SEASONAL PASSERINE MIGRATORY MOVEMENTS OVER THE ARID SOUTHWEST

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Abstract. Biannually, millions of Neotropical and Nearctic migratory birds traverse the arid southwestern US-Mexico borderlands, yet our knowledge of avian migration patterns and behaviors in this region is extremely limited. To describe the spatial and temporal patterns of migration, we examined echoes from weather surveillance radar sites across the American Southwest from southern Texas to southwestern Arizona during spring 2005 and 2006 and fall 2005. After taking steps to identify radar echoes dominated by birds, we determined migrants' speeds, directions, and altitudes. Our results show that in spring, migrants generally flew lower and faster than in fall, although much of this overall pattern may be driven by higher fall altitudes and higher ground speeds at some of the easternmost sites in the borderlands. Seasonal differences in migrants' altitudes can be partially explained by seasonal differences in the altitudes of favorable winds. Seasonal differences in migrant ground speeds might arise for many reasons including variation in winds aloft or the presence of naïve hatch-year birds in fall. In addition, migrating bats may also be present throughout the region in varying degrees in radar data. Flight directions across the region were generally north in spring and south in fall, but also were consistent with the premise that songbird migration in North America is comprised of distinct regional migratory systems.

Key Words: altitude, Arizona, borderlands, Doppler, landbirds, migration, New Mexico, radar, Texas, velocity.

MOVIMIENTOS MIGRATORIOS ESTACIONALES DE AVES PASSERIFORMES SOBRE EL SUROESTE ÁRIDO

Resumen.Millones de aves migratorias neotropicales y neárticas atraviesan dos veces por año el área fronteriza del suroeste árido de los Estados Unidos y México, y aún así nuestro conocimiento sobre los patrones y el comportamiento migratorio es extremadamente limitado. Para describir los patrones espaciales y temporales de la migración, examinamos los ecos de radares de vigilancia climatológica a lo largo del suroeste Norteamericano, desde el sur de Texas al suroeste de Arizona durante las primaveras de 2005 y 2006, y el otoño de 2005. Después de identificar los ecos del radar dominados por aves migratorias, determinamos sus velocidad, dirección y altitud. Nuestros resultados muestran que en primavera, los migrantes generalmente vuelan más bajo y más rápido que en otoño, aunque este patrón general puede deberse a altitudes mayores en el otoño y a mayores velocidades con respecto al terreno en algunos de los sitios más al este en el área fronteriza. Las diferencias estacionales en la altitud de los migrantes pueden explicarse parcialmente por diferencias estacionales en la altitud de los vientos dominantes. Las diferencias estacionales en la velocidad de las aves migratorias con respecto al terreno pueden ser debidas a diversas razones incluyendo la variación en los vientos ascendentes o la presencia de aves del primer año sin experiencia en el otoño. Además, murciélagos migratorios pudieron estar presentes en toda la región en mayor o menor medida en los datos del radar". La dirección general de vuelo en la región fue hacia el norte en primavera y al sur en otoño, pero también fue consistente con la premisa de que la migración de aves canoras en Norteamérica incluye distintos sistemas migratorios regionales.

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 et al. 1995, Hutto 1998, Moore 2001, Heglund and Skagen 2005). Migration is arguably the most hazardous period of a migratory bird's annual life cycle (Sillett and Holmes 2002). Birds must overcome multiple natural challenges including high energy demands, competition, predation, severe weather, and finding suitable foraging and resting habitat in unfamiliar terrain. 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 et al. 1995, Root et al. 2003, MacMynowski et al. 2007). However, it is less common to consider the physical atmosphere as migration habitat. Flying migratory wildlife requires what could be called migration aerohabitat. Migratory birds, bats, and insects are uniquely susceptible to atmospheric disturbances and human use of the air space. Tall anthropogenic structures

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such as communication towers and wind turbines (Manville 2001, Cooper et al. 2004), and meteorological and climatic phenomenon (e.g., storms, adverse wind speeds and directions) represent threats to migratory birds in their aerohabitat. Conversely, migrating birds themselves present risks to humans via bird-aircraft collisions. Much remains unknown about patterns in bird flight altitude, speed, direction of travel, abundance, and density, as well as the seasonal and annual variation in these migration characteristics, all occurring across broad regional 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 et al. 2005). In addition, documenting historical regional-scale migration patterns and behaviors provides baseline data needed to predict or model future changes in these patterns in response to factors such as climate change.

Moore et al. (1995) and Kelly and Hutto (2005) point out that what we know about passerine migration in North America is largely based on research conducted east of the Mississippi River. However, many factors potentially affect western migrants that are unique to the western landscape or at the very least are manifested in a different way and affect our ability to understand western migration dynamics. Western migrants face physical obstacles such as the Rocky Mountains and vast arid ecosystems that dominate the landscapes they must cross. These relatively unpopulated expanses also present logistical challenges to the field-based research 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 help guide future research.

The Sonoran and Chihuahuan Deserts, the Sierra Madre Occidental, and the Tamaulipan brushlands of the US-Mexico borderlands region typify the sort of potentially inhospitable landscapes that western birds must traverse during migration. 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 et al. 1999, Finch and Yong 2000, Skagen et al. 2005, Paxton et al. 2007). We know much less about migrant use of other habitat types or larger-scale migrant distributions and behavior

aloft in this region. Continuing research will take advantage of additional weather surveillance radar products not analyzed for this paper and begin to describe densities of migratory birds aloft and make associations with stopover habitat.

We report here on the first results of a larger study examining migratory behavior and patterns across the 1,500 km of the US-Mexico borderlands region. Using data collected by weather surveillance radars, we identified biological targets likely to be migratory birds. We determined the altitude, speed, and direction of birds during migration and explored how these general flight behaviors varied seasonally and among sites in the borderlands region.

METHODS

We retrieved data from seven WSR-88D (weather surveillance radar, 1988 design year, Doppler capable) sites across the American Southwest (Fig. 1; Table 1). These so-called Level II data include reflectivity, a measure of radar echo intensity determined by the density and size of targets, and radial velocity, a measure of target velocity relative to the radar (Crum et al. 1993). Both reflectivity and radial velocity measurements are made in discrete volumes of atmosphere or pulse volumes whose dimensions are determined by how space is partitioned along radii from the radar (1 km intervals for reflectivity and 0.25 km for velocity) and the width of the pulsed radar beam (~1°). A sweep comprises a complete rotation of the radar (360°) at a specific elevation angle of the radar's beam. Depending on a radar's mode of operation, elevations range from 0.5° to 19.5°. This study is confined to data from 3.5° elevation sweeps

FIGURE 1. Locations of seven WSR-88D radars used in this study.

TABLE 1. GEOGRAPHIC COORDINATES OF RADARS ACROSS THE SOUTHWEST THAT WERE USED IN THIS STUDY (LISTED WEST TO EAST).

WSR-88D call sign	City	North latitude (°)	West longitude (°)
KFSX	Flagstaff, AZ	34.57	-111.20
KEMX	Tucson, AZ	31.89	-110.63
KABX	Albuquerque, NM	35.15	-106.82
KEPZ	El Paso, TX	31.87	-106.70
KMAF	Midland, TX	31.94	-102.19
KDFX	Del Rio, TX	29.27	-100.28
KBRO	Brownsville, TX	25.92	-97.42

taken approximately three hours past the end of local civil twilight (when the sun is 6° below the horizon) from 20 March to 20 May 2005 and 2006, and from 10 August to 20 October 2005. Sampling data from this time period allowed us to avoid bias associated with variation in target speed and direction during the onset of nocturnal migration. Hereafter, we refer to any sweep from a specific date at a specific radar site as simply a representative sweep, unless otherwise specified.

We identified radar echoes caused by migrants in a two-step process. First, by visual inspection, we rejected reflectivity sweeps that contained non-biological echoes—usually caused by precipitation or ground clutter. Second, we distinguished migrants from other biological echoes by their airspeeds, which we determined by vector subtracting wind velocity from ground velocity (Gauthreaux and Belser 1998).

ESTIMATING WIND VELOCITY

The number of radars used in this study was limited by the availability of radiosonde data for target identity; radiosonde launch stations coincide with seven WSR-88D stations in the borderlands region. 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). We retrieved archived data on vertical profiles of wind speed and direction gathered using these radiosondes. Balloons are typically 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 nearest peak nocturnal migration, the focus of this study, across most of the borderlands region. Therefore, wind and target ground velocity data (see below) used in target identity are separated by either four or five hours, depending on time zone. Other sources of winds aloft information either did not improve

spatial and temporal coverage or were not sufficiently accurate.

ESTIMATING TARGET GROUND VELOCITY

We determined target ground velocities using Level II radial velocity data from ~3.5° sweeps during the peak of nocturnal migration (local civil twilight plus 3 hr). These higher elevation sweeps have several advantages over lower elevation sweeps when estimating target ground velocities. Loss of data through beam obstruction caused by relief in terrain is nearly absent, and there is less ambiguity in altitude-specific measures of speed and direction (particularly of higher altitude targets). Also, there is less spatial separation between radar and radiosonde data, because the beam intersects the migratory layer relatively close to the radar site. Finally, data from higher elevation angles are less affected by refraction, because the beam propagates through rather than along horizontal moisture and temperature gradients.

We constructed vertical profiles of target speed and direction for ~3.5° radial velocity sweeps using methods outlined by Browning and Wexler (1968) and implemented in SAS (SAS Institute 2003). We present a variation on methods well established in the meteorological literature, so they are reviewed only briefly here. The approach determines speed and direction from velocity-azimuth displays (VADs) calculated from radial velocity data centered on a focal range and including velocities within a ±1 km range window. In the typical VAD, radial velocities for all available azimuths within a sweep are modeled as a function of the horizontal and vertical Cartesian coefficients comprising target velocity in three-dimensional space (Browning and Wexler 1968, eq. 1). These coefficients are estimated using non-linear least-squares minimization, and speed and direction are in turn calculated from the coefficients. The window is then advanced one range bin (250 m) away from the radar and the VAD recalculated. This process is repeated out to the maximum range of available velocity data, which varies

depending primarily on the height of targets. Because the radar's ~3.5˚ elevation beam travels up and away from the earth (which simultaneously curves out from beneath the beam), an increase in range corresponds to a predictable increase in altitude (Diehl and Larkin 2005, eq. 1). Therefore the succession of VADs calculated at incrementally increasing range enables the construction of vertical profiles of target speed and direction (in m ASL). For each least-squares minimization on data from a focal range, we compute an adjusted r^2 as a measure of how well predicted radial velocities explain variation in observed velocity data. These, in addition to visual correspondence between observed and predicted radial velocities (Fig. 2a, b), offered statistical and heuristic feedback respectively on the reliability of ground speed and direction estimations used in calculating target airspeeds.

IDENTIFYING TARGETS

For each date, target ground velocities were combined with wind velocity data according to altitude ASL. We calculated targets' headings and air speeds across altitudes during the hours around peak nocturnal migration by subtracting available wind velocities from targets' ground velocities. We determined that targets were migrants if airspeed was ≥6 m/s (Schaefer 1976, Larkin 1991, Gauthreaux and Belser 1998). From the resulting profile of migrant-dominated velocities (Table 2), we determined which altitude stratum corresponded with the mode, or highest reflectivity (i.e., the stratum with the highest migrant density (Gauthreaux and Belser 1998)) on that given day. From these modal strata, migrants' flight altitudes, speeds (relative to both the ground and air), and directions of travel were retained for further statistical analysis. Where we specify directions of travel in this paper, we are indicating the migrants' (or winds') directions of travel over ground. We subsequently subtracted radar tower elevations (meters ASL) from the modal strata altitudes to determine migrants' above ground level (meters AGL) altitudes for use in statistical analyses. Some migrants were probably present at altitudes that were not considered in analyses. However, by using the modal observation we selected altitudes where migrants were most dominant. Modal migrant altitudes are subsequently referred to simply as migrant altitudes.

Considering Bruderer's (1997) accounts of airspeeds of fast and slow intermittent flapping bird species (all ≥11 m/s), it is more likely we have mistaken some insects for birds rather than mistaken any birds for insects. We considered migrating bats to be indistinguishable from birds and that they could be present locally in large numbers in some of our data. As an example, in reflectivity data we observed patterns typical of biological targets entering the radar beam from point locations (Russell and Gauthreaux 1998). These patterns were observed shortly before and after local civil twilight and were closely associated
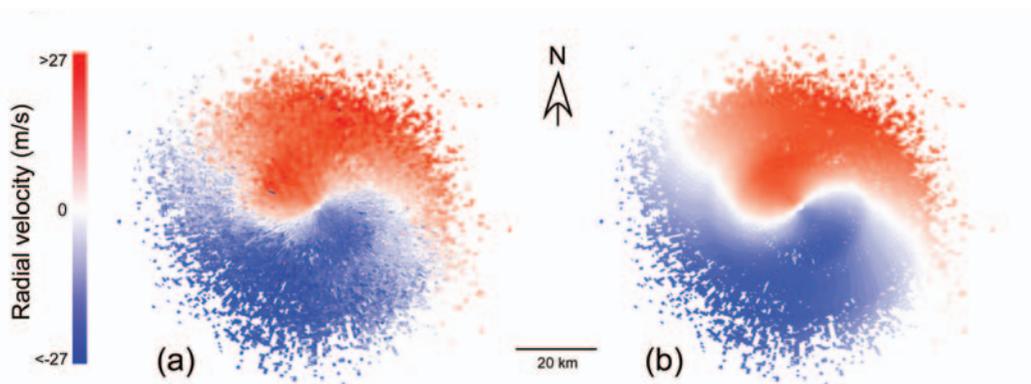

FIGURE 2. Vertical wind direction shear in observed (left) and predicted (right) data. (a) Observed radial velocity data from a 3.5° beam elevation sweep at Del Rio, Texas 27 March 2006, 0424 UTC where blue indicates movement toward the radar; red is movement away. The S-shaped Doppler null (in white; a region where movement is tangential to the radar) shows typical direction shear; in this case targets' directions of travel shift from being toward the NW to toward the NNE with increased distance from the radar (and so also with increased altitude). (b) Predicted radial velocities from VADs of observed data used to estimate speed and direction. Close correspondence between observed and predicted radial velocities demonstrate how accurately VADs estimate speed and direction from radial velocity data.

TABLE 2. VERTICAL PROFILE OF WIND VELOCITIES AND TARGET GROUND AND AIR VELOCITIES, AN EXAMPLE FROM DFX ON 27 MARCH 2006 AT 0424 UTC.

Altitude ASL (m) [a]	Wind direction (°)	Wind speed (m/s)	Target ground direction (°)	Target ground speed (m/s)	Target heading (°)	Target air speed (m/s)
610	325	11.3	320.9	12.8	293.6	1.7
771	330	11.3	326	14.2	310.4	3
914	335	11.8	330.9	15.5	318.1	3.8
1,219	335	12.9	345.6	17.3	12.4	5.3
1,488	335	12.9	6	16.4	56.7	8.6 [b]
1,737	335	11.3	16.3	17.3	56.7	11.5 [b]
1,829	335	10.8	17.8	17.5	55.2	12.1 [b]
2,068	22	6.2	20.6	17.7	19.8	11.6 [b]
2,134	35	5.1	22	18.1	17	13.2 [b]
2,438	60	6.2	29.1	18.1	15.2	13.1 [b]
2,743	55	7.2	37.4	17.8	26.1	11.1 [b]
3,105	50	10.8	46.8	16.8	41.2	6.0 *

[a] Altitudes shown are those provided in the radiosonde report from Del Rio, Texas on 27 March 2006 at 0000 UTC.
[b] Movements characterized by air speeds ≥6 m/s are considered to be dominated by birds.

geographically with several known colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) in the easternmost range of our study area (B. French, pers. comm.). However, these patterns dissipated, and resembled ambient reflectivity before the times when sweep data were collected for target identification. Like Able (1977), we assume that migrating bats are rare relative to birds in most geographical locations; however, the relative abundances of migrating bats and birds remain poorly understood and likely vary geographically and seasonally.

STATISTICAL APPROACH

We examined the effects of geographic location (i.e., radar site) and season on migrant altitude, ground speed, and ground direction across seven radar sites and three seasons. Nonparametric 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 altitudes (AGL) and ground speeds. We used simple correlation analyses on the seasonal median values for each site to describe to what extent seasonal flight altitudes were similar on a site-by-site basis. We used the same Kruskal-Wallis approach to test for differences in altitude and ground speed between sites within seasons, and within sites between seasons. Where overall differences in altitudes or ground speeds were significant among seasons across sites, among sites within seasons, or within sites among seasons, nonparametric Tukey-type multiple comparisons

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% and 75% quantiles) 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, we used Tukey-type multiple comparison tests of circular ranks (*Q* statistic) to identify differences among specific sites.

RESULTS

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 analysis—235 in 2005 (56%) and 180 in 2006 (43%). Of the 504 sweeps evaluated in fall 2005 (10 August–20 October), we retained 214 (45%) for analysis. The number of migrant-dominated evenings at an individual radar site during a season varied from 17 at Brownsville (BRO), Texas in spring 2006 to 40, also at Brownsville, in spring 2005. Most rejected sweeps were excluded from analysis due to the presence of precipitation. 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 (i.e., target airspeeds fell below 6 m/s; Table 3).

Shear—variation in the speed or direction of the wind with altitude (Fig. 3 in Diehl and

TABLE 3. NUMBER OF 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 analysis (N)	235	214	180

Larkin [2005]; Fig. 9 in Larkin [2005]) — occurred at all sites in all seasons. Shear was particularly common, and its specific structure conspicuously stable, at Midland (MAF) and Del Rio (DFX), Texas. At Del Rio, 34 of 39 migrant-dominated sweeps in fall 2005 exhibited some degree of shear, and the specific structure of shear in spring (Fig. 2a) at this site varied relatively little (see below). Although wind velocities that vary with altitude may be advantageous at times for multiple, separate, and simultaneous layers of migrants traveling in different directions, reflectivity data at Midland and Del Rio failed to support the presence of such a pattern in this case. Further visual review confirmed that reflectivity data at these sites were dominated by single, continuous, layers of migrants.

FLIGHT ALTITUDE

Flight altitudes differed among seasons when pooled across all sites (χ^2 = 40.92, P < 0.0001, df = 2); migrants flew significantly lower in both springs than in fall (Table 4a). Within each season, migrants used significantly different altitudes among sites (spring 2005: χ^2 = 80.45, P < 0.0001, df = 6; fall 2005: χ^2 = 73.82, P < 0.0001, df = 6; spring 2006: χ^2 = 25.22, P = 0.0003, df = 6), but showed no apparent geographical pattern (Table 4a). Median flight altitudes for each season and where among-site significant differences occurred within each season are presented in Table 4a.

Additionally, radar-site median migrant altitudes in spring 2005 and spring 2006 were significantly positively correlated (r = 0.76, P < 0.05), suggesting that birds on a site-by-site basis migrated at consistent altitudes in spring. In contrast, radar-site median migrant altitudes in fall 2005 were not correlated with altitudes in either spring (r = 0.17, P = 0.72, spring 2005 v. fall 2005; r = 0.35, P = 0.44, spring 2006 v. fall 2005) indicating that site-specific differences exist in flight altitudes between spring and fall. We determined (by within-site among-season analysis of variance by ranks) that site-specific

seasonal differences in altitude occurred at Flagstaff (FSX), Arizona (χ^2 = 15.40, P = 0.0005, df = 2), Midland (χ^2 = 43.12, P < 0.0001, df = 2), Del Rio (χ^2 = 30.14, P < 0.0001, df = 2), and Brownsville (χ^2 = 9.26, P < 0.01, df = 2); which seasons at these sites are significantly different are presented in Table 5. We found no among-season differences in altitude at Tucson (EMX), Arizona, Albuquerque (ABX), New Mexico, and El Paso (EPZ), Texas (each site P ≥ 0.29). At Midland and Del Rio in particular, fall altitudes were much higher than those of both springs. The large differences at these two sites explain most of the significant difference in altitudes between seasons across all sites (Fig. 3; Table 4a).

GROUND SPEED

Migrants' ground speeds were significantly different among seasons when pooled across all sites (χ^2 = 67.48, P < 0.0001, df = 2; Fig. 4); migrants flew significantly faster in spring than in fall (Table 4b). However, most of this difference can be attributed to variation at three of the seven sites, Midland, Del Rio, and Brownsville (Tables 4b, 5). Midland (χ^2 = 11.34, P = 0.003, df = 2), Del Rio (χ^2 = 38.13, P < 0.0001, df = 2), and Brownsville (χ^2 = 18.02 , P < 0.0001, df = 2) were the only sites with significant differences in ground speed within sites among seasons; which seasons are significantly different at these sites are presented in Table 5.

We found no significant differences in ground speeds within season among sites during spring 2005 (χ^2 = 9.24, P = 0.16, df = 6) or fall 2005 (χ^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 4b). 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 4b).

TABLE 4. SUMMARY OF STATISTICS FOR DAILY MIGRANT (A) FLIGHT ALTITUDE, (B) GROUND SPEED, AND (C) GROUND DIRECTION OF TRAVEL AT EACH WSR-88D SITE FOR EACH SEASON.

	FSX	EMX	ABX	EPZ	MAF	DFX	BRO	All Sites
(a) Flight altitude (m AGL)								
Spring 2005								
N	32	35	30	31	31	36	40	235
Median	817.6	1,708.5	971.8	896.9	600.6	1,194.5	1,846.9	1,206.7
25% quantile	473.3	1409.7	363.1	574.7	554.7	915.5	1,515.2	641.2
75% quantile	1,352.7	1,962.2	1,415.3	1,206.7	969.5	1,661.0	2,471.5	1,846.9
MC[a]	C	AB	C	C	C	ABC	A	
Fall 2005								
N	25	25	25	27	36	39	37	214
Median	1,352.7	1,535.2	995.0	1,456.7	2,213.9	2,665.9	2,133.8	1,785.5
25% quantile	856.1	819.9	671.8	574.7	1,669.0	2,021.9	1,578.1	953.9
75% quantile	1,384.0	1,803.5	1,384.0	1,898.6	2,410.9	3,123.6	2,698.4	2,335.4
MC	D	BCD	D	CD	ABC	A	AB	
Spring 2006								
N	24	32	24	26	23	34	17	180
Median	1,384.0	1,621.9	942.3	1,167.8	985.0	1,515.2	1,515.2	1384.0
25% quantile	875.3	1,132.9	336.6	574.7	615.9	1,066.5	1,233.4	881.5
75% quantile	1,872.9	2,022.0	1,474.3	1,934.5	1,295.9	17,99.8	2,006.3	1841.4
MC	AB	A	AB	AB	AB	B	AB	
(b) Flight ground speed (m/s)								
Spring 2005								
Median	11.64	11.64	12.52	12.44	13.09	13.40	14.17	12.44
25% quantile	9.63	9.01	9.87	8.63	9.77	10.19	10.45	9.74
75% quantile	15.74	13.04	15.43	15.44	18.76	16.44	17.71	15.86
MC	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
25% quantile	7.90	7.14	8.39	7.45	7.60	5.76	6.77	7.38
75% quantile	11.44	10.83	14.85	11.90	12.33	10.48	11.87	11.86
MC	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
25% quantile	7.97	9.55	9.32	7.01	10.13	11.92	10.06	9.27
75% quantile	12.73	13.67	15.58	12.42	17.50	17.95	14.49	15.39
MC	BC	BC	ABC	C	AB	A	ABC	
(c) Flight direction (°)								
Spring 2005								
Median	359.03°	335.42°	42.90°	73.30°	23.68°	7.52°	22.97°	
25% quantile	329.04°	322.70°	2.00°	331.91°	358.30°	355.95°	13.13°	
75% quantile	37.88°	350.78°	86.08°	90.06°	51.87°	28.44°	32.53°	
MC	AB	A	B	B	B	B	B	
Fall 2005								
Median	157.02°	173.36°	161.92°	160.95°	187.31°	196.54°	175.27°	
25% quantile	113.08°	154.12°	140.14°	126.04°	160.08°	169.14°	169.22°	
75% quantile	182.30°	182.36°	179.28	228.22°	211.18°	212.70°	189.30°	
MC	AB	AB	B	AB	AB	A	B	

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	FSX	EMX	ABX	EPZ	MAF	DFX	BRO	All Sites
(c) Flight direction (°)								
Spring 2006								
Median	322.52°	335.83°	6.49°	18.16°	3.42°	9.02°	22.49°	
25% quantile	308.88°	329.35°	352.87°	339.26°	345.54°	3.07°	11.20°	
75% quantile	349.04°	1.59°	86.53°	67.87°	16.00°	19.65°	34.76°	
MC	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 flight altitude, ground speed, and ground direction.

Migrants' median daily ground speed across all seven sites in spring 2006 was slightly lower than the previous spring (Table 4b). 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 4b).

FLIGHT DIRECTION

Median directions of travel at all sites in spring 2005 were seasonally appropriate (i.e., 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. 5; Table 4c). 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% quantiles); smallest variations in direction occurred at easternmost sites Del Rio and Brownsville (Fig. 5; Table 4c).

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 (i.e., 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. 5; Table 4c).

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. 5; Table 4c). 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. 5; Table 4c). Fifty-five degrees separated the median directions of travel at El Paso between spring 2005 and spring 2006.

DISCUSSION

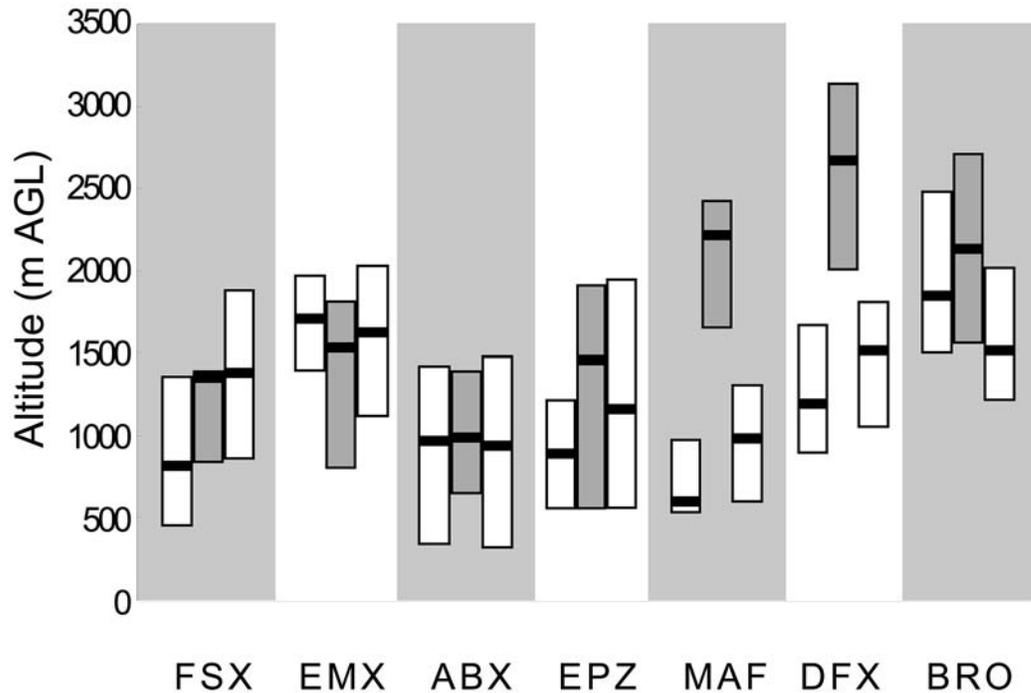In summary, our results show that in spring, migrants generally flew lower and faster than in

FIGURE 3. Median daily altitudes AGL (± 25% quantiles) of migrant-like targets at each radar site during spring 2005 (left white bar), fall 2005 (middle grey bar), and spring 2006 (right white bar).

TABLE 5. WITHIN-SITE AMONG-SEASON COMPARISONS OF FLIGHT ALTITUDES AND GROUND SPEEDS USING NON-PARAMETRIC MULTIPLE COMPARISONS OF RANKS TESTS (Q).

Radar site	FSX	EMX	ABX	EPZ	MAF	DFX	BRO
Flight ground speed							
Spring 2005	-	-	-	-	A	A	A
Fall 2005	-	-	-	-	B	B	B
Spring 2006	-	-	-	-	A	A	AB
Flight altitude							
Spring 2005	B	-	-	-	B	B	AB
Fall 2005	AB	-	-	-	A	A	A
Spring 2006	A	-	-	-	B	B	B

Note: Different letters indicate significant differences within sites among seasons. Significant differences are those comparisons with Q values >$Q_{(0.017), 3}$ = 2.827, an estimated critical value adjusted for comparisonwise error rates (Table B.15 in Zar 1999), indicates $Q_{(0.02), 3}$ = 2.713 and $Q_{(0.01), 3}$ = 2.936). Dashes indicate non-significance.

fall, although much of this overall pattern may be driven by patterns at a few of the radar sites.

Much of the seasonal variation in migrant flight altitude across the region may be explained by the seasonal differences at Midland and Del Rio. Spring migrants at these two locations might have experienced more favorable and less variable winds than did fall migrants, perhaps owing to relatively consistent directional wind shear in spring. In such conditions where winds are stable from day to day, birds typically concentrate at certain altitudes, selecting winds favorable for migration or avoiding winds unfavorable for

migration (Richardson 1978). Winds aloft data at these sites might suggest the former condition (selection of favorable winds) may be at work in spring and the latter (avoidance of unfavorable winds) at work in fall. However, caution should be exercised in evaluating such hypotheses with winds aloft data; the combined spatial and temporal separation of winds aloft data (provided by radiosondes) from the representative sweeps we analyzed was as much as 50 km and 5 hr (Midland). Such separation in place and time makes it difficult to define what winds aloft are favorable or unfavorable using our methods.
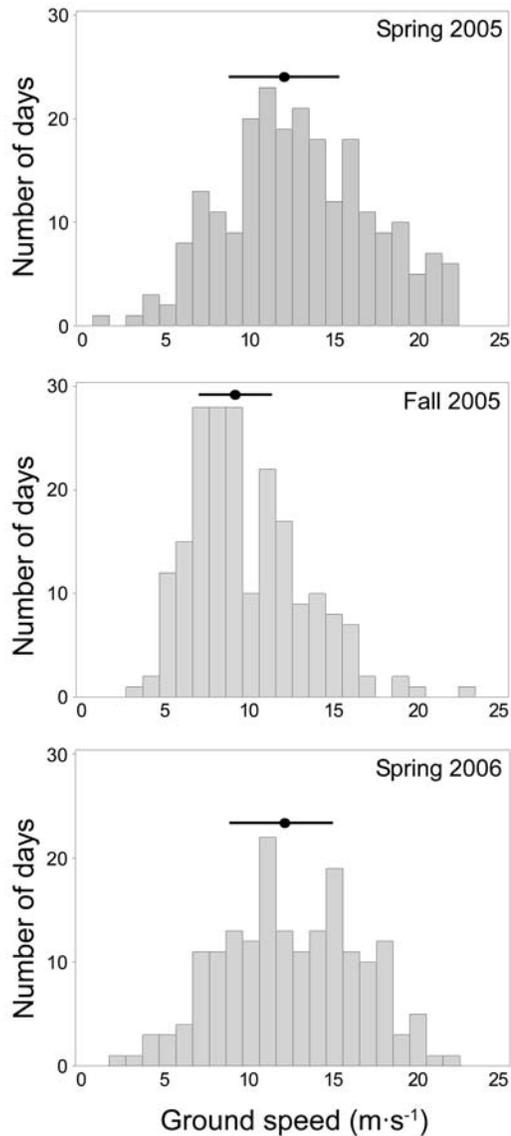
FIGURE 4. Histogram of ground speed estimates during spring 2005, fall 2005, and spring 2006 where each observation represents one ground speed estimate per day. Error bars represent season median ground speeds ± one quartile.

Proceeding with caution, however, we can say, based on comparison of winds (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. During both springs at Midland and Del Rio, more favorable southerly winds occurred at lower altitudes, which is where migrants tended

to concentrate, whereas wind directions above 2 km AGL were from the west. Winds were generally unfavorable for fall migration at all altitudes at Midland and Del Rio, but higher altitude migrants at these two sites at least had some chance of encountering more favorable winds due to the winds' greater variability in direction. The northerly winds presumably favorable to fall migrants were scarce but had a greater likelihood of occurring at higher altitudes, which is where migrants tended to concentrate. To more accurately interpret any winds effects at these or any site would require comparisons of prevailing winds at every altitude and migrants' possible responses therein on a day-by-day basis, and then only after closer spatial and temporal association between radar and winds aloft data is achieved. Such a full analysis was beyond the scope of this study, but would be useful in further understanding the patterns observed here.

Radar data suggest that the majority of spring migrants are found at altitudes ranging from 650 to 1850 m (AGL) and fall migrants at altitudes ranging from 950 to 2,350 m (AGL). However, these results should not be interpreted to mean that migrants did not fly at lower altitudes. WSR-88D radars in general are ill-suited for studies of low flying targets, particularly when using higher beam elevation data such as that from the 3.5° sweeps used in this study. This geometry, together with the constraints 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 occurs above 500 m AGL, we were not able to detect low altitude movements. Despite these limitations of the data, the resulting increased knowledge of regional and seasonal patterns in migratory movement offers guidance for future research and management as regulatory agencies and organizations implement bird conservation activities in the borderlands region.

Migrant ground speeds were higher in spring than fall, which is consistent with hypotheses concerning the selective pressures for Neotropical and Nearctic migrants to arrive early on breeding grounds in the spring. However, a number of factors may affect (reduce) migrant ground speeds in fall. (1) Greater variability in fall migrant directions of travel within a sweep results in lower measured ground speeds as a consequence of the way speed is measured using large Doppler radars. At their highest resolution, these radars quantify the Doppler velocity of all targets within relatively large volumes of airspace; for our sweeps these volumes were typically
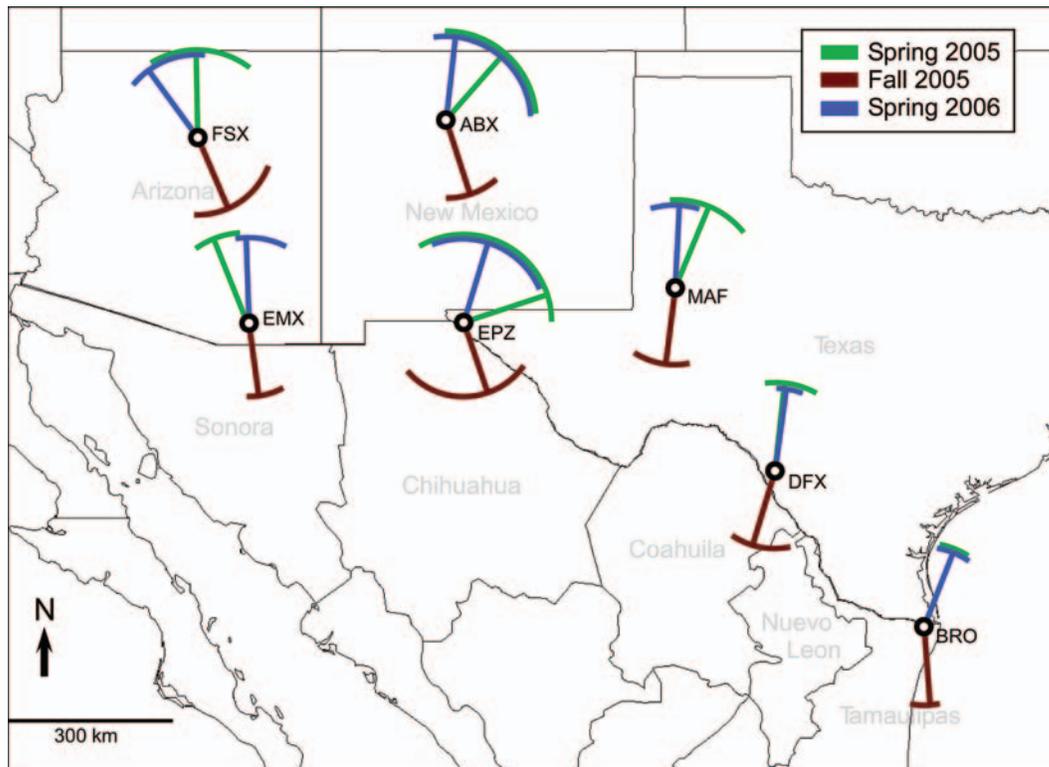
FIGURE 5. Directions of migration for spring and fall 2005 and spring 2006 at seven radar sites in the southwestern US. Green, red, and blue flags indicate seasonal median migrant directions (with 25% and 75% quantile whiskers) traveling away from the radar site.

3.0×10^7 m^3 to 4.7×10^7 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. (2) Birds experience less favorable winds in fall than in spring. (3) The proportion of naïve hatch-year birds that show more variable orientations (Ralph 1981, Woodrey 2000) is higher in fall. (4) Fall data retain a higher proportion of arthropods or non-migratory bats (Cleveland et al. 2006).

We attribute much of the seasonal variation in ground speed to differences at three sites, Midland, Del Rio, and Brownsville. These are the easternmost sites in the study area, making the greatest seasonal differences in ground speed somewhat concentrated geographically. This suggests that the causal factors are also geographically limited to the same area. Synoptic winds may be structured across the borderlands region such that birds migrating through Texas in fall encounter unfavorable winds. Alternatively, Del Rio's location in southcentral

Texas places it near a region of high insect and bat activity. Although insect migration through central Texas generally occurs below 1,000 m (Beerwinkle et al. 1994), foraging bats regularly reach altitudes characteristic of fall bird migration in this area. Despite efforts to retain data only from bird-dominated movements, this prospect of contamination by bats stresses the need for more sophisticated methods of target identification.

The direction of movement patterns we documented for spring and fall in 2005 and 2006 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 et al. 2003). They are also consistent with two major overland migratory systems suggested for North American wood warblers (Kelly and Hutto 2005), assuming that patterns in wood warbler migration are representative of more general passerine migration through the southwest captured by radar. Direction of movement patterns for our westernmost sites (Flagstaff and Tucson) in Arizona (Fig. 5) suggest dominance by species

that migrate between the Sierra Madre Occidental or Baja California and the Pacific coast (Kelly and Hutto 2005; Cooke 1915). However, directions of travel in the central and eastern borderlands suggest that some component of these migrants may be from midwestern or eastern North America. High variation in directions of movement in the central sites in New Mexico (Albuquerque) and west Texas (El Paso and Midland) suggests that these areas may draw migrants from intermountain west and central-eastern North America in fall. This is consistent with Yong and Finch's (2002) findings that their sites on the Rio Grande in New Mexico (near Albuquerque) were used by both western and eastern breeding species. Paxton et al. (2007) found similar west-east patterns in the breeding destinations of migrating Wilson's Warblers (*Wilsonia pusilla*), although the easternmost borderlands site they studied was in southeastern Arizona. The directions of movement in the easternmost sites in Texas (Del Rio and Brownsville) to the NNE in spring and the SSW in fall are most consistent with species that migrate between various locations in Mexico (or further south) and central and eastern North America.

This paper focuses on migrant movement behavior (migrant altitude, speed, and direction) and not on the intensity of migration across the borderlands region. Our ongoing research addresses remaining questions concerning large-scale structure in migrant density, which may be particularly relevant if multiple migratory systems converge within the region.

ACKNOWLEDGMENTS

Authors' Note: For literature cited in this paper, see the separate PDF of the complete <u>Literature Cited</u> for Studies in Avian Biology no. 37.