

**METHODS FOR STUDYING STOPOVER ECOLOGY OF MIGRATING  
LANDBIRDS WITH WEATHER SURVEILLANCE RADAR**

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment  
of the requirements for the degree of Master of Science in Wildlife Ecology

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## ABSTRACT

Populations of numerous migratory landbird species in the eastern United States are declining and these populations may be limited during their migratory journey. Weather surveillance radar is a useful tool for monitoring large scale movements of birds during migration and particularly for mapping stopover distributions of migratory landbirds because it detects birds low to the ground as they initiate nocturnal migratory flight. This approach is sensitive to the time when flight exodus is sampled because the number of birds in the air at this time changes rapidly. Thus, in order to use radar to map densities of migrant birds on the ground, an empirical determination is needed to identify an unbiased method to sample migrant density in the air. I assessed the relationship between seasonal mean migrant bird ground densities and seasonal mean radar reflectivity, an estimate of emigrant bird density aloft, sampled at a series of sun elevation angles ranging from  $1.5^{\circ}$  to  $10^{\circ}$  below the horizon at 26 sites in Delaware, Maryland, and Virginia within 80 km of the Dover, Delaware (KDOX) and Wakefield, Virginia (KAKQ) WSR-88D stations during fall 2013 and 2014. Additionally, because the timing of flight exodus varied among nights within and among radars, I fit a logistic growth curve to the change in mean reflectivity through time during the onset of nocturnal flight to determine the sun angle at the inflection point of the curve (i.e., at the maximum growth rate) for each sampling night by radar. I computed correlations between ground bird densities and mean reflectivity among the series of radar sampling times and among a series of times relative to the inflection point of daily exodus curves. Sampling radar at the inflection point of daily exodus curves provided a consistent moderate to strong

correlation and this approach is likely robust to broad spatio-temporal changes in the timing of exodus that would not be accounted for by using an absolute sun angle. Placing stopover sites for migratory landbirds into a functional framework based on intrinsic and extrinsic factors may be a key to conserving declining populations. Landbirds typically use numerous stopover sites during migration, which vary in usefulness regarding replenishment of energetic resources. To classify stopover sites across a broad spatial scale, I determined relative stopover duration at study sites mentioned above combined with data collected using similar protocols during a previous study in Alabama and Louisiana by integrating ground transect data with weather surveillance radar data. Functional types within the function framework initially included “fire escape,” “convenience store,” and “service hotel”, but clustering resulted in four distinct groups, which I redefined as “coastal fire escape,” “inland rest stop,” “convenience store,” and “full service hotel.”, a novel designation for landbirds.

I incorporated hardwood forest within 5 km, distance to the coast, and insect density into the analysis as potential drivers of stopover duration. One third of our study sites were deemed as full service hotels, making the majority of our study sites coastal fire escapes, inland rest stops, or convenience stores, which typically receive less attention in conservation planning. There were regional differences, where the mid-Atlantic lacked full service hotels and the Gulf Coast lacked coastal fire escapes. Using a system of functional types facilitates the prioritization of stopover sites because I can evaluate sites within each functional type rather than across functional types. Each functional type serves a purpose and all are necessary in conservation, but all sites cannot be protected, so using a functional type system allows us to prioritize sites

more easily and efficiently. Using weather surveillance radar and ground surveys allowed me to assess stopover use at a broad spatial scale, which is difficult to do with more traditional methods.

## **Chapter 1**

# **WHEN IS THE BEST TIME TO SAMPLE MIGRATING BIRDS WITH WEATHER SURVEILLANCE RADAR TO DETERMINE STOPOVER DENSITY?**

## **Introduction**

In the eastern United States, some migratory landbird populations are decreasing (Ballard et al. 2003), (Robbins et al. 1989), (Terborgh 1989), (Finch 1991), (Hagan and Johnston 1992). Investigating population dynamics during the annual cycle of migratory landbirds may be the key to conserving species and determining population limitations (Webster et al. 2002). The annual cycle of migratory landbirds consists of four parts: a breeding season in which birds are stationary, a migration period to the non-breeding grounds, a stationary non-breeding season, and a return migration to the breeding grounds (Newton 2010). Migration is one of the most taxing (McWilliams et al. 2004) and least understood parts of a migrant's annual cycle (Ewert and Hamas 1996). The majority of birds that breed in northern latitudes migrate to less harsh areas with greater available resources annually during the non-breeding season (Faaborg et al. 2010). Migration is generally broken up into two phases, flight and stopover (Newton 2010) and occurs over two to four months during spring and fall combined (Keast and Morton 1980), (Webster et al. 2005). These long-

distance movements pose relatively high risk of mortality for adult birds (Sillett and Holmes 2002) and may limit some migrant populations (Newton 2010).

Migrating landbirds spend more time at stopover locations than in migratory flight (Hedenstrom and Alerstam 1997). Selected stopover sites provide the necessary fuel and/or a place to rest before continuing migratory flight (McWilliams et al. 2004). Length of stopover can range from hours (Moore and Aborn 1996) to many days (Seewagen et al. 2010) and depends in part on how quickly an individual can replenish fuel for the next period of flight (Moore and Kerlinger 1987), (Lindstrom and Alerstam 1992). Ideal stopover locations are free of predators and competitors, and contain abundant energy resources, but these areas are scarce and distributed unevenly across the landscape (Newton 2010). This usually isn't the case and migratory species frequently encounter interspecific and intraspecific species competition (Moore et al. 2005).

Migratory stopover use has been studied using various methods and metrics (Bruderer 1997), including mist-netting and transect and point counts (Reynolds et al. 1980). Stopover use by landbirds during migration can also be assessed using the national network of weather surveillance radars (WSR-88D) in the United States (Diehl et al. 2003). Researchers first noted that birds were detectable on surveillance radars in the 1940s (Lack and Varley 1945) and since then, migratory movements of landbirds have been monitored and quantified using radar technology (Eastwood 1967). There are two useful data products from the WSR-88D for quantifying bird migration and assessing stopover use of migrating landbirds: radar reflectivity and

radial velocity. From these data products, bird densities, flight speed, and overall flight direction can be quantified (Gauthreaux Jr. et al. 2003) out to 80 km from the radar (Buler and Diehl 2009).

Methods for using weather surveillance radar to map stopover distribution of landbirds have improved since it was first done by Gauthreaux Jr. et al. (2003) where they visually selected two to five volume scans near the onset of nocturnal flight for each day to quantify densities of birds emerging from ground sources. Bonter et al. (2008), Buler and Diehl (2009), Buler and Moore (2011), and Ruth et al. (2012) modified this approach by visually selecting a single volume scan near the onset of nocturnal flight for each day to serve as an instantaneous sample of birds exiting ground sources. Later, Buler et al. (2012), and Buler and Dawson (2014) introduced an approach to spatially and temporally interpolate reflectivity data between scans to a fixed sun angle near the onset of nocturnal landbird migration (around civil twilight, 30 to 40 min after sunset) for each day in order to instantaneously sample birds low to the ground as they depart for flight. Each of these sampling methods may lead to sampling time bias, because not all landbirds initiate nocturnal migration at the same time every night in all locations (Akesson et al. 1996) and it is difficult to train radar data screeners to consistently select volume scans that accurately represent bird distributions on the ground.

Although the timing of the initiation of nocturnal migration can vary, the majority of birds generally being leaving within one hour after sunset (Akesson et al. 1996). For example, Song Thrushes (*Turdus philomelos*) in autumn in southern

Sweden departed between 30 and 34 min after sunset (Alerstam 1976). Timing of departure is also influenced by other factors such as latitude and time of year and may vary among and within species (Akesson et al. 1996). Akesson et al. (1996) found that, on average, birds departed when the sun was  $-6^{\circ}$  below the horizon in autumn, but ranged from  $8^{\circ}$  to  $30^{\circ}$  below the horizon. The majority of Swainson's Thrushes (*Catharus ustulatus*) departed from Fort Morgan, Alabama, on the Gulf of Mexico, within one hour after sunset (Smolinsky et al. 2013). Furthermore, there are birds that leave well after the end astronomical twilight (sun elevation angle of 18 degrees below the horizon), such as the European Robin (*Erithacus rubecula*) that, depending on fuel stores, leaves between 83 and 482 min after sunset (Bolshakov et al. 2007).

Birds may begin migratory flight around civil twilight for several reasons. The direction of sunset, skylight polarization pattern, and stars visible at twilight provide navigational cues to migrants (Able 1993). In addition, atmospheric conditions, such as cooler temperatures and calmer winds, are most favorable for migration near civil twilight (Kerlinger and Moore 1989). Because the number of birds in the airspace increases quickly and can double every few minutes after civil twilight (Hebrard 1971), choosing the time to sample the flight exodus is critical. The WSR-88D can only be used to sample the first landbirds initiating in nocturnal migration because once birds are aloft and begin their migratory flight, they obscure the departure of landbirds migrating at a later time (Buler and Diehl 2009).

Deciding on a dynamic (across days and radars), yet consistent relative sampling time, is critical for making accurate stopover maps and reducing sampling

time bias. Precise stopover maps can be used for conservation planning. By using a dynamic sampling time, sampling error from the coarse sampling (one volume scan every 10 min) of the WSR-88D combined with the bias of any geographic differences in the initiation of nocturnal migration as birds get displaced from their stopover sites (Buler and Diehl 2009), should be reduced.

My objectives were to 1) assess at which fixed sun angle across all nights and radars to sample radar data at the onset of bird flight produced the most accurate estimates of stopover densities of birds at the ground and 2) assess whether using a dynamic relative sampling time to sample radar data, which was related to the nature of how the number of birds aloft changes during exodus performed better than sampling radar data at a fixed sampling sun angle to map bird densities at the ground. To accomplish objective 1, I followed the work of Buler et al. (2012) to identify the optimal time to sample migrant density in the air for mapping ground densities. I compared densities of birds on the ground during stopover to emigrant densities on the radar at sun elevation angles between  $1.5^{\circ}$  and  $10^{\circ}$  below the horizon. The point of strongest correlation should be the optimal sampling time. Based on previous work done by Buler et al. (2012) and Buler and Dawson (2014), I expected that the optimal time to sample migrants would be when the sun is at an elevation of  $5.5^{\circ}$  below the horizon. In contrast, the dynamic approach used in objective 2 does not determine an absolute sun elevation angle to sample migrant density in the air, but rather uses a variable sampling time that is dependent on the magnitude and timing of the initiation of nocturnal landbird migration.

## Methods

During the autumns of 2013 and 2014, I conducted bird surveys at 26 forested sites in Delaware, Maryland, and Virginia between August 15 and November 7 (Figure 1). Transect locations were chosen based on seasonal mean observed reflectivity values during fall 2008 & 2009 as determined by Buler and Dawson (2014) and were stratified in each of three distance bands (10-20 km, 20-50 km, 50-80 km) from the WSR-88D radars near Dover, Delaware (KDOX) and Wakefield, Virginia (KAKQ), in areas with observed high and low reflectivity values determined by (Buler and Dawson 2014). This stratification among distances from the radar was important to accurately assess the effective radar range (80 km). I used hardwood forest sites because they are the most abundant and consistent habitat type in the region and most migrants are forest-dwelling species. Birds were sampled along a transect during a 30-min period (a pace of 1 km per hour) from sunrise to four hours post-sunrise approximately every four days (four days = one sampling period). Species, number of individuals, perpendicular distance from transect, distance from observer, and height above ground were recorded for each detection. Height and distances were recorded in distance classes because there is much measurement error in estimating distances (Alldredge et al. 2007); 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m, 25-50 m, and >50 m within habitat. Flyovers and flythroughs were also recorded, but were not used in further analyses.

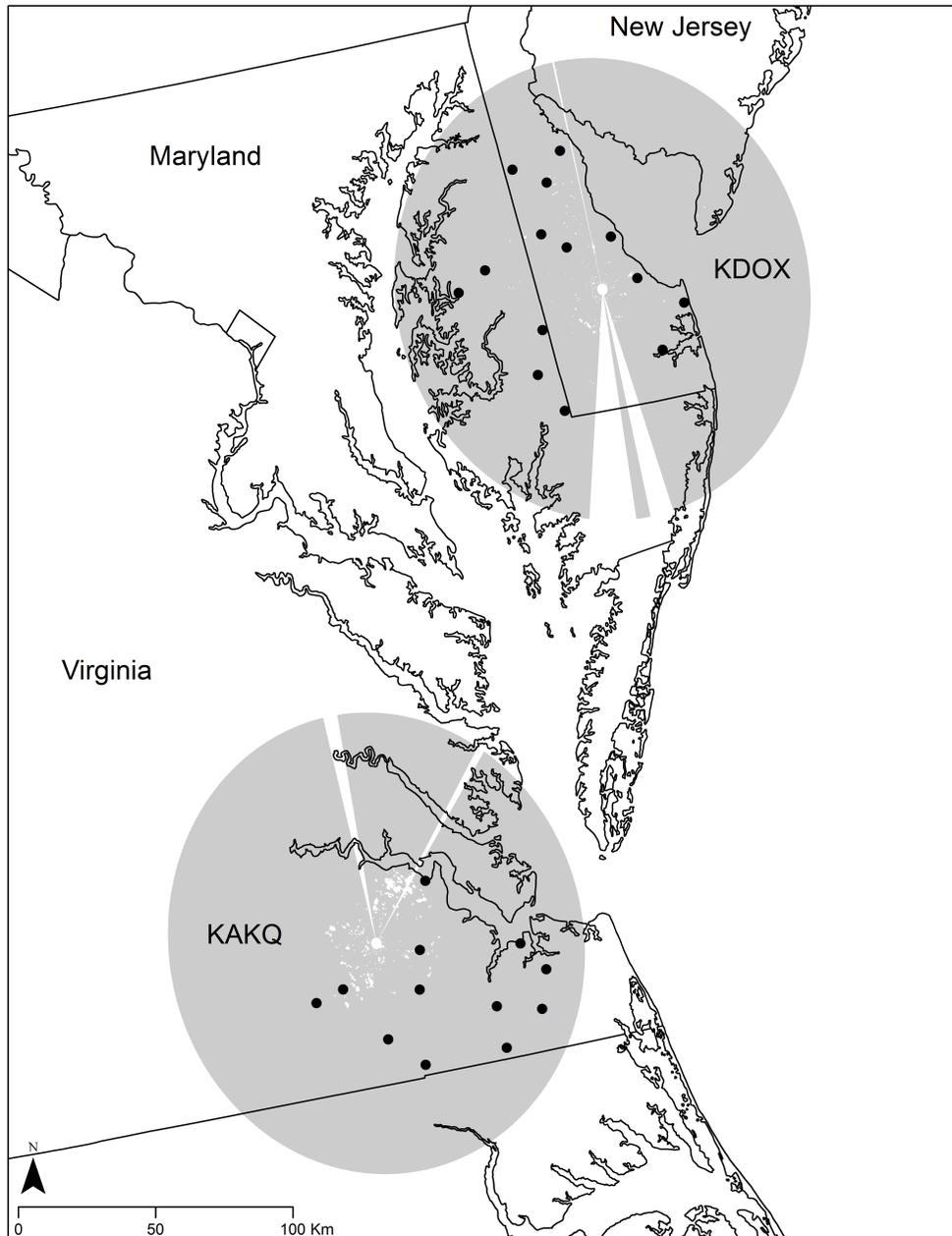


Figure 1 Locations of transect sites (dots) where I surveyed migratory landbirds and the names and locations of two WSR-88D radar stations and their associated 80 km radius coverage areas used in this study.

I estimated detection probabilities to derive daily migrant densities from the ground surveys within R (R Core Team 2012) using the “gdistsamp” function in the extension package “unmarked” (Fiske et al. 2011). Temperature, wind (Beaufort scale), sky measurements, and observer were incorporated as covariates. All covariates except for observer were scaled within R (R Core Team 2012) before analysis. I incorporated multiple covariates, individual covariates, and no covariates into both half-normal and hazard rate detection functions. To determine detection probabilities of nocturnal migrants (Classification of species in Table 1 and Table 2), I pooled species (Neotropical migrants, temperate migrants, and non-resident breeding species) to ensure adequate sample size. I used Akaike’s Information Criterion adjusted for small sample sizes (Hurvich and Tsai 1989) to rank models base on their ability to explain the data (Akaike 1992). I ran the top-ranked model through goodness of fit testing to ensure the chosen model predicted the data well. Then, I computed a mean visit density of nocturnally migrating birds (birds/ha/visit) for each transect, which I used for all analyses.

I quantified stopover densities from radar data similarly to Buler and Diehl (2009) and Buler and Dawson (2014). From the National Climatic Data Center archive, I downloaded Level-II radar data, collected at KDOX and KAKQ during autumn 2013 and 2014 (August 15 – November 7). WSR-88D radars transmit horizontally polarized electromagnetic radiation at a wavelength of ~10 cm (s-band) and a nominal peak power of 750 kW with a half-power beamwidth (3 dB) of 0.95° (Crum and Albery 1993). I used two data products produced by the radar: reflectivity,

which is a measure of radar echo strength in units of  $Z$  ( $\text{mm}^6 \text{m}^{-3}$ ) that is determined by the density and size of the targets in the sampled volume, and mean radial velocity, which is a measure of the mean target velocity (in knots) relative to the radar. Radar data from the  $0.5^\circ$  elevation angle were screened to identify nights contaminated with precipitation, sea breeze fronts, smoke, and anomalous beam propagation (Buler and Diehl 2009). Nights that were not contaminated were processed for biological target identification.

Biological targets (i.e., birds and insects) were distinguished by quantifying target airspeeds by vector-subtracting the wind velocity from the target ground velocity. Radar radial velocity data from the  $2.5^\circ$  elevation angle during the peak of nocturnal activity ( $\sim 3$  h after sunset) were used to determine target flight directions and airspeeds in conjunction with high-resolution data on winds aloft archived by the North American Regional Reanalysis (NARR) following Farnsworth et al. (2014). These high-resolution modeled wind data are available in three-hour composites across the United States at  $\sim 0.3$  degrees (or as fine as 32 km) resolution. I used these data to determine air speeds (u and v wind components) at nine geopotential heights ranging from 650-1000 mb within the 100-km range of each radar. Mean air speeds were then computed by weighting speeds by the relative density of biological targets at each height interval based on vertical profiles of reflectivity calculated using methods outlined by Buler and Diehl (2009). Radar scans with mean target air speeds greater than or equal to 5 m per s were considered bird dominated (Larkin 1991), (Gauthreaux and Belser 1998). Only bird-dominated nights were used in the analysis.

For all bird-dominated nights, I used reflectivity measures interpolated to sun elevation angles between  $1.5^\circ$  and  $10^\circ$  below the horizon following sunset at  $0.5^\circ$  intervals to determine the optimal sampling time for migrant land birds during the onset of nocturnal migration. Each  $1^\circ$  change in sun elevation is approximately a time span of four to five minutes.

Additionally, for each sampling night, I fit a logistic growth curve through a time series of mean radar reflectivity during the onset of nocturnal flight to determine the sun angle at the inflection point, the point of the curve of maximum growth rate (Figure 2). For all sampling nights, I interpolated reflectivity measures to sun elevation angles at the inflection point and  $\pm 1^\circ$  at  $0.5^\circ$  intervals surrounding the inflection point.

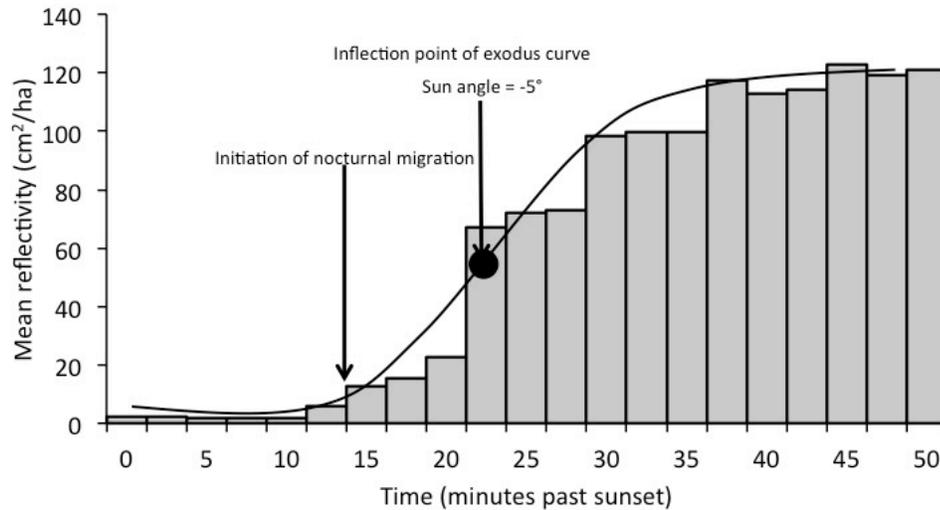


Figure 2 Time series of bird density aloft during nocturnal migratory flight exodus for an example night. A modeled logistic growth curve is drawn.

I processed the WSR-88D radar data using w2birddensity, which is part of the Warning Decision Support System – Integrated Information software package (WDSS-II), to correct reflectivity measures for several sources of measurement bias (see Buler and Dawson 2014) for each sun angle. I plotted the ground survey transects in a geographic information system (GIS) and built a 50 m buffer perpendicular to each transect, which corresponds to the effective detection distance for ground surveys. I georeferenced radar data to a static polar coordinate grid created for each radar (hereafter referred to as a basegrid) and identified areas where the radar beam was blocked (by topography, buildings, or other human infrastructure), limiting

coverage, using clutter maps developed by Buler and Dawson (2014). I then intersected the radar sample volumes (mean reflectivity is extracted from each sample volume) from the KDOX and KAKQ basegrids with the transect buffer. The intersection created polygons of various sizes (area in hectares), in which corrected reflectivity measures were extracted from each transect location. I then compared the corrected reflectivity measures at each sun elevation angle to the observed bird density on the ground.

### **Analysis**

I used Pearson correlation tests to assess the relationship between mean daily observed bird densities and mean reflectivity measures at each static sun angle (2.5° - 10° below the horizon at 0.5° degree intervals) for each transect. I also assessed the relationship between ground densities and sun angles relative to the inflection point (inflection point  $\pm 1^\circ$  below the horizon at 0.5° intervals) using the same correlation tests. To obtain 95% confidence intervals for correlation coefficients, I bootstrapped the correlations using the “boot” package (Canty and Ripley 2014) within R (R Core Team 2012). I then identified the sun angle that produced the strongest correlation with mean visit density for each transect (Buler et al. 2012).

Furthermore, I used data from 11 radars from Buler and Dawson (2014) and 7 radars analyzed in La Puma and Buler (2013) to assess and compare the distribution of the nightly sun angles at the inflection point of flight exodus curves to the static sun

elevation angle of 5.5° degrees below the horizon that Buler and Dawson (2014) used to map densities of landbirds on the ground.

## **Results**

I detected 983 migrants (n=167 surveys) in 2013 and 684 migrants (n=137 surveys) in 2014 during daily transect counts within the KDOX radar range (Table 1), and 603 migrants (n=121 surveys) in 2013 and 437 migrants (n=105 surveys) in 2014 during daily transect counts within the KAKQ radar range (Table 2).

Table 1 Complete list of bird species and species groups detected during fall 2013 and fall 2014 among 16 transect locations within range of KDOX. Migration status classifications (mi – transient, su – summer breeder, wi – winter resident, yr – year-round), total detections, and nocturnal migrant classification indicated by Yes (Y) or No (N) are also presented.

Common Name	Scientific Name	Migration Status	Nocturnal Migrant	Total Detections 2013	Total Detections 2014
Acadian Flycatcher	<i>Empidonax vireescens</i>	su	Y	104	76
Accipiter sp.	<i>Accipiter</i> sp.	yr	N	1	1
American Crow	<i>Corvus brachyrhynchos</i>	yr	N	67	70
American Goldfinch	<i>Spinus tristis</i>	yr	N	37	19
American Redstart	<i>Setophaga ruticilla</i>	su	Y	39	30
American Robin	<i>Turdus migratorius</i>	yr	N	444	753
American Woodcock	<i>Scolopax minor</i>	yr	Y	3	1
Baltimore Oriole	<i>Icterus galbula</i>	su	Y	0	7
Barn Owl	<i>Tyto alba</i>	yr	N	1	0
Barred Owl	<i>Strix varia</i>	yr	N	7	2
Belted Kingfisher	<i>Megasceryle alcyon</i>	yr	N	2	0
Bird sp.			N	309	92
Black Vulture	<i>Coragyps atratus</i>	yr	N	4	0
Black-and-white Warbler	<i>Mniotilta varia</i>	su	Y	49	15
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	mi	Y	74	40

Black-throated Green Warbler	Setophaga nigrescens	mi	Y	3	3
Blackbird sp.			N	33	0
Blackburnian Warbler	Setophaga fusca	mi	Y	1	1
Blackpoll Warbler	Setophaga striata	mi	Y	12	6
Blue Grosbeak	Passerina caerulea	su	Y	2	2
Blue Jay	Cyanocitta cristata	yr	N	354	412
Blue-gray Gnatcatcher	Poliophtila caerulea	su	Y	3	5
Blue-headed Vireo	Vireo solitarius	mi	Y	3	1
Blue-winged Warbler	Vermivora cyanoptera	su	Y	1	0
Brown Creeper	Certhia americana	wi	Y	49	20
Brown Thrasher	Toxostoma rufum	yr	Y	1	3
Brown-headed Cowbird	Molothrus ater	yr	N	13	2
Canada Goose	Branta canadensis	yr	N	0	46
Canada Warbler	Cardellina canadensis	mi	Y	2	0
Cape May Warbler	Setophaga tigrina	mi	Y	0	4
Carolina Chickadee	Poecile carolinensis	yr	N	695	508
Carolina Wren	Thryothorus ludovicianus	yr	N	491	360
Catharus Thrush	Catharus sp.	mi	Y	1	4
Cedar Waxwing	Bombycilla cedrorum	yr	N	47	33
Chestnut-sided Warbler	Setophaga pensylvanica	mi	Y	4	4
Chipping Sparrow	Spizella passerina	su	Y	3	2
Common Grackle	Quiscalus quiscula	yr	N	2	250
Common Yellowthroat	Geothlypis trichas	su	Y	0	1
Cooper's Hawk	Accipiter cooperii	yr	N	1	2
Dark-eyed Junco	Junco hyemalis	wi	Y	2	23
Downy Woodpecker	Picoides pubescens	yr	N	215	255

Eastern Bluebird	<i>Sialia sialis</i>	yr	N	3	4
Eastern Phoebe	<i>Sayornis phoebe</i>	su	Y	6	2
Eastern Screech-Owl	<i>Megascops asio</i>	yr	N	1	0
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	yr	Y	11	17
Eastern Wood-Pewee	<i>Contopus virens</i>	su	Y	160	123
Empidonax sp.	<i>Empidonax sp.</i>		Y	9	2
Field Sparrow	<i>Spizella pusilla</i>	su	N	1	0
Fox Sparrow	<i>Passerella iliaca</i>	wi	Y	1	0
Golden-crowned Kinglet	<i>Regulus satrapa</i>	wi	Y	332	242
Gray Catbird	<i>Dumetella carolinensis</i>	su	Y	13	10
Gray-cheeked Thrush	<i>Catharus minimus</i>	mi	Y	4	4
Great Blue Heron	<i>Ardea herodias</i>	yr	N	1	3
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	su	Y	48	40
Great Horned Owl	<i>Bubo virginianus</i>	yr	N	1	3
Hairy Woodpecker	<i>Picoides villosus</i>	yr	N	130	33
Hermit Thrush	<i>Catharus guttatus</i>	wi	Y	67	103
House Wren	<i>Troglodytes aedon</i>	su	Y	5	0
Indigo Bunting	<i>Passerina cyanea</i>	su	Y	5	5
Kinglet sp.	<i>Regulus sp.</i>	wi	Y	1	0
Magnolia Warbler	<i>Setophaga magnolia</i>	mi	Y	12	1
Mourning Dove	<i>Zenaidura macroura</i>	yr	N	16	23
Northern Cardinal	<i>Cardinalis cardinalis</i>	yr	N	321	171
Northern Flicker	<i>Colaptes auratus</i>	wi	Y	159	206
Northern Parula	<i>Setophaga americana</i>	mi	Y	9	3
Oriole sp.	<i>Icterus sp.</i>	su	Y	1	0
Ovenbird	<i>Seiurus aurocapillus</i>	su	Y	35	22



Warbler sp.				Y	223	213
Warbling Vireo	Vireo gilvus	su		Y	2	0
White-breasted Nuthatch	Sitta carolinensis	yr		N	70	98
White-eyed Vireo	Vireo griseus	su		Y	17	22
White-throated Sparrow	Zonotrichia albicollis	wi		Y	22	43
Wild Turkey	Meleagris gallopavo	yr		N	3	3
Winter Wren	Troglodytes hiemalis	wi		Y	40	28
Wood Duck	Aix sponsa	yr		N	0	1
Wood Thrush	Hylocichla mustelina	su		Y	54	59
Woodpecker sp.				N	38	25
Worm-eating Warbler	Helmitheros vermivorus	su		Y	15	4
Wren sp.				N	0	1
Yellow-bellied Flycatcher	Empidonax flaviventris	mi		Y	0	1
Yellow-bellied Sapsucker	Sphyrapicus varius	wi		Y	5	4
Yellow-billed Cuckoo	Coccyzus americanus	su		Y	31	18
Yellow-rumped Warbler	Setophaga coronata	wi		Y	215	103
Yellow-throated Vireo	Vireo flavifrons	su		Y	3	1
Yellow-throated Warbler	Setophaga coronata	su		Y	2	0

Table 2 Complete list of bird species and species groups detected during fall 2013 and fall 2014 among 16 transect locations within range of KAKQ. Migration status classifications (mi – transient, su – summer breeder, wi – winter resident, yr – year-round), total detections, and nocturnal migrant classification indicated by Yes (Y) or No (N) are also presented.

Common Name	Scientific Name	Migratory Status	Nocturnal Migrant	Total Detections 2013	Total Detections 2014
Accipiter sp.	Accipiter sp.	yr	N	1	1
Acadian Flycatcher	Empidonax vireescens	su	Y	34	60
American Crow	Corvus brachyrhynchos	yr	N	247	137
American Goldfinch	Spinus tristis	yr	N	43	5
American Redstart	Setophaga ruticilla	su	Y	49	39
American Robin	Turdus migratorius	yr	N	333	122
American Woodcock	Scolopax minor	yr	Y	0	2
Bald Eagle	Haliaeetus leucocephalus	yr	N	1	2
Baltimore Oriole	Icterus galbula	su	Y	0	2
Black-and-white Warbler	Mniotilta varia	su	Y	13	22
Black-billed Cuckoo	Coccyzus erythrophthalmus	mi	Y	3	0
Bay-breasted Warbler	Setophaga castanea	mi	Y	2	0
Barred Owl	Strix varia	yr	N	11	15
Belted Kingfisher	Megasceryle alcyon	yr	N	3	0
Blue-gray Gnatcatcher	Poliptila caerulea	su	Y	0	4
Brown-headed Cowbird	Molothrus ater	yr	N	1	0
Brown-headed Nuthatch	Sitta pusilla		N	0	13
Blue-headed Vireo	Vireo solitarius	mi	Y	3	6
Blackburnian Warbler	Setophaga fusca	mi	Y	0	1

Blue Grosbeak	Passerina caerulea	su	Y	2	6
Blue Jay	Cyanocitta cristata	yr	N	157	102
Blackpoll Warbler	Setophaga striata	mi	Y	16	0
Brown Creeper	Certhia americana	wi	Y	3	6
Brown Thrasher	Toxostoma rufum	yr	Y	12	12
Black-throated Blue Warbler	Setophaga caeruleascens	mi	Y	11	24
Carolina Chickadee	Poecile carolinensis	yr	N	369	301
Canada Goose	Branta canadensis	yr	N	5	15
Carolina Wren	Thryothorus ludovicianus	yr	N	554	348
Cedar Waxwing	Bombycilla cedrorum	yr	N	4	0
Chipping Sparrow	Spizella passerina	su	Y	2	0
Chimney Swift	Chaetura pelagica	su	N	5	1
Common Grackle	Quiscalus quiscula	yr	N	164	214
Common Yellowthroat	Geothlypis trichas	su	Y	5	5
Chestnut-sided Warbler	Setophaga pensylvanica	mi	Y	1	2
Downy Woodpecker	Picoides pubescens	yr	N	95	129
Eastern Bluebird	Sialia sialis	yr	N	6	11
Eastern Phoebe	Sayornis phoebe	su	Y	10	4
Eastern Screech-Owl	Megascops asio	yr	N	2	4
Eastern Towhee	Pipilo erythrophthalmus	yr	Y	57	13
Eastern Wood-Pewee	Contopus virens	su	Y	38	46
Empidonax sp.	Empidonax sp.		Y	6	0
Tufted Titmouse	Baeolophus bicolor	yr	N	295	297
European Starling	Sturnus vulgaris	yr	N	33	1
Fish Crow	Corvus ossifragus	yr	N	1	1
Field Sparrow	Spizella pusilla	su	N	0	7

Fox Sparrow	Passerella iliaca	wi	Y	0	3
Great Blue Heron	Ardea herodias	yr	N	2	2
Great Crested Flycatcher	Myiarchus crinitus	su	Y	13	14
Golden-crowned Kinglet	Regulus satrapa	wi	Y	179	92
Gray-cheeked Thrush	Catharus minimus	mi	Y	1	2
Great Horned Owl	Bubo virginianus	yr	N	3	0
Gray Catbird	Dumetella carolinensis	su	Y	38	13
Hairy Woodpecker	Picoides villosus	yr	N	27	22
Hermit Thrush	Catharus guttatus	wi	Y	59	64
House Finch	Haemorhous mexicanus	yr	N	0	1
Hooded Warbler	Setophaga citrina	su	Y	23	23
Indigo Bunting	Passerina cyanea	su	Y	2	1
Killdeer	Charadrius vociferus	yr	N	2	0
Magnolia Warbler	Setophaga magnolia	mi	Y	3	1
Mourning Dove	Zenaida macroura	yr	N	59	44
Yellow-rumped Warbler	Setophaga coronata	wi	Y	82	28
Northern Bobwhite	Colinus virginianus	yr	N	1	2
Northern Cardinal	Cardinalis cardinalis	yr	N	499	352
Northern Mockingbird	Mimus polyglottos	yr	N	10	1
Northern Parula	Setophaga americana	su	Y	13	9
Northern Waterthrush	Parkesia noveboracensis	mi	Y	4	3
Ovenbird	Seiurus aurocapillus	su	Y	6	9
Pine Warbler	Setophaga pinus	yr	Y	137	122
Pileated Woodpecker	Dryocopus pileatus	yr	N	118	145
Prothonotary Warbler	Protonotaria citrea	su	Y	7	2
Rose-breasted Grosbeak	Pheucticus ludovicianus	mi	Y	0	3

Red-breasted Nuthatch	<i>Sitta canadensis</i>	wi	Y	0	2
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	yr	N	161	180
Ruby-crowned Kinglet	<i>Regulus calendula</i>	wi	Y	14	13
Red-eyed Vireo	<i>Vireo olivaceus</i>	su	Y	20	42
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	yr	N	21	15
Red-shouldered Hawk	<i>Buteo lineatus</i>	yr	N	31	14
Red-tailed Hawk	<i>Buteo jamaicensis</i>	yr	N	1	6
Ruby-throated Hummingbird	<i>Archilochus colibris</i>	su	N	4	0
Scarlet Tanager	<i>Piranga olivacea</i>	su	Y	0	6
Song Sparrow	<i>Melospiza melodia</i>	yr	N	3	1
Summer Tanager	<i>Piranga rubra</i>	su	Y	10	17
Swamp Sparrow	<i>Melospiza georgiana</i>	wi	Y	1	0
Swainson's Thrush	<i>Catharus ustulatus</i>	mi	Y	2	0
Swainson's Warbler	<i>Limnolophus swainsonii</i>	su	Y	1	0
Turkey Vulture	<i>Cathartes aura</i>	yr	N	1	0
Blackbird sp.			N	0	2
Buteo sp.	<i>Buteo sp.</i>		N	1	0
Hawk sp.			N	4	0
Hummingbird sp.		mi	N	1	0
Icterid sp.	<i>Icterus sp.</i>	su	N	100	0
Bird sp.			N	218	32
Thrush sp.			Y	2	0
Vireo sp.	<i>Vireo sp.</i>		Y	0	2
Warbler sp.			Y	49	72
Woodpecker sp.			N	61	24
Veery	<i>Catharus fuscescens</i>	mi	Y	0	5

Warbling Vireo	Vireo gilvus	su	Y	1	0
White-breasted Nuthatch	Sitta carolinensis	yr	N	61	88
White-eyed Vireo	Vireo griseus	su	Y	38	51
Worm-eating Warbler	Helmitheros vermivorus	su	Y	1	5
Wild Turkey	Meleagris gallopavo	yr	N	14	20
Winter Wren	Troglodytes hiemalis	wi	Y	27	20
Wood Duck	Aix sponsa	yr	N	0	1
Wood Thrush	Hylocichla mustelina	su	Y	4	9
White-throated Sparrow	Zonotrichia albicollis	wi	Y	28	17
Yellow-breasted Chat	Icteria virens	su	Y	1	2
Yellow-billed Cuckoo	Coccyzus americanus	su	Y	9	24
Yellow-bellied Flycatcher	Empidonax flaviventris	mi	Y	1	0
Yellow-bellied Sapsucker	Sphyrapicus varius	wi	Y	10	6
Northern Flicker	Colaptes auratus	wi	Y	137	102
Yellow-throated Vireo	Vireo flavifrons	su	Y	24	24

Detection-corrected estimates of ground densities ranged from 2.02 to 7.11 (mean =  $3.14 \pm 0.41$ ) birds per hectare per visit in 2013 and 1.17 to 5.37 (mean =  $3.08 \pm 0.28$ ) birds per hectare per visit in 2014 within the KDOX radar range, and from 1.23 to 3.83 (mean =  $2.40 \pm 0.26$ ) birds per hectare per visit in 2013 and 1.26 to 2.92 (mean =  $2.04 \pm 0.17$ ) birds per hectare per visit in 2014 within the KAKQ radar range.

I analyzed the onset of evening flights from the KDOX radar for 12 days during fall 2013 and 10 days during fall 2014, and from the KAKQ radar for 15 days during fall 2013 and 7 days during fall 2014.

The sun elevation angle at which bird density aloft was most closely-correlated to bird density at the ground was -1.5 at KAKQ in 2013 and -6.0 in 2014 (Table 3). The optimal sun elevation angle was different at KDOX, which we calculated to be -3.0 in 2013 and -6.5 in 2014. When pooled across radars, the strongest correlated sun elevation angle was -2.0 ( $r=0.45$ ) in 2013 and -6.5 ( $r=0.69$ ) in 2014.

Table 3 Sun elevation angle when the strongest correlation between ground data and mean radar reflectivity occurred by radar and among angles ranging from  $-1.5^{\circ}$  to  $-10^{\circ}$  at KAKQ and KDOX in fall 2013 and 2014. Upper and lower CI represent 95% confidence intervals for each correlation coefficient presented.

Radar	Year	Sun Angle	<i>r</i>	Lower CI	Upper CI
KAKQ	2013	-1.5	0.36	-0.22	0.83
	2014	-6.0	0.57	-0.13	0.88
KDOX	2013	-3.0	0.44	0.00	0.89
	2014	-6.5	0.63	0.11	0.89
Pooled	2013	-2.0	0.45	0.01	0.76
	2014	-6.5	0.69	0.36	0.89

Inflection points derived from daily exodus curves (hereafter “peak exodus”) varied within years and among radars, ranging from sun angles of  $3.06^{\circ}$  to  $8.12^{\circ}$  (mean =  $5.38 \pm 0.47$ ) below the horizon in 2013 and from  $3.28^{\circ}$  to  $10.16^{\circ}$  (mean =  $6.41 \pm 0.65$ ) in 2014 for KDOX. For KAKQ, the sun angle at peak exodus of the curve ranged from  $3.01^{\circ}$  to  $10.03^{\circ}$  (mean =  $5.45 \pm 0.5$ ) in 2013 and from  $3.05^{\circ}$  to  $8.6^{\circ}$  (mean =  $5.24 \pm 0.7$ ) in 2014.

The sun elevation angle relative to peak exodus that had the strongest correlation between air and ground densities of birds was  $0.5^{\circ}$  at KAKQ in 2013 and  $-1.0^{\circ}$  in 2014 (Table 4). The optimal sun elevation angle in relation to peak exodus was different at KDOX, which I calculated to be  $-1.0^{\circ}$  in 2013 and  $0.5^{\circ}$  in 2014 (Table 4). When pooled across radars, the optimal sun elevation angle in relation to peak exodus

determined by the Pearson correlation test was  $-0.5^\circ$  ( $r=0.31$ ) in 2013 and  $0.5^\circ$  ( $r=0.67$ ) in 2014 (Table 4). Furthermore, peak exodus at a given radar and year increased as the autumn season progressed (Figure 3).

Table 4 Sun elevation angle relative to inflection point ( $0^\circ$ ) of exodus growth curve for each night when the strongest correlation between ground data and mean radar reflectivity occurred at KAKQ and KDOX in fall 2013 and 2014. Relative sun angles range within  $1^\circ$  of the inflection point angle.

Radar	Year	Sun Angle	<i>r</i>	Lower CI	Upper CI
KAKQ	2013	0.5	-0.33	-0.81	0.28
	2014	-1.0	0.37	-0.46	0.85
KDOX	2013	-1.0	0.38	-0.31	0.98
	2014	0.5	0.60	0.01	0.87
Pooled	2013	-0.5	0.31	-0.25	0.83
	2014	0.5	0.67	0.37	0.84

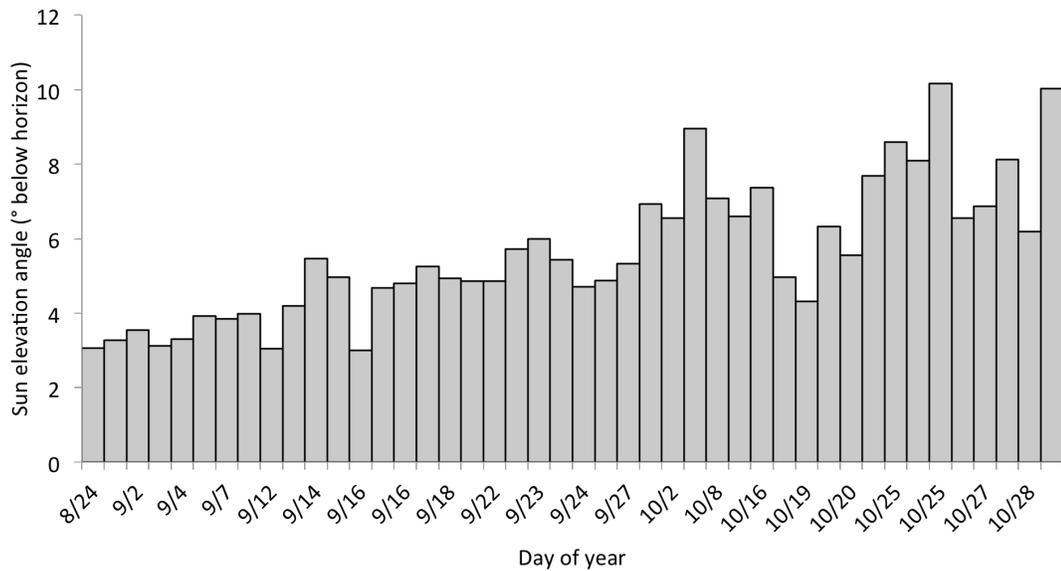


Figure 3 Sun elevation angle at the inflection point of flight exodus for individual sampling nights during autumn 2013 and 2014 at KDOX and KAKQ. Note some dates have two measures; one from each radar.

When pooled across radars, the bootstrapped mean Pearson correlation of seasonal mean radar at the target sun elevation angle in relation to peak exodus to ground bird densities was similar to that of radar data sampled at the nearest static sun elevation angle across days and radar (5.5°) (Figure 4). The mean correlation also varied little among sun angles. Sampling radar data at the time of peak exodus for a given night and radar produced more consistent stopover maps of migrant distributions for individual nights when compared to maps of radar data sampled at the static 5.5° below horizon (Figure 5).

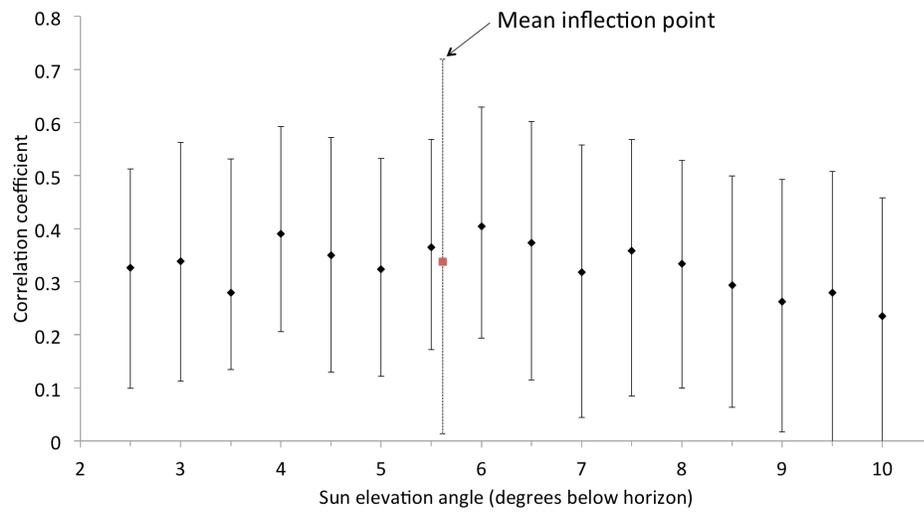


Figure 4 Pearson correlations between seasonal average migrant density at the ground and aloft at KAKQ and KDOX sampled at a series of sun angles and at the mean daily inflection point sun angle of exodus among days. Error bars are bootstrapped 95% CI.

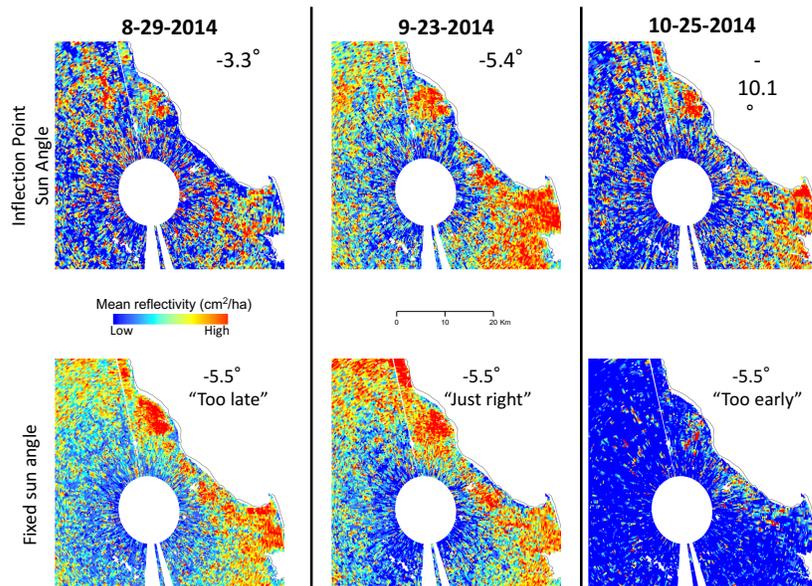


Figure 5 Mapped bird stopover density (mean reflectivity) on three nights in fall 2013 sampled at either the daily inflection point of exodus (top) or a fixed sun angle of  $-5.5^\circ$  (bottom) at the KDOX WSR-88D radar station.

This was also apparent at the radar scale when I compared the range of peak exodus determined for individual sampling nights for 18 radars in the eastern United States (Figure 6). Latitudinal differences in timing of flight indicated that some radars were always sampled too early in the flight exodus when using the  $5.5^\circ$  sun angle as in Buler and Dawson (2014).

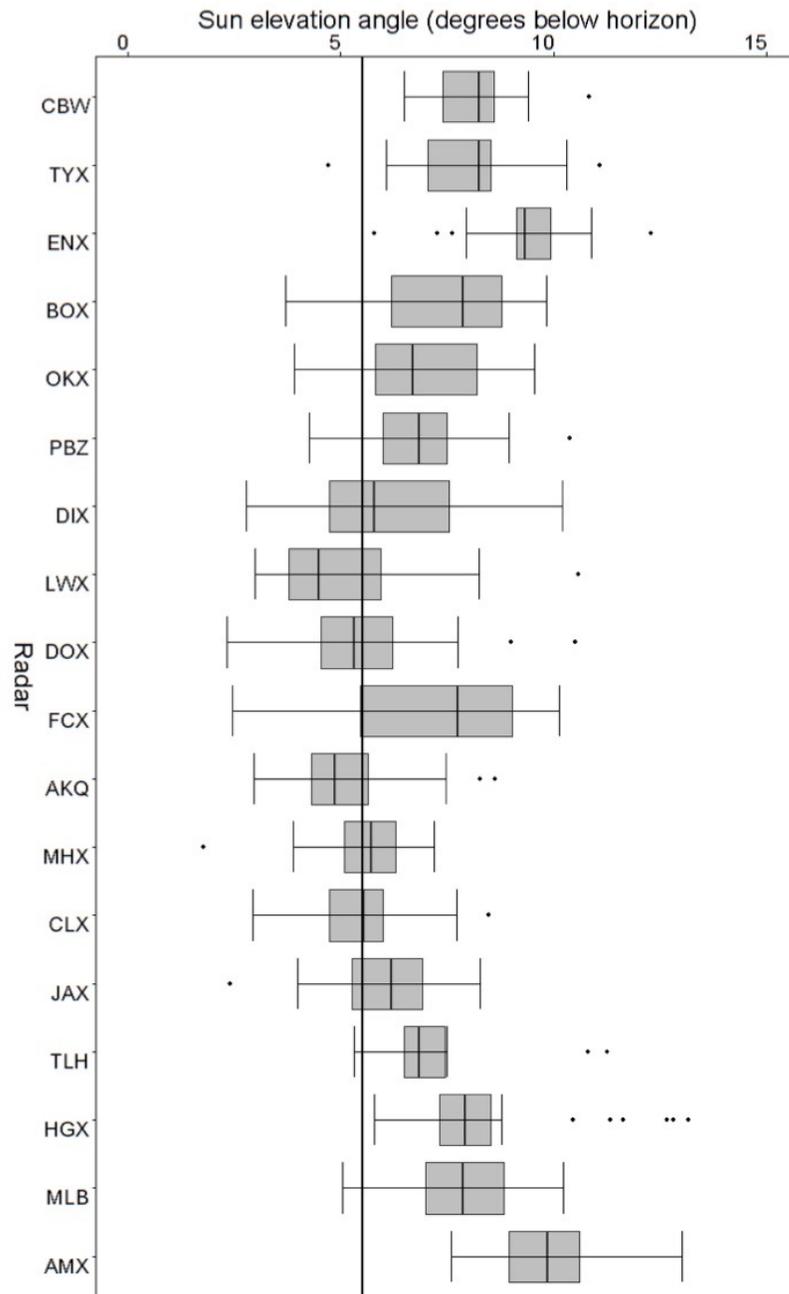


Figure 6 Boxplots of the distribution of the nightly sun angles at the inflection point of flight exodus curves for autumn sampling nights at 18 radar stations in the eastern United States (Table 5). Radars decrease in latitude from top to bottom. Vertical line denotes the sun angle of  $5.5^\circ$  below horizon.

Table 5 Unique identifier and locations for 18 WSR-88D radars.

Radar Identifier	Location
CBW	Caribou, Maine
TYX	Montague, New York
ENX	Albany, New York
BOX	Boston, Massachusetts
OKX	Upton, New York
PBZ	Pittsburgh, Pennsylvania
DIX	Mt. Holly, New Jersey
LWX	Sterling, Virginia
DOX	Dover, Delaware
FCX	Blacksburg, Virginia
AKQ	Wakefield, VA
MHX	Newport/Morehead, North Carolina
CLX	Charleston, South Carolina
JAX	Jacksonville, Florida
TLH	Tallahassee, Florida
HGX	Houston/Galveston, Texas
MLB	Melbourne, Florida
AMX	Miami, Florida

### Discussion

I found that timing of peak flight exodus of migrating birds varies night-to-night within and among radars and migrating landbirds appear to leave at different times each night, ranging from roughly 24 to 80 min after sunset. This range of sampling times may be due to time of year, the species composition of migrating landbirds, and individual departure decisions (Akesson et al. 1996). Age and condition of individuals may also provide insight as to why I saw this range of exodus timings. For example, (Smolinsky et al. 2013) found that the majority of radio-tagged Swainson's Thrushes leaving after astronomical twilight were lean, hatch-year birds.

On average, I found that birds left slightly earlier in 2013 than in 2014 when pooled across radars. This is problematic when choosing an optimal static sampling time because birds in the airspace can double every couple of minutes (Hebrard 1971).

There are several biases that may influence the relationship between mean radar reflectivity and the density of landbirds on the ground, which may result in confounding relationships, including the difference in sampling days between radar and ground data, the influence of sun angle and weather conditions on departure timings of migratory landbirds, and variable stopover length.

Buler and Diehl (2009) found differences in slopes of the relationship between ground bird densities and radar reflectivity among migration seasons and radars. These differences may be due to the way weather surveillance radars quantify echoes caused by migrating birds and the spatial variation in sun elevation. Sampling error from the WSR-88D can occur because of the coarse sampling rate (one volume scan every 10 min) and because the data collection is not synchronized with the onset of nocturnal migration, which can result in drastic differences in the magnitude of reflectivities between radars (Buler and Diehl 2009).

Stopover length of migratory landbirds is extremely variable and depends on how quickly birds can refuel (Moore and Kerlinger 1987), (Lindstrom and Alerstam 1992). Because I sampled sites approximately every four days, I may not have captured complete turnover since stopover can range from hours (Moore and Aborn 1996) to many days (Seewagen et al. 2010). Ground surveys reflect daily bird use rather than the number of passage migrants at a site. Furthermore, birds that were

counted on the ground during surveys may not have left the following night and may have stayed longer than four days or moved on to a different food source within the same patch of habitat, but not within the effective detection distance of the observer. Thus, the relationship between mean radar reflectivity and mean daily bird density on the ground can be confounded if stopover length varies among sites.

When considering the potential biases when comparing radar data to ground data, fitting daily exodus curves to the radar data and using the mean reflectivity at peak exodus should eliminate most, if not all of the biases. Fitting daily exodus curves at each radar allows us to control for sampling differences among radars and for the differences in exodus timings between nights and throughout the season. Although fitting daily exodus curves may not directly aid in fixing the sample days bias, I think it gives us the most accurate day-to-day snapshot of birds leaving their stopover sites.

Sampling radar at the sun angle of peak exodus for each day provided a consistent moderate to strong correlation between ground data and mean radar reflectivity and this approach is likely robust to broad spatio-temporal changes in the timing of exodus that would not be accounted for by using the same sun angle among sampling days. When using WSR-88D for mapping stopover use of migratory landbirds and conservation planning, researchers need to take the variability in exodus timing throughout the season and between radars into consideration. By using a dynamic sampling time at the point of peak exodus, I captured the variability within and among radars and this should provide the most accurate and precise stopover maps for conservation use.

## Chapter 2

# DETERMING RELATIVE STOPOVER DURATION MEASURES OF NOCTURNAL MIGRANT LANDBIRDS BY INTEGRATING GROUND SURVEYS AND WEATHER SURVEILLANCE RADAR

### Introduction

Migrating landbirds spend more time at stopover locations than in migratory flight (Hedenstrom and Alerstam 1997). Stopover sites provide the necessary fuel and/or a place to rest before continuing migratory flight (McWilliams et al. 2004). Duration of stopover can range from hours (Moore and Aborn 1996) to many days (Seewagen et al. 2010) and depends in part on how quickly an individual can replenish fuel for the next period of flight (Moore and Kerlinger 1987). Ideal stopover locations are free of predators and competitors, and contain abundant energy resources, but these areas are scarce and distributed unevenly across the landscape (Newton 2010). Most locations are not ideal, however, and migratory species frequently encounter competition with and among species for resources (Moore et al. 2005).

Quantifying the duration of time that migratory landbirds spend at stopover sites can provide insight into migratory behavior, including the role of stopover in serving the metabolic needs of migrant landbirds, and determining which sites contribute most towards a successful migration. Moreover, if one can pinpoint which stopover sites increase survivorship best by classifying them based on their ecological function (Mehlman et al. 2005), conservation decisions will become easier. The ecological function of stopover spans a spectrum from 1) “fire escape” sites that offer

a temporary place for migrants to rest without access to food resources during dire situations, 2) “convenience store” sites that offer a moderately safe place to rest with moderate food resources to allow some or prolonged refueling, and 3) “full-service hotel” sites that offer a safe place with plentiful food resources for quick refueling. Fire escapes are generally small, isolated patches of habitat surrounded by unsuitable habitat, are coastal, have very little food, and function as a rest stop. Examples of fire escapes include barrier islands and, in certain situations, oil rigs and ships in large bodies of water, all of which serve the sole purpose of survival. On the contrary, full service hotels (i.e., extensive tracts of forest) have abundant food and high forest cover, allowing birds to refuel safely and efficiently. In between fire escapes and full service hotels, convenience stores have moderate amounts of food and forest cover, giving birds the opportunity to refuel slowly. Due to a high amount of fragmentation and development in the eastern US, convenience stores, which may include city parks, small forest patches, or woodlots, may be the most common of the functional types.

In addition to collecting data on food availability, measuring the mean stopover duration of individual migrants over the course of a season can help determine a site’s general functional type.

There are different methods to determine stopover duration, but the traditional and most-used approach is mark-recapture (Cherry 1982). Determining stopover duration through traditional mark-recapture methods via mist-netting requires intense sampling effort and thus is usually only done at a few sites at a time (Cherry 1982), (Lyons and Haig 1995), (Morris et al. 1996). O’Neal et al. (2012) proposed an

approach to estimate stopover duration for waterfowl (i.e., days per duck) by dividing the total number of ducks counted from frequent aerial surveys (i.e., how many total days of stopover use by ducks) with radar measures of the nightly density of duck emigrants leaving a site over the course of a migration season (i.e., total number of ducks that used the site). A similar approach combining radar data and ground surveys of migrants could be used for more-feasibly determining relative stopover duration of landbirds across multiple sites over a broad geographic extent. This would aid in recognizing stopover functional types and their composition on the landscape, which is important for identifying regions with minimal stopover habitat, where fire escapes may be absent, or where consistently used stopover sites may be lost (Mehlman et al. 2005).

My first objective was to implement an analogous approach of O'Neal et al. (2012) to determine the relative stopover duration of migratory landbirds at 27 stopover sites in the mid-Atlantic (Delaware, Maryland, and Virginia) and 18 stopover sites along the Gulf Coast (Alabama and Louisiana). Subsequently, I used stopover duration estimates with three other factors influencing how migrants either rested or refueled to assign each site to the functional stopover framework developed by Mehlman et al. (2005). This analysis could help empirically validate the existence of different functional types within the framework. I hypothesized that stopover duration would be different between sites and would follow a bell-shaped curve with regard to the coast, where stopover duration is short at coastal sites, increases at sites farther from the coast, and then becomes shorter again at sites that are farthest inland (Figure

7). Additionally, I hypothesized that locations with minimal food and low forest cover would have low stopover duration; locations with moderate amounts of food and low to modest amounts of forest cover would have high stopover duration; and that locations with high amounts of food and forest cover would have moderate stopover duration.

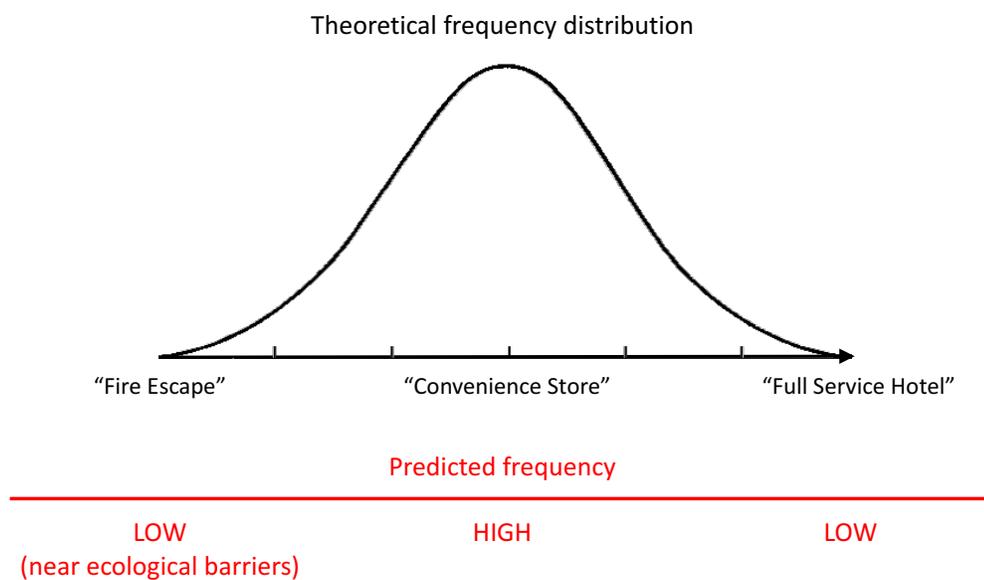


Figure 7 Theoretical frequency distribution of stopover duration with respect to fire escapes, convenience stores, and full service hotels in the functional framework described by Mehlman et al. (2005).

## **Methods**

The study area was composed of 45 sites located in the mid-Atlantic and Gulf of Mexico coasts (Figure 8). Within the mid-Atlantic, I chose transect locations based on seasonal mean observed reflectivity values during fall 2008 & 2009 as determined by Buler and Dawson (2014). Twenty-seven of the sites were located throughout Delaware, Maryland, and Virginia in hardwood, pine, and mixed forests and within 80 km of the weather surveillance radars at Dover, Delaware (KDOX) and Wakefield, Virginia (KAKQ). Fifteen survey sites were located within the range of KDOX and twelve surveys sites were located within the range of KAKQ. Additionally, 18 sites were located in Alabama and Louisiana within 80 km of the Mobile, Alabama (KMOB) and Slidell, Louisiana (KLIX) weather surveillance radars. Gulf coast sites were from a previously published study that followed identical protocols for ground survey data collection (Buler et al. 2007).

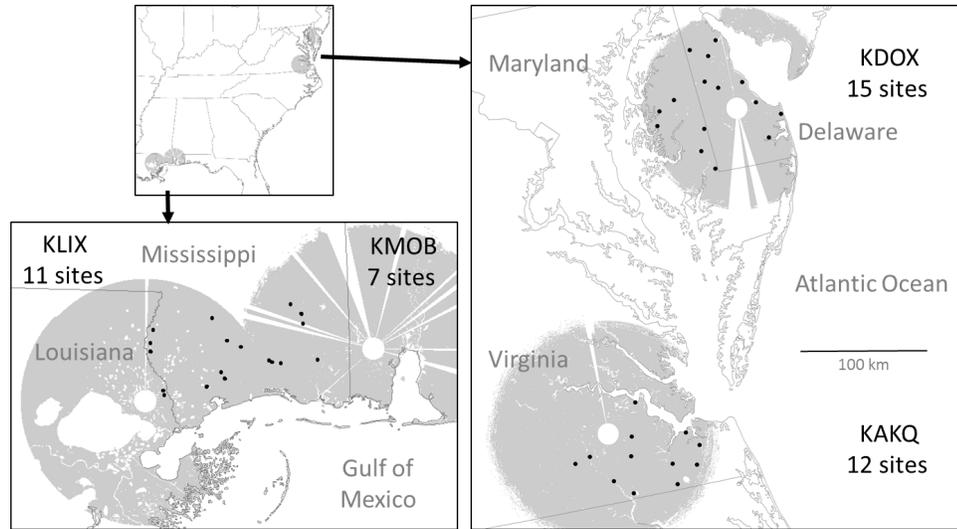


Figure 8 Locations of 45 hardwood forest transect survey sites where bird surveys were conducted for determination of stopover duration and the coverage areas (shaded in grey) and names of 4 associated NEXRAD sites.

I surveyed birds along a 500 m long transect during a 30-min period (at a pace of 1 km per hour) from sunrise to four hours post-sunrise approximately every four days (four days = one sampling period) from August 15<sup>th</sup> to November 7<sup>th</sup> in 2013 and 2014 in the mid-Atlantic and recorded species, number of individuals, perpendicular distance from transect, distance from observer, and height above ground for each detection. Bird surveys were conducted from August 15<sup>th</sup> to November 7<sup>th</sup> in 2002 and 2003 along the Gulf of Mexico Coast. Additionally, I recorded height and distances in distance classes because there is much measurement error in estimating distances (Alldredge et al. 2007); 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m, 25-50 m, and >50 m within habitat. I also recorded temperature, wind (Beaufort scale), and sky measurements.

I estimated detection probabilities to derive daily migrant densities from the ground surveys within R (R Core Team 2012) using the extension package “unmarked” (Fiske et al. 2011). Temperature, wind (Beaufort Scale) and sky measurements, and observer were incorporated as covariates. All covariates except for observer were scaled within R (R Core Team 2012) before analysis. To determine detection probabilities of nocturnal migrants, I pooled species (Neotropical migrants, temperate migrants, and non-resident breeding species) to ensure adequate sample size. Using the detection probabilities, I computed a mean visit density of nocturnally migrating birds (birds/ha/visit) for each transect, which I used for all analyses.

I quantified stopover densities from radar data using methods similar to Buler and Diehl (2009) and Buler and Dawson (2014). From the National Climatic Data Center archive, I downloaded Level-II WSR-88D radar data, collected at KDOX and KAKQ during autumn 2013 and 2014 (August 15 – November 7) and KLIX and KMOB during autumn 2002 and 2003 (August 15 – November 7). WSR-88D radars transmit horizontally polarized electromagnetic radiation at a wavelength of ~10 cm (s-band) and a nominal peak power of 750 kW with a half-power beamwidth (3 dB) of 0.95° (Crum and Albery 1993). I used two data products recorded by the radar: reflectivity, which is a measure of radar echo strength in units of  $Z$  ( $\text{mm}^6 \text{m}^{-3}$ ) that is determined by the density and size of the targets in the sampled volume, and mean radial velocity, which is a measure of the mean target velocity (in knots) relative to the radar. Radar data from the 0.5° elevation angle were screened to identify nights contaminated with precipitation, sea breeze fronts, smoke, and anomalous beam

propagation (Buler and Diehl 2009). Nights that were not contaminated were processed for biological target identification.

Biological targets (i.e., birds and insects) were distinguished by quantifying target airspeeds by vector-subtracting the wind velocity from the target ground velocity. Radar radial velocity data from the 3.5° elevation angle during the peak of nocturnal activity (~3 h after sunset) were used to determine target flight directions and airspeeds in conjunction with high-resolution data on winds aloft archived by the North American Regional Reanalysis (NARR) following Farnsworth et al. (2014). These high-resolution modeled wind data are available in three-hour composites across the United States at ~0.3 degrees (or as fine as 32 km) resolution. I used these data to determine air speeds (u and v wind components) at nine geopotential heights ranging from 650-1000 mb within the 100-km range of each radar. Mean air speeds were then computed by weighting speeds by the relative density of biological targets at each height interval based on vertical profiles of reflectivity calculated using methods outlined by Buler and Diehl (2009). Radar scans with mean target air speeds greater than or equal to 5 m per s were considered bird dominated (Larkin 1991), (Gauthreaux Jr. and Belser 1998). Only bird-dominated nights were used in the analysis.

For all bird-dominated nights, I fit a spline function to the time series of mean radar reflectivity during the onset of nocturnal flight to determine the sun angle at the point of the maximum rate of increase in reflectivity (i.e. peak exodus). For all sampling nights, I interpolated reflectivity measures among observed samples to the sun angle at the point of peak exodus for each night. I processed the WSR-88D radar

data using w2birddensity, which is part of the Warning Decision Support System – Integrated Information software package (WDSS-II), to correct reflectivity measures for several sources of measurement bias (see Buler and Dawson 2014) for each year.

I plotted the ground survey transects in a geographic information system (GIS) and built a 50 m buffer perpendicular to each transect, which corresponded to the effective detection distance for ground surveys. I georeferenced radar data to a static polar coordinate grid of the two-dimensional extent of individual sample volumes at the ground created for each radar (hereafter referred to as a basegrid) and identified areas where the radar beam was blocked (by topography, buildings, or other human infrastructure), limiting coverage, by developing clutter maps following Buler and Dawson (2014). I then intersected the radar sample volumes (mean reflectivity is extracted from each sample volume) from the KDOX, KAKQ, KLIX, and KMOB basegrids with the transect buffer. I calculated weighted average reflectivity over each transect using the area of the intersected polygons to weight the averages.

I used National Land Cover Data (Homer et al. 2015), specifically hardwood, mixed, and pine forests and forested wetland. I constructed a 5-km buffer around each transect and computed the proportion of total forest cover within each buffer using Geospatial Modeling Environment (GME), (Beyer 2012). I used the Euclidean Distance tool within a GIS to determine the distance to the coast for each transect location. Before computing distance, I converted a United States boundary shapefile (Downloaded from [https://www.census.gov/geo/maps-data/data/cbf/cbf\\_nation.html](https://www.census.gov/geo/maps-data/data/cbf/cbf_nation.html))

from polygon to polyline and then determined the Euclidean distance from each transect location to the “coast.”

Arthropod abundance was estimated by sampling in the field along the transect during each visit. Six 20-m x 20-m plots were placed alongside each transect at every 75 m. During each visit, insects were sampled at three of six plots using a branch clipping method, in which I counted all insects on a branch and then weighed the branch to get a density of insects (insects/g) available for birds to eat (Johnson 2000).

Stopover Duration (days/bird) is simply the quotient of seasonal average bird use days/ seasonal average stopover bird density (sensu O’Neal et al. 2012). I computed a relative stopover length in days using seasonal mean ground bird density from surveys [birds/ha/day] divided by the seasonal mean number of estimated emigrants leaving at the onset of migration [birds/ha]. Emigrant numbers were estimated by dividing seasonal mean radar reflectivity of emigrants [cm<sup>2</sup>/ha] by the estimated mean radar cross section of migrant birds for NEXRAD (11 cm<sup>2</sup>/bird) as determined by Diehl et al. (2003). Although the units for stopover duration are in days, the estimate should be treated as a relative index rather than a precise measure of stopover duration. This is because the radars only sample an unknown, but small, proportion of emigrants leaving habitats at the initial onset of migration and, thus, bias estimates low.

## Analysis

This approach to measure relative stopover duration assumes that the mean daily averages of birds on the ground and birds emigrating measured by each technique are unbiased. However, given that not all sample volumes of radar data (pulse volumes) over survey sites were composed purely of forested habitat, they may reflect aggregate emigrants from a mixture of habitats (i.e., agriculture, wetlands, urban) that likely do not harbor the same migrant densities as forests and introduce measurement bias. Typically, when a pulse volume is not completely filled with hardwood forest, stopover duration is biased high. I attempted to statistically control for this potential measurement bias of emigrants emanating from non-forested habitats by fitting a linear regression between the amount of forest cover within radar sample volumes over sites and stopover duration. I then used the residuals of the regression as measure of relative stopover duration.

I clustered transect sites into three *a priori* stopover functional groups (fire escape, convenience store, full service hotel) based on 4 variables: relative stopover duration, amount of forest cover within 5 km, distance of site to the nearest coastline, and seasonal mean insect density at the site using the Partitioning Around Medoids (PAM) algorithm of Reynolds et al. (2006) and package “cluster” in R (Maechler et al. 2015), which calls function “princomp” to conduct a Principle Component Analysis (PCA). This approach minimizes dissimilarity among members within clusters.

Because cluster group sizes differed and may have had unequal variances, I used a Games-Howell Post Hoc test (Games and Howell 1976) to determine if there were significant differences in clustering variables between functional types. Because initial clustering produced groupings of only 2 classes within each geographic region, I increased the number of clusters to 4 post hoc (coastal fire escape, inland rest stop, convenience store, full service hotel) so that each region had at least 3 clusters represented. Functional types were identified based on the values of clustering variables within each cluster post hoc, where full service hotels had the highest forest cover and arthropod density and coastal fire escapes had the lowest forest cover and the least arthropod density. Convenience stores had the longest stopover duration and inland rest stops had stopover duration in between convenience stores and coastal fire escapes.

## **Results**

Detection-corrected estimates of daily bird use ranged from 2.02 to 7.11 (mean =  $3.14 \pm 0.41$ ) birds per ha per day in 2013 and 1.17 to 5.37 (mean =  $3.08 \pm 0.28$ ) birds per ha per day in 2014 within the KDOX radar range, and from 1.23 to 3.83 (mean =  $2.40 \pm 0.26$ ) birds per ha per day in 2013 and 1.26 to 2.92 (mean =  $2.04 \pm 0.17$ ) birds per ha per day in 2014 within the KAKQ radar range. Detection-corrected estimates of daily bird use ranged from 0.67 to 3.21 (mean =  $1.42 \pm 0.19$ ) birds per ha per day in

2002 and 0.42 to 3.98 (mean =  $1.38 \pm 0.24$ ) birds per ha per day in 2003 within the KLIX radar range, and from 0.73 to 2.24 (mean =  $1.29 \pm 0.22$ ) birds per ha per day in 2002 and 0.48 to 1.64 (mean =  $0.88 \pm 0.17$ ) birds per ha per day in 2003 within the KMOB radar range.

I analyzed the onset of evening flights from the KDOX radar for 12 days during fall 2013 and 10 days during fall 2014, and from the KAKQ radar for 15 days during fall 2013 and 7 days during fall 2014. Reflectivity as a measure of bird density ranged from 0.47 to 2.54 ( $\text{cm}^2/\text{ha}$ , mean =  $1.54 \pm 0.21$ ).

I analyzed the onset of evening flights from the KLIX radar for 5 days during fall 2002 and 6 days during fall 2003, and from the KMOB radar for 5 during fall 2002 and 7 days during fall 2003. Reflectivity as a measure of bird density ranged from 1.55 to 9.27 ( $\text{cm}^2/\text{ha}$ , mean =  $5.52 \pm 1.33$ ).

Relative stopover duration ranged from 0.01 to 57.7 (Table 3, mean =  $4.25 \pm 1.59$ ) and residual stopover duration ranged from -2.80 to 4.03 (mean =  $2.22 \pm 1.97$ ). Proportion of forest cover within radar sample volumes ranged from 0.23 to 0.99 (mean =  $0.86 \pm 0.02$ ). Proportion of hardwood within 5 km of each transect ranged from 0.01 to 0.89 (mean =  $0.40 \pm 0.03$ ). Distance to the coast (km) ranged from 0.7 to 71.4 (mean =  $27.1 \pm 2.67$ ). Insect density (insects/gram of branch) ranged from 0.02 to 3.87 (mean =  $0.84 \pm 0.14$ ).

I identified four well-defined groups from the cluster analysis (Figure 9), which is based on PCA components one and two, which explained the highest proportions of variance (Table 6).

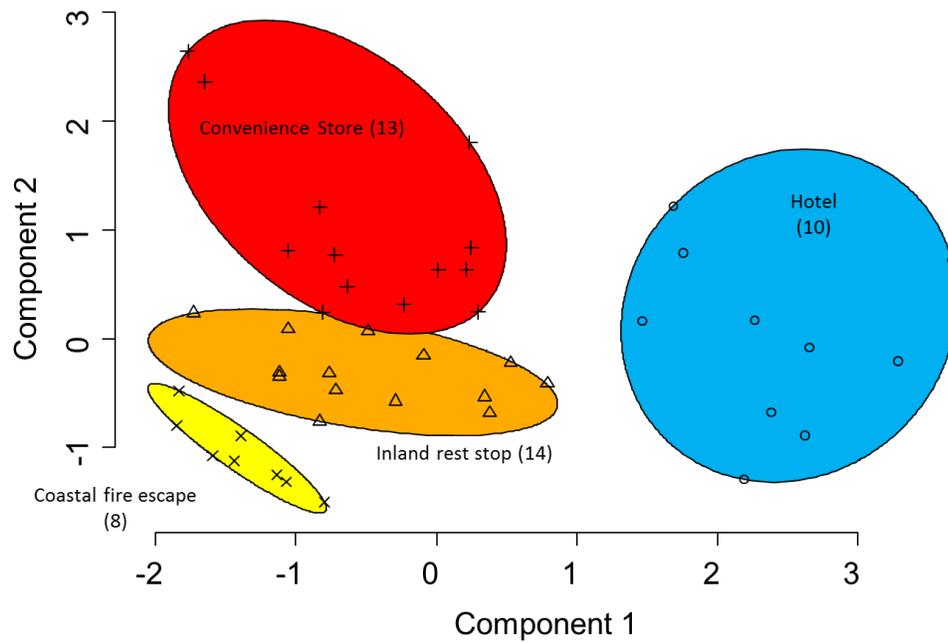


Figure 9 Cluster plots of 45 transect sites along two component axes and designated as members of four labeled stopover functional types by colored ellipses. The number of sites within each cluster group is presented in parentheses under cluster label name. Component 1 is nearly equal weighted by all of the variables with increasing forest cover, distance from the coast, insect density, and decreasing stopover duration as you move left to right. Component 2 is heavily weighted by stopover duration and should primarily be greater with longer stopover duration.

Table 6 Summary of Principle Component loadings from clustering analysis. Loadings for each variable within each component presented as well as the proportion of variance explained for each component.

	Component 1	Component 2	Component 3	Component 4
Proportion or hardwood forest within 5 km	0.59		-0.37	0.72
Distance to coast (km)	0.46	0.31	0.83	
Insect Density (# insects / g of branch)	0.55	0.34	-0.39	-0.65
Residual Stopover Duration	-0.37	0.89	-0.14	0.23
Proportion of Variance Explained	0.54	0.21	0.17	0.08

Based on the values of the four predictor variables, I assigned functional types to each cluster (Figure 10). I ended up with 8 coastal fire escapes, 14 inland rest stops, 10 full service hotels, and 13 convenience stores. On average, coastal fire escapes were distinguished by having short stopover duration, were located closest to the coast, had the lowest amount of forest cover in the landscape, and the least amount of insect density (Table 7). Inland rest stops had moderate stopover duration, low insect density (intermediate but not statistically different from fire escapes and convenience stores), were located away from the coast, and had a moderate amount of forest cover in the landscape. Convenience store sites had the longest stopover duration, were located away from the coast, had moderate forest cover in the landscape, and moderate amounts of insects. Hotel sites had short stopover duration (not different from fire

escapes), and the greatest amounts of forest cover and insect density and were located farthest from the coast. All hotel sites were located within extensive forested wetlands and inland areas along the Gulf Coast (Figure 11). All fires escapes were located in coastal and highly urbanized areas of the mid-Atlantic. Inland rest stops occurred primarily along the Delmarva Peninsula. Convenience stores were generally located along inland riparian forests within both Gulf Coast and mid-Atlantic regions.

Table 7 Values of predictor variables to determine stopover functional type classification of 45 transects sites (Table 8) in the mid-Atlantic and Gulf Coast regions. Data are sorted by region and functional type.

Transect	Region	Relative stopover duration (days per emigrant at onset of exodus)	Proportion hardwood forest within sample volumes	Proportion hardwood forest within 5km	Distance to coast (km)	Insect density (#/g veg)	Residual stopover duration	Functional type
NW2	Gulf Coast	0.38	0.92	0.31	37.8	1.525	-1.36	2) Inland rest stop
SE3	Gulf Coast	0.96	0.98	0.19	17.2	0.832	-0.30	2) Inland rest stop
SW2	Gulf Coast	1.81	0.61	0.37	12.7	1.413	0.04	2) Inland rest stop
NW3	Gulf Coast	7.29	0.96	0.33	32.6	2.208	1.67	3) Store
SE1	Gulf Coast	45.88	0.88	0.18	19.1	1.126	3.40	3) Store
SE2	Gulf Coast	57.70	1.00	0.17	17.8	1.191	4.03	3) Store
SW1	Gulf Coast	7.51	0.80	0.31	8.5	1.039	1.54	3) Store
SW3	Gulf Coast	9.04	0.91	0.35	16.2	1.095	1.80	3) Store
NE3	Gulf Coast	0.01	0.87	0.53	56.5	2.114	-2.80	4) Hotel
NE4	Gulf Coast	0.18	0.94	0.76	51.3	2.835	-2.07	4) Hotel
NE5	Gulf Coast	0.69	0.75	0.69	45.0	2.185	-0.86	4) Hotel
NW1	Gulf Coast	0.51	0.92	0.39	52.9	1.800	-1.05	4) Hotel
NW4	Gulf Coast	0.35	1.00	0.73	53.9	3.868	-1.08	4) Hotel
NW5	Gulf Coast	0.33	0.98	0.79	45.6	2.187	-1.37	4) Hotel

NW6	Gulf Coast	0.19	1.00	0.76	41.0	1.757	-1.69	4) Hotel
SE4	Gulf Coast	0.12	0.98	0.80	24.1	1.770	-2.38	4) Hotel
SW4	Gulf Coast	3.40	1.00	0.85	22.8	2.447	1.20	4) Hotel
SW6	Gulf Coast	2.15	1.00	0.89	20.2	2.244	0.74	4) Hotel
BFLP	mid-Atlantic	0.65	0.77	0.29	4.1	0.051	-0.92	1) Coastal fire escape
BHNW	mid-Atlantic	0.91	1.00	0.05	5.8	0.077	-0.16	1) Coastal fire escape
CHSP	mid-Atlantic	1.08	0.65	0.21	2.1	0.063	-0.46	1) Coastal fire escape
HCWP	mid-Atlantic	1.55	0.41	0.11	0.7	0.307	-0.18	1) Coastal fire escape
MCWS	mid-Atlantic	0.95	0.84	0.17	9.6	0.040	-0.50	1) Coastal fire escape
MNWA	mid-Atlantic	0.36	1.00	0.38	3.3	0.043	-1.14	1) Coastal fire escape
PACP	mid-Atlantic	3.95	0.23	0.01	13.1	0.094	0.69	1) Coastal fire escape
PHWA	mid-Atlantic	0.53	0.97	0.29	3.8	0.038	-0.93	1) Coastal fire escape
THWO	mid-Atlantic	4.46	0.98	0.28	5.9	0.022	1.20	1) Coastal fire escape
BLWA	mid-Atlantic	1.21	0.88	0.35	20.8	0.066	-0.23	2) Inland rest stop
CPSP	mid-Atlantic	0.84	0.88	0.38	26.3	0.236	-0.60	2) Inland rest stop
FBNP	mid-Atlantic	0.93	0.90	0.35	14.7	0.024	-0.48	2) Inland rest stop
GDNW	mid-Atlantic	0.75	0.99	0.61	21.7	0.475	-0.51	2) Inland rest stop
GDSE	mid-Atlantic	0.78	0.88	0.65	24.2	0.173	-0.67	2) Inland rest stop
GDSW	mid-Atlantic	0.97	0.95	0.61	36.3	0.234	-0.37	2) Inland rest stop
KPSP	mid-Atlantic	1.53	0.96	0.28	17.0	0.046	0.09	2) Inland rest stop
NWWA	mid-Atlantic	2.36	0.95	0.51	22.6	0.027	0.51	2) Inland rest stop
TUSP	mid-Atlantic	1.45	0.88	0.21	21.7	0.043	-0.05	2) Inland rest stop
CBSN	mid-Atlantic	2.69	0.83	0.36	52.8	0.190	0.53	3) Store
CSNA	mid-Atlantic	1.75	0.94	0.30	60.0	0.364	0.19	3) Store
IDYL	mid-Atlantic	1.96	0.99	0.41	39.7	0.095	0.45	3) Store
MAHO	mid-Atlantic	2.93	0.79	0.28	30.8	0.151	0.60	3) Store

MASP	mid-Atlantic	3.72	0.59	0.24	24.9	0.129	0.76	3) Store
MSBT	mid-Atlantic	6.07	0.56	0.38	27.8	0.275	1.23	3) Store
RACP	mid-Atlantic	2.04	0.93	0.27	71.4	0.091	0.34	3) Store
SOQU	mid-Atlantic	1.74	0.71	0.37	50.0	0.460	0.04	3) Store
ZUNI	mid-Atlantic	4.49	0.93	0.32	32.5	0.333	1.12	3) Store

Table 8 Acronym, name, and general location (State) for 45 transect sites where bird surveys were conducted.

Transect Acronym	Transect Name	State
BFLP	Bullseye Ferry Landing Preserve	Delaware
BHNW	Bombay Hook NWR	Delaware
BLWA	Blackiston Wildlife Area	Delaware
CHSP	Cape Henlopen State Park	Delaware
FBNP	Fork Branch Nature Preserve	Delaware
KPSP	Killens Pond State Park	Delaware
MCWS	Mill Creek Wildlife Sanctuary	Delaware
MNWA	Milford Neck Wildlife Area	Delaware
NWWA	Norman G. Wilder Wildlife Area	Delaware
PHWA	Prime Hook Wildlife Area	Delaware
NW6	NW6	Louisiana
SE4	SE4	Louisiana
SW4	SW4	Louisiana
SW6	SW6	Louisiana
IDYL	Idylwild	Maryland
MAHO	Marshy Hope	Maryland
MASP	Mardella Springs	Maryland
THWO	Third Haven Woods	Maryland
TUSP	Tuckahoe State Park	Maryland
NE3	NE3	Mississippi
NE4	NE4	Mississippi
NE5	NE5	Mississippi
NW1	NW1	Mississippi
NW2	NW2	Mississippi
NW3	NW3	Mississippi
NW4	NW4	Mississippi
NW5	NW5	Mississippi
SE1	SE1	Mississippi
SE2	SE2	Mississippi
SE3	SE3	Mississippi
SW1	SW1	Mississippi
SW2	SW2	Mississippi

SW3	SW3	Mississippi
CBSN	Cypress Bridge Swamp NAP	Virginia
CPSP	Chippokes Plantation State Park	Virginia
CSNA	Chub Sandhill NAP	Virginia
GDNW	Great Dismal Swamp NWR Northwest Jericho Ditch	Virginia
GDSE	Great Dismal Swamp NWR East	Virginia
GDSW	Great Dismal Swamp NWR Southwest	Virginia
HCWP	Hoffler Creek Wildlife Preserve	Virginia
MSBT	Mill Swamp Blackwater Tract	Virginia
PACP	Paradise Creek Park	Virginia
RACP	Raccoon Creek Pinelands	Virginia
SOQU	South Quay	Virginia
ZUNI	Zuni	Virginia

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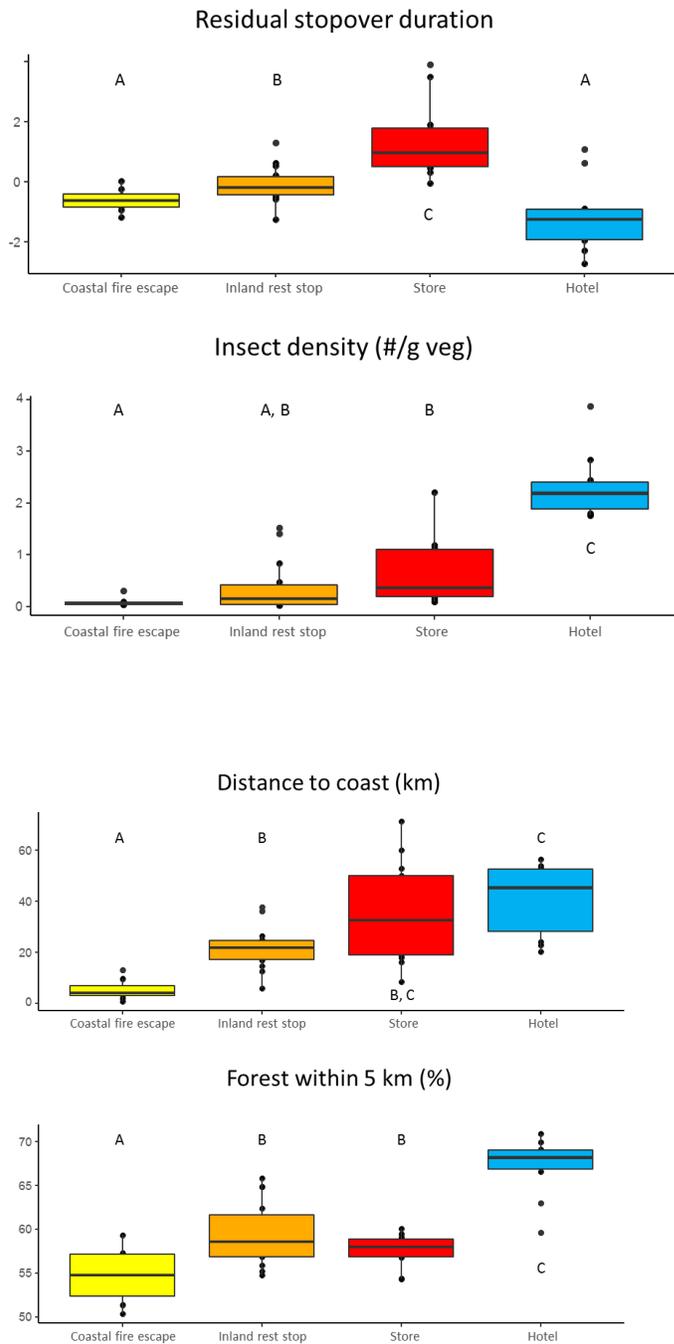


Figure 10 Boxplots of values of residual migrant stopover duration, insect density, distance to coast, and forest cover within 5km among 4 stopover site functional type clusters (coastal fire escape, inland rest stop, convenience store, and hotel) composed of 4.

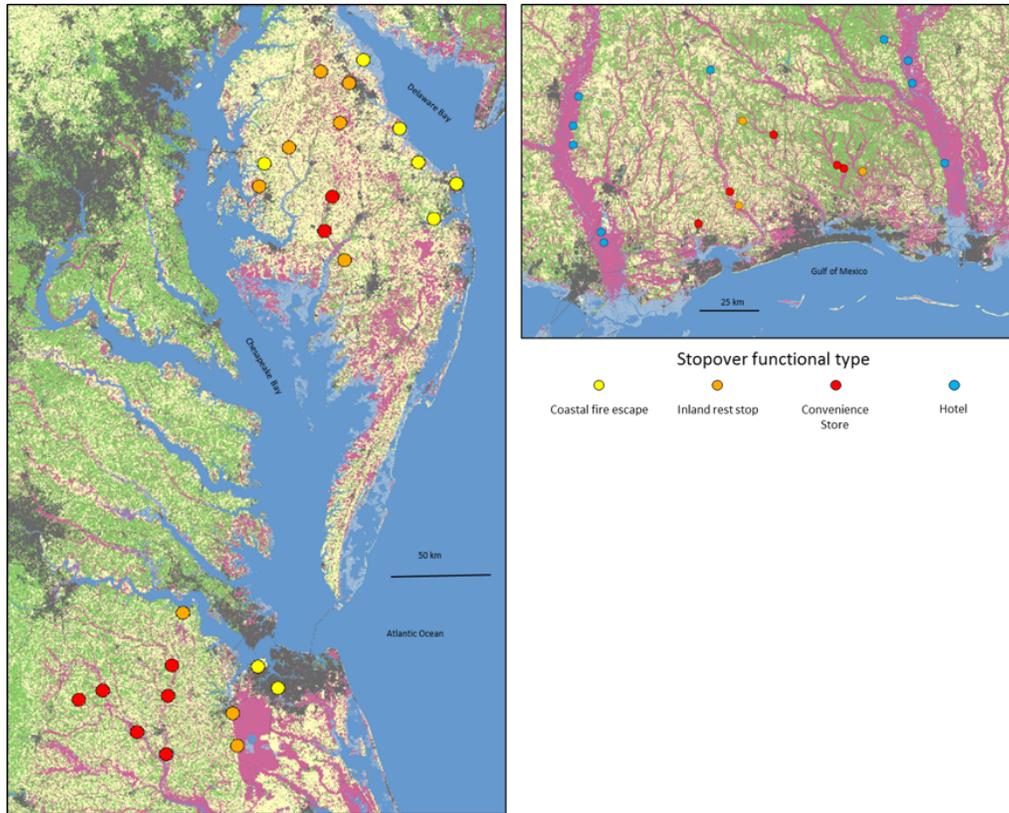


Figure 11 Maps of classified fall migration stopover functional types for 45 transect sites across the mid-Atlantic (top panel) and Gulf of Mexico (bottom panel) coasts.

## Discussion

Determining relative stopover duration by integrating radar and ground surveys similar to O’Neal et al. (2012), in conjunction with measuring food resources, proximity to the coast, and the fraction of hardwood forest cover in the landscape, allowed me to assess how migrants use specific stopover sites and classify them into four categories similar to the framework outlined by Mehlman et al. (2005). Stopover duration varied in accordance with empirical

data on the relationship between the propensity to leave a site and fuel deposition rate (Schaub et al. 2008). Namely, birds exhibited the lowest stopover duration in sites with the least amount of food (coastal fire escapes) and the most amount of food (full service hotels), while sites with moderate amounts of food were associated with the longest stopover duration (convenience stores). The explanation for this observation is that birds that refuel quickly can spend less time at a stopover site. If there are only moderate amounts of food, it will take longer for migrants to refuel to levels suitable for a long-distance migratory flight. This also begs the question as to whether convenience stores may be ecological traps and confer negative fitness consequences to migrants.

I could have lumped coastal fire escapes with inland rest stops because they both serve as temporary rest areas where birds likely cannot refuel due to low food resources. Collectively, they represented half of all stopover sites. However, the significant difference in their proximity to the coast may reflect an important difference. Coastal fire escapes offer a safe landing place for landbirds that may have just completed an open water crossing and tend to be used in greater and more consistent densities of emigrants than inland rest stops. This runs counter to the description by Mehlman et al. (2005) for fire escapes, which is that they are only used infrequently by migrants. Thus, researchers may need to realize that fire escape sites in close proximity to coasts are used rather consistently over the course of a season.

I found that the mid-Atlantic lacked full service hotels, while the majority of study sites in the Gulf Coast were classified as full service hotels. The lack of full service hotels in the mid-Atlantic emphasizes the importance of conserving areas classified as convenience stores and fire escapes. Buler and Dawson (2014) found that, on a local scale, hardwood forests in agricultural-dominated landscapes (convenience stores) had consistent high bird stopover density as well as shoreline habitats (fire escapes), (Archibald et al. 2017). Bonter et al. (2008) also found that shoreline habitats and forest patches in developed landscapes were characterized by high bird density. On a regional scale, much of the Delmarva Peninsula, which contains many of my study sites, was characterized by high, consistent bird stopover density (Buler and Dawson 2014).

In contrast, the Gulf Coast lacked true fire escapes, but the sites located closest to the coast were characterized as convenience stores and inland rest stops. As mentioned earlier, the majority of sites on the Gulf Coast were full service hotels. Migrating landbirds that encounter these convenience stores and inland rest stops may not find them suitable for fueling up before crossing an ecological barrier (i.e., Gulf of Mexico) and therefore may undertake a “reverse migration” or “relocation flight” to find a more resourceful stopover location (Alerstam 1978).

Convenience stores seemed to be concentrated in narrow riparian forests in both the mid-Atlantic and Gulf Coast. Narrow floodplain or riparian

forests are consistently used throughout the migration period in the mid-Atlantic (Buler and Dawson 2014). Also of interest were the two coastal fire escapes located in urban forests in Virginia, where birds are likely to stopover in city parks and small forest patches (Matthews and Rodewald 2010) in urban-dominated landscapes because natural vegetation is not present (Bonter et al. 2008).

Classifying stopover sites into the functional framework following Mehlman et al. (2005) should be useful in conservation planning as each functional type is important for stopover and allowing comparisons within each functional type rather than across types, which may bias the conservation of full service hotels and leave fire escapes and convenience stores unprotected. Each functional type serves certain needs for migrating landbirds, therefore prioritizing stopover locations classified under each functional type may be the most appropriate method to increasing survival during migration.

The needs of migrants and quality of stopover sites undoubtedly change annually. Using radar data, we can determine which stopover sites are consistently meeting metabolic demands of migrants. Time spent at stopover sites is often longer than time spent in flight (Hedenstrom and Alerstam 1997), therefore increasing survivorship during periods of stopover is of value for conservationists. High quality stopover habitat should contain high forest cover, abundant food resources, and minimal predation and competition.

Most areas under protection or that are included in conservation plans are likely considered full service hotels. Therefore, future conservation plans and studies should also focus on fire escapes and convenience stores because those are the sites that are likely not under protection already and therefore are in danger of disappearing (Mehlman et al. 2005).

A stopover site plays a significant role during migration, giving a migrant a place of shelter and an opportunity to refuel, thus contributing to the overall survival of a species. The time it takes a migrant to refuel is very important (Jenni and Schaub 2003) and depends highly on the quality of stopover site they choose. Categorizing stopover sites is a difficult, but necessary task, especially when funding for conservation is inadequate. Using a system of functional types facilitates the prioritization of stopover sites because one can evaluate sites within each functional type rather than across functional types. Each functional type serves a purpose and all are necessary in conservation, but all sites cannot be protected, so using a functional type system allows us to prioritize sites more easily and efficiently (Mehlman et al. 2005).

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