturnal and stopover migrants in this study. Little migration research or monitoring has been conducted in grassland or scrub/shrub habitats. However, a study of habitat associations of migrating and wintering grassland birds in southern Texas (Igl and Ballard, 1999) found that grassland birds overall were most abundant during migration in the two most structurally simple habitats (grassland and shrub-grassland) that most closely resembled their breeding habitats, although they used other habitats with woody canopy cover to some extent. Although there is reason to believe that grassland and shrubland birds may use a wider range of habitats during the nonbreeding season (Emlen, 1972; Hutto, 1992; Igl and Ballard, 1999), Igl and Ballard (1999) also found that species that were considered grassland specialists on their breeding grounds tended to be more habitat specific during the nonbreeding season than shrub-grassland specialists.

In addition to meeting the habitat requirements of grassland and shrubland specialists during migration, large arid grassland and shrubland habitat blocks provide, to an unmeasured extent, stopover habitat for species usually thought of as forest-dwelling migrants. On occasions, large numbers of spring migrant warblers, tanagers, and flycatchers have been observed using sagebrush and other arid habitat types in Idaho (J. Carlisle, personal commun., 2010), sometimes even when presumably more "preferred" willow and cottonwood habitat is available nearby. J. Carlisle (personal commun., 2010) suggests that this may be because the desert in Idaho is at its most productive from March to June and provides sufficient food resources for migrants. Similarly, warblers usually considered to be forest-dwelling, have been observed using xeric arroyo habitats in the Sonoran Desert (B. Wolf, personal commun., 2009). Obviously these patterns would vary depending on precipitation, seasonal productivity patterns, and available habitat types in different locations.

There is another perspective that could be applied to the observations that grasslands and shrublands are supporting lower densities of migrants. In habitats where food resources are more limited, the availability of broad spatial extents may allow migrating grassland and shrubland specialists to spread out at lower densities to acquire needed resources while avoiding competition. In addition, these arid habitats exhibit substantial annual and seasonal geographic variation in resource availability (driven largely by precipitation), as well as subtle habitat heterogeneity which frequently is poorly distinguished by land cover classification. The existence of large, heterogeneous landscapes could ensure necessary resources at different places in different years for stopover migrants. Mehlman and others (2005) provide a valuable conceptual framework for conserving stopover habitat for forest-dwelling, nocturnal migrants by distinguishing among different types of stopover site functions. However, the concepts they introduce may be more difficult to apply in arid, nonforested landscapes where the location of habitats that serve different functions for migrants may not be easily identified, the knowledge about relative availability of resources and services provided is more limited, and functions, resources, and habitat quality show more seasonal or annual variation.

A number of factors may affect the bird-habitat association results in this study: occultation, migrant displacement, presence of bats or insects in data, radar scale and resolution issues, and temporal differences between radar and land cover data.

Occultation likely contributes significant variation to habitat analyses. Across the study area, radar site occultation varies from none at Brownsville and Midland to more than 50 percent at El Paso and Tucson (Figs. 2 and 5). In the case of our analyses, data were further constrained by the use of reflectivity data (and therefore land cover data) only within a band extending from 35 to 50 km from the radar, where habitat associations may be considered comparable (explained in Methods section). Because of these two constraints, at several sites substantial amounts of habitat could not be analyzed because it occurred behind the occultation filter or outside the 35 to 50 km ring analyzed. In Flagstaff, Tucson, and Albuquerque, for example, upland forest habitat is under-represented in our analyses.

Displacement of migrants from their actual stopover habitat between the time they take flight and the time that they intersect the radar beam can affect bird-habitat associations (Diehl and Larkin, 2005), especially for small habitat patches or narrow, linear habitat types like riparian corridors. Over a time interval shorter than the temporal resolution of the radar sweep, migrant songbirds may take off from a small habitat patch and become associated with surrounding habitat types. In these instances migrants will be inaccurately associated with the incorrect stopover habitat type. A likely example of the effects of displacement in our results is related to the high migrant densities in Flagstaff in spring 2005 that were associated with open water/wetland habitat (not key stopover habitat for passerine migrants). Further review of radar and habitat data in GIS around Flagstaff detect strong echoes (high target densities) throughout a section of forest that contains two of the largest patches of open water (lakes) in the area 21 km north-northeast of the Flagstaff radar. Although it is possible that some migrating waterfowl taking off from these lakes contribute to the target pool, based on the timing of migration it is most likely that these open water-associated echoes were a result of passerine migrants dispersing from the surrounding forested habitats. Migrant displacement combined with the narrow, linear shape of riparian habitats, may mean that our estimates of stopover migrant densities in forested/shrub wetlands may be underestimates. Proximity effects such as these might be common throughout the study area, especially given the spatial and temporal resolution of the radar reflectivity data. Proximity effects can result in over- or under-estimation of densities associated with a particular habitat.

As mentioned previously, the remaining presence of local, high-density concentrations of bats or the broad presence of bats at low densities in our data could either cause or obscure patterns or associations between birds and stopover habitats.

Differences between the scale of the data used, and the scale of the biological phenomenon described affected our ability to relate birds to their stopover habitats (Gergel and others, 2002; O'Neill and Smith, 2002). Limits to spatial resolution are largely a radar data problem. Radar and land cover data differ in their resolution. Land cover data are Cartesian-raster, and defined in 30-m by 30-m grid cells. Radar reflectivity data are polar-vector with a resolution of 1° by 1,000 m increments and had to be converted to raster grids of the same resolution as land cover data within GIS. Landbird migrants may be distributed within the habitats at scales much smaller than WSR-88D radars are capable of measuring. Likely, this is the case with small and narrow, linear riparian corridors and arroyos in the arid Southwest. Land cover data already exist that approximately match the scale of migration stopover for the most part, although there may be exceptions for the same small habitat patches and narrow riparian habitats that pose problems for radar data. For example, a study in the Sonoran Desert (B. Wolf, personal commun., 2009) indicates that passerine migrants are stopping over in xeric riparian (arroyo) habitats that most likely are classified as scrub/shrub in these land cover data. While higher resolution weather radar data have become more available, the problem of bird dispersion into the atmosphere during takeoff persists, and this prevents the estimation of higher resolution habitat-migrant associations. Models currently under development based on radar data may be capable of high resolution habitat-migrant associations (Diehl and Wang, 2007).

Limits to temporal resolution have both radar and land cover components. As discussed in the Methods section, there is temporal separation between the time when wind speeds are sampled by radiosondes and when radar is sampling bird targets in the middle of the night. Secondly, there is temporal separation between the time when birds initiate migration from stopover and migration in the middle of the night, the time when target identity is determined. Because it is unreliable to attempt target identification when bird are initiating migration, we had to rely on middle of the night target identification to identify days that were dominated by bird targets for our analyses (described in Methods section). Finally, the temporal scales of radar data and habitat data are not similar. Satellite imagery used to derive the habitat data we analyzed were collected in 2001 (U.S. Geological Survey, 2008). At least four years passed between the habitat data collection and the migrant density data collection, and land cover could have changed considerably in certain parts of the study area. We would expect habitat data to be less reliable especially near centers of anthropogenic activity.

Finally, it is important to recognize the limitations associated with assigning importance to stopover habitats based solely on numbers of birds. We have already discussed the problems with making such interpretations solely based on densities of birds departing stopover habitats, especially when considering habitats which cover broad geographic expanses. In addition, relying on densities or total numbers of birds to assign habitat importance fails to address questions related to how migrants are using particular habitats (for example, do they stopover for longer periods in some habitats? Do they gain mass faster in some habitats than others? Is survivorship greater in some habitats?).

Discussion Summary and Implications for Future Work

Despite any limitations of the data and analyses used in this study, the results provide new information about regional and seasonal patterns in migratory movement in the U.S./Mexico borderlands area which offers guidance for future research and management, as regulatory agencies and organizations implement bird conservation activities in the borderlands region. Our observations regarding high migrant densities in forested/shrub wetlands, upland forest, and developed habitats support existing literature and observations. However, our results suggesting that large expanses of scrub/shrub and grassland/herbaceous habitats may support larger numbers of stopover migrants than previously thought are noteworthy and have implications for future research and migratory bird conservation.

The results of this study emphasize the need for further work to: (1) characterize passerine migratory systems and bird-habitat associations in the American Southwest (Kelly and Hutto, 2005; Carlisle and others, 2009); (2) improve methods for analyzing radar data and improving target identification for the study of migration and other bird movements, such as use of artificial intelligence methods for analyzing radar data and identifying bird targets (Mead and others, 2008; Doktor and others, 2009); (3) improve knowledge about the subtle habitat characteristics that allow arid landscapes to support migrants; (4) improve land cover classification methods to better distinguish among arid habitat types (especially among grassland types and desert shrubland types) that may be important for migrant stopover; and (5) inform decisionmakers crafting and implementing biological conservation policy affecting migrating birds (Ruth and others, 2005).

Our study analyzed data from two spring seasons and only one fall season. Given the between-season and among-site variations we documented, analysis of additional years of data are required to get a clearer picture of the patterns and variation in bird migration through the borderlands region. Additional, more detailed analyses of wind patterns (speed, direction, and structure) as they are associated with bird migration behaviors would improve our understanding of how wind affects migration speed, direction, and elevation.

More traditional on-the-ground migration ecology research and migration monitoring, in conjunction with the collection of further long-range and short-range radar data, are critical, particularly in habitats that are rarely studied during migration (scrub/shrub, grassland/herbaceous, and developed) and that may be supporting more migrants at low densities than is currently recognized. This future research should focus on “ground truthing” the patterns presented here from analyses of long-range radar data and gathering the additional information needed to understand how migrants are using these stopover habitats. Collaborative work among researchers studying migration throughout the West will assist in painting the full picture of migration through the Southwest borderlands region and throughout the West. The value of riparian habitats in the arid West and the threats facing this important migration stopover habitat are well documented elsewhere. However, semidesert and plains grasslands and desert scrub/shrub habitats in the Southwest also are highly threatened from multiple factors (for example, habitat conversion for agriculture, urban/exurban, or energy development, livestock overgrazing, shrub encroachment, changes in fire regimes, climate change) (McClaran and Van Devender, 1995; Merola-Zwartjes, 2004; Ingelfinger and Anderson, 2004; Pruett and others, 2009). Research is needed to provide managers with the information needed to guide management of grasslands, desert shrublands, and other habitats for migratory birds. In addition, more research is needed using radar technologies to determine whether passerine migrants are moving in broad fronts as generally assumed, or if they may be navigating in the middle of the night using linear landscape features like riparian corridors (Skagen and others, 2005) or mountain ridges.

We are not the first to identify the importance of aerohabitat for migrating birds and other flying wildlife. However, application of this concept to migration research and migratory habitat conservation requires a change in perspective. Compared to the terrestrial stopover habitats we are used to thinking about in migration ecology, aerohabitat is a lot more dynamic; the favorable or unfavorable nature of aerohabitat in relation to migrants can change dramatically on a daily (or hourly) basis. Our results have barely touched on the importance of wind speed, direction, and vertical structure for migrating birds. For the most part, we do not have any control over the atmosphere, but in meteorology we do have the ability to predict atmospheric changes (for example, weather patterns) and in radar technology an increasingly sophisiticated ability to detect biological targets in the atmosphere. These resources can be used to inform management decisionmakers and enable the protection of aerohabitat close to the ground for migrants (for example, powering down wind turbines in the face of approaching migrants and predicted bad weather that might drive migrants to low elevations).

In summary, based on our results it is overly simplistic and paints an incomplete picture to: (1) consider the arid west as a largely inhospitable landscape in which there are only relatively small oases of habitat that provide the resources needed by all migrants; (2) think of western riparian and upland forest habitat as the preferred habitat for all migrants; or (3) consider a particular habitat type unimportant migrant stopover habitat based solely on migrant densities. In reality western landscapes are a complex mosaic of habitats through which a complex assemblage of migrants passes twice a year, stopping to refuel in the specific habitats that meet their needs.

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