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Comparing transect survey and WSR-88D radar methods for monitoring daily changes in stopover migrant communities

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ABSTRACT. For decades, researchers have successfully used ground-based surveys to understand localized spatial and temporal patterns in stopover habitat use by migratory birds. Recent technological advances with WSR-88D radar now allow such investigations on much broader spatial scales. Both methods are assumed to accurately quantify patterns in migrant bird communities, yet information is lacking regarding relationships between radar estimates of migration and different ground-based monitoring methods. From 2005 to 2007, we monitored migrant communities on or near two Department of Defense installations in the spring (Ft. Polk Military Complex, LA; U.S. Army Test and Evaluation Command, Yuma Proving Ground, AZ) and on two installations in the fall (Ft. Polk Military Complex, LA; Eglin Air Force Base, FL) using both ground-based transect surveys and radar imagery of birds aloft. We modeled daily changes in migrant abundance and positive and negative species turnover measured on the ground as a function of radar estimates of migrant exodus and input densities. Radar data were not significant predictors of any response variable in any season either in the southeastern or southwestern United States, indicating a disparity between the results obtained using different methods. Multiple unique sources of error associated with each technique likely contributed to the conflicting outcomes, and researchers should take great care when selecting monitoring methods appropriate to address research questions, effects of management practices, or when comparing the results of migration studies using different survey techniques.

RESUMEN. **Comparando censos de transeptos y el método de radar WSR-88D para monitorear, diariamente, cambios en paradas de comunidades de migratorios**
Por décadas los investigadores han utilizado exitosamente censos terrestres para tratar de entender los cambios espaciales y temporales de migratorios en lugares de paradas. Los recientes avances tecnológicos con el radar WSR-88D, permiten, actualmente, este tipo de investigación en una escala espacial más amplia. Se asume, que ambos métodos indicados cuantifican con precisión los patrones migratorios en comunidades de aves, aunque falta información referente a las relaciones entre los estimados con el radar y los de otros métodos de censos terrestres. De 2005 al 2007, monitoreamos comunidades migratorias durante la primavera, en o cerca de dos instalaciones del Departamento de Defensa (complejo militar Ft. Polk, LA; Comando de Pruebas y Evaluación del ejercito de los EUA, Yuma, Arizona) y otras dos durante el otoño (complejo militar Ft. Polk, LA; la base Eglin de la Fuerza Aérea, Fl), utilizando censos terrestres e imágenes de radar. Modelamos diariamente los cambios en la abundancia de migratorios y los cambios positivos o negativos de especies al usar censos en el terreno y como función de los estimados del radar en el éxodo migratorio y su aportación en las densidades. Los datos del radar no permitieron predecir, de forma significativa, ninguna variable de respuesta, en ninguna de las dos temporadas, y en ninguna de las dos localidades al sureste o suroeste de las Estados Unidos, e indicaron disparidad entre los resultados obtenidos utilizando diferentes métodos. Errores múltiples, asociados a cada técnica, contribuyeron a los resultados conflictivos, por lo que los investigadores deben tener cuidado cuando seleccionen el método de monitoreo más apropiado para contestar preguntas particulares, o el efecto de prácticas de manejo o cuando quieran comparar los resultados de estudios sobre migratorios que usen diferentes técnicas.

Key words: avian migration, NEXRAD, riparian, stopover, transect surveys, WSR-88D weather radar

Approximately half of all bird species that nest in the United States are classified as Neotropical migrants. These species, including about 340 species of songbirds, shorebirds, waterfowl, and birds of prey, move annually between breeding grounds in North America and wintering areas in Mexico, Central America, South America, and the Caribbean. Seasonal bird migration

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is a time-consuming, energetically expensive behavior that imposes numerous risks on the survival of individuals, with potential implications for long-term viability of populations (Alerstam 1990, Moore et al. 1995). Although many landbird migrants are capable of making nonstop flights over large ecological barriers, few migrants actually engage in nonstop flights between seasonal ranges. Instead, migration is divided into alternating phases of flight and stopover, with each stopover lasting a few hours to a few days. Often, the cumulative amount of time spent at stopover sites far exceeds time spent in flight and largely determines the total duration of migration (Alerstam 1990). Thus, migrants are dependent on the availability of high-quality stopover habitats with sufficient food and cover resources for refueling and avoiding predators (Morrison et al. 1992, Moore et al. 1995, 2005).

Complicating this process is decades of urban growth and agricultural expansion that has fragmented and eliminated key migratory stopover areas, such as riparian habitats (e.g., Askins et al. 1990, Askins 1993, Gauthreaux and Belser 2003). Loss and degradation of migratory stopover areas are frequently cited as key contributors to the observed long-term declines of migratory landbirds (Hutto 1985, Askins et al. 1990, Moore et al. 1995, Mehlman et al. 2005), and conservation organizations (e.g., American Bird Conservancy and The Nature Conservancy) rank protection of stopover areas in the United States as a very high priority. Furthermore, Donovan et al. (2002) suggested that mapping migration stopover areas should be one of the highest research priorities for the conservation of migratory birds. Therefore, it is important that we not only develop tools to help identify important migration stopover sites, but that we also evaluate and compare the effectiveness of those tools.

Field surveys (e.g., point counts, transect surveys, or mist-netting) have historically been the standard and recommended method of investigating demographic characteristics of migrant bird communities (Hussell and Ralph 1995). However, large-scale field studies can be tedious and costly because they are generally time and labor intensive. Additionally, field studies are often spatially limited by logistical constraints associated with environmental and legal accessibility issues. Since the early 1990s, technological advances in obtaining and interpreting output from Weather Surveillance Radar 1988 Doppler (WSR-88D), also known as NEXRAD (NEXt Generation RADar), have greatly enhanced our ability to monitor broad-level migration patterns, assess annual trends of migratory bird passage, determine geographical areas of high stopover use, and gather information on the quantity, speed, and altitude of flying birds (Gauthreaux and Belser 1998, 2003, Diehl and Larkin 2005). This technology allows investigations of migratory patterns on spatial and temporal scales that are not feasible with field surveys. However, radar investigations have their own drawbacks because WSR-88D data tend to be limited in resolution, complex in interpretation, and can be hampered by displacement biases (Diehl and Larkin 2005). Data from both field censuses and radar are important to help identify specific, high-quality migratory stopover habitats and to understand their roles in sustaining migratory bird populations. However, these methods are fundamentally different in the way they estimate migrant bird abundances, and thus it is important to understand how these estimates differ to determine when each technique is appropriate and to help compare results from studies using different methods.

Few studies have actually compared indices of bird abundance on the ground with data from radar observations, and the results of those studies have been somewhat inconsistent. For example, Simons et al. (2004) found a strong correlation between migration data from WSR 57 radar and mist-net captures at sites within 100 to 150 km of radar stations along the coast of the Gulf of Mexico in the United States. In contrast, DiGaudio et al. (2008) failed to detect significant relationships between mist-net captures and radar data in California. Still fewer studies have compared radar-estimated migrant densities to abundance indices based on census data (e.g., point counts or transect surveys). Buler and Diehl (2009) found a significant relationship between bird densities recorded using transect surveys and nightly bird exodus densities estimated from WSR-88D radar stations along the Gulf of Mexico coast in the United States when they averaged daily values across seasons. Peckford and Taylor (2008) also found a significant relationship between the actual daily changes in migrant birds recorded using a variety of ground survey techniques (e.g., mist-net and transect survey data) and nightly estimates of migrating birds recorded using a mobile marine radar in Nova Scotia. However, most mobile radars used for monitoring bird movements cannot detect individual small birds beyond 1 km and, because the radars are not Doppler, the detection of ground clutter and its removal can severely limit detection of birds in areas of interest. Moreover, mobile radar units must be deployed in specific target locations to collect appropriate data; they are frequently used, for instance, on military airfields to detect local-scale movements of birds to reduce bird-aircraft strike hazards. WSR-88D radar stations, on the other hand, are already distributed throughout the country, have a narrow beam width (1°), detect flocks of birds out to a range of 200 km, operate continuously, and data are regularly archived. Therefore, WSR-88D radar data at the National Climatic Data Center are free and relatively easy to collect over the internet, though bird densities can only be assessed at broad scales. To our knowledge, no studies have compared daily changes in migrant abundances recorded on the ground with nightly migrant input and exodus density estimates based on WSR-88D radar technology. We investigated this relationship on or near three military installations in the United States from 2005 to 2007. Our specific objective was to determine if changes in migrant abundance or species composition on the ground could be explained by migratory events captured on radar. Such knowledge will improve our understanding of the types of migration studies for which each method is most accurate and useful.

METHODS

Study sites. This research took place within the context of a larger study aimed at identifying military installations that serve as important stopover habitat for migratory birds in the spring and fall (Fischer et al. 2011). The United States Department of Defense administers over 12 million hectares of land for the primary purposes of training troops and testing weapons platforms to ensure military readiness (Benton et al. 2008). Military installations often contain large, undeveloped landscapes that provide habitat for birds in all phases of their life cycle. These areas may be particularly valuable for migrating birds requiring stopover habitat. We selected two installations in both the spring and fall to use for our comparison of radar and ground-based migrant estimates. In the spring, we monitored sites on Ft. Polk Military Complex, LA (31° N, 93° W; hereafter, Ft. Polk) and adjacent to the U.S. Army Test and Evaluation Command, Yuma Proving Ground, AZ (32° N, 114° W; hereafter, Yuma); in the fall, we monitored sites on Ft. Polk and Eglin Air Force Base, FL (30° N, 86° W; hereafter, Eglin AFB). These locations were selected because of the consistent patterns of large, radar-indicated migration exodus events observed on or near the installations during the respective migration seasons, and the relative ease of access to field sites suitable for establishing transects (see Fischer et al. 2011 for more detail). Originally, we proposed to compare ground and radar migration estimates on one eastern and one western study site during both fall and spring seasons. However, clearly identifying fall migrant hot spots on western installations proved difficult because migration was either too dispersed, or installations suffered from beam blockage from mountainous terrain. Thus, a second eastern site (Eglin AFB) was selected for study during the fall.

We identified three riparian drainages (sites) on or adjacent to each installation to be surveyed simultaneously using line-transects. We focused our bird sampling along riparian areas because radar studies have shown eastern (Gauthreaux and Belser 1998, 2005) and western (Skagen et al. 1998, Kelly and Hutto 2005) migrants to be highly dependent on riparian areas for stopover during migration. Specific riparian sites were selected because they had been identified as stopover "hotspots" based on multiple years of compiled radar data (Fischer et al. 2011). Because it was not logistically feasible to conduct ground transect surveys encompassing entire installations, we assumed that surveying these hotspots would provide us with a reasonable index of migrants present in the region from 1 d to the next. At each site, we established from five to seven 500-m transects and each had a numbered start and end point. Transects were laid end-to-end where possible and followed riparian habitat along stream drainages.

During fall 2005, we established transects at three different sites at Eglin AFB, each with well-defined, transitional habitats between upland and floodplain forests. Regional uplands were typically dominated by extensive longleaf pine (*Pinus palustris*) sandhills, a sparse midstory of oaks (*Quercus* spp.) and other hardwoods, and a diverse groundcover. Riparian areas at Eglin AFB were comprised of a wide variety of hardwood tree species including magnolia (*Magnolia* spp.), sweetgum (*Liquidambar* spp.), poplar (*Populus* spp.), hickory (*Carya* spp.), ash (*Fraxinus* spp.), and maple (*Acer* spp.).

We established transects at four different sites at Ft. Polk. Transects at three sites were established in fall 2005, but, after that season, one site could no longer be accessed because of military training restrictions. Therefore, we established another transect in a nearby drainage (and within a radar-identified hotspot) in spring 2006. All transects were located in bottomland hardwood floodplains dominated by a variety of oak, hickory, ash, and other hardwood species.

During spring 2006 in southwestern Arizona, we established two transects along the Colorado River, and a third along an abandoned channel adjacent to the All-American Canal. These sites were located near Yuma Proving Ground and were dominated by a variety of trees and shrubs, including palo verde (*Parkinsonia* spp.), Fremont cottonwood (*Populus fremontii*), willow (*Salix* spp.), mesquite (*Prosopis* spp.), creosote bush (*Larrea tridentata*), and saltcedar (*Tamarix* spp.).

Bird surveys. Experienced birders conducted simultaneous transect surveys at sites during migration from fall 2005 through spring 2007. Sampling took place between 25 March and 15 May during spring migration and between 28 September and 21 October during fall migration. Because of logistical constraints, only two drainages each were surveyed at Yuma, AZ, and at Fort Polk during spring 2006 and 2007, respectively. Each morning, field crews began surveys at or shortly after sunrise, with each surveyor at a different site. Surveyors used a hand-held GPS unit pre-loaded with numbered waypoints that denoted the beginning and end of each 500-m transect, walking each transect at the site in succession and recording each bird detected. If a bird could not be identified to species, we categorized it to the lowest taxonomic level possible. Each 500-m transect was completed in ~30 min, and thus each site survey could be completed in ~3 h (surveys usually ended by ~10:00). All sites were surveyed daily during the study period, except in cases of inclement weather or logistical constraints (38 of 255 possible sampling events were missed in the fall, and 56 of 411 in the spring), and surveyors rotated among sites daily.

Radar data. We downloaded all nightly WSR-88D radar data (National Climatic Data Center, Ashville, NC) captured over our study areas between sunset and sunrise for all days when ground surveys were conducted. Data were recorded by radar station KEVX for Eglin AFB, by station KPOE for Ft. Polk, and by station KYUX for Yuma; all sample sites were within 70 km of associated radar stations. Data were processed following methods described by Gauthreaux and Belser (2003) and Gauthreaux et al. (2008). Each evening, we recorded two migration density values over each installation, with one representing the peak migrant exodus density (exodus) and a second representing peak nightly migration over the study area (input). Exodus values were treated as an index for the number of migrants emigrating from our stopover sites, and input values as an index for the number that could potentially use the areas as stopover habitat the next day. Peak exodus density values occurred between 45 and 120 min after sunset (see Hebrard 1971, Buler and Diehl 2009). Peak migration density values occurred any time between the end of nocturnal exodus and sunrise, with most peaks between 21:00 and 23:00; this timing corresponds with the results of a previous study that compared hourly nocturnal migration densities calculated from WSR-88D in Mobile, Alabama, with captures of migrants in mist nets the following morning in Fort Morgan, Alabama, and found the highest R^2 value (0.578) occurred during the 22:00 h (22:00–23:00), or ~3 h after sunset (Gauthreaux, unpubl. data). Input and exodus values were generated by selecting the peak pixel reflectivity measured in dBZ (minimum of 10 pixels) over a study area and then translating that into mean birds per cubic kilometer (MBPCKM; Gauthreaux and Belser 2003, Gauthreaux et al. 2008). In some instances, estimating one or both of these values for a particular evening was not possible because radar images were contaminated by weather, insects, or particles (e.g., smoke).

Statistical analyses. We first classified each species recorded during transect surveys into migratory categories (i.e., nocturnal migrant, diurnal migrant, or permanent resident) then eliminated all diurnal migrants and permanent residents from analyses. When a bird could not be identified to species, we assigned it to the most likely migratory category (e.g., unknown warblers, flycatchers, and thrushes were classified as nocturnal migrants, and unknown herons, raptors, and swallows were classified as diurnal migrants). These steps ensured that we were only modeling the relationship between migratory events captured on evening radar scans and changes in abundance of birds that had the potential to be captured by those radar scans. We did not attempt to account for avian detection probability because we were not interested in densities of individual species, but rather wanted an index that represented changes in all nocturnal migrants combined, and no good method exists to account for detection probability in large-scale, multi-species monitoring surveys (Johnson 2008). Each morning an installation was sampled, we summed the number of spring or fall migrants recorded at all sites and divided it by the total distance walked (migrants/km) that morning (this value was not necessarily constant because observers sometimes had to avoid or stop sampling transects for a number of logistical reasons). We then calculated the change in migrant abundance between days by using the formula:

$$\Delta\text{migrants/km}_d = \text{migrants/km}_d - \text{migrants/km}_{d-1},$$

where d = the survey date of interest. We also calculated positive and negative species turnover from 1 d to the next, with positive turnover defined as the number of species present on day_d that were not present on day_{d-1}, and negative turnover as the number of species not present on day_d that were present on day_{d-1}. Although we acknowledge that WSR-88D radar stations are not able to collect species-level information, we wanted to test the hypothesis that substantial migratory events captured on radar might be reflected in changes in migrant composition on the ground.

Because ground surveys were conducted on consecutive days at the same sites, we were concerned that our response variables might be temporally auto-correlated. In other words, the change in migrant abundance or species composition on a given night may be influenced to varying degrees by changes that took place over the previous few nights. Thus, we first examined autocorrelation and partial autocorrelation functions (PROC ARIMA, SAS v. 9.2, SAS Institute, Cary, NC) among each of the three response variables (change in migrant abundance, positive species turnover, and negative species turnover). We assumed that any autocorrelation would affect all regions, years, and seasons similarly, so we pooled all data for this step.

For change in migrant abundance, we found evidence of temporal autocorrelation at a 1-d lag with a moving average corresponding to a 5-d lag (i.e., an AR[1], MA[5] model). Thus, we output the residuals from this analysis and modeled them as a linear function of input and exodus radar data simultaneously (PROC MIXED, SAS v. 9.2, SAS Institute, Cary, NC). In this step, each installation-by-season combination was analyzed separately, with year included as a fixed effect. Because these linear mixed models tended to be extremely poor fits for the data, we also modeled the effect of input and exodus on the residuals of the AR(1), MA(5) model using a non-linear mixed model (PROC NLMIXED, SAS v. 9.2, SAS Institute, Cary, NC) to free the parameter estimates from the constraints of having to be normally distributed and linearly related. We assessed the fit of the linear mixed models by calculating χ^2/df, and models with a value much greater than 1 were considered a poor fit (McCullagh and Nelder 1989). We assessed the fit of the nonlinear mixed models by comparing the –2 log-likelihood values of the model of interest and an intercept-only model. If the deviance was ≤ 4, then models were considered a good fit (McCullagh and Nelder 1989).

There was no evidence for temporal autocorrelation for either positive or negative species turnover. Thus, we modeled positive species turnover as a function of migrant input density data recorded on radar, and negative species turnover as a function of exodus density, assuming a negative binomial distribution (PROC GLIMMIX, SAS version 9.2, SAS Institute, Cary, NC). We again modeled each installation-by-season combination separately, including year as a fixed effect, and assessed goodness-of-fit using χ^2/df. For all three response variables, we used an $\alpha = 0.05$ significance level to determine if radar variables were significant predictors of data recorded on the ground.

Table 1. Summary of sampling effort and birds detected during spring and fall migration transect surveys on three military installations from 2005 to 2007.

Season	Installation	Year	Sampling days	Total transect distance sampled (km)	Effort (km/day)	Total birds	Nocturnal migrants (% of all birds)	Nocturnal migrants detected per day
Fall	Eglin AFB	2005	10	83	8.30	2268	818 (36)	81.8
		2006	18	157	8.72	8214	3749 (46)	208.3
		2007	17	142	8.35	6989	3496 (50)	205.7
	Ft. Polk	2005	14	97	6.93	2921	513 (18)	36.6
		2006	17	116	6.82	2895	688 (24)	40.5
Spring	Ft. Polk	2006	36	316.5	8.79	13,147	6360 (48)	176.7
		2007	33	152	4.61	5979	3349 (56)	101.5
	Yuma Proving Ground	2006	38	219.5	5.78	50,404	15,095 (30)	397.2
		2007	43	416	9.67	31,133	16,354 (53)	380.3

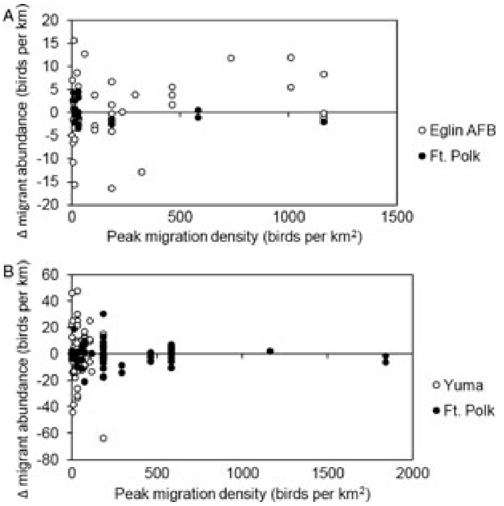

Fig. 1. Relationship between peak nightly bird migration density (as recorded by WSR-88D radar stations) and change in nocturnal migrant abundance recorded on consecutive days by observers conducting transect surveys during (A) fall migration, and (B) spring migration on or near three military installations (Eglin AFB, FL; Ft. Polk, LA; and Yuma Proving Ground, AZ) from 2005 to 2007. After the effects of temporal autocorrelation were taken into account (PROC ARIMA, SAS v. 9.2, SAS Institute, Cary, NC), peak migration density was not a significant predictor ($\alpha = 0.05$) of change in migrant abundance at any installation in any season.

RESULTS

From fall 2005 to spring 2007, bird surveys yielded 123,950 detections of 271 species (Table S1). We conducted transect surveys on 45 mornings at Eglin AFB, 100 mornings at Ft. Polk (fall and spring combined), and 81 mornings near Yuma Proving Ground (Table 1). Approximately 60% of species and 40% of total detections were likely nocturnal migrants. Species richness tended to be greater during spring surveys and was greater at Yuma, AZ, than at either Ft. Polk or Eglin AFB. For all installations and seasons combined, we had estimates of both input and change in migrant abundance for 192 nights, and we had both exodus and change in migrant abundance estimates for 179 nights. We were able to estimate all three variables on 170 nights.

The relationship between change in migrant abundance and input (Fig. 1) or exodus (Fig. 2) radar data revealed no clear patterns in either season. Indeed, analyses of the residuals output from the ARIMA procedure on the change in migrant abundance values revealed no evidence that either input or exodus radar data were significant predictors of change in migrant abundance observed using transect surveys (Table 2). The linear models were extremely poor fits for the data ($\chi 2/\mathrm{df} \geq 3.90$) at all installations during all seasons. Although the nonlinear models seemed to fit the data better, parameter estimates for input and exodus were still not significantly different from 0 in any of the analyses. Hence, relationships between radar data and change in migrant abundance described by the nonlinear modeling were not useful.

Examination of the positive species turnover models also indicated no significant relationship with input radar data (Fig. 3). The linear models comparing these variables fit the data well for all

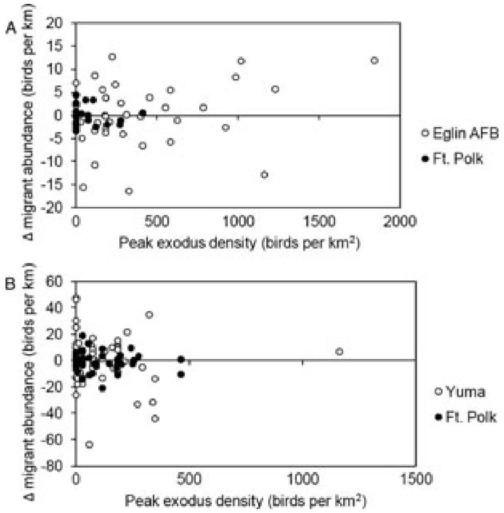

Fig. 2. Relationship between peak nightly bird exodus density (as recorded by WSR-88D radar stations) and change in nocturnal migrant abundance recorded on consecutive days by observers conducting transect surveys during (A) fall migration, and (B) spring migration on or near three military installations (Eglin AFB, FL; Ft. Polk, LA; and Yuma Proving Ground, AZ) from 2005 to 2007. After the effects of temporal autocorrelation were taken into account (PROC ARIMA, SAS v. 9.2, SAS Institute, Cary, NC), peak exodus density was not a significant predictor ($\alpha = 0.05$) of change in migrant abundance on any installation in any season.

installations in all seasons, yet input was not a statistically significant predictor of positive species turnover in any case (Table 3). Similarly, there appeared to be little relationship between exodus radar data and negative species turnover (Fig. 4). Again, although linear models appeared to be a good fit for the data, parameter estimates for exodus values were not significantly different from 0 (Table 4) for any installation in any season.

DISCUSSION

For years, researchers have used ground-based techniques (e.g., census and mist-netting) to monitor spatial (e.g., Skagen and Knopf 1994, Hardy et al. 2004, Rodewald and Brittingham 2004) and temporal (Moore et al. 1990, Simons et al. 2004) patterns of stopover habitat use by migrating birds. However, use of WSR-88D radar data to address similar questions has become more common in recent decades because it allows analysis of migratory movements on a broader scale (Gauthreaux et al. 2003, Diehl and Larkin 2005, Felix et al. 2008). Our results revealed that nightly estimates of exodus and input recorded using WSR-88D radar data were not significant predictors of the daily change in migrant abundance or species turnover as recorded with ground-based transect surveys. Because our results suggest that the two survey methods yield disparate results, great care should be taken when selecting appropriate methods to meet specific objectives in future migration studies or when comparing migrant stopover data gathered using different techniques.

In contrast, Buler and Diehl (2009) compared radar- and ground-estimated bird densities at 24 sites in Mississippi and Louisiana and found that radar reflectivity of birds aloft near the onset of migratory flight was positively correlated with bird densities on the ground. They averaged temporal ground and radar data across seasons and used several sites as replicates, whereas we used days as replicates at a small number of sites. Unfortunately, we were unable to use their same analytical approach for a direct comparison because, in the context of their experimental design, we only had three study sites. However, the contrasting outcomes of these two studies may reveal some insightful details about the relationship between ground and radar migration surveys, namely that unique sources of error associated with each technique may introduce so much variability that it could preclude finding a relationship when examined at the temporal scale of 1 d.

Our methods assumed that all birds departing stopover sites left during the early evening, and that birds that did not leave remained in the same general area until departure. Although we included only primarily nocturnal migrants in our analyses, some birds may arrive or depart during the day, avoiding capture on nightly radar images (Lowery and Newman 1955). In addition, birds using an area as a stopover site do not establish territories as they would in breeding areas and so may not be found in the same place on consecutive days, despite being present. Migrants often move in flocks, especially during the fall (Morse 1989), and changes in abundance recorded during surveys could also be influenced by whether or not flocks were near transects on a

Table 2. *P* values associated with parameter estimates for variables used to explain nightly change in migrant abundance detected during migration transect surveys on or near three military installations from 2005 to 2007.

				P value of parameter[a]			Model fit
Type of model	Season	Installation	*N*	Input	Exodus	Year	statistic[b]
Linear mixed model	Fall	Eglin AFB	38	0.17	0.09	<0.01[c]	27.8
		Ft. Polk	21	0.18	0.34	0.49	3.9
	Spring	Ft. Polk	43	0.34	0.74	0.30	44.6
		Yuma Proving Ground	68	0.95	0.15	0.22	212.2
Nonlinear mixed model	Fall	Eglin AFB	38	0.25	0.32	0.61	3.6
		Ft. Polk	21	0.20	0.39	0.47	1.8
	Spring	Ft. Polk	43	0.35	0.74	0.23	1.3
		Yuma Proving Ground	68	0.99	0.13	0.19	2.6

[a] Nightly input and exodus values were recorded using WSR-88D radar.

[b] χ 2/df for linear mixed models and deviance for nonlinear mixed models.

[c] Parameter estimate is significantly different from 0 ($\alpha = 0.05$).

given day. Large fluctuations in daily abundance of permanent residents during some seasons in our study support the hypothesis that not all changes in the number of migrant birds encountered were due to individuals leaving or arriving at stopover sites. These sources of error may create variability in both radar and ground estimates of daily changes in migrant communities, making it difficult to find a correlation between methods. By averaging daily ground and radar estimates across seasons, Buler and Diehl (2009) may have improved their ability to detect a relationship by reducing the influence of daily variability.

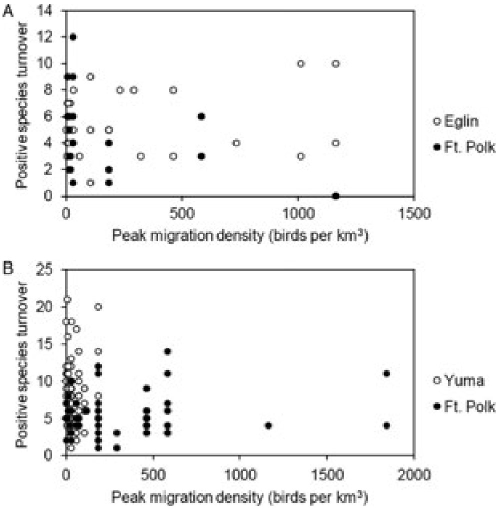

Fig. 3. Relationship between peak nightly bird migration density (as recorded by WSR-88D radar stations) and positive species turnover (as recorded by observers conducting transect surveys) during (A) fall migration, and (B) spring migration on or near three military installations (Eglin AFB, FL; Ft. Polk, LA; and Yuma Proving Ground, AZ) from 2005 to 2007. Peak migration density was not a significant predictor ($\alpha = 0.05$) of positive species turnover on any installation in any season.

Other factors could also have confounded our ability to detect a relationship between the results of transect and radar surveys. First, our methods assumed that all observers were equally able to detect and identify birds. This assumption was almost certainly violated because previous studies have shown that observer bias can influence estimates of bird abundance (e.g., Sauer et al. 1994). Moreover, examination of our data indicated that observer bias may have been a problem because we noted systematic asymmetry in the number of birds counted by different observers during at least one field season.

Second, there were discrepancies between the ground- and radar-survey data both in terms of the spatial extent and scale of the measurements. Transect surveys were conducted along relatively narrow riparian strips in distinct drainages within a larger landscape matrix. However, because of the coarse scale of the radar data, our estimates of input and exodus also included areas between and around drainages. Thus, transect surveys only measured a small portion of the area surveyed by radar, and we assumed that daily changes observed within this subsample of riparian habitat were indicative of changes

Table 3. *P* values associated with parameter estimates for variables used to explain nightly positive bird species turnover detected during migration transect surveys on or near three military installations from 2005 to 2007.

			P value of parameter[a]		
Season	Installation	*N*	Input	Year	χ^2/df
Fall	Eglin AFB	39	0.72	0.43	1.1
	Ft. Polk	21	0.14	0.13	1.2
Spring	Ft. Polk	57	0.55	0.05[b]	1.0
	Yuma Proving Ground	75	0.69	0.79	1.1

[a] Nightly input values were recorded using WSR-88D radar.

[b] Parameter estimate is significantly different from 0 ($\alpha = 0.05$).

in the area surveyed by radar. We feel this was a legitimate assumption, particularly in the western United States, because riparian habitats sampled in and near Yuma were located in desert landscapes, and thus represented virtually all available stopover habitat. However, riparian areas at the eastern installations (Ft. Polk and Eglin AFB) were embedded in a much larger matrix of upland forest, where migrants may have been more dispersed. If true, the limited extent of our transect surveys would have made it difficult to accurately quantify temporal changes in migrant communities at the same scale as those detected on radar. Finer-scale radar data, which are not available with current WSR-88-D technology, would have allowed us to generate metrics for individual sites; the resolution of the WSR-88D is too coarse to detect individual birds as they depart from stopover areas. High-resolution mobile radar units like the enhanced BirdRad radar (eBirdRad; Nohara et al. 2005) can be moved and placed in strategic locations where individual birds can be tracked as they depart from stopover habitats, and should be considered for use in future studies (e.g., Peckford and Taylor 2008). Use of such radar, particularly in discrete riparian habitats such as those along the Colorado River, would allow quantification of echo size, flight direction, flight speed, and number of migrant birds leaving specific locations.

Lastly, although we can reasonably assume that most birds recorded by radar during an exodus event were leaving the study region, an unknown proportion of birds detected by radar during peak nightly migration (input) were actually arriving. Moreover, that proportion may change during the night depending on weather conditions and when radar reflectivity values were calculated. Peckford and Taylor (2008), for instance, found that the correlation between their ground census and radar data varied during the night, peaking just before sunrise on nights with unfavorable headwinds and just after sunset on nights with favorable tailwinds. Most of our input data were collected between 21:00 and 23:00 and, although we had evidence to suggest this timing would be ideal for correlation with census data, our input estimates may have been a poor index for the actual number of birds settling in each study area. Radar data collected at a smaller spatial scale and over a larger temporal scale than ours may be required to accurately estimate how many birds are actually arriving on any given night.

Many sources of error mentioned are not unique to our study, but would be inherent in

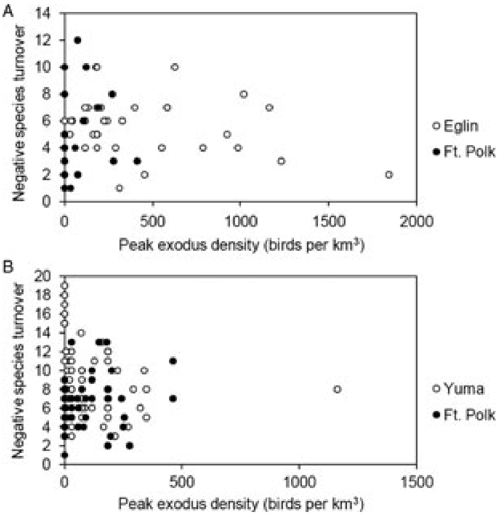

Fig. 4. Relationship between peak nightly bird exodus density (as recorded by WSR-88D radar stations) and negative species turnover (as recorded by observers conducting transect surveys) during (A) fall migration, and (B) spring migration on or near three military installations (Eglin AFB, FL; Ft. Polk, LA; and Yuma Proving Ground, AZ) from 2005 to 2007. Peak exodus density was not a significant predictor ($\alpha = 0.05$) of negative species turnover on any installation in any season.

Table 4. *P* values associated with parameter estimates for variables used to explain nightly negative bird species turnover detected during migration transect surveys on or near three military installations from 2005 to 2007.

			P value of parameter[a]		
Season	Installation	*N*	Exodus	Year	χ^2/df
Fall	Eglin AFB	38	0.26	0.48	1.0
	Ft. Polk	25	0.36	0.14	1.1
Spring	Ft. Polk	44	0.22	0.57	1.1
	Yuma Proving Ground	72	0.38	0.44	1.0

[a] Nightly exodus values were recorded using WSR-88D radar.

any attempt to model a relationship between ground and WSR-88D radar estimates of migratory events. The sources of error are, however, unique for each method, making it difficult to draw a correlation between the two and likely explaining why we found no significant relationship between methods. Several recent studies have shown that mist-netting may be the ground-sampling method that yields results most reflective of migratory events captured on radar (Simons et al. 2004, Peckford and Taylor 2008). Unlike mist-netting, transect censuses cannot tell us if the migrants detected have been present for several days or are the result of migration input. Similarly, on days with low numbers of detections on the ground, we cannot determine whether birds left stopover sites or simply dispersed through the landscape beyond the transect area. Daily numbers of transient migrants varied greatly at all of our study regions and future studies should focus on gaining a better understanding of this variation because it has significant implications for understanding the relationship between ground and radar migration surveys and for the identification, validation, and conservation of important migratory stopover areas.

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Supporting Information

The following supporting information is available for this article online:

Table S1. All bird species recorded (Y) during spring (Ft. Polk and Yuma Proving Ground) and fall (Ft. Polk and Eglin AFB) migration surveys from 2005 to 2007 on or near three military installations.