

MIGRATING BIRDS' USE OF STOPOVER HABITAT IN THE SOUTHWESTERN UNITED STATES

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Abstract. In the arid Southwest, migratory birds are known to use riparian stopover habitats; we know less about how migrants use other habitat types during migratory stopover. Using radar data and satellite land-cover data, we determined the habitats with which birds are associated during migration stopover. Bird densities differed significantly by habitat type at all sites in at least one season. In parts of Arizona and New Mexico upland forest supported high densities of migrants, especially in fall. Developed habitat, in areas with little upland forest, also supported high densities of migrants. Scrub/shrub and grassland habitats supported low to intermediate densities, but because these habitat types dominate the Southwestern landscape, they may provide stopover habitat for larger numbers of migratory birds than previously recognized. These results are complicated by continuing challenges related to target identity (i.e., distinguishing among birds, arthropods and bats). Our results suggest that it is too simplistic 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 forests as supporting the majority of migrants in all cases, and (3) consider a particular habitat unimportant for stopover solely on the basis of low densities of migrants.

Key words: *bird migration, borderlands, radar, Southwest, stopover habitat use.*

Uso de Hábitats de Parada por Aves Migratorias en el Suroeste de los Estados Unidos

Resumen. En el suroeste árido de Norteamérica, se sabe que las aves migratorias utilizan hábitats ribereños como paradas migratorias; sabemos menos sobre cómo estas aves migratorias usan otros tipos de hábitat durante estas paradas. Utilizando datos de radar y datos de cobertura del suelo proveniente de satélites, determinamos los hábitats con los que se asocian las aves durante las paradas migratorias. Hubo diferencias significativas en las densidades de aves entre los tipos de hábitat en todos los sitios en al menos una estación. El hábitat de bosque montano en partes de Arizona y Nuevo México sustenta densidades altas de aves migratorias, especialmente en el otoño. Hábitats modificados, en áreas con poco hábitat de bosque montano, también sustentaron densidades altas de aves migratorias. Los hábitats de matorral y matorral-pastizal sustentaron densidades de aves migratorias bajas a intermedias, pero debido a que estos hábitats dominan el paisaje del suroeste, éstos pueden proveer hábitat de parada para números mayores de aves migratorias que los reconocidos previamente. Estos resultados se ven complicados por retos persistentes relacionados con la identidad de los objetivos (es decir, confusión con aves, artrópodos y murciélagos). Nuestros resultados sugieren que es demasiado simplista: (1) considerar al oeste árido como un paisaje inhóspito en el que sólo existen oasis relativamente pequeños de hábitat que proporcionan los recursos necesarios para todas las aves migratorias, (2) pensar en el hábitat ribereño y hábitat de bosque montano del oeste como el sustento de la mayoría de las aves migratorias en todos los casos, y (3) considerar a un tipo particular de hábitat poco importante como hábitat de parada basado únicamente en bajas densidades de aves migratorias.

INTRODUCTION

To accomplish conservation of migratory birds over their full life cycle (Berlanga et al. 2010), we need to understand more about migration patterns, ecology, and the value of stopover sites to migrating birds (Moore et al. 1995, Heglund and Skagen 2005, Carlisle et al. 2009, Faaborg et al. 2010a). Migration

is arguably the most hazardous period of a migratory bird's annual life cycle; Sillett and Holmes (2002) and E. H. Paxton et al. (2007) have shown that a disproportionately large amount of mortality occurs in the relatively short migration periods of the annual cycle. Birds must overcome multiple natural challenges including high energy demands, competition, predation, severe weather, geographic barriers, and

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the need to find habitat suitable for foraging and resting in unfamiliar terrain.

Much remains unknown about patterns in bird density and use of stopover habitat, as well as the seasonal and annual variation in these characteristics, especially at regional and continental scales. However, our knowledge about migration ecology in western North America has increased substantially during the past 10–15 years (Carlisle et al. 2009). In the West, migration is largely overland (Kelly and Hutto 2005), and western migrants face physical obstacles such as the Rocky Mountains and vast arid ecosystems. Much of what we know about western migration comes from site-specific data focused on documenting the critical importance to migrants of riparian stopover habitats (Finch and Yong 2000, Skagen et al. 2005, K. L. Paxton et al. 2007). Very little has been published on the broader-scale distribution of migrants in the West (Gauthreaux et al. 2003), and little is known about how birds are distributed among available habitats beyond those studies that focus on riparian areas. The relatively unpopulated expanses of the West present logistical challenges to the field-based studies and monitoring efforts that characterize most bird-migration research. Methods 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 (Gauthreaux and Belser 2003, Diehl and Larkin 2005). However, almost no studies have used these radars to evaluate migrants' use of stopover habitats at a landscape scale (Bonter et al. 2009, Buler and Moore 2011).

Here we combine weather radar and land-use data from south Texas to central Arizona to study geographical patterns in densities of migrant landbirds (passerines) and quantify associations between migrants and their stopover habitats.

METHODS

STUDY SITES

The U.S.–Mexico borderlands comprise the U.S. states of Texas, New Mexico, Arizona, and California and the Mexican states of Tamaulipas, Nuevo León, Coahuila, Chihuahua, Sonora, and Baja California, stretching for 1500 km from the Gulf of Mexico to the Pacific Ocean. This region supports a wide diversity of nearctic and neotropical biotic communities including temperate and tropical–subtropical forests, woodlands, scrublands, deserts, temperate grasslands, and the riparian and wetland communities embedded within each of these (Brown et al. 2007). Substantial numbers of western migratory landbirds appear to move in broad fronts through this region (Kelly and Hutto 2005, Faaborg et al. 2010a). 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.

DATA SELECTION

In this study we used seven WSR-88D (Weather Surveillance Radar, 1988 design year, Doppler capable) sites across

the Southwest (Felix et al. 2008)—Flagstaff, AZ (FSX), Tucson, AZ (EMX), Albuquerque, NM (ABX), El Paso, TX (EPZ), Midland, TX (MAF), Del Rio, TX (DFX), and Brownsville, TX (BRO) (see Appendix 1, available at <http://dx.doi.org/10.1515/cond.2012.120020> for detailed location information). For analysis, we selected radar data from these sites for days during spring migration (20 March to 20 May) in 2005 and 2006 and fall migration (10 August to 20 October) in 2005 (for ease of reference we refer to these day-site combinations simply as “day-sites”). Limited resources precluded us from analyzing an additional fall season. We downloaded level II radar data from the National Climatic Data Center's archive and vertical profiles of wind-velocity data from radiosonde (balloon-launched packages of meteorological instruments) stations that coincided with these radar sites for these day-sites. Unlike the analyses of Felix et al. (2008), which focused solely on patterns of full-migration movement in the middle of the night, for this study we visually screened reflectivity data from radar sweeps at the lowest beam elevation (0.5° above the horizon) for each day-site from local civil twilight (when the sun is between 0° and 6° below the horizon) until 4 hr later. A sweep includes a complete rotation of the radar (360°) at a specific elevation angle of the radar's beam (see Crum et al. 1993 for other operational characteristics). We excluded from analysis any day-sites at each radar site where echoes caused by precipitation, ground clutter (e.g., tall buildings, bridge overpasses, or relief in terrain), or refraction greater than standard refraction (Bech et al. 2002) were present. We considered day-sites that passed visual screening to be dominated by biological targets; all radar data (reflectivity and velocity data at multiple beam elevations) from these day-sites were retained and were the focus of further target discrimination and other analyses.

We evaluated 434 representative sweeps for each spring season and 504 sweeps for fall 2005, finding 15–24% of the original sweeps were dominated by migrants and appropriate for analyses of migrant–habitat associations for each season. Sweeps were rejected for various reasons, primarily the presence of precipitation. The number of retained 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.

To address issues related to complete or partial blockage of the radar beam, referred to as occultation, we created occultation maps (Fig. 1). To account for occultation effects more conservatively, we chose not to rely solely on existing occultation maps produced from mapping beam geometry and the beam's intersection with terrain relief (defined by digital elevation models; National Oceanic and Atmospheric Agency 2006). We created occultation filters (Fig. 1) based on boundaries defined by those existing maps, but only after reviewing radar reflectivity data from the 0.5° beam elevation to identify likely partial beam blockage or other terrain effects. These more conservative filters excluded areas showing both full- and partial-beam obstruction from subsequent analyses. Occultation at the lowest

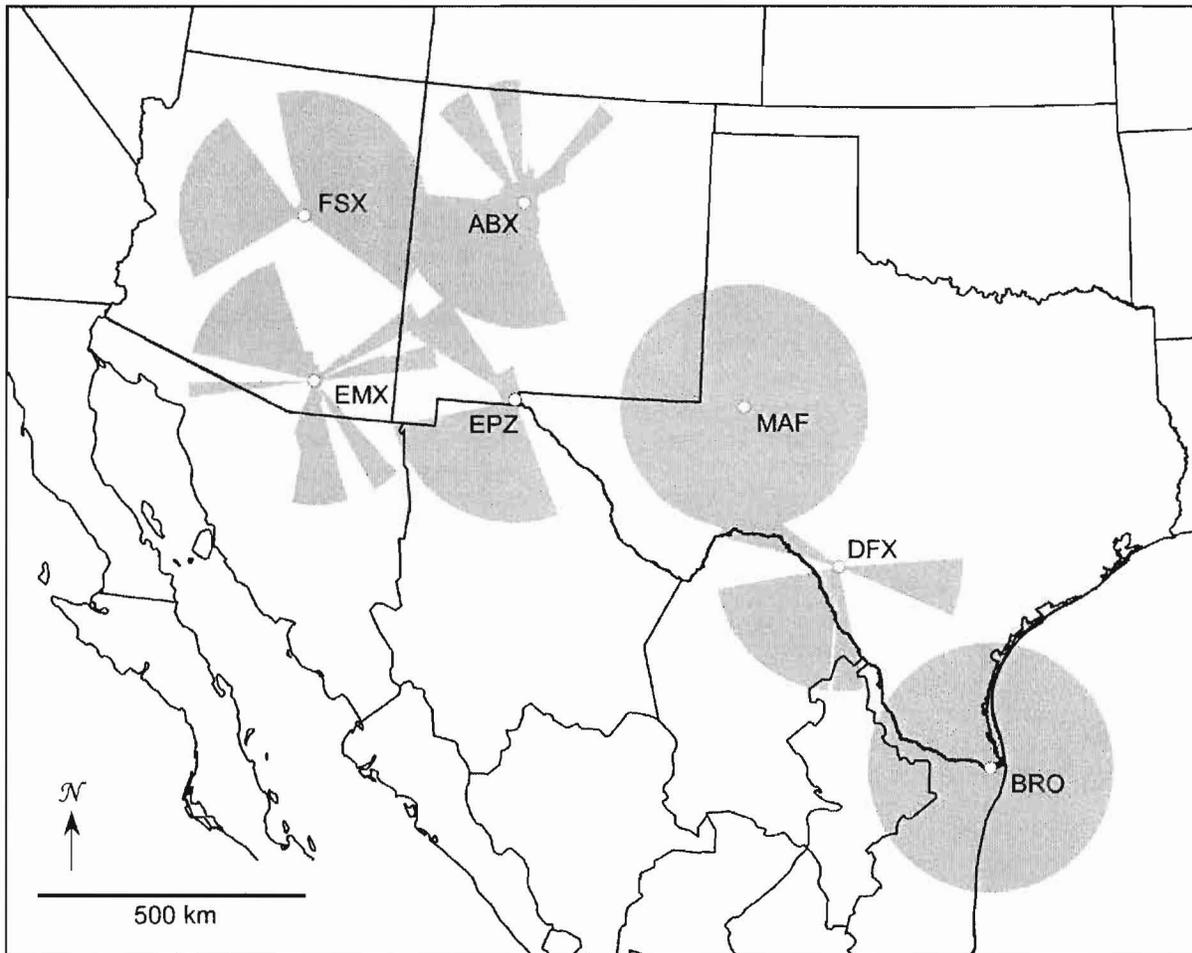


FIGURE 1. Location of the seven radars used in this study (open circle) and their occultation at the $\sim 0.5^\circ$ beam elevation. Gray regions around each radar indicate where data are not obscured out to a 230-km radius. Radar site acronyms: Flagstaff, AZ (FSX); Tucson, AZ (EMX); Albuquerque, NM (ABX); El Paso, TX (EPZ); Midland, TX (MAF); Del Rio, TX (DFX); and Brownsville, TX (BRO).

elevation of the radar beam had the greatest effect on analyses of migrants' use of stopover habitat because at some sites the gcospatial filters eliminated a substantial area around the radar from analyses of both target densities and land cover (see below). By comparison, occultation effects decrease as beam elevation increases and were nonexistent at beam elevations used to identify vertebrate targets.

VERTEBRATE TARGET IDENTITY AND INTENSITY

Having identified day-sites dominated by biological targets with a conservative approach by using the data from 0.5° radar beam elevations, we used radar data from the 3.5° beam elevation (a representative sweep from approximately 3 hr past the end of civil twilight) to distinguish vertebrate from invertebrate targets during night migration and to analyze densities during that time. Using data from higher beam elevations reduces sources of bias by (1) generating more accurate and

precise height-specific measures of the targets' speed and direction, (2) avoiding occultation effects, (3) quantifying targets in smaller volumes of space closer to the radar, and (4) gathering target data that are spatially closer to the source of wind-velocity data. It is also unreliable to attempt target identification by airspeed when birds are initiating migratory flight, which is detected at lower elevations of the radar beam. We computed the targets' ground velocity and, using wind-velocity data, calculated their air speeds at all heights to distinguish birds from other biological targets (insects) (Gauthreaux and Belser 1998, Felix et al. 2008). We assessed the vertical distribution of airspeeds at altitudinal strata determined by the resolution of radiosonde data. If the majority (usually much more than 50%) of the targets' air speeds were $>6 \text{ m sec}^{-1}$ we considered the day-site to be dominated by birds (Schaefer 1976, Larkin 1991, Gauthreaux and Belser 1998) and retained it for further analysis of migrant-habitat associations.

Higher values of z , or radar-reflectivity factor, represent stronger radar echoes and are considered representative of bird densities (Rinehart 1997), and we used z to represent the density of migrants.

Methods used in these analyses cannot distinguish bats from migrating birds. The flight of migrating bats is similar enough to that of migrating birds that targets are indistinguishable by airspeed-based techniques, and the flight of migrating bats is not understood well enough for algorithms distinguishing them from migrating birds to be developed (Cryan and Diehl 2009). Although we assume that birds represent the majority of targets in most instances (Able 1977), the relative abundances of bats and migrating birds remain poorly understood and likely vary geographically and seasonally. Where we observed patterns typical of bats emerging from caves (Horn and Kunz 2008), especially around Del Rio, those patterns dissipated over time and resembled ambient reflectivity before the times when we selected radar data for target identification. However, migrant-habitat analyses use lower-elevation data from twilight when birds initiate migration; concentrations of bats are highest as they leave their roosts at approximately the same time. 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 analyses of migrant-habitat associations, limiting our analyses to the remaining six radar sites.

MIGRANTS' USE OF STOPOVER HABITAT

Descriptions of migrants' stopover-habitat associations are possible with a combination of WSR-88D reflectivity data, which provide a measure of the targets' density, and satellite-derived land-cover data, which provide a measure of habitat type. Radar data from the 0.5° WSR-88D beam elevation around evening civil twilight are used to capture the departure of landbirds from stopover habitat. When the radar beam is at its lowest elevation, departing migrants enter the radar-swept airspace approximately over the site of their stopover. Stronger radar echoes (higher z values) are generally associated with habitats in which higher densities of migrants had concentrated during stopover (Buler and Diehl 2009). Using the day-sites dominated by bird targets, 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. Again we visually screened representative sweeps, eliminating day-sites with nonbiological echoes.

For habitat analyses, we used the most recent satellite-based Land Use and Land Cover (LULC) data from the National Map Seamless Server administered by the U. S. Geological Survey (USGS 2008), derived from imagery recorded in 2001. These data provide classification of land cover at a 30-m resolution. We downloaded the LULC data for the regions surrounding the seven radars used in this study and derived our land-cover types from the class II definitions of the National Land Cover Data 2001 (Multi-Resolution Land

Characteristics Consortium 2001). We reduced the number of land-cover types by combining categories (e.g., we combined all upland forest types—deciduous, mixed, and evergreen forests—into upland forest). This reclassification resulted in eight land-cover categories for our analyses: scrub/shrub, grassland/herbaceous, upland forest, open water/wetland, forested/shrub wetland, agriculture, developed, and barren. Brownsville had an additional no-data cover type that we omitted from analyses. (See Appendix 2 online for details about land-cover classification).

The area around each radar that could be used as a basis for migrant-habitat associations was limited by a number of factors. We chose to restrict analysis of land cover and migrants' reflectivity to a narrow 15-km band—35 to 50 km away from each radar—to limit the effect of range bias (Fig. 2). This bias limits comparison of how migrants use habitat at considerably different distances from the radar. Also, at greater distances from the radar, determining habitat associations is less reliable because the radar beam passes farther above the earth's surface and therefore migrants are displaced farther from the site of their stopover in the time it takes for them to fly up into the beam (Diehl and Larkin 2005, Larkin 2005). At shorter distances from the radar, low-altitude radar data are more likely to be affected by clutter caused by relief in terrain or artificial structures (Diehl and Larkin 2005). Range-adjustment techniques described in Buler and Diehl (2009) aim to address this problem and allow use of more of the radar data, but attempts to apply these adjustments to our analyses often resulted in overcorrection. We also excluded additional land-cover and radar data within the 35- to 50-km band from analysis if they lay within the filtered regions of full or partial beam occultation (Figs. 1 and 2). Finally, we were not able to get comparable land-cover data where radar coverage extended into Mexico, nor did we use the portion of radar coverage at Brownsville that extended over the Gulf of Mexico.

With a geographic information system (GIS) we verified that all radar-reflectivity data and land-cover data were accurately georeferenced (datum WGS 1984, among UTM zones 12N, 13N, and 14N). Radar and land-cover data differ in their resolution. Land-cover data are Cartesian-raster and defined in 30- by 30-m grid cells. Radar-reflectivity data are polar-vector with a resolution of 1° by 1000-m increments and had to be converted to raster grids of the same resolution as the land-cover data with a GIS. Using a model constructed within a GIS, for each site we processed each radar-reflectivity data sweep at the onset of migration in relation to the underlying land-cover data. For each sweep we determined zonal (areal) means and standard deviations of the density of migrants associated with each of eight major land-cover types, statistics we 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 and calculating a surface (2-dimensional) density for that habitat type as z per unit area.

Statistical approach. Daily mean densities of targets (daily mean z values) for given habitats failed to meet assumptions of normality and homoscedasticity, even when transformed. We relied on nonparametric Kruskal–Wallis analysis of variance by ranks to test for differences in daily mean density of targets by habitat type or season within each site. 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 were markedly different, as described below.

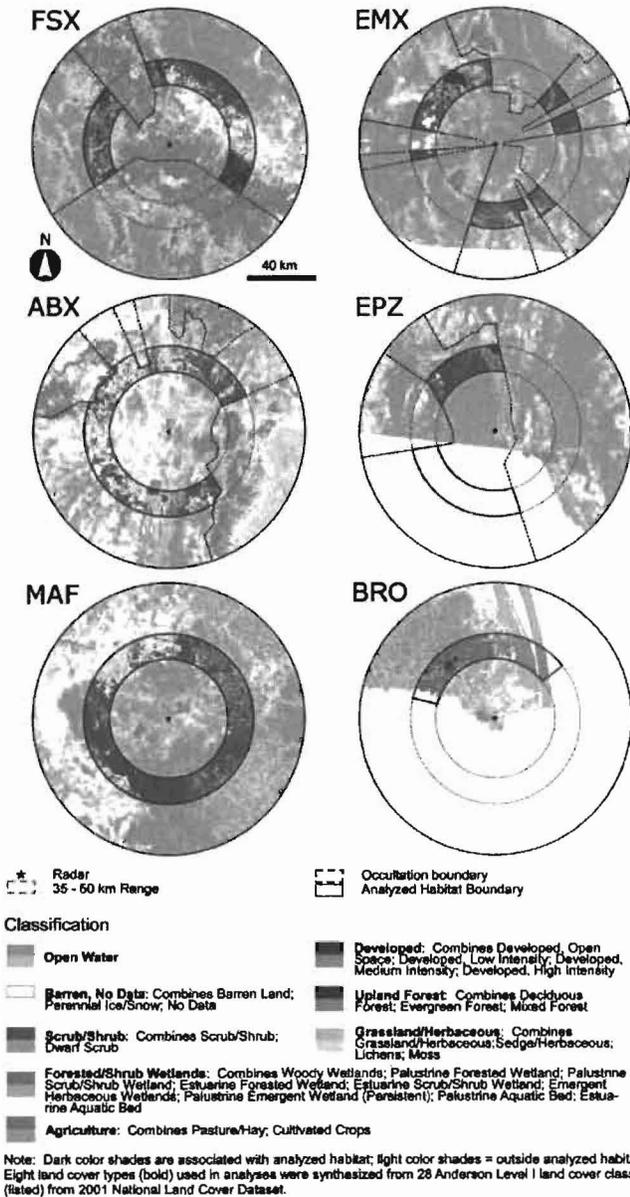


FIGURE 2. Land cover surrounding the six radars where data were analyzed for migrant–habitat associations, showing occultation masks of radar beams and the band extending from 35 to 50 km away from the radar within which data were analyzed. Radar site acronyms are defined in Figure 1.

RESULTS

Scrub/shrub was the most abundant habitat type by area sampled at five of the six sites (all but Brownsville); grassland/herbaceous also occurred in high abundance at Albuquerque and Midland. Agriculture was most abundant around Brownsville, at which the composition of land-cover types was also more even than at other sites. Forest was most abundant around Flagstaff. In spite of the ecological importance in the Southwest of forested riparian corridors (incorporated into the forested/shrub wetland category), this habitat was not one of the major ones at any of our sites. See Appendix 3 online for additional details about the area of each habitat sampled at each site.

At two sites—Flagstaff and Tucson—bird densities differed significantly by habitat within a season for both springs and fall (Table 1), and those habitat-use patterns were relatively consistent across seasons (Fig. 3). Around Flagstaff densities of migrants were highest in developed, upland forest and open water/wetland habitats in both springs and fall (Fig. 3). Conversely, some of the lowest densities of birds were in agricultural habitat. At Tucson, densities of migrants were highest in upland forest, with no clear pattern among the other habitat types. Figure 4 presents an example of this pattern, with concentrations of migrants taking off from upland forest associated with the mountains around Tucson.

TABLE 1. Results of χ^2 tests comparing densities of migrants (differences in daily mean z) in eight land-cover types within site by season.

Radar site and season	χ^2	<i>P</i>	<i>n</i>
Flagstaff, AZ (FSX)			
Spring 2005	45.5	<0.001	17
Fall 2005	30.3	<0.001	12
Spring 2006	18.8	<0.01	14
Tucson, AZ (EMX)			
Spring 2005	105.1	<0.001	27
Fall 2005	45.5	<0.001	16
Spring 2006	29.2	<0.001	18
Albuquerque, NM (ABX)			
Spring 2005	0.7	1.00	9
Fall 2005	10.6	0.16	12
Spring 2006	5.6	0.59	14
El Paso, TX (EPZ)			
Spring 2005	10.5	0.11	18
Fall 2005	20.8	<0.01	15
Spring 2006	22.4	<0.01	14
Midland, TX (MAF)			
Spring 2005	1.6	0.98	12
Fall 2005	18.8	<0.01	21
Spring 2006	1.9	0.97	12
Brownsville, TX (BRO)			
Spring 2005	8.3	0.31	30
Fall 2005	33.6	<0.001	26
Spring 2006	6.3	0.51	16

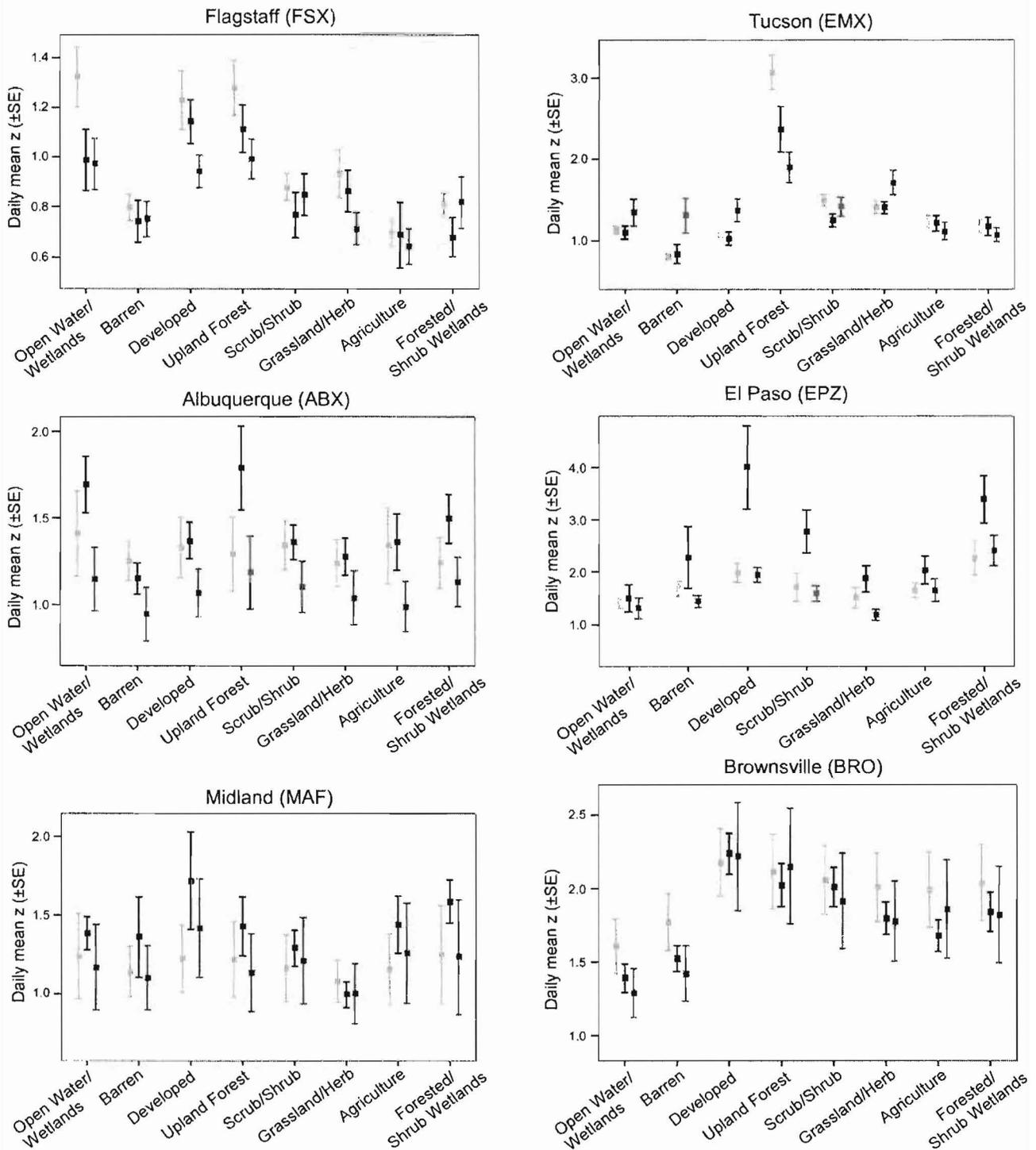


FIGURE 3. Densities of migrants as they are associated with major habitat types at each radar site by season (daily mean $z \pm 1$ SE). Within a habitat type, squares represent spring 2005 (left light gray), fall 2005 (middle black), and spring 2006 (right medium gray). Vertical scales for daily mean z are different for each site.

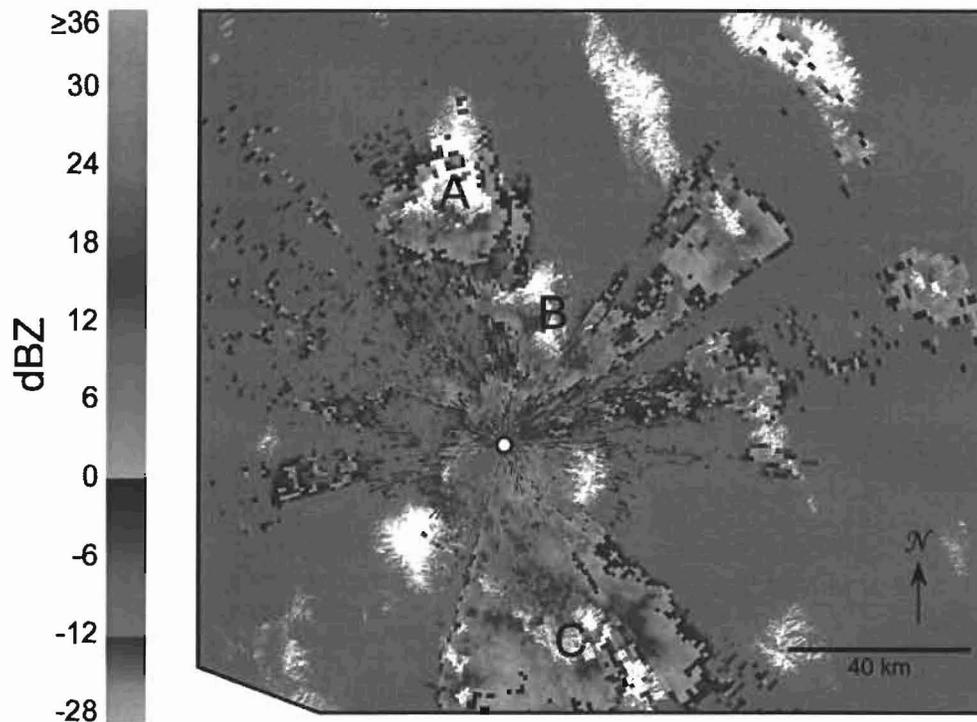


FIGURE 4. Radar reflectivity superimposed over simplified land cover around the Tucson, AZ, radar (white dot), 14 May 2005, 19:47 MST. Upland forest is shown in white, all other land-cover types in gray. Mountain ranges that interfere with radar-beam propagation are labeled: (A) Santa Catalina Mts., (B) Rincon Mts., and (C) Huachuca Mts. Voids in the radar data occur around montane forested areas where peaks cause the radar to reject reflectivities as ground clutter. The red/purple radar targets, frequently surrounding the upland forest and/or tall mountain peaks, indicate concentrations of migrants taking off to initiate migration.

At three sites—El Paso, Midland, and Brownsville—bird densities differed significantly by habitat in fall 2005 (Table 1); El Paso also showed significant differences in spring 2006. At all three of these sites the densities of fall migrants were highest in developed habitats (Fig. 3). At El Paso and Midland the second highest fall densities were in forested/shrub wetlands, and in Brownsville the next highest fall densities were in upland forest and scrub/shrub habitats. At one site—Albuquerque—bird densities did not differ significantly by habitat in either spring or fall (Table 1). In fall 2005, however, there was a relatively strong pattern like that at the three previous sites that was not quite statistically significant (Table 1). At Albuquerque, densities of fall migrants appeared highest in upland forest, open water/wetland, and forested/shrub wetland habitats (Fig. 3).

DISCUSSION

USE OF STOPOVER HABITAT

Our results indicate significant differences in bird densities by type of stopover habitat at all sites in at least one season. The recent review of research on landbird migration in the

West by Carlisle et al. (2009) acknowledges that much study of western migration has focused on riparian habitats and only recently has broadened its focus to the wide range of stopover habitats available in the West. One of the emerging questions they identified was “what is the relative importance of all habitat types to migrants?” Migrants’ selection of stopover habitat involves a hierarchical decision-making process (Hutto 1985a, Moore et al. 1995) at continental and regional scales as well as at local habitat and microhabitat scales. Recognizing these scale-dependent relationships allows us to determine the best tools for answering questions at different scales (Moore et al. 2005, Buler and Moore 2011); weather-surveillance radar allows us to document migrants’ movements at broad geographic scales and can provide rough estimates of the density of migrants associated with various stopover habitats (Moore et al. 2005, Carlisle et al. 2009). We have used this tool to provide the first descriptions of the relative densities of migrants using major stopover habitat types in the Southwest and to discuss the implications of these results for our understanding of migration ecology in this region and for future research that is clearly needed to supplement and confirm the patterns we documented.

We were quite conservative in our evaluations of migrant-habitat associations, 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. New methods are being developed (Buler and Diehl 2009) to address some of the limitations we faced, methods that will enable use of more of the available data in the future. Two sites—Flagstaff and Tucson—show evidence of differential habitat use by migrants in both spring and fall and that those habitat-use patterns are similar at both seasons. For the remaining four sites there is evidence of differential use of habitat in the fall but no clear pattern in the spring. Such seasonal differences in habitat use can be pronounced and may be associated with seasonally related constraints or opportunities such as food availability or physiological limitations (Hutto 1985b, 2000, Farley et al. 1994, Petit 2000). We analyzed data from a single fall, so the scope of inference from habitat-use patterns in fall, and comparison of those patterns with data from two springs is limited to the years sampled. However, these patterns were observed at multiple sites and are consistent with available literature on migration in this region, as described in more detail by habitat type below.

The fact that riparian habitats support large numbers of migrants during stopover in arid landscapes has long been recognized (Carlisle et al. 2009). Our results are generally consistent with this observation, but they do not provide strong evidence for the high densities suggested in the literature (but see discussions below regarding displacement of migrants and issues with the spatial resolution of land cover). At all sites, forested/shrub wetlands are among the least abundant habitats, yet they supported the second or third highest densities of fall migrants at Albuquerque, El Paso, and Midland, indicating their value as stopover habitat.

The importance of higher-elevation habitats, especially montane deciduous and coniferous forests, for fall migrants has been recently documented (Carlisle et al. 2005, 2009, DeLong et al. 2005). At the three sites with large areas of upland forest (Fig. 2)—Flagstaff, Tucson, and Albuquerque—these montane forests had high densities of migrants in fall, as did those at Flagstaff and Tucson in spring. Our results are consistent with ground-based studies of migration in the Manzano Mountains southeast of Albuquerque (DeLong et al. 2005) and in the Santa Rita, Huachuca, and Santa Catalina mountains surrounding Tucson (J. L. Kellermann, pers. comm.). These studies found that montane forested habitats supported substantial numbers of migrants; some species were found primarily, or in higher numbers, in montane forested habitats than in lower-elevation habitats. High-elevation habitats may provide cooler microclimates and more food than do lowlands, especially during fall migration (Carlisle et al. 2009); this may be particularly the case in very arid locations such as Tucson and Albuquerque.

Our sites are also located near substantial human population centers. Developed habitats supported high densities of

stopover migrants at four sites: at Flagstaff in one spring and in fall, and at El Paso, Brownsville, and Midland in fall; in contrast there was no such pattern at Tucson or Albuquerque. In the arid Southwest, developed areas (urban and exurban), although often considered inhospitable habitats (Hansen et al. 2005), support some breeding species of native birds (Germaine et al. 1998, Bock et al. 2008). Elsewhere, developed habitats also have been associated with high concentrations of migrants (Bonter et al. 2009). More lush vegetation and free water available in urban and exurban areas can provide resources and shelter for birds in arid landscapes (Germaine et al. 1998, Bock et al. 2008). In arid landscapes with little or no upland forest available to migrants (El Paso, Midland, and Brownsville), especially in the fall (Carlisle et al. 2009), developed habitats may provide valuable refuges for some migrating species.

Scrub/shrub habitat is one of the most widely distributed habitats in the borderland region. Similarly, grassland/herbaceous is the second most abundant habitat at two sites, Albuquerque and Midland, and occurs at intermediate coverage levels at all other sites. At no site did either of these habitat types support high densities of migrants, although at many sites they supported low to intermediate densities similar to those of a number of other habitats (Fig. 3). Research on or monitoring of migration has been limited in scrub/shrub and grassland habitats, so there is little with which to compare our results. Puschock (1998) found that spring and fall migrants through New Mexico used both riparian habitat and various scrub/shrub habitat types. In south Texas, Igl and Ballard (1999) found that grassland migrants were more abundant in grassland and shrub-grassland than in parkland, brushland, and woodland. In New Mexico, Agudelo et al. (2008) found that shrubland migrants were more abundant than grassland migrants in shrub-encroached grasslands. Scrub/shrub and grassland habitat may support birds at densities more modest than those in riparian, upland forest, or developed habitat, but the abundance of scrub/shrub and grasslands in the southwestern landscape implies that these habitat types may support larger absolute numbers of migrants (DeLong et al. 2005) than previously recognized.

Grassland/herbaceous and scrub/shrub are also important to migrants as stopover habitats because not all migrants traversing the borderlands region have similar habitat requirements. Much migration research, by virtue of its location in forested ecosystems, has focused on migration stopover of long-distance neotropical migrants, whereas many shrubland and grassland birds are short-distance migrants that breed across the western U.S. and southern Canada and pass through the southwestern U.S. in migration or remain and winter there and in northern Mexico. Our results are consistent with the concept that many species have basic, consistent, year-round associations with broad habitat types (Petit 2000). They are also consistent with the literature from this region that indicates grassland and shrubland birds use

grasslands and scrub/shrub in migration and avoid or occur less frequently in other habitat types. Igl and Ballard (1999) found that grassland migrants were most abundant in the habitats that most closely resembled their breeding habitats, and grassland specialists tended to be more habitat-specific during the nonbreeding season than shrub-grassland specialists. Agudelo et al. (2008) found that, during migration in shrub-encroached grasslands of New Mexico, the grassland bird guild consistently responded negatively to shrub density, and the shrubland bird guild was strongly and positively associated with shrub density, although there were associations with other vegetation variables. The value of scrub/shrub and grassland habitats for these migrants is important in light of the significant population declines of many grassland and shrubland species (Peterjohn and Sauer 1999, North American Bird Conservation Initiative 2009, Sauer et al. 2011).

In addition to meeting the habitat requirements of grassland and shrubland specialists during migration, large arid grassland and shrubland habitats provide, to an unmeasured extent, stopover habitat for species usually thought of as forest-dwelling. 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, pers. comm.), sometimes even when presumably more "preferred" willow and cottonwood habitat is available nearby. Similarly, in the Sonoran and Chihuahuan deserts, forest-dwelling birds use xeric arroyos during spring migration (Hardy et al. 2004, Kozma et al. 2012). Hutto (2000) reported good numbers of species that breed in high-elevation conifer habitats using Sonoran desert scrub in spring migration.

There are several potential problems associated with assigning importance to stopover habitats solely on the basis of numbers of birds present or, in our case, relative densities of birdlike targets leaving a habitat. These problems influence our current abilities to understand migration-stopover ecology. We present some evidence of the problem with assessing the value of stopover habitat solely on the basis of bird densities, especially when habitats cover broad geographic expanses. In addition, and beyond the scope of this study, relying on either densities or total numbers of birds to assign habitat importance fails to address questions related to habitat quality (Mehlman et al. 2005) and how migrants are using different habitats (e.g., length of stopover, relative mass gain, survivorship).

CONCERNING METHODS

Target identity and displacement present the greatest challenges to interpretation of radar data and may affect the results we present (Diehl and Larkin 2005). In addition, scale, resolution, and temporal differences between radar and land-cover data, as well as occultation, may be issues.

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 migrant-habitat associations (Diehl and Larkin 2005), especially for small habitat patches or narrow, linear habitats like riparian corridors. Over an interval shorter than the temporal resolution of the radar sweep, migrant songbirds may take off from one habitat type and be detected above another. In these instances migrants will be associated with the incorrect stopover habitat type (Diehl and Larkin 2005). Displacement of migrants combined with the narrow, linear shape of riparian habitats may mean that our estimates of migrants' densities in forested/shrub wetlands are underestimates. Proximity effects result in over- or under-estimation of densities associated with a particular habitat. In addition, understanding the influence of displacement becomes more challenging in conditions where relief in terrain may bias measures of reflectivity associated with birds during the onset of migratory flight.

Target identification (particularly the ability to distinguish birds from bats and insects) remains a challenge in radar analyses. Several species of invertebrate pests migrate through Texas (Wolf et al. 1990, Showers et al. 1993), and their movements are readily detected by weather radar (Wolf et al. 1990). It is possible that some migrating insects may fly at velocities high enough that they cannot be distinguished from birds by airspeed (Larkin 1991, Alerstam et al. 2011). Cryan (2003) documented several species of migratory bats in the region during our sampling periods. These migrating bats may be present and indistinguishable from migrating birds in our data; locally foraging bats may also be present in the data. The Southwest supports by far the highest diversity of the 45 species of bats that occur in the United States and Canada, (Humphrey 1975, McCoy and Connor 1980, Willig and Selcer 1989). Bats typically emerge from their colonies before sunset to begin foraging (Lee and McCracken 2001). Foraging (and perhaps migrating) bats occur locally in extremely high densities, as in central Texas (Horn and Kunz 2008), but bats are also broadly present at lower densities across much of the arid Southwest. For example, in our reflectivity data we observed patterns typical of bats emerging from cave roosts (Horn and Kunz 2008) in south and central Texas (Fig. 5). These patterns were observed shortly before and after local civil twilight and were closely associated geographically with several known colonies of the Mexican Free-tailed Bat (*Tadarida brasiliensis*). Despite efforts to retain data only from bird-dominated movements, it is possible that bats, insects, or both could be represented locally in large numbers in some of these data, which could either generate spurious migration patterns or associations between birds and stopover habitats or obscure real ones.

There are challenges to linking the different spatial and temporal resolutions of data types used in these analyses. 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 et al. 2002, O'Neill and

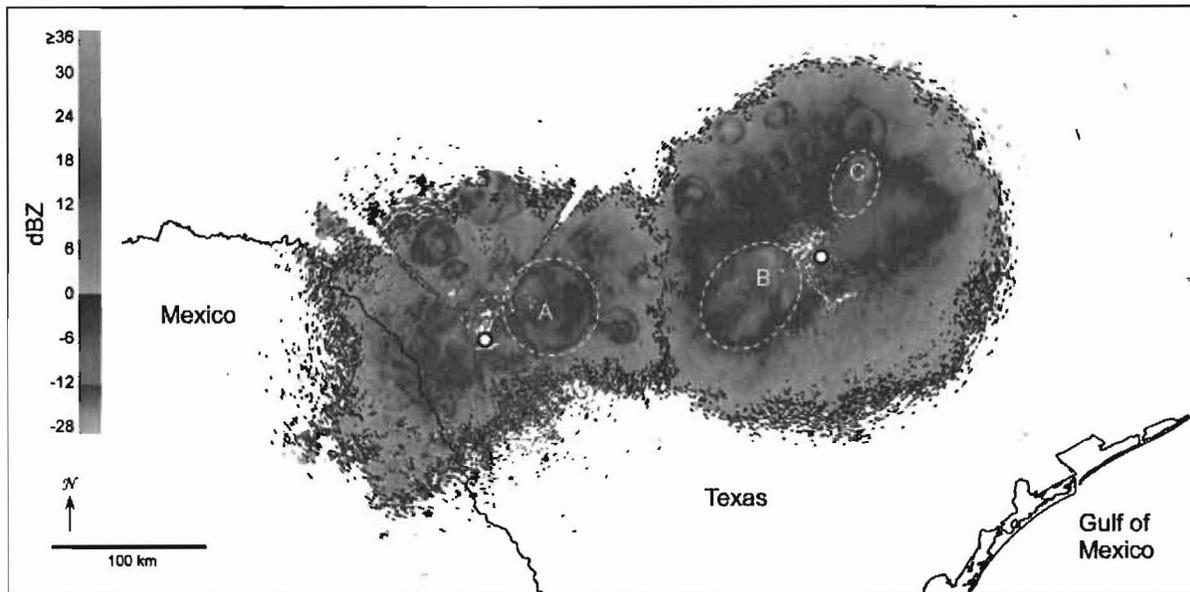


FIGURE 5. Reflectivity data from radars at Del Rio and New Braunfels, TX (white dots), from 14 October 2005 at ~19:00 CST. Labeled dashed circles highlight three roosts of the Mexican Free-tailed Bat, Frio Cave (A), Bracken Cave (B), and the Congress Ave. Bridge in Austin, TX (C). Many other roosts are visible in this image.

Smith 2002). Migrating landbirds may be distributed within the habitats at scales much smaller than WSR-88D radars are capable of resolving. Similarly, habitats of importance to migrants may be distributed across the landscape at scales that current land-cover data are incapable of distinguishing from surrounding habitat. The current 30-m spatial resolution of Landsat image data is too coarse to delineate the vegetation along narrow riparian corridors, yielding poor classifications (Congalton et al. 2002, Johansen et al. 2007). This is particularly pertinent in the Southwest where the courses of intermittent streams (arroyos) are important to migrants (Hardy et al. 2004, Kozma et al. 2012) and yet are poorly delineated in land-cover data. Moreover, the temporal scales of radar and habitat data are not similar. Satellite imagery on which habitat data are based (USGS 2008) was taken 4 years before the radar data from which we calculated densities of migrants. In addition, there is temporal separation of 4 to 5 hr between the time when radiosondes sample wind velocity and the time when radar is detecting migrating birds in the middle of the night. Also, there is temporal separation between the time when birds initiate migration from stopover and migration in the middle of the night, the time when a target is identified.

A significant number of WSR-88D sites in the western U.S. are located where relief in terrain (e.g., mountains) obstructs the radar's beam in ways that interfere with detection of biological targets at low altitude. Across the study area, occultation at radar sites varies from none at Brownsville and Midland to more than 50% at El Paso and Tucson (Fig. 1). As a result, at several sites we could not analyze substantial

amounts of habitat because it lay behind the feature obstructing the radar beam.

IMPLICATIONS FOR FUTURE WORK

Our results provide new information about migrants' use of various stopover habitats in the U.S./Mexico borderlands area and offer guidance for future research and management. In particular, our results suggesting that in large expanses of scrub/shrub and grassland/herbaceous habitats larger numbers of migrants stop over than previously acknowledged are noteworthy and have implications for future research and conservation of migratory birds.

The results of this study emphasize the need for further work to (1) characterize migrant's habitat associations in the Southwest (Carlisle et al. 2009, Faaborg et al. 2010a), with a focus on scrub/shrub and grassland habitats, (2) improve methods for analyzing radar data and identifying targets, especially distinguishing birds from bats and insects, (3) address the problems posed by extensive occultation of large-scale radar beams in the West, and (4) improve knowledge about the subtle habitat characteristics that allow arid landscapes to support migrants.

Many questions about migration ecology cannot be answered with radar data only. Future research should take a scale-dependent approach (Moore et al. 1995, 2005). More traditional ground-based monitoring and research in migration ecology, in conjunction with use of long-range and short-range radar and other technologies, will be needed, particularly in habitats that are rarely studied during migration

(scrub/shrub, grassland, and developed). Collaborative research focused on verifying the patterns presented here and gathering additional information about how migrants use these habitats for stopover will assist in painting a more complete picture of migration stopover throughout the West.

The value of riparian habitats in the arid West and the threats facing these habitats important for migration stopover are well documented elsewhere. However, semidesert and plains grasslands and desert scrub/shrub habitats in the Southwest also are highly threatened by multiple factors (e.g., habitat conversion for agriculture, urban/exurban development, energy development, overgrazing by livestock, shrub encroachment, changes in fire regimes, climate change) (McClaran and Van Devender 1995, Merola-Zwartjes 2004, Prucutt et al. 2009). Research is needed to provide managers with information they need to conserve migratory birds and to guide management of the grasslands, desert shrublands, other terrestrial habitats, and aerial habitat that birds use during migration (Heglund and Skagen 2005, Kelly and Hutto 2005, Carlisle et al. 2009, Faaborg et al. 2010b).

In summary, our results suggest that 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 habitats as supporting the majority of migrants in all cases, or (3) consider a particular habitat type unimportant to migratory birds during stopover solely on the basis of low densities of migrants. In reality western landscapes are a complex mosaic of habitats through which a complex assemblage of migrants passes twice a year.

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