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Migration Ecology of American Woodcock (*Scolopax minor*)

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Migration Ecology of American Woodcock (*Scolopax minor*)

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

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University of Pittsburgh
Bachelor of Science in Biological Sciences, 2010

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This thesis is approved for recommendation to the Graduate Council.

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ABSTRACT

Improving the understanding of American woodcock (*Scolopax minor*) migration ecology has been identified as a priority information need for woodcock management. Developments in remote tracking technology and analytical techniques present an opportunity to gain insight into woodcock migratory connectivity and migration phenology and to evaluate the degree in which the current two-region (Eastern and Central) basis for woodcock management represents migratory movements. To analyze woodcock migration using band return records, I excluded observations that took place during the migratory period. Using this dataset, 17.9% of records showed crossover between management regions, higher than the < 5% crossover found in studies including non-migratory band returns. During autumn migration, woodcock from the Central Region largely migrated to destinations within the Central Region, whereas woodcock from the Eastern Region migrated to destinations across their wintering range, mixing with individuals from the Central Region. Between 2013 and 2016, I deployed 75 satellite transmitters on woodcock. I tracked the migration paths of 61 woodcock and documented 88 woodcock migrations. Average migration duration was longer during spring migration (53 days) than during autumn migration (31 days) because woodcock made a higher number of close-together migratory stopovers, not because woodcock stayed at individual stopovers longer during spring migration. Woodcock captured in the Central Management Region used 2 primary migration routes: a Western Route and a Central Route. The Western Route ran north-south, connecting the breeding and wintering grounds of the Central Management Region. The hourglass-shaped Central Route connected an area on the wintering grounds reaching from Texas to Florida, to sites throughout northeastern North America. Woodcock following the Central Route funneled between the Appalachian Mountains and the Mississippi Alluvial Valley in western Tennessee during both autumn and spring migration. A higher than anticipated

percentage (36%, $n = 12$) of marked woodcock captured in Texas and Louisiana and monitored during spring migration migrated to breeding-period sites in the Eastern Management Region, raising questions about the biological basis of managing woodcock as separate populations. The supplementary material includes woodcock capture information (Appendix I), information on individual stopovers (Appendix II), and migration maps for individual woodcock (Appendix III).

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INTRODUCTION

American woodcock (*Scolopax minor*, hereafter woodcock), a migratory bird in family Scolopacidae, are found throughout eastern North America. Woodcock are managed as an Eastern and Central population (Fig. 1), with the border between management regions following the boundary of the Atlantic and Mississippi Flyways (Cooper and Rau 2015). Woodcock are a popular game bird; woodcock hunters spent an estimated 347,300 days afield and harvested an estimated 200,100 woodcock within the United States during the 2014-2015 season (Cooper and Rau 2015). Woodcock are associated with early successional forest (Dessecker and McAuley 2001). However, long-term declines in the availability of early successional habitat alongside increased urban/industrialized development have contributed to long-term woodcock population declines (Dwyer et al. 1983, Dessecker and McAuley 2001, Trani et al. 2001). The U.S Fish and Wildlife Service calculates annual woodcock population indices for the Eastern and Central management region using the results from the Singing-ground Survey (SGS). This survey exploits the conspicuous courtship display of singing males. The results of the SGS are used to create an annual index of the number of singing males per survey route and to identify short-term, 10-year, and long-term population trends. Since initiating the current form of the SGS in 1968, indices for these populations in both regions have undergone significant long-term annual decline (Eastern: -1.06%/year, Central: -0.71%/year). Additionally, the Eastern Region has shown a declining 10-year trend (-1.56%/year), whereas there has been no significant 10-year trend in the Central Region (Cooper and Rau 2015).

Migratory connectivity is defined as “the movement of individuals between summer and winter populations, including immediate stopover sites” (Webster et al. 2002:77). An appreciation of the migratory connectivity of a species is vital to understanding the movement of

individuals between disparate areas throughout the annual cycle and how these movements influence regional population dynamics (Johnson et al. 1988, Taylor and Norris 2009, Taylor and Stutchbury 2016). This is especially important because woodcock populations have experienced range-wide, long-term population (Cooper and Rau 2015) and woodcock are subject to both harvest and natural mortality during the breeding period, wintering period, and throughout the migratory period. In addition, knowledge of migratory phenology (seasonal temporal patterns) is necessary to determine annual harvest pressure on woodcock across management regions and political boundaries (Blankenship 1957, Myatt and Krementz 2007*a*).

Though woodcock migratory patterns have been a subject of study for a considerable period (Mendall and Aldous 1943), many details of their migratory connectivity remain poorly understood (McAuley et al. 1994). Techniques used to study woodcock migration including radio-telemetry (Krementz et al. 1994, Myatt and Krementz 2007*b*, Meunier et al. 2008), band returns (Glasgow 1958, Coon et al. 1977), phylogenetics (Rhymer et al. 2005), and stable isotopes (Sullins et al. 2016) have provided insight into woodcock migration. However, many details of woodcock migration remain unclear because previously used methods were limited by either focusing on a single geographic area, being unable to provide information on more than one relocation per individual, or by only providing information on large-scale geographic movements.

Band return data has been the basis of many geographic scale studies of woodcock migration and has been used to hypothesize woodcock migration routes and develop woodcock management regions (Glasgow 1958, Sheldon 1967, Coon et al. 1977, fig. 1). Estimates of the proportion of woodcock that cross between management regions during migration have varied from less than 5% to 25% depending on the criteria used to incorporate band return records into

the study (Martin et al. 1969, Coon et al. 1977). I investigated woodcock migratory connectivity by using a range-wide sample of band returns that only included observations of woodcock banded during a period when most woodcock were on their breeding grounds and encountered during a period when most woodcock were on their wintering grounds and vice versa (i.e., I excluded observation that took place during the migratory period). Additionally, advances in geographic information systems, spatial statistics, and analytical techniques allowed me to use band return records to determine the extent of crossover between management regions and to describe woodcock migratory connectivity.

Technology has advanced to the point where satellite transmitters are light enough to deploy on woodcock. These transmitters can relay multiple relocations of an individual over the course of a migratory season and/or throughout the full year, offering an opportunity to observe migratory movements and timing. Between September 2013 and February 2016, I deployed 75 satellite transmitters on woodcock at sites on their breeding and wintering grounds, focusing on the United States portion of the Central Region. I used data from these transmitters to (1) investigate migratory connectivity including migratory routes and major stopover regions, (2) document migratory phenology and other characteristics of migration such as distance traveled during migration, and (3) investigate whether there was variation based on age, year, or season for these variables.

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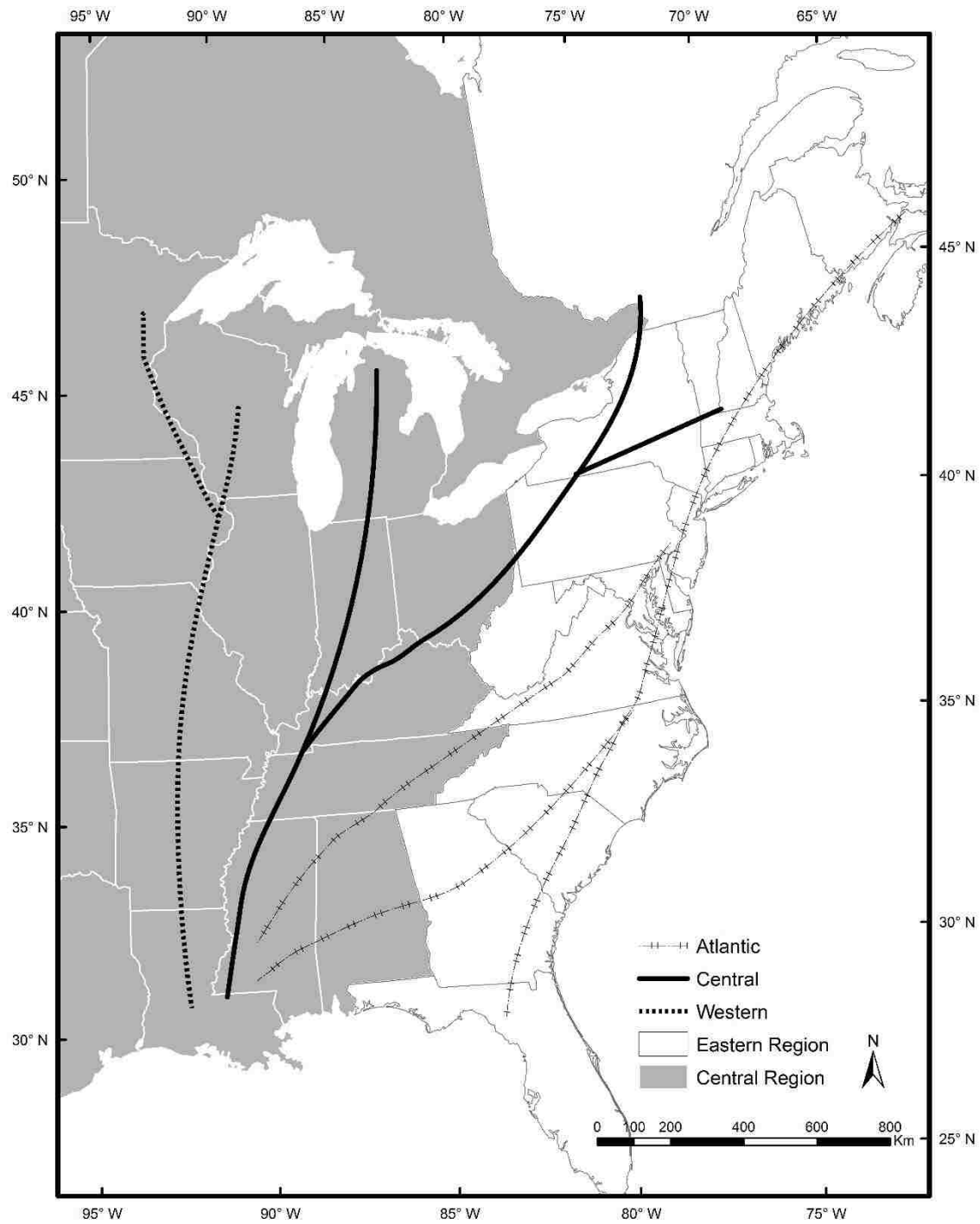


Figure 1. Glasgow's (1958) hypothesized migration routes of American woodcock overlaid on current Eastern and Central American woodcock Management Regions.

Chapter I

Migratory Connectivity of American Woodcock Using Band Return Data

Joseph D. Moore

ABSTRACT

American woodcock (*Scolopax minor*) are managed as a Central and an Eastern population with management region boundaries analogous to those of the Atlantic and Mississippi Flyways. Band return data showing little crossover between populations or management regions have been used as biological justification for these Central and Eastern Management Regions. However, the observed proportion of crossover between management regions depends on the criteria used to subset the band return dataset. I analyzed the amount of crossover between management regions using only band return records representing complete migrations between the breeding and wintering grounds by using only band return records in which the capture took place during the breeding season and the encounter took place during the wintering season or vice versa (n = 224). Additionally, I applied spatial statistics and a clustering algorithm to investigate woodcock migratory connectivity using this subset of migratory woodcock band return records. Using raw counts, 17.9% of records showed crossover between management regions, a higher proportion than the < 5% crossover found in studies that did not use only migratory band returns. My results showed woodcock from the breeding grounds in the Central Region largely migrate to destinations within the Central Region, whereas woodcock from the breeding grounds in the Eastern Region migrate to destinations across the entire wintering range and mix with individuals from the Central Region. Using the division coefficient, I estimated that 54% of woodcock from the breeding grounds of the Eastern Region migrate to the Central Region. My result that many woodcock from separate regions of the breeding grounds mix on the wintering grounds has implications for the present two-region basis for woodcock management. Elucidating finer scale movement patterns among regions provides a basis for reassessing the boundaries to ensure optimal conservation and management of the species.

INTRODUCTION

Migratory connectivity describes the links between the geographic distribution of breeding and non-breeding populations of a migratory species, including ‘the degree to which individuals from the same breeding site migrate to the same wintering site’ (Webster et al. 2002, Trierweiler et al. 2014). Understanding the patterns of connectivity over an annual cycle is important because events at one site, such as habitat loss, can affect individuals and population dynamics at connected sites (Marra et al. 1998, Taylor and Norris 2009). The strength of connectivity describes the extent to which individuals from separate breeding populations mix on the wintering grounds. When migratory connectivity is strong, individuals near each other on the breeding or wintering grounds remain near each other after migrating (Webster et al. 2002). Strong connectivity can be caused by parallel migration (pattern transference in Ambrosini et al. 2009) where the spatial structure between individuals on the breeding grounds is maintained on the wintering grounds, i.e., longitudes on the breeding and wintering grounds are positively correlated (Newton 2008). Strong migratory connectivity can also result when distinct groups from separate breeding or wintering regions remain in their distinct groups after migrating. These groups can be thought of as ‘sub-populations’ (Ambrosini et al. 2009). These sub-populations can remain separate due to geographic barriers (Brooks 1952, Fraser et al. 2013), genetics, or social behavior (Noordwijk et al. 2006). When migratory connectivity is weak, individuals near each other on the breeding or wintering grounds scatter after migrating and mix with individuals from other regions. When migratory connectivity is moderate, the majority of individuals near each other on the breeding or wintering grounds remain near other individuals that they shared breeding or wintering areas with after migrating but with some mixing between groups (Webster

et al. 2002). Understanding migratory connectivity is important because events at wintering sites are shown to affect population dynamics at breeding season sites (Sillett et al. 2000).

American woodcock (*Scolopax minor*, hereafter woodcock) are a migratory game bird widespread throughout eastern North America. Woodcock are managed as an Eastern and Central population (Fig. 1), with the border between management regions following the boundary of the Atlantic and Mississippi Flyways (Cooper and Rau 2015). Indices for these populations in both regions have undergone significant long-term declines (Eastern: -1.06%/year, Central: -0.71%/year) since the initiation of a standardized annual survey in 1968. The Eastern Region has shown a declining 10-year trend (-1.56%/year), whereas there has been no significant 10-year trend in the Central Region (Cooper and Rau 2015). Woodcock population decline has been largely attributed to habitat loss (Dessecker and McAuley 2001, Kelley et al. 2008). It is unknown whether habitat loss on the breeding grounds, wintering grounds, or along migration routes is primarily responsible for this decline. Though woodcock migratory patterns have been a subject of study for a considerable period (Mendall and Aldous 1943), many details of their migratory connectivity remain poorly understood (McAuley et al. 1994). An improved understanding of migratory connectivity can be instrumental in directing population-specific conservation strategies and in modeling population dynamics over the full annual cycle (Johnson 1988, Rushing et al. 2016, Taylor and Stutchbury 2016).

Glasgow (1958) and Sheldon (1967) plotted woodcock band returns to infer three primary migration routes: Atlantic, Central, and Western (Fig. 1). However, limited band recovery data were available (Glasgow: $n = 175$, Sheldon: $n = 400$) and few of the returns represented complete migratory movements. Band returns that do not represent complete migratory movements between breeding and non-breeding sites offer some insight into migratory

routes and phenology but have limited use in determining the connectivity between regions of the breeding and wintering grounds because the bird's origin or destination is uncertain. Many later studies explored woodcock migratory connectivity using band returns originating from one state or management region (Martin et al. 1969, Krohn and Clark 1977, Myatt and Kremetz 2007a) or used a sample of band returns inappropriate for quantifying migratory connectivity because the sample included birds that had yet to complete migration (Coon et al. 1977). Studies using only band returns from individual states or management regions provide insight into migration phenology, population dynamics, and migratory connectivity within a limited area but may not represent range-wide trends.

Coon et al. (1977) recommended the current configurations of the Eastern and Central Management Regions based on limited crossover (3.0% unweighted, 4.4% weighted) between the two management regions. Their analysis used only direct and indirect returns but no additional criteria to restrict the dataset to observations of complete migratory movements. A direct return is when a band recovery takes place in the first hunting season following banding. An indirect return is when a band recovery takes place in a hunting season after the first hunting season following banding. Much of the harvest may have taken place before the initiation of autumn migration or early in migration; 73% of band returns used in Coon et al.'s (1977) analysis were from the same state or province where the individual woodcock was banded. Using only band returns representing complete migratory movement by excluding returns that took place during the migratory period, rather than using all direct and indirect returns may more accurately depict migratory connectivity and the extent of crossover between management regions.

Previous studies have not considered spatial autocorrelation while investigating woodcock migration, i.e. the extent to which the migratory behavior of an individual can be predicted by the behavior of nearby individuals. Incorporating spatial autocorrelation and spatial structure into an analysis of migratory connectivity allows the strength of migratory connectivity to be quantitatively measured and allows for the identification of ‘sub-populations’ of individuals that are near each other both on the breeding and on the wintering grounds (Ambrosini et al. 2009).

My objective was to investigate woodcock migratory connectivity by using a range-wide sample of band returns that only included observations that represented full migratory movements and by taking into account the spatial structure on the breeding and wintering grounds. My goals were to (1) determine the extent of crossover between management regions, (2) quantify and describe the strength of migratory connectivity, and, if possible, (3) identify subpopulations based on the correlation between the spatial structure on the breeding and the wintering grounds.

METHODS

Data Set

I used band return data from the U.S. Geological Survey Bird Banding Laboratory database, which provides information on banding and subsequent encounters of banded birds for the United States and Canada including information on location, location precision, date, and how the bird was encountered. The majority of locations was reported with precision at the 10-minute block scale (18.5 km east-west by 14.2 km north-south at 40°N). As of 29 March 2016, there were 6,587 encounter records resulting from 123,132 banded woodcock. I filtered these

data to include only returns representing full migratory movements using the ‘dplyr’ package in R (Wickham and Francois 2015, R Core Team 2016). I included only birds banded during a period when most woodcock were on their breeding grounds and encountered during a period when most woodcock were on their wintering grounds and vice versa. I defined the period when most woodcock are on their breeding grounds as 15 May through 15 September (Myatt and Krementz 2007a) and the period when most woodcock are on their wintering grounds as 15 December through 31 January (Glasgow 1958, Myatt and Krementz 2007b). I also included any woodcock banded as a nestling, fledgling, or “local” (i.e., a young bird incapable of sustained flight, U.S. Geological Survey Bird Banding Laboratory, Patuxent, MD, USA) banded north of 36°N that were encountered during the winter season and any woodcock banded as a nestling, fledgling, or local banded south of 36°N that were encountered during the breeding season. In many cases, banding and encounter records had a month recorded but no associated day. These records were included if the entire month fell within the windows defined. I removed implausible observations by filtering out all woodcock banded or encountered west of 105°W or banded and encountered within the same state or province. Due to the periods used, 97% of birds included in the dataset were banded on the breeding grounds and encountered on the wintering grounds (hunting takes place during the wintering period but not the breeding period). My filtering process created a dataset of 217 woodcock banded on the breeding grounds and reencountered on the wintering grounds, and a dataset of 7 woodcock banded on the wintering grounds and reencountered on the breeding grounds. I categorized each banding and encounter location as belonging to one of four groups based on whether it took place during the breeding or wintering season and whether it was located within the Eastern or Central Region (e.g., north-central,

north-eastern, south-central, south-eastern). Due to the low number of observations, I did not group data by period and used data from all available years (1960-2016).

Crossover Between Management Regions

For spring and autumn migration, I used the filtered dataset to calculate how many woodcock belonged to each of the four groups, the number and proportion of woodcock that migrated to either the Eastern or Central Region from each group, the extent of overall crossover between regions, and to plot migratory movements. Because there were limited data for spring migration ($n = 7$), I only analyzed observations representing autumn migration ($n = 217$) after this step.

I determined the division coefficient and bootstrapped confidence intervals for each management region using the method described by Kania and Busse (1987) with the R package ‘birdring’ (Korner-Nievergelt et al. 2010, Korner-Nievergelt and Robinson 2015). The division coefficient is the proportion of the woodcock population from each management region on the breeding grounds that migrate to each region on the wintering grounds. It is determined by taking into account “area-specific reencounter probabilities” by using the total number of woodcock banded in each region on the breeding grounds and the number of woodcock encountered in each region on the wintering grounds that originated from each region on the breeding grounds (Kania and Busse 1987). This method was used to determine the origin of Eurasian woodcock wintering in France (Bauthian et al. 2007).

To visualize the destinations of migratory movements I used the kernel density tool in ArcMap 10.3 (ESRI, Inc.) to create kernel density estimates using a search radius of 150 km and a grid size of 10 x 10 km. I created separate kernel density estimates for the migratory

destinations or origins of woodcock from each of the four groups (i.e., wintering locations of woodcock that were in the Central Region during the breeding season, breeding locations of woodcock that were in the Central Region during the wintering season, etc.).

Migratory Connectivity

I used a Mantel test following the procedure described in Ambrosini et al. (2009) to quantify the strength of migratory connectivity between the breeding and wintering range of woodcock. For both the breeding and wintering grounds, I created a distance matrix, calculating the great-circle distance (the shortest distance along the curvature of sphere) between each pair of individual woodcock using the R package ‘fossil’ (Vavrek 2011). I subsequently used these distance matrices to investigate the correlation between the spatial structure of individuals on the breeding grounds and the spatial structure of the same individuals on the wintering grounds. I used the R package ‘ecodist’ (Goslee and Urban 2007) to conduct a Mantel test between these distance matrices with 10,000 permutations to determine significance. If there is a correlation among the reciprocal position of individuals on breeding and on the wintering grounds, the Mantel test will show a statistically significant positive Mantel correlation coefficient (R_M). The R_M value “corresponds to a simple Pearson product moment correlation coefficient between the two matrices” and indicates the strength of migratory connectivity (Sokal and Rohlf 1995, Ambrosini et al. 2009:205).

To investigate the possibility of parallel migration, I regressed the longitude of locations on the breeding ground with the longitude of locations on the wintering grounds using a linear model. I used the Mantel test and linear models to investigate range-wide connectivity and migratory connectivity within each region using a p-value of 0.05 to assess significance for both tests.

Identification of Sub Ranges

I used a clustering technique to identify possible sub-ranges based on the observed distribution of individuals following the procedure described in Ambrosini et al. (2009). I used the *pam* clustering algorithm (partitioning around medoids - an algorithm similar to K-means that minimizes a sum of dissimilarities) to determine if connectivity was due to clustering of individuals that stay together on the breeding and wintering grounds (Ambrosini et al. 2009). The overall average silhouette width (*oasw*) is a measure of the “goodness of the overall classification of points in a given number of clusters” (Ambrosini et al. 2009:205). A higher *oasw* value signifies a higher degree of validity to the clustering: “*oasw* values lower than 0.25 indicate that no substantial structure has been found in the data, values between 0.26 and 0.50 indicate a ‘weak’ structure, between 0.51 and 0.70 a ‘reasonable’ structure and values larger than 0.71 a ‘strong’ structure” (Rousseeuw 1987, Ambrosini et al. 2009:205). I used the *oasw* to determine the appropriate number of clusters and to determine whether the clustering represents a “structure actually present in the data” (Rousseeuw 1987). I created kernel density estimates for each cluster on the breeding and wintering grounds to visualize the boundaries of each cluster using the same method I used to visualize the point distributions based on management regions. Because there was significant clustering as indicated by the *oasw* and R_M values, I repeated the Mantel’s test and clustering procedure for each cluster to investigate the possibility of sub-clusters within the data (Ambrosini et al. 2009).

RESULTS

Crossover Between Management Regions

For autumn migration, 17.5% ($n = 38$) of woodcock were encountered in the region other than the one in which they were banded (Table 1, Fig.2, Fig. 3). The majority of this crossover was from the breeding grounds of the Eastern Region to the wintering grounds of the Central Region. From the Eastern Region, 37.9% of birds crossed over to sites in the Central Region. Only 3.8% of birds crossed over to the wintering grounds of the Eastern Region from the breeding grounds of the Central Region. On the wintering grounds, 21.0% of birds in the Central Region had origins in the Eastern Region whereas only 8.5% of birds in the Eastern Region had origins in the Central Region. For spring migration, all woodcock ($n = 7$) were banded in the Central Region and 28.6% ($n = 2$) of these woodcock were encountered in the Eastern Region. Between spring and autumn migration combined, 17.9% ($n = 40$) of woodcock were encountered in a region other than the one in which they were banded.

More than twice as many woodcock were banded during the breeding season in the Central Region ($n = 56,266$) than in the Eastern Region ($n = 27,153$). The reencounter probability was 0.002 in the wintering grounds of the Central Region (95% CI: 0.002-0.003) and 0.004 in the Eastern Region (95% CI: 0.003-0.010). Using the division coefficient approach, I found the proportion of the banded woodcock population from the breeding grounds of the Central Region that migrated to destinations within the Central Region to be 0.98 (95% CI: 0.95-1.00). The proportion of the banded woodcock population from the breeding grounds in the Eastern Region that migrated to destinations within the Eastern Region was 0.46 (95% CI: 0.21-0.65, Table 2).

The kernel density estimate for the wintering locations of birds that were in the Central Region during the breeding season was largely contained within the southern portion of the Central Region. The kernel density estimate for the wintering locations of birds that were in the

Eastern Region covered an area encompassing the wintering range in both the Eastern and Central Regions (Fig. 4).

The kernel density estimate for the breeding season locations of birds that were in the Central Region during the winter had the highest densities in Wisconsin and Michigan but included sections of New York, Maine, and West Virginia. The kernel density estimate for the breeding locations of birds that were in the Eastern Region during the wintering season was largely contained within the boundaries of the Eastern Region but included sections of northern Michigan and Wisconsin (Fig. 4).

Migratory Connectivity

Moderate migratory connectivity between the breeding and wintering grounds was found at the range-wide scale using linear regression on longitude and the Mantel test ($R^2 = 0.46$, $P < 0.01$, Mantel test: $R_M = 0.42$, $P < 0.01$, Table 3). I found no correlation between breeding season and wintering locations using subsets of returns based on management region in the north-central and south-eastern bins (Table 3). In the northeastern bin there was a significant correlation based on longitude ($R^2 = 0.07$, $P = 0.01$), but no indication of a correlation with the Mantel test ($R_M = 0.03$, $p = 0.24$). In the south-central bin, there was a significant relationship based on longitude ($R^2 = 0.11$, $P < 0.01$; Mantel test ($R_M = 0.14$, $P < 0.01$), indicating a weak within-management-region migratory connectivity.

Identification of Sub-Ranges

Using pam clustering to identify sub-ranges based on observed locations of individuals, I found that two clusters were the best fit for the data. The two clusters had “reasonable structure” with an *oasw* value of 0.59 (Rousseeuw 1987, Ambrosini et al. 2009:205). On the breeding

grounds, the clusters were analogous to the Eastern and Central Regions (with some overlap on the border between regions in New York and West Virginia), and the clusters on the wintering grounds overlapped similarly to the overlap shown by grouping woodcock by management region origin (Fig. 5). I found no significant connectivity for within-cluster movements (Cluster 1: $R_M = -0.07$, $P = 0.94$ Cluster 2: $R_M = -0.02$, $P = 0.69$). Additionally, I found no evidence for sub-clusters. Pam clustering on the two original clusters resulted in creating clusters with “weak” structure (Cluster 1: $oasw = 0.45$, Cluster 2: $oasw = 0.40$).

DISCUSSION

My results of 17.9% crossover between regions (Table 1) showed more crossover than the < 5% crossover found by Coon et al. (1977), most likely because my dataset only included woodcock that had completed migration instead of including woodcock that had yet to initiate migration or were harvested early in migration before they had an opportunity to cross between management regions. Perhaps most surprising, I estimated a 37.9% crossover from the Eastern Region to the Central Region during autumn migration. This high northeast-to-southwest crossover is in contrast to the low rate of crossover between the northern portion of the Central Region and the southern portion of the Eastern Region (3.9% of birds from the Central Region during autumn migration).

A higher proportion of the banded woodcock population may have crossed from the northern portion of the Eastern Region to the Central Region than was suggested by the raw counts alone (division coefficient; 0.54, 95% CI: 0.35-0.78). The higher proportion of crossover can be attributed to a higher banding effort in the Central Region (Table 2) and a higher recovery probability in the Eastern Region. The division-coefficient approach to modeling the distribution of woodcock after migration has four requirements: (1) groups must have equal reencounter

probabilities within destination areas, (2) reencounter probabilities and woodcock distribution should not change within the time of the study, (3) reencounter probabilities must be uniform within each destination area, and (4) all destination areas should combine to make up the possible area to which banded birds could migrate (Korner-Nievergelt et al. 2010). My study meets assumptions one and four. Because of the limited number of band returns available ($n = 216$), I used all available data (1960 - 2016) and may not have met the second assumption. However, I have no evidence that the reencounter probabilities or woodcock distribution have changed during the period used. Additionally, I may not have met assumption three because of the possibility of uneven hunting pressure within management regions.

Whereas the total amount of crossover is useful on its own, incorporating spatial structure into my analysis provided additional insight into the nature and extent of the crossover. Using kernel density estimates to visualize migratory destinations and origins demonstrated that this crossover is not just due to birds crossing a political border between management regions. Instead, they show that the wintering range of woodcock breeding in the Eastern Region completely overlaps the wintering range of woodcock breeding in the Central Region, with Louisiana having one of the highest concentrations of recoveries of woodcock banded in the Eastern Region. The clustering analysis complements this hypothesis. The natural clustering in the dataset corresponded to the current management region boundaries on the breeding grounds, and therefore the clusters overlapped in the Central Region on the wintering grounds

At a range-wide scale, woodcock show moderate migratory connectivity, i.e., the majority of individuals from separate breeding sites migrate to distinct wintering sites, with some crossover among sites (Webster et al. 2002). However, connectivity does not appear to be constant between regions. The breeding grounds in the Central Region connect strongly to the

wintering grounds in the Central Region. However, the wintering grounds in the Central Region show moderate connectivity, with most birds originating from the Central Region, but with 21% (using raw counts) of woodcock originating from the Eastern Region. The breeding grounds in the Eastern Region show weak connectivity, with birds scattering throughout the entire woodcock wintering range. Yet, the wintering grounds in the Eastern Region connect strongly to the breeding grounds in the Eastern Region.

I found weak within-region migratory connectivity. Although the breeding grounds in the Central Region connect strongly to the wintering grounds in the Central Region, woodcock throughout the breeding grounds of the Central Region mix on the wintering grounds all the way from Texas to Alabama. This weak connectivity within regions is true for all four groups (weak or no correlation based on longitude or the Mantel test). The longitudinal correlation between the summer and wintering locations of woodcock that are in the Eastern Region in the summer may have been influenced by the likelihood of woodcock that were banded in or to the west of the Appalachian Mountains (i.e., in West Virginia) being more likely to travel southwest instead of crossing high-elevation areas to winter in the Eastern Region. The association between breeding and wintering areas in the south-central bin (based on longitude and the Mantel test) may be because none of the six woodcock banded in Minnesota during the breeding season and encountered during the winter season were encountered east of Louisiana, and because there was a higher banding effort in the breeding grounds of the Central Region than there was in the Eastern Region (Table 2).

Woodcock migrating in relation to geographic barriers could explain clustering at the range-wide scale. Woodcock are known to follow rivers and coastlines while migrating (Mendall and Aldous 1943). The Appalachian Mountains could be acting as a natural barrier that prevents

woodcock that breed in the Central Region from wintering in the southeastern United States. Woodcock that breed in the Eastern Region may migrate along the western edge of the Appalachian Mountains to wintering grounds in the Central Region in addition to migrating along the Atlantic coast. These possible migration routes correspond to the migration routes hypothesized by Glasgow (1958) and Sheldon (1967, Fig. 1). Despite the correlation between longitude on the breeding and wintering grounds at a range-wide scale, it seems that the strength of connectivity is due to clustering based on whether woodcock migrate on the east or the west side of the Appalachian Mountains.

I documented a much higher percentage woodcock crossover between management regions than reported in previous range-wide studies. Coon et al. (1977) found 3.0% crossover between management regions using all direct and indirect band recoveries. Sullins et al. (2016) investigated woodcock migratory connectivity using stable isotopes. They incorporated band return data into their model as a prior probability to predict natal origin of harvested woodcock. Their banding dataset incorporated 1,818 direct band recoveries and showed 1% crossover from birds harvested in the Eastern Region and 2% crossover from birds harvested in the Central Region. With these prior probabilities, Sullins et al. (2016) assigned most woodcock harvested from Texas and Louisiana to origins within the Central Region and assigned most woodcock harvested from West Virginia to origins within the Eastern Region. Conversely, Martin et al. (1969) used only migratory returns from Louisiana-banded woodcock and found 25% crossover between regions, which is similar to my results. Results from Martin et al. (1969) and this study show higher proportions of crossover because these studies included only records representing migration. Direct and indirect recoveries that take place before or at the beginning of migration

provide insight on the distribution and derivation of harvest but do not accurately represent migratory connectivity between breeding and wintering grounds.

Rhymer et al. (2005) investigated whether woodcock populations show “geographic genetic structure” between management regions using mitochondrial DNA samples collected in the primary breeding grounds. They found “high levels of genetic variability among individuals” but “no correlation with geographic region” (Rhymer et al. 2005:122). They attributed the lack of geographic structure to rapid range expansion following Pleistocene glaciation and to ongoing gene flow from the Eastern Region to the Central Region. They hypothesized that because woodcock breed on their wintering grounds in addition to their primary breeding grounds (Roboski and Causey 1981, Whiting and Boggus 1982), individuals mixing on the wintering grounds can cause gene flow between regions.

Band return data are important for investigating woodcock migratory connectivity over long periods; however, uneven banding and hunting (recovery) effort bias band return data. On the breeding grounds, banding locations clustered in Wisconsin, Michigan, New York, and Maine (Fig. 4). Very few banding or recovery locations were in Canada even though Sullins et al. (2016), using a stable isotope analysis, determined the majority of harvested woodcock were produced north of 44°N. On the wintering grounds, it is likely that high hunting effort in Louisiana caused recovery locations to cluster there (Fig.2). To help mitigate this effect, I included band returns resulting from both hunter harvest and from other sources. The final dataset for autumn migration consisted of 90% of recoveries from harvested woodcock. Of the twenty-one returns from other sources, only two returns were in Louisiana. However, including these recoveries did not completely offset the disproportionately high number of band returns in Louisiana. With current banding and return rates, it is not likely that it will be possible to

overcome these limitations using only band-return data. However, recent developments in the miniaturization of satellite transmitters (PTTs) now allow satellite telemetry of American woodcock. Systematically tagging woodcock throughout their range would allow for determining woodcock migratory connectivity without biases due to uneven banding and hunting effort.

MANAGEMENT IMPLICATIONS

An improved understanding of between-region and within-region migratory connectivity can help managers recognize how range-wide population dynamics and conservation efforts may affect regional populations. Specifically, the weak within-region migratory connectivity suggests that habitat management in one area on the breeding, wintering, or migratory grounds could positively affect woodcock that use a broad extent of the connected grounds during the course of the annual cycle. A high proportion of woodcock cross between management regions. Consequently, many woodcock breeding in the Eastern region are affected by management decisions and hunting pressure within the Central Region. My result that many woodcock from separate regions of the breeding grounds mix on the wintering grounds has implications for the present two-region basis for woodcock management. Elucidating finer scale movement patterns among regions provides a basis for reassessing the boundaries to ensure optimal conservation and management of the species.

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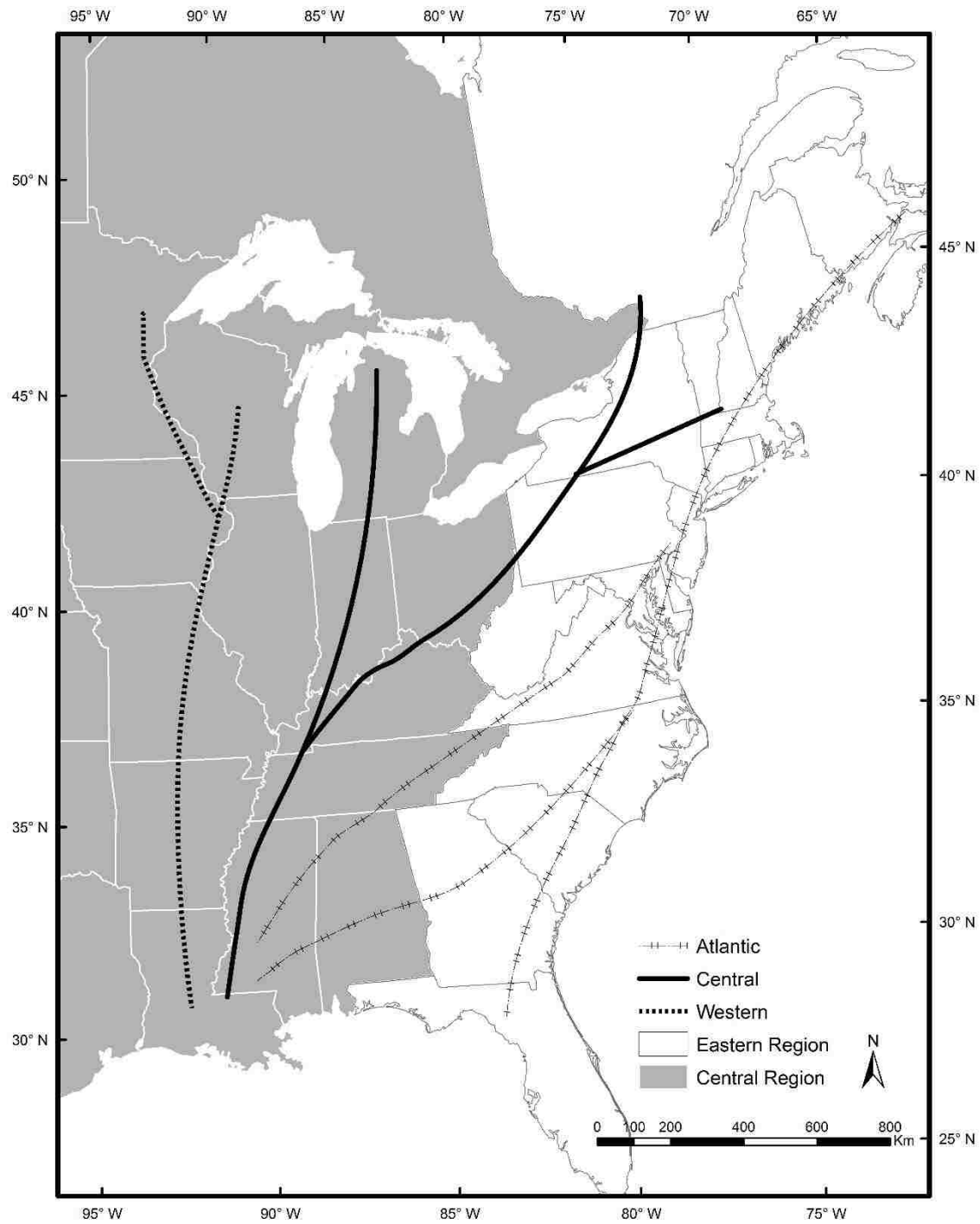


Figure 1. Glasgow's (1958) hypothesized migration routes of American woodcock overlaid on current Eastern and Central American woodcock Management Regions.

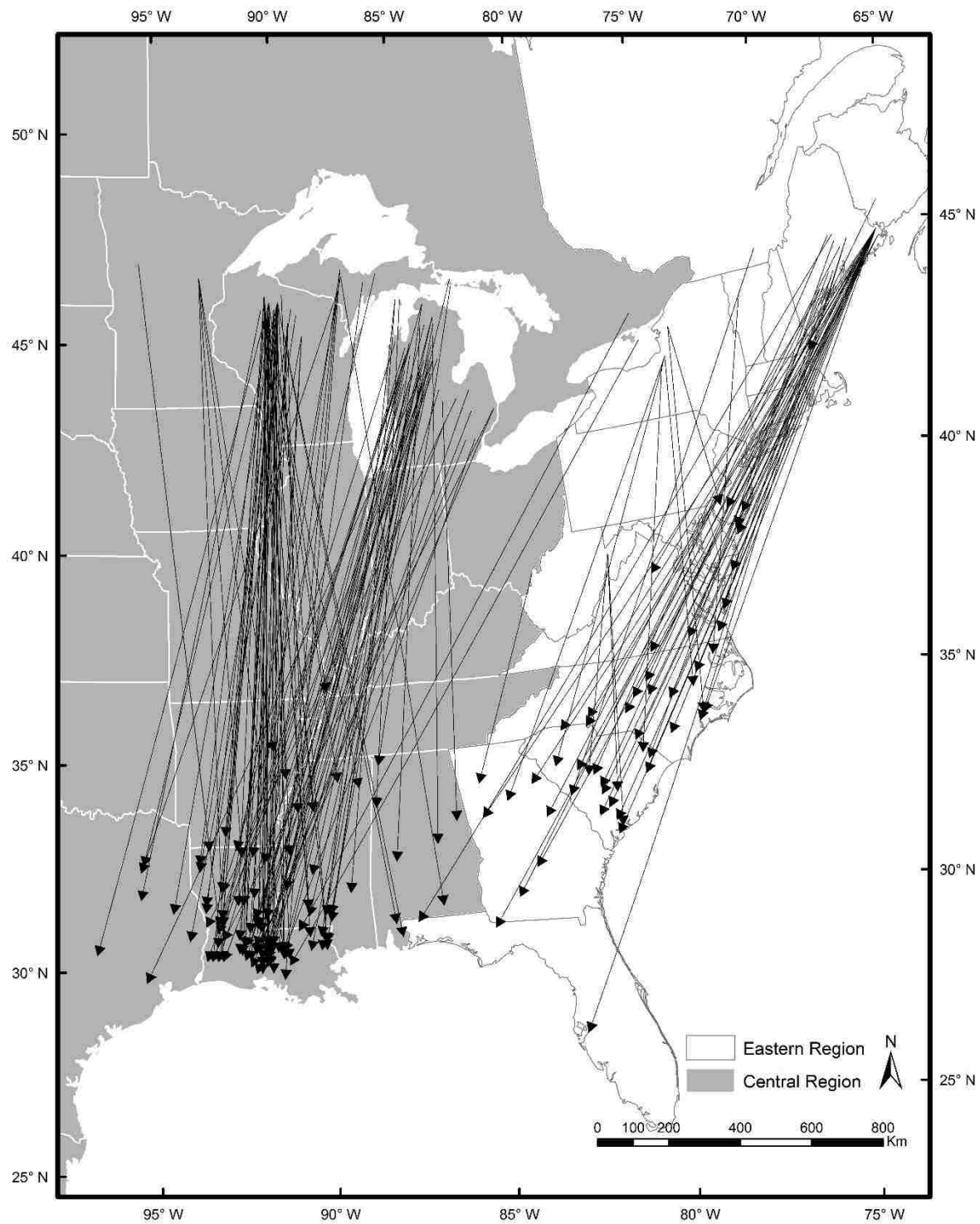


Figure 2. Within-management-region migration movements of American woodcock banded during the summer and encountered in the winter.

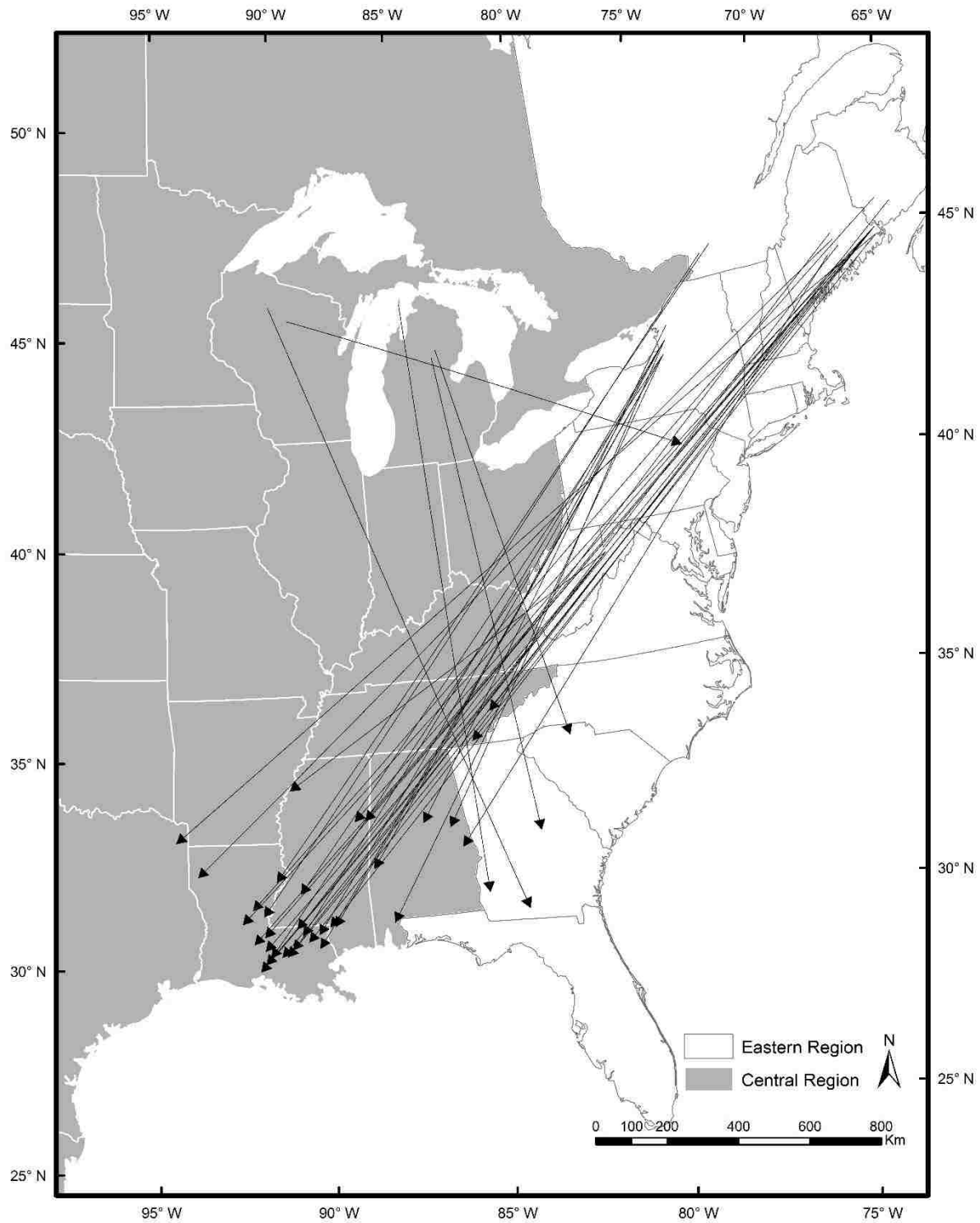


Figure 3. Between-management-region migration movements of American woodcock banded during the summer and encountered in the winter.

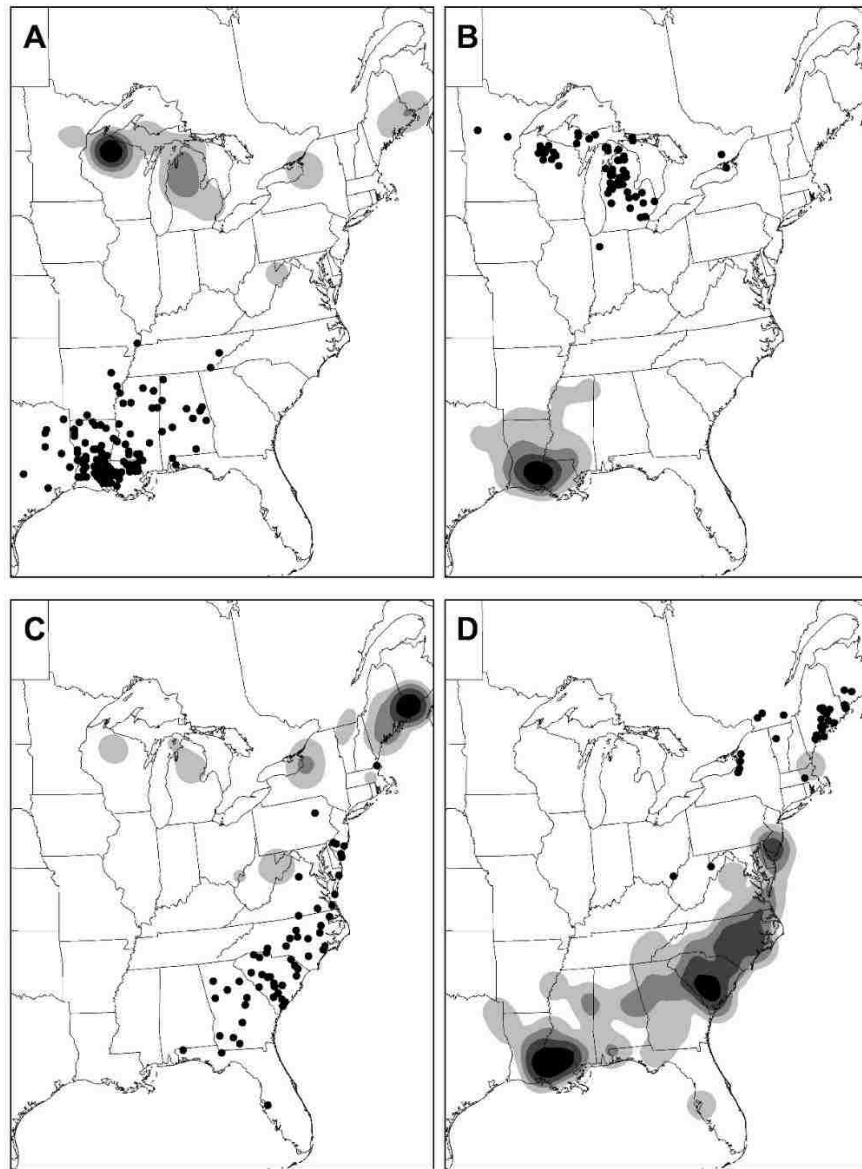


Figure 4. Kernel density estimates (KDE) of migratory origins and destinations of American woodcock banded during the summer and encountered in the winter. The density surface is categorized into five classes, with darker classes having a higher density of American woodcock records. A) KDE of woodcock banding locations that migrate to wintering locations in the Central Region. Points show wintering destinations. B) KDE of woodcock wintering locations that migrate from summer locations within the Central Region. Points show summer origins. C) KDE of woodcock banding locations that migrate to wintering locations in the Eastern Region. Points show wintering destinations. D) KDE of woodcock wintering locations that migrate from breeding locations within the Eastern Region. Points show summer origins.

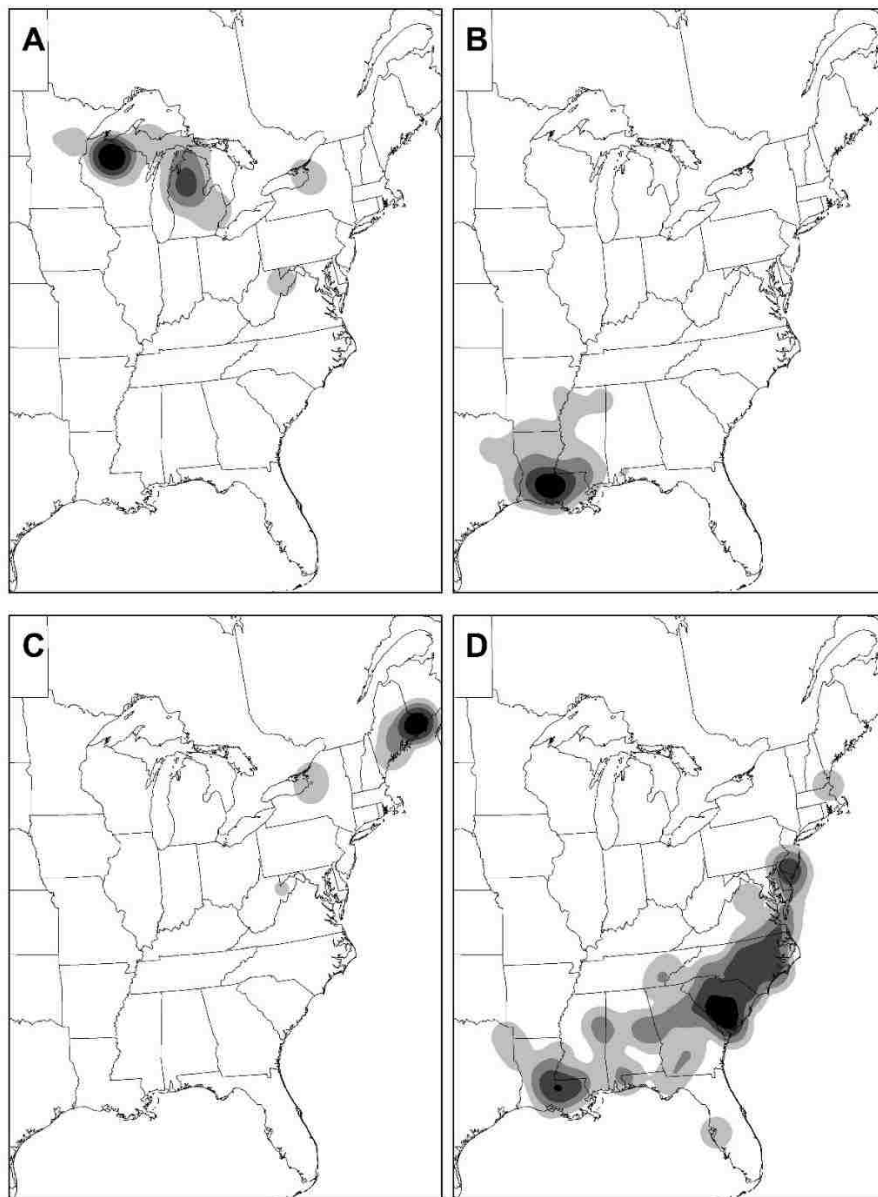


Figure 5. Kernel density estimates (KDE) of migratory origins and destinations of American woodcock banded during the summer and encountered in the winter. The density surface is categorized into five classes, with darker classes having a higher density of American woodcock records. American woodcock were divided into two groups based on clustering. The first cluster had breeding locations (A) and wintering locations (B) largely within the Central Region. The second cluster had breeding locations (C) largely within the Eastern Region and wintering locations (D) in both the Eastern Region and Central Region.

Table 1. American woodcock origins and destinations by management region during autumn migration and the amount of crossover between management regions during autumn migration, spring migration, and the total crossover including both seasons.

	<i>n</i>	Central	Eastern	% Crossover
Destination region of Eastern Region origin woodcock	87	33	54	37.9%
Destination region of Central Region origin woodcock	130	125	5	3.8%
Origin region of Eastern Region wintering woodcock	59	5	54	8.5%
Origin region of Central Region wintering woodcock	158	125	33	21.0%
Crossover in Autumn Migration	217	-	-	17.5%
Crossover in Spring Migration	7	-	-	28.6%
Total Crossover	224	-	-	17.9%

Table 2. Proportion of American woodcock from both the Central and Eastern Management Regions that migrate to destinations within either the Central or Eastern Management Regions during autumn migration

Banding Region	Total Banded	<u>Central</u>			<u>Eastern</u>		
		<i>n</i>	<i>p</i>	95% CI	<i>n</i>	<i>p</i>	95% CI
Central	56,266	124	0.98	0.95-1.00	5	0.02	0.00-0.05
Eastern	27,153	33	0.54	0.35-0.79	54	0.46	0.21-0.65

Table 3. Results of linear models and Mantel’s tests showing the relationship based on the longitude of breeding season sites and the longitude of wintering season sites of individual American woodcock banded during the summer and encountered in the winter.

	R²	P	R_M	P
Range-wide	0.46	<0.01	0.42	<0.01
Woodcock captured in the Central Region	0.02	0.10	-0.04	0.75
Woodcock captured in the Eastern Region	0.07	0.01	0.03	0.24
Woodcock encountered in the Central Region	0.11	<0.01	0.14	<0.01
Woodcock encountered in the Eastern Region	0.06	0.07	0.07	0.20

Chapter II

Migratory Connectivity and Migration Phenology of American Woodcock

Joseph D. Moore

ABSTRACT

As with many migratory birds, details about the migratory ecology of American woodcock (*Scolopax minor*) are largely unknown. Understanding the migratory connectivity and migration phenology of a species is important to understand the factors that influence survival and fitness over the full annual cycle. Traditional methods, including analysis of band return records, led to managing woodcock on the basis of an Eastern and a Central Management Region with management region boundaries analogous to those of the Atlantic and Mississippi Flyways. Advances in the miniaturization of satellite transmitters now allow remote tracking of woodcock. To investigate woodcock migratory connectivity and migratory phenology during spring and autumn migration, I deployed 75 satellite transmitters on woodcock, primarily in the Central Management Region of the United States. From 2014 through 2016, I documented migration paths of 61 individual woodcock and 88 autumn or spring woodcock migrations. Average migration duration was longer during spring migration (53 days) than during autumn migration (31 days) because woodcock made a higher number of close-together migratory stopovers, not because woodcock stayed at individual stopovers longer during spring migration. Woodcock captured in the Central Management Region used 2 primary migrations routes: a Western Route and a Central Route. The Western Route ran north-south, connecting the breeding and wintering grounds of the Central Management Region. The hourglass-shaped Central Route connected an area on the wintering grounds reaching from Texas to Florida, to sites throughout northeastern North America. Woodcock following the Central Route funneled between the Appalachian Mountains and the Mississippi Alluvial Valley in western Tennessee during both autumn and spring migration. A higher than anticipated percentage (36%, $n = 12$) of marked woodcock captured in Texas and Louisiana and monitored during spring migration migrated to breeding-

period sites in the Eastern Management Region, raising questions about the biological basis of managing woodcock as separate populations.

INTRODUCTION

The time, energy, and risks associated with migration mark the time transiting between the breeding grounds and winter grounds as a critical period for migratory birds (Alerstam and Lindström 1990, Colwell 2010:105). However, as with many migrants the migratory connectivity and migratory phenology of American woodcock (*Scolopax minor*, hereafter woodcock) remain poorly understood (McAuley et al. 1994). Migratory connectivity is defined as “the movement of individuals between summer and winter populations, including immediate stopover sites” (Webster et al. 2002:77). An appreciation of the migratory connectivity of a species is vital to understanding the movement of individuals between disparate areas throughout the annual cycle and how these movements influence regional population dynamics (Johnson et al. 1988, Taylor and Norris 2009, Taylor and Stutchbury 2016). This is especially important because woodcock populations have experienced range-wide, long-term population declines since the initiation of a standardized population survey in 1968 (Cooper and Rau 2015) and woodcock are subject to both harvest and natural mortality during the breeding period, wintering period, and throughout the migratory period. In addition, knowledge of migratory phenology (seasonal temporal patterns) is necessary to determine annual harvest pressure on woodcock across management regions and political boundaries (Blankenship 1957, Myatt and Kremetz 2007a).

Although woodcock habitat use on the breeding and wintering grounds is well documented, little is known about habitat use during migration (Case and Sanders 2010). To understand what factors influence decisions about where and how long to stop during migration,

it is useful to take a hierarchical, scale-dependent approach (Saab 1999, Buler et al. 2007). At the geographic scale, birds may choose a region to stop during migration based on factors other than habitat, e.g., a stopover site may be along a predetermined migration route (Hutto 1985), constrained by geographical barriers (e.g., a bird may choose to rest before crossing a large body of water), or be influenced by weather events (Buler et al. 2007). At the landscape scale, stopover site selection may be influenced by the available cover type and patch dynamics (Moore et al. 2005), whereas at the local scale birds may choose foraging locations based on food availability (Buler et al. 2007).

Previously, woodcock migration has been studied using radio-telemetry (Krementz et al. 1994, Myatt and Krementz 2007*b*, Meunier et al. 2008), band returns (Glasgow 1958, Coon et al. 1977), phylogenetics (Rhymer et al. 2005), and stable isotopes (Sullins et al. 2016). These studies have provided insight into woodcock migration; however, previous studies were limited by either focusing on a single geographic area, being unable to provide information on >1 relocation per individual or by only providing information on large-scale geographic movements. Advances in the miniaturization of satellite transmitters, or Platform Transmitter Terminals (PTTs), now allow remote tracking of smaller birds including woodcock. These devices facilitate much more detailed understanding of migratory connectivity, migratory phenology, and stopover site selection because they allow for multiple relocations of the same individual over the full annual cycle without geographic constraints. My objective was to use satellite telemetry to characterize the spring and autumn migration of woodcock. Specifically, I: (1) investigated migratory connectivity including migratory routes and major stopover regions, (2) documented migratory phenology and other characteristics of migration such as distance traveled during

migration, and (3) investigated whether there was variation based on age, year, or season for these variables.

STUDY AREA

Woodcock are found throughout eastern North America and are managed on the basis of an Eastern and a Central Management Region. Management region boundaries are analogous to those of the Atlantic and Mississippi Flyways (Fig. 1). I captured the majority of woodcock within the United States portion of the Central Management Region, with the exception of two woodcock captured at a site in the Eastern Management Region (New Jersey). I captured woodcock at sites during the breeding and wintering periods except for 1 woodcock likely caught during migration in northwestern Arkansas (Fig. 1). I captured woodcock at 21 sites in Arkansas, Louisiana, Michigan, Minnesota, New Jersey, Texas, and Wisconsin between September 2013 and February 2016 (Table 1). To represent woodcock across the breeding-period and nonbreeding-period distribution within the Central Management Region, I captured woodcock across a large area in the northern and southern portion of the Central Management Region within the United States and chose specific capture sites that would facilitate woodcock capture. In addition to woodcock capture sites, my study area included the locations to which PTT-marked woodcock migrated, including portions of the Eastern Management Region.

METHODS

Capture

I trapped woodcock using spotlights and hand-nets at night both while on foot and from all-terrain vehicles; I also trapped woodcock using mist-nets during the crepuscular period (McAuley et al. 1993) and captured 1 woodcock with a hand-net and a trained pointing dog

during daylight. I tagged woodcock close to the initiation of migration to reduce the risk of mortality or transmitter failure before migration began. In the winter, I captured woodcock between 5 January and 16 February (with the exception of 1 woodcock captured in Arkansas on 10 March). In the autumn, I captured woodcock between 18 September and 3 November. I aged, sexed, and weighed all captured woodcock (Martin 1964) and I banded all captured woodcock with a U.S. Geological Survey-issued aluminum band. I attached satellite transmitters using a modified thigh harness where the PTT rested on the synsacrum, secured by loops over each leg (Rappole and Tipton 1991, Streby et al. 2015). I constructed PTT harnesses with two strands of 0.7 mm Stretch Magic elastic plastic cord (Pepperell Braiding Company, Pepperell, Massachusetts, USA) threaded through Tygon tubing (Hughes et al. 1994) and crimped with metal rings. I performed this study under the auspices of the Institutional Animal Care and Use Committee (IACUC) at the University of Arkansas, protocol # 15011, and the IACUC at the University of Minnesota, protocol # 1408-31777A.

Transmitters

I tracked woodcock using 3 types of PTTs: a 9.5-g PTT, a 5-g PTT, and a 4.9-g GPS PTT. The 9.5-g and 5-g PTTs (Microwave Telemetry, Columbia, MD) were solar-powered and transmitted messages on a 10-hour-on and 48 hour-off-duty cycle. The Argos Data Collection and Location System (Service Argos Inc., Landover, Maryland, USA) collected woodcock locations for these PTTs. This system used instruments flown on polar-orbiting satellites to estimate woodcock locations using the Doppler shift of transmissions originating from the PTTs (Argos 2016). Associated with each location was a location class (LC) that provides estimated error. Reported location errors were: LC 3, <250 m; LC 2, 250–500 m; LC 1, 500–1,500 m; LC 0, >1,500 m; LC A, No estimation; LC B, No estimation (Argos 2016). These PTTs had

auxiliary sensors that provided information on temperature, voltage, and activity. I censored location data from the PTTs when the auxiliary sensors indicated that the tag was no longer moving and the temperature had dropped to ambient, or when I stopped receiving messages from a PTT. The battery powered 4.9-g GPS PTTs (Lotek Wireless, Newmarket, Ontario, Canada) had only enough charge to collect 30 locations along one migration path. Before deployment, I programmed the times and dates these 30 GPS locations would be collected. After collecting the GPS locations, the tag attempted to transmit all the location data to the Argos system on a 6-hour-on and 6-hour-off duty cycle. The Argos system used Doppler shift to collect additional locations while the GPS PTTs transmitted GPS locations. In autumn 2015, I programmed the GPS transmitters to record 1 location every 3 days between 18 October and 19 January. In spring 2016, I programmed the GPS transmitters to record 1 location 24 January, 1 location 31 January, a location every 3 days from 7 February to 1 May, and a final location on 8 May. Though our transmitters had off periods of 48 hours, 72 hours, or 1 week, we often had larger gaps between observations. A possible cause of these gaps was that the thick cover used by woodcock prevented the solar-powered transmitters from charging or prevented both types of transmitters from successfully transmitting or receiving messages from a satellite. Transmitter mass did not exceed 5% of the individual's body mass (I received an exception from the U.S. Geological Survey Bird Banding Laboratory to exceed the usual 3% body mass restriction). I deployed 9.5-g PTTs only on females weighing > 200 g. I deployed 5-g PTTs and 4.9-g GPS PTTs on males and females weighing > 150 g.

Data Analysis

I used the *movebank* tracking data map (Kranstauber et al. 2011, Wikelski and Kays 2016) to identify clusters of location points and to classify them as migratory stopovers,

wintering sites, or breeding-period sites. I defined the first wintering site as a site where a woodcock remained for > 25 days and had no further movement over 50 km southward. I defined subsequent sites as wintering sites until northward movement began. I defined the first breeding-period site as a site where a woodcock remained for > 25 days and had no further movement over 50 km northward. I defined subsequent sites as breeding-period sites until southward movement began. I classified sites between breeding-period and wintering sites as migratory stopovers. I mitigated the influence of implausible Argos locations by only using clusters of ≥ 2 successive Argos locations to define stopover sites. I used location proximity, time lag between locations, and Argos location class to determine whether locations were clustered under the assumption “that accurate locations obtained during a period when the animal has moved little will cross-validate one another” (Douglas et al. 2012:6, i.e., spatial and temporal autocorrelation confirm the validity of locations). Because woodcock migrate nocturnally, I classified single diurnal GPS locations as stopovers, but I only classified clusters of ≥ 2 nocturnal GPS locations as stopovers. I determined the coordinates of each stopover by taking the median center of all locations within the cluster (Arizaga et al. 2014).

I determined the date of initiation for spring and autumn migration by using the median date between the last known location at the breeding-period or wintering site and the first migratory location (Arizaga et al. 2014, Olson et al. 2014). I determined the date of arrival at a breeding or wintering site by using the date midway between the last known migratory location and the first location at a breeding-period or wintering site. I did not consider arrival or departure dates where the gap between the last known location at a site and the first migratory location was > 10 days (Martell et al. 2001, Arizaga et al. 2014, Olson et al. 2014). I determined the duration of migration using the period between the date of migration initiation and the arrival date and I

excluded migration durations where the amount of uncertainty in migration duration was > 10 days. I determined the number of days spent at a stopover as the period between the first and last locations recorded at that site. Because transmitters typically had 48-72 hours “off” duty cycles, and because of additional gaps from transmitters missing “on” duty cycles, the number of days at each stopover represents a minimum number of days. In addition, there may have been stopovers that I was not able to record or account for; therefore, the number of stopover sites identified is a minimum.

I determined the distance traveled during autumn migration as the great-circle distance (the shortest distance between 2 points along the surface of a sphere) between the last breeding-period site, all known stopover sites, and the first wintering site. I determined the distance traveled during spring migration as the distance between the last wintering site, all known stopover sites, and the first breeding-period site. The total migration distance represents a minimum possible distance because each woodcock may have made more stopovers than recorded and did not necessarily make straight-line movements between transmitter-derived locations. I determined the net displacement during autumn migration as the distance between the last breeding-period site and the first wintering site. I determined the net displacement during spring migration as the distance between the last wintering site and the first breeding-period site. I determined the rate of migration by dividing the net displacement by the duration of migration. I excluded records of distance, net displacement, rate, and the number of stopovers from the analysis if I was unable to document a complete migration path (i.e., if a woodcock had an undetermined origin or final destination). If I had data for multiple spring or autumn migrations for an individual woodcock, I used only the first recorded instance of a migration metric to avoid pseudoreplication. I tested for the effects of age, year, and season on migration initiation date,

migration end date, migration duration, number of stopovers during migration, rate of migration, net displacement between the start and end of migration, stopover duration, and the distance between stopovers using one-way ANOVA. I tested for sex effects in both spring and autumn migration, but tested for age effects only during spring migration and year effects only between spring 2015 and spring 2016 (excluding spring 2014) due to small group sample sizes. I used $\alpha = 0.10$ for the significance of statistical tests because of the small group sample sizes and the observational rather than experimental nature of this study.

I visualized geographic areas with high densities of migratory stopovers using the kernel density tool in ArcMap 10.3 (ESRI, Inc.). I used a search radius of 150 km and a grid size of 10 x 10 km. I created separate kernel density estimates for autumn migration stopovers, spring migration stopovers, and an aggregate of stopovers among individuals from both autumn and spring migration. For spring and autumn stopover regions, I only included stopover sites from the first autumn or spring of the first year if I monitored a woodcock for multiple years. For the aggregate kernel density estimate combining spring and fall migrations, I only included stopover sites from the first year and season if I monitored a woodcock for multiple years or seasons. I used natural breaks (Jenks 1967) to classify and symbolize each kernel density estimate into 5 categories based on stopover density.

I visualized migration routes, i.e. collections of concentrated migration paths, using the line density tool in ArcMap 10.3 (ESRI, Inc.). I used a search radius of 75 km and a grid size of 10 x 10 km. I created separate line density estimates for autumn migration, spring migration, and for spring and autumn migration combined. For autumn migration, I only included autumn migration paths from woodcock captured during the breeding period. For spring migration, I only included spring migration paths from woodcock captured during the wintering period. For

spring and autumn migration, I only included paths from the first autumn or spring of the first year in which a woodcock was monitored. For the aggregate of spring and fall migrations, I only included path from the first year and season if I monitored a woodcock during multiple years or seasons. I used natural breaks (Jenks 1967) to classify and symbolize each line density estimate into 5 categories based on path density.

To model the distribution of woodcock relocations by latitude and date for autumn and spring migration, I created a subset of all location points containing only 1 location per transmitter duty cycle using the Douglas-Argos filter (Douglas et al. 2012). For autumn migration I further filtered this dataset to only include the last known breeding-period location (this location was removed if it was before 1 October), all autumn locations, and the first winter location. For spring migration, I filtered the dataset to include only the last known wintering location, all spring locations, and the first breeding-period location. For each migration season, I fitted a smoothed line using local polynomial regression fitting on latitude vs. date using the *loess* function in R (R Core Team 2016) with the default smoothing parameter of 0.75.

RESULTS

I tagged 75 woodcock between September 2013 and February 2016 (Fig. 1) and deployed transmitters on 55 females (Adult: $n = 25$, Juvenile: $n = 30$) and 20 males (Adult: $n = 8$, Juvenile $n = 12$, Table 1) using 44 9.5-g PTTs, 10 5-g PTTs, and 21 4.9-g GPS PTTs (Table 2). I monitored woodcock during autumn migration in 2013, 2014, and 2015 and I monitored woodcock during spring migration in 2014, 2015, and 2016. I monitored the migration paths of 61 individual woodcock (Fig. 2) and documented 67 complete migrations (migrations in which both the breeding and wintering sites were known) and 21 partial migrations (some migration data, but the migratory origin and/or destination were unknown, Table 3).

Autumn Migration

During 2013, 2014, and 2015 I documented the autumn migration paths of 30 individual woodcock; 26 females (16 adult, 10 juvenile) and 4 males (1 adult, 3 juvenile; Table 1). I monitored all woodcock during 1 season, except for 1 woodcock that I monitored in both 2013 and 2014, for 31 total migration paths (Fig. 2), which included 23 complete migration paths and 8 partial migration paths. Autumn migration data were from woodcock tagged in Michigan ($n = 8$), Minnesota ($n = 8$), and Wisconsin ($n = 3$, Table 4) prior to autumn migration and the autumn migrations of woodcock tagged in Texas ($n = 3$) and Louisiana ($n = 8$) that had migrated in spring to Maine ($n = 1$), New Brunswick ($n = 1$), New York ($n = 1$), Ontario ($n = 3$), Quebec ($n = 1$), Vermont ($n = 2$), and Wisconsin ($n = 2$).

Migration Paths

Woodcock captured in Minnesota with complete autumn migration paths ($n = 6$) migrated southward through Iowa and Missouri to winter sites in Arkansas ($n = 2$), Louisiana ($n = 1$), and Texas ($n = 3$). Two woodcock captured in Minnesota were censored (unknown fate) during autumn migration after reaching locations in Missouri and Tennessee. Woodcock captured in Wisconsin and a nearby site in the Upper Peninsula of Michigan with complete fall migration paths ($n = 6$) migrated either southwest to winter sites in Arkansas ($n = 1$) and Texas ($n = 1$), or southeast to winter sites in Alabama ($n = 1$), Mississippi ($n = 1$), and Florida ($n = 2$). Woodcock captured prior to fall migration in the Lower Peninsula of Michigan with complete migration paths ($n = 5$) migrated either southwest to winter sites in Arkansas ($n = 1$) and Texas ($n = 1$) or south to winter sites in Alabama ($n = 2$) and Mississippi ($n = 1$). Overall, 15 woodcock migrated to winter sites in the Central Management Region and 2 woodcock migrated to winter sites in the Eastern Management Region. I monitored 1 woodcock both in autumn 2013 and in autumn 2014;

this woodcock had a similar migration path both years. That woodcock and 5 other woodcock captured during the breeding-period had 2 known winter sites, each from a different year. For 3 of these woodcock, the center of the winter sites were < 1 km apart between years, 1 woodcock had winter sites approximately 5 km apart between years, and 2 woodcock had winter sites that were between 50 and 100 km apart between years (Table 5)

Woodcock breeding in the Central Management Region showed 2 primary migration routes, a Western and a Central Route (Fig. 3). Woodcock that used the Western Route moved south to Arkansas, Louisiana, and Texas with main stopover regions (Fig. 3) in southwest Iowa, central Missouri, the Arkansas Ozarks, and depending on winter destination, the northeast corner of Texas or the western edge of the Louisiana portion of the Mississippi Alluvial Valley (MAV). Woodcock using the Central Route moved southeast from Wisconsin, Minnesota, and the Upper Peninsula of Michigan and south from Lower Michigan to Alabama, Florida, and Mississippi with concentrations of stopovers in northern Illinois, southwestern Ohio, and the central hardwoods area of Kentucky and Tennessee west of the Appalachian Mountains.

Migration Phenology and Movement Patterns

The mean autumn departure date was 3 November (SE = 2.0, $n = 21$, Table. 6) and there was no age effect ($F_{1, 19} = 2.30$, $P = 0.146$) on departure date. The mean arrival date to a wintering site was 6 December (SE = 3.8, $n = 17$) and juveniles (15 December, SE = 8.3, $n = 6$) arrived at wintering sites later than adults (30 November, SE = 3.1, $n = 11$; $F_{1, 15} = 4.22$, $P = 0.058$). The mean duration of autumn migration was 31.2 days (SE = 4.0, $n = 17$) with a range of 9 to 68 days and there was no age effect ($F_{1, 15} = 1.92$, $P = 0.186$) on the mean duration of autumn migration. Monitored woodcock progressed southward at a constant rate through autumn migration (Fig. 4) and averaged 2.4 stopovers (SE = 0.4, $n = 22$) with a mean distance of 456 km

(SE = 40 n = 93) between stopover sites. There was no age effect on the number of stopovers ($F_{1, 20} = 0.01$, $P = 0.917$) or on the mean distance between sites ($F_{1, 91} < 0.01$, $P = 0.979$). The mean minimum duration at a stopover site was 5.1 days (SE = 0.7, n = 68) and juveniles (9.1 days, SE = 2.5, n = 14) stayed at stopovers longer than adults (4.1 days, SE = 0.6, n = 54; $F_{1, 66} = 8.60$, $P = 0.005$). Monitored woodcock had a mean net displacement of 1,612 km (SE = 81, n = 22), and traveled at a rate of 69.1 km per day (SE = 9.4, n = 17) and there were no age effects on net displacement ($F_{1, 20} = 1.62$, $P = 0.218$) or migration rate ($F_{1, 15} = 0.57$, $P = 0.461$).

Spring Migration

During 2014, 2015, and 2016 I monitored spring migration paths of 49 individual woodcock; 37 females (16 adult, 21 juvenile) and 12 males (4 adult, 8 juvenile; Table 1). I monitored 41 woodcock during 1 spring migration and 8 woodcock during 2 spring migrations for 57 total migration paths (Fig. 2), which included 44 complete migration paths and 13 partial migration paths. Spring migration paths were from woodcock tagged in Arkansas (n = 1), Louisiana (n = 31), New Jersey (n = 1), and Texas (n = 9, Table 7) and the spring migrations of woodcock tagged in Michigan (n = 3) and Minnesota (n = 4) that had migrated during autumn to Alabama (n = 1), Arkansas (n = 1), Louisiana (n = 1) and Texas (n = 4).

Migration Paths

Nine woodcock captured in Texas had complete migration paths and most of these woodcock (n = 7) migrated northward through Arkansas to breeding-period sites in Manitoba (n = 1), Minnesota (n = 1), Missouri (n = 2), western Ontario (n = 2) and South Dakota (n = 1). Two woodcock captured in Texas migrated northeast to eastern Ontario (n = 1) and New York (n = 1). One woodcock captured in Arkansas migrated northwest into Kansas before being

censored. Nine woodcock captured in Louisiana west of the MAV had complete migration paths and 4 had partial migration paths. Four of these woodcock with complete migration paths migrated generally northward through Arkansas to breeding-period sites in Minnesota ($n = 1$), western Ontario ($n = 2$), and the Upper Peninsula of Michigan ($n = 1$), and 1 woodcock with a partial migration path was censored in Minnesota. The remaining 5 woodcock with complete migration paths captured in Louisiana west of the MAV migrated northeast to breeding-period sites in New Hampshire ($n = 1$), eastern Ontario ($n = 2$), and Quebec ($n = 2$) and 3 partial migration paths ended in Illinois ($n = 1$), Michigan ($n = 1$), and Mississippi ($n = 1$). Fifteen woodcock captured in the Louisiana portion of the MAV migrated to breeding-period sites in Maine ($n = 2$), Michigan ($n = 3$), New Brunswick ($n = 1$), Ontario ($n = 2$), Pennsylvania, ($n = 1$), Quebec ($n = 2$), Vermont ($n = 2$), and Wisconsin ($n = 2$) and 3 partial spring migration paths ended in Iowa ($n = 1$), Kentucky ($n = 1$), and Missouri ($n = 1$). Most ($n = 14$) of the 18 woodcock captured in the MAV migrated through western Mississippi into Tennessee before spreading out to their breeding-period sites. Of the remaining 4 woodcock, 1 migrated along the east side of the Appalachian Mountains to a breeding-period site in Maine, 1 made a stopover on the west side of the MAV in Arkansas before completing spring migration in Vermont, and 2 had no recorded stopovers early in spring migration and their migration paths were unclear. One woodcock captured in New Jersey had a partial migration ending in Pennsylvania. Overall, 21 woodcock migrated during spring to breeding-period sites in the Central Management Region and 12 woodcock migrated to breeding-period sites in the Eastern Management Region. Most woodcock captured in Texas (89%) migrated to breeding-period sites in the Central Management Region, whereas just over half of woodcock captured in Louisiana (54%) remained in the Central

Management Region. Of these tagged woodcock, 45% ($n = 15$) of tagged woodcock migrated to breeding-period sites in Canada.

There were sufficient data from 7 woodcock to compare spring migration paths between years. Six woodcock had similar spring migration paths between years and the only woodcock that used different migration paths between years migrated from Louisiana to Maine on the east side of the Appalachian Mountains during spring 2014, had no recorded locations in the following autumn and winter, and then migrated on the west side of the Appalachian Mountains during spring 2015. I documented 2 years of breeding-period sites for 11 woodcock. Six of these woodcock had centers of their breeding-period sites < 1.5 km apart between years. One woodcock had successive breeding-period sites approximately 25 km apart between years and 4 had successive breeding-period sites that were between 200 and 1,000 km apart between years (Table 5).

I observed 2 primary migration routes north from sites in Texas and Louisiana (Fig. 3), a Western Route and a Central Route. The Western Route went from Texas and the portion of Louisiana west of the MAV north through Arkansas and Missouri before ending at breeding-period sites west of Lake Michigan. A main stopover region along this route extended from the Arkansas Ouachita Mountains to the southern border of Iowa, with the highest concentration of stopovers in the Arkansas Ozarks and in northern Missouri (Fig. 3). A second area with a high concentration of stopovers was along the Mississippi River on the border between Wisconsin and Minnesota. The Central Route was used by most woodcock that wintered in the Louisiana portion of the MAV and by some of the woodcock that wintered west of the MAV in Louisiana and Texas. This route followed the eastern edge of the MAV through Mississippi into Tennessee before ending at breeding-period sites in areas extending from Wisconsin to New Brunswick. A

main stopover region along this route extended from northern Mississippi through western Tennessee, western Kentucky, and the bootheel of Missouri, with a lower density of stopover sites extending north into southern Illinois and Indiana. Other areas with high stopover-site density included northeastern Wisconsin, along the southern shoreline of Lake Michigan (with the highest density near Chicago), northern Michigan, and along the western half of the border between New York and Pennsylvania.

Migration Phenology and Movement Patterns

The mean departure date for spring migration was on 23 February (SE = 1.6, $n = 41$, Table. 8) and juveniles (27 February, SE = 2.01, $n = 23$) departed later than adults (18 February, SE = 2.21, $n = 18$; $F_{1,39} = 9.98$, $P = 0.003$). Transmitter-marked woodcock departed on spring migration earlier in 2016 (22 February, SE = 1.85, $n = 25$) than in 2015 (28 February, SE = 3.67, $n = 12$; $F_{1,35} = 3.29$, $P = 0.078$) and arrived at breeding-period sites on average on 17 April (SE = 3.6, $n = 37$) with no age ($F_{1,35} = 0.19$, $P = 0.670$) or year effect ($F_{1,31} = 1.36$, $P = 0.252$). The mean duration of spring migration was 53.2 days (SE = 3.8, $n = 37$) with a range of 16 to 91 days. There was no age effect ($F_{1,35} = 0.39$, $P = 0.538$) or year effect ($F_{1,31} = 0.03$, $P = 0.858$) on spring migration duration. Transmitter-marked woodcock moved northward at a constant rate throughout spring (Fig. 5). The mean minimum number of stopovers was 6.0 (SE = 0.6, $n = 40$) with a distance of 301 km (SE = 15, $n = 303$) between sites and there was no age or year effect on number of stopovers (Age: $F_{1,38} = 0.56$, $P = 0.461$; Year: $F_{1,34} = 0.07$, $P = 0.796$) or on the distance between stopover sites (Age: $F_{1,301} = 1.92$, $P = 0.167$; Year: $F_{1,271} < 0.01$, $P = 0.976$). The mean minimum duration at a stopover site was 5.9 days (SE = 0.5, $n = 254$) with no age effect ($F_{1,252} = 0.09$, $P = 0.771$) or year effect ($F_{1,226} = 0.68$, $P = 0.412$). Woodcock had a mean net displacement of 1,898 km (SE = 71, $n = 40$), and traveled at a rate of 41.4 km per day (SE =

2.9, $n = 37$) and there were no age or year effects on net displacement (Age: $F_{1, 38} = 0.14$, $P = 0.708$; Year: $F_{1, 34} = 0.45$, $P = 0.505$) or migration rate (Age: $F_{1, 35} = 0.39$, $P = 0.537$, Year: $F_{1, 31} = 0.11$, $P = 0.742$).

Differences between autumn and spring migration

Migration Paths

I observed both autumn and spring migration paths from 18 woodcock; I captured 7 of these woodcock in the autumn and 11 in the winter. There were sufficient data to compare autumn and spring migration paths from 12 of the 18 woodcock with both autumn and spring migration records. Six of these had similar migration paths in both autumn and spring, and 6 had paths that differed substantively between autumn and spring migration. One woodcock migrated through the northwest corner of Ohio on its way from Louisiana to Vermont in the spring, but in the autumn returned through southern Ohio. A second woodcock migrated through northwestern Pennsylvania, crossing the Appalachian Mountains in New York, on its way from Louisiana to New Brunswick in the spring. Then, in the autumn, this woodcock followed the Atlantic Ocean coast to New Jersey and crossed the Appalachian Mountains in West Virginia. The following spring, this same bird again migrated through northwestern Pennsylvania and New York. A third woodcock migrated through Tennessee and Kentucky on its way from Texas to New York in spring 2015 and 2016. In the autumn of 2015, however, it returned through Missouri. A fourth woodcock migrated through Iowa during autumn 2015 on its migration from Minnesota to Arkansas and returned to Minnesota the following spring through Illinois, Indiana, and Wisconsin. A fifth woodcock migrated through western Missouri on its way from Minnesota to Texas in autumn 2015 and then returned the following spring to Minnesota through eastern Missouri and Illinois. The final woodcock for which I monitored sequential migrations migrated

in spring 2014 from Louisiana, along the west side of the Appalachian Mountains, and then crossed the Appalachian Mountains in northwestern Pennsylvania and New York to a breeding-period site in Maine. In the autumn of 2015, it migrated along the east side of the Appalachian Mountains to the border of North Carolina and Virginia before being censored.

Migration Phenology and Patterns

Overall, the duration of spring migration (53.2 days, SE = 3.8 $n = 37$) was longer than the duration of autumn migration (31.2 days, SE = 4.0, $n = 17$, $F_{1, 52} = 12.66$, $P < 0.001$) and there was a slower rate of migration in spring (Spring: 41.4 km/day, SE = 2.9, $n = 37$; Autumn: 69.1 km/day, SE = 9.4, $n = 17$, $F_{1, 52} = 13.41$, $P < 0.001$). The longer migration duration was influenced by woodcock making more stopovers in the spring (Spring: 6.0, SE = 0.6, $n = 40$; Autumn: 2.4, SE = 0.4, $n = 22$, $F_{1, 60} = 16.81$, $P < 0.001$) that were closer together (Spring: 301 km, SE = 15, $n = 303$; Autumn: 456 km, SE = 40, $n = 93$, $F_{1, 394} = 20.32$, $P < 0.001$). However, there was no difference in the stopover duration between spring and fall migration (Spring: 5.9 days, SE = 0.5, $n = 254$; Autumn: 5.1 days, SE = 0.7, $n = 68$, $F_{1, 320} = 0.69$, $P = 0.406$).

DISCUSSION

Previous studies inferred woodcock migration routes using band-return data and aerial very high frequency telemetry (Glasgow 1958, Sheldon 1967, Myatt and Krementz 2007b). These methods usually allowed only 2 locations per individual, the point of banding or tagging and the point of relocation. Therefore, there were 2 possible outcomes. Either the migratory origin and destination of an individual were known, but the path and stopovers used were unknown; or, the origin and a single stopover of an individual were known, but the ultimate migratory destination was unknown. Remote tracking of woodcock with PTTs facilitated a much

more detailed understanding of woodcock migration routes because PTTs allowed for multiple relocations of the same individual over the full annual cycle without geographic constraints.

Glasgow (1958) and Sheldon (1967) proposed 3 primary woodcock migration routes: Western, Central, and Atlantic (Fig. 6). Glasgow's proposed Western Route starts in the wintering grounds of Texas and Louisiana. Heading north, woodcock use disparate routes through Arkansas and Missouri before converging on and following the Mississippi River. Woodcock then diverge towards their breeding-period sites in Minnesota and Wisconsin. I observed a similar route used by woodcock captured in Texas, Louisiana (west of the MAV), Minnesota, Wisconsin, and Michigan's Upper Peninsula (Fig. 3). As an addition to Glasgow's Western Route, I also observed diffuse movement through Iowa and many woodcock continued farther north to breeding-period sites in Ontario and Manitoba (Fig. 3). Monitoring woodcock captured on the wintering grounds enabled me to document this northern extension of the Western Route.

Myatt and Krementz (2007b) proposed a route similar to Glasgow's Western Route based on observations made using aerial radio telemetry of woodcock marked in Minnesota, Wisconsin, and the Upper Peninsula of Michigan. As an addition to this route, they proposed a Mississippi Route that branches south from the Western Route in the boot heel of Missouri and follows the eastern edge of the MAV into Missouri. I observed limited use of this route during spring migration. In addition, I observed a migration route that headed southeast from Wisconsin and the Upper Peninsula of Michigan to the portion of Tennessee between the MAV and the Appalachian Mountains and then spread out to wintering sites extending from Louisiana to Florida. Whereas both sections of this route (Wisconsin to Tennessee, and Tennessee to Alabama

and Florida) were previously undescribed, this route acts as an extension to Glasgow's Central Route.

Glasgow described the Central Route as heading north from Louisiana and Mississippi, crossing western Tennessee and Kentucky, continuing northeast parallel to the Ohio River, and then crossing Pennsylvania and New York into Quebec. Glasgow described additional spurs on this route as crossing New York to breeding-period sites in New England and the Maritime Provinces of Canada and as crossing Illinois and Ohio to breeding-period sites in Michigan. I documented extensive use of this Central Route by woodcock captured in the MAV, and I documented use to a lesser extent by woodcock captured in Texas and in Louisiana west of the MAV. In addition, I observed woodcock following this route to continue north to breeding-period sites in Ontario after crossing Lake Superior, Lake Huron, or Lake Erie. Satellite telemetry revealed the Central Route to be an hourglass-shaped route connecting an area on the wintering grounds reaching from Texas to Florida to sites throughout eastern North America, with western Tennessee as an important migratory corridor for woodcock using this route. Importantly, this route connects woodcock populations that winter in the Central Management Region to breeding-period populations in both the Central and Eastern Management Regions.

By capturing woodcock primarily in the Central Management Region, my sample did not include woodcock likely to use Glasgow's Atlantic Route, which runs between the Appalachian Mountains and the Atlantic Coast. However, I observed 1 tagged woodcock following the Atlantic Route; this woodcock's spring migration route from Louisiana followed the eastern edge of the Appalachian Mountains to a breeding-period site in Maine (Fig. 2). The high proportion of monitored woodcock that migrated to breeding-period sites in Canada during spring migration complements the high harvest derivation from the northern portion of the woodcock's range

found by Sullins et al. (2016) using stable isotopes. It is important to note that the routes described above are broad migration routes with many branches between them and spurs to spatially disparate breeding-period sites.

Although I observed and described general migration routes, there were a large number of migration destinations. Newton (2008:684–685) described this pattern where “birds from a small part of the breeding range can spread out to occur across a wide part of the winter range or vice versa” as fan migration. Fan migration has been previously observed in Peregrine Falcons (*Falco peregrinus*) tagged on the Gulf of Mexico (McGrady et al. 2002) during autumn and spring migration. Fan migration is in contrast to the more commonly displayed parallel migration in which the east-west distribution of individuals on the breeding grounds is maintained on the wintering grounds (Newton 2008). Whereas woodcock tagged during the breeding period in the Central Management Region largely remained within the Central Management Region during the wintering period, woodcock tagged during the wintering period in the Central Management Region migrated to breeding period sites in both the Eastern and Central Management Regions. The connectivity between management regions shown using PTTs contradicts band return studies showing <5% crossover between regions (Coon et al. 1977) that have been used as the biological justification for monitoring and managing woodcock as 2 populations.

The 377 migratory stopovers used by transmitter-marked woodcock in my sample were widely distributed throughout eastern North America, but not distributed randomly. There were regions with a higher density of migratory stopovers (Fig. 3), suggesting that some regions are more important to woodcock during migration than others. To some extent, these stopover regions may be determined by extrinsic (non-habitat) factors such as mountain ranges acting as

barrier to movement or by woodcock following rivers or other natural features during migration (Hutto 1985). For example, an area in northern Mississippi (Fig. 3) with high stopover density is approximately 300 to 400 km from our capture sites in Louisiana (Fig. 1), which was a frequently observed distance for a woodcock to travel in 1 night (Table. 8). This stopover region extends into western Tennessee and Kentucky and is bounded on the east by the Appalachian Mountains, which appear to act as a physical barrier that woodcock migrate around rather than migrate over. Additional examples of major stopover regions that may be due to extrinsic factors include western New York south of the Great Lakes and north of the Appalachian Mountains, the area along the southern edge of Lake Michigan, and the area along the Mississippi River in Illinois, Iowa, Michigan, and Wisconsin. Although extrinsic factors likely influence the location of migratory routes and stopover locations, intrinsic landscape habitat factors also influence where woodcock migrate and stop during migration (Moore et al. 2005). For example, along both the Western and Central Routes there are high stopover densities in the more forested regions such as northwestern Arkansas. This is in contrast to the low stopover densities observed in agriculturally dominated regions such as the Arkansas, Louisiana, and Mississippi portion of the MAV and central Illinois. This suggests that woodcock would make stopovers during migration in the low stopover density regions if suitable habitat became available, although the landscape-level factors that influence migratory stopover location are poorly understood.

The mean autumn departure date of 3 November was similar to the date of 28 October observed by Meunier et al. (2008) and the peak departure taking place in the first week of November by Sepik and Derleth (1993) and by Myatt and Krementz (2007a). Woodcock showed the same rate of fidelity to both wintering sites and breeding-period sites between years. In both periods, tagged woodcock returned to sites < 5 km from their previous site in the subsequent year

66.7% of the time. This a similar proportion to that found by Diefenbach et al. (1990) using band return data (1939-1960: males = 75%, females = 55%; 1962-1977: males = 57%, females = 67%).

Although the median stopover duration in both spring and autumn migration was 3 days, stopover duration was variable within seasons. Stopovers lasted for as long as 28 days in autumn and for as long as 43 days in the spring. This pattern of primarily shorter stopovers, intermixed with extended stopovers is similar to the minimum stopover durations ($n = 22$) between 1 and 14 days observed by Myatt and Krementz (2007*b*) using aerial telemetry. The extended stopovers during spring migration may have been a result of nest attempts during migration or due to waiting for more favorable weather conditions to continue northward movement (Taylor et al. 2016). Spring migration took longer than autumn migration because woodcock made more migratory stopovers during spring migration compared to autumn migration, not because woodcock stayed at individual stopovers longer in the spring. This behavior is in contrast to the majority of species, which show a shorter migration duration in the spring (Nilsson et al. 2013). Many migratory birds are thought to display a shorter spring migration as part of a competition for early arrival to the breeding grounds which is shown to enable higher reproductive performance (Kokko 1999, Moore et al. 2005). Piersma (1987) described hop, skip, and jump migration strategies based on whether an individual completes migration in a series of short flights with many stopovers or with long flights between infrequent stopovers. Woodcock made more migratory stopovers during spring migration (median = 6, max = 18) than in autumn migration (median = 2, max = 9). Woodcock exemplified a hopping migration strategy by taking multiple stopovers along a relatively short migratory distance during spring migration and either a hopping or skipping migration strategy during autumn migration. The short hops are

energetically favorable due to the high metabolic cost of transporting extra fat to fuel longer flights (Piersma 1987). Hops also allow migrants to assess environmental and phenological conditions during migration, and therefore adapt their migration rate to arrive at their destinations when conditions are right (Taylor et al. 2016). Woodcock begin to arrive at their breeding-period sites as early as March and April and winter conditions may persist during migration. Woodcock may adapt to adverse conditions encountered during migration, such as low temperature and snow cover, and choose to stopover instead of continuing northward. Adapting to local conditions may explain the slower migration rate and more frequent stopovers taken by woodcock during spring migration compared to autumn migration. Because woodcock depart the winter grounds early (Table 8) and display an energetically favorable hopping migration strategy during spring migration, they may arrive on the breeding grounds early with increased fitness compared to departing the wintering grounds late and making a less metabolically efficient migration with few stopovers. Though woodcock stand out from many other migrants by exhibiting a protracted spring migration (Nilsson et al. 2013), this behavior may be part of a similar competition to arrive on the breeding grounds early and in good physiological condition.

MANAGEMENT IMPLICATIONS

High stopover density regions along migration routes may represent areas that are important for migrating woodcock and low stopover density regions may represent areas where appropriate management may make habitat available for migrating woodcock. Managers should consider these regions when making land management and acquisition plans for migrating woodcock. Documenting woodcock migration routes provides an improved understanding of the connection between woodcock populations on the breeding and wintering grounds. I observed a

higher than expected proportion of woodcock travel from the Central Management Region to the Eastern Management Region during spring migration, raising questions about the biological basis of managing woodcock as 2 separate populations. Managers can use the observed dates of autumn migration initiation and arrival on winter grounds along with the scatterplot showing the latitude and date that tagged woodcock made migratory stopovers during migration to identify the periods in which woodcock migrate through individual states and the periods in which both migrating woodcock and woodcock yet to initiate migration are present. Depending on management goals, states can use these data to choose woodcock season dates within the framework established by the U.S. Fish and Wildlife Service to maximize the likelihood of woodcock being present or to minimize harvest on the local population.

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Table 1. The number of American woodcock captured and outfitted with a satellite transmitter between September 2013 and February 2016 by state, sex and age

State	Adult Female	Juvenile Female	Adult Male	Juvenile Male	Total
Arkansas	1	0	0	0	1
Louisiana	8	15	5	8	36
Michigan	5	2	2	2	11
Minnesota	5	3	0	0	8
New Jersey	0	2	0	0	2
Texas	4	7	1	2	14
Wisconsin	2	1	0	0	3
Total	25	30	8	12	75

Table 2. The number of 9.5-g PTTs, 5-g PTTs, and 4.9-GPS PTTs deployed on American woodcock between September 2013 and February 2016. Autumn denotes woodcock captured during September through November in Michigan, Minnesota, New Jersey, and Wisconsin. Winter denotes woodcock captured during January and February in Texas and Louisiana and 1 woodcock captured in Arkansas during March.

Season	9.5-g PTT	5-g PTT	4.9-g GPS PTT	Total
Autumn 2013	1	0	0	1
Autumn 2014	3	0	0	3
Autumn 2015	10	0	10	20
Winter 2014	5	0	0	5
Winter 2015	8	10	0	18
Winter 2016	17	0	11	28
Total	44	10	21	75

Table 3. The number of complete (migratory origin and destination are both known) and partial (some data for migration) migration routes of transmitter-marked American woodcock per season.

Season	Male	Female	Complete	Partial	Total
Autumn 2013	0	1	1	0	1
Autumn 2014	0	6	2	4	6
Autumn 2015	4	20	20	4	24
Spring 2014	0	5	4	1	5
Spring 2015	6	12	13	5	18
Spring 2016	8	26	27	7	34
Total	18	70	67	21	88

Table 4. Migratory destinations of transmitter-marked American woodcock captured in the autumn before the start of autumn migration with known wintering sites

Winter Destination	State Captured			Total
	Michigan	Minnesota	Wisconsin	
Alabama	3	0	0	3
Arkansas	1	2	1	4
Florida	0	0	2	2
Louisiana	0	1	0	1
Mississippi	2	0	0	2
Texas	2	3	0	5
Central Region	8	6	1	15
Eastern Region	0	0	2	2
Total	8	6	3	17

Table 5. The distance between breeding-sites between years and the distance between wintering sites between years for individual American woodcock marked with satellite transmitters.

ID	Age	Sex	Capture Date	State Captured	Destination	Distance between Breeding Sites (km)	Distance Between Wintering Sites (km)
Woodcock 1	Adult	Female	9/17/2013	Minnesota	Texas	0.8	5.7
Woodcock 2	Juvenile	Female	1/16/2014	Louisiana	Vermont	0.3	-
Woodcock 4	Juvenile	Female	1/16/2014	Louisiana	Maine	0.6	-
Woodcock 7	Juvenile	Female	10/1/2014	Minnesota	Louisiana	0.9	-
15TX01	Adult	Female	1/22/2015	Texas	Ontario	349.1	0.8
15LA04	Adult	Female	1/22/2015	Louisiana	New Brunswick	0.3	1.0
15TX02	Juvenile	Female	1/24/2015	Texas	Ontario	-	0.7
15TX06	Juvenile	Male	2/1/2015	Texas	New York	1.4	52.0
15LA11	Juvenile	Male	2/12/2015	Louisiana	Wisconsin	-	94.5
15UP01	Adult	Female	9/23/2015	Michigan	Texas	24.3	-
15MN01	Adult	Female	9/28/2015	Minnesota	Arkansas	0.7	-
15MI01	Adult	Female	10/6/2015	Michigan	Alabama	924.8	-
15MI03	Adult	Female	10/11/2015	Michigan	Texas	231.7	-
15MN02	Juvenile	Female	10/27/2015	Minnesota	Texas	337.9	-

Table 6. Migration departure date, arrival date at destination, migration duration, number of stopovers, rate of movement during migration, minimum distance traveled during migration, net displacement (distance between winter sites and breeding-period sites), stopover duration, and distance between stopover sites for American woodcock monitored during autumn migration in 2013, 2014, and 2015.

	Mean	95 % CI	Standard Error	Median	Min	Max	<i>n</i>
Departure	3 Nov	30 Oct – 7 Nov	2.0	4 Nov	14 Oct	21 Nov	21
Arrival	6 Dec	28 Nov – 14 Dec	3.8	3 Dec	21 Nov	9 Jan	17
Duration (Days)	31.2	22.7- 39.7	4.0	32	9	68	17
Number of Stopovers	2.4	1.5 - 3.3	0.4	2	0	9	22
Rate (km/day)	69.1	49.3 – 88.9	9.4	62.1	24.7	146.9	17
Minimum Distance (km)	1669	1496 - 1842	83	1622	1097	3094	22
Net Displacement (km)	1612	1444- 1780	81	1539	1097	2958	22
Stopover Duration (days)	5.1	3.7 - 6.6	0.7	3	1	28	68
Distance between Sites (km)	456	377 – 535	40	359	9	1987	93

Table 7. Migratory destinations of transmitter-marked American woodcock captured in the winter before the start of spring migration with known breeding-period sites.

Summer Destination	State Captured		Total
	Louisiana	Texas	
Maine	2	0	2
Manitoba	0	1	1
Michigan	4	0	4
Minnesota	1	1	2
Missouri	0	2	2
New Brunswick	1	0	1
New Hampshire	1	0	1
New York	0	1	1
Ontario	6	3	9
Pennsylvania	1	0	1
Quebec	4	0	4
South Dakota	0	1	1
Vermont	2	0	2
Wisconsin	2	0	2
Central Region	13	8	21
Eastern Region	11	1	12
Total	24	9	33

Table 8. Migration departure date, arrival date at destination, migration duration, number of stopovers, rate of movement during migration, minimum distance traveled during migration, net displacement (distance between winter sites and breeding-period sites), stopover duration, and distance between stopover sites for American woodcock monitored during spring migration in 2014, 2015, and 2016.

	Mean	95 % CI	Standard Error	Median	Min	Max	<i>n</i>
Departure	23 Feb	20 Feb – 26 Feb	1.6	19 Feb	1 Feb	18 Mar	41
Arrival	17 Apr	9 Apr – 24 Apr	3.6	18 Apr	8 Mar	25 May	37
Duration (Days)	53.2	45.6 – 60.8	3.8	51	16	91	37
Number of Stopovers	6.0	4.8 – 7.2	0.6	6	0	18	40
Rate (km/day)	41.4	35.6 – 47.2	2.9	35.6	21.8	97.4	37
Minimum Distance (km)	2069	1893 – 2245	87	2049	666	3341	40
Net Displacement (km)	1898	1755 – 2042	71	1907	621	2959	40
Stopover Duration (days)	5.9	5.0 – 6.9	0.5	3	1	43	254
Distance between Sites (km)	301	272 – 330	15	249	7	1782	303

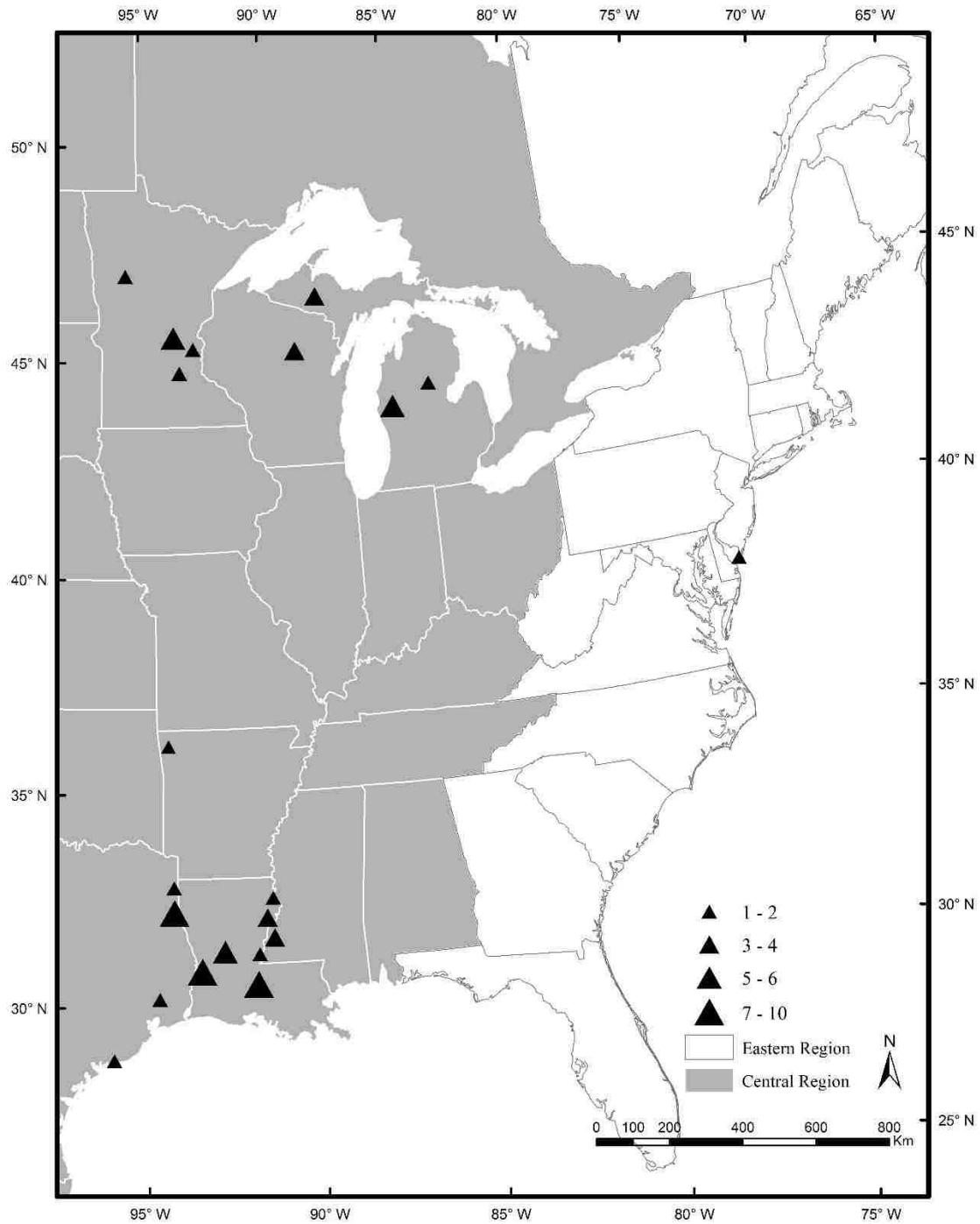


Figure 1. American woodcock capture sites. The size of the triangle represents the number of woodcock captured and outfitted with a PTT. Overlapping symbols were jittered. States and provinces filled in grey are part of the Central Management Region. States and provinces filled with white are part of the Eastern Management Region.

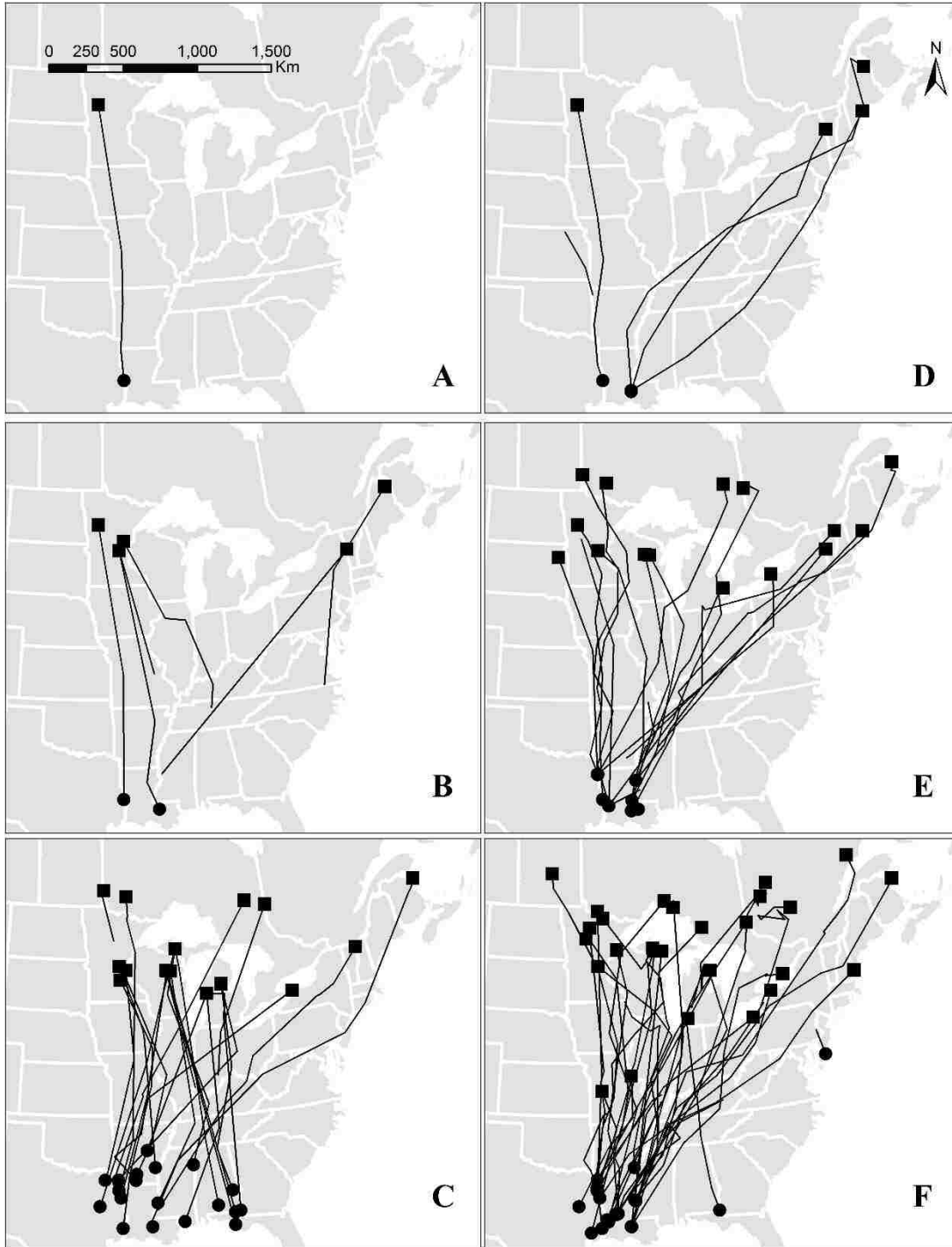


Figure 2. The spring and autumn migration routes of American woodcock ($n = 61$) tracked during autumn migration 2013 (A), 2014 (B), and 2015 (C); and during spring migration 2014 (D), 2015 (E), and 2016 (F). One woodcock was monitored during 2 autumn migrations, 8 woodcock were monitored during 2 spring migrations, and 18 woodcock were monitored during both autumn and spring migrations. Squares represent breeding-period sites, and circles represent winter sites.

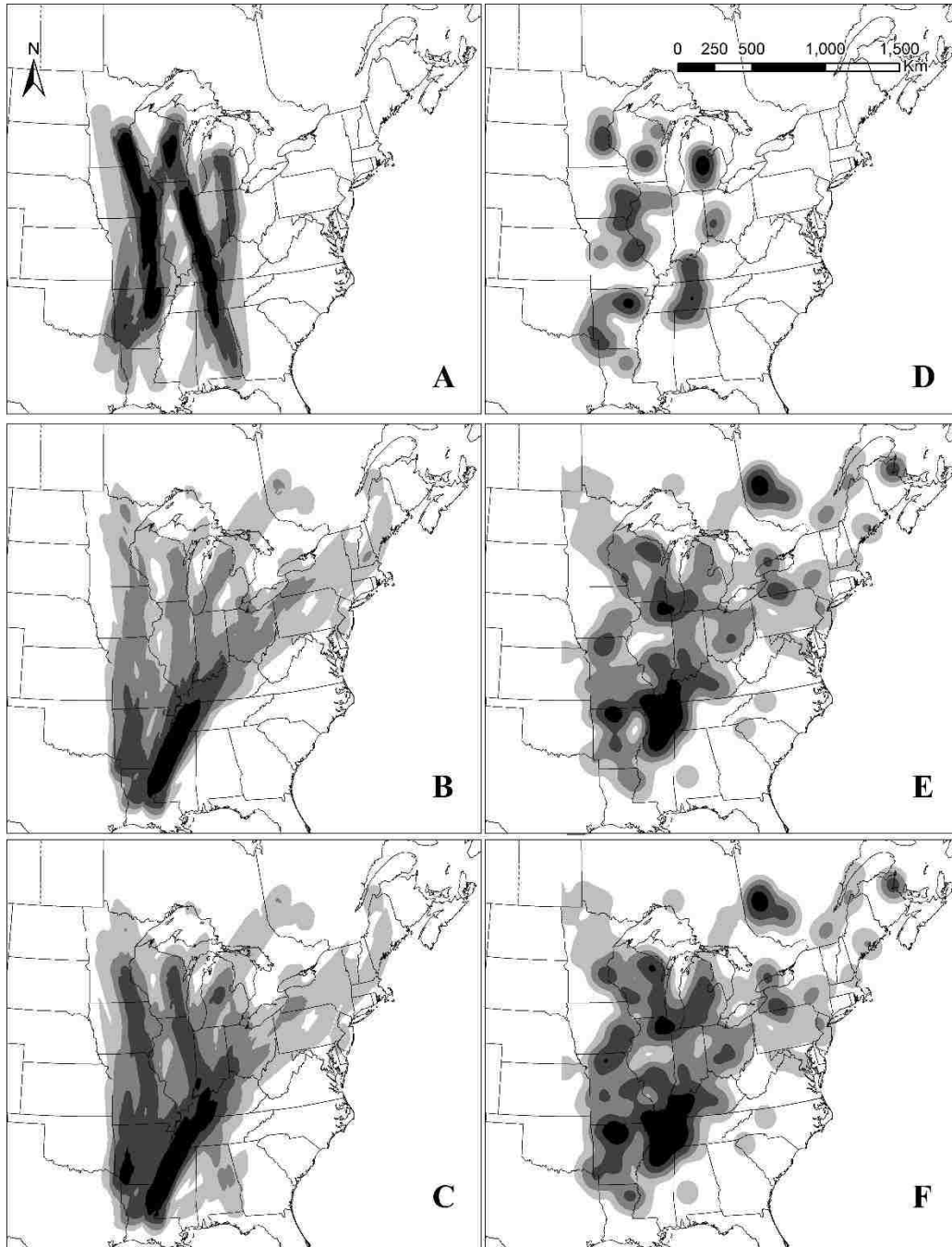


Figure 3. Migration routes and stopover regions of American woodcock, primarily captured within the Central Management Region, monitored with PTTs. Autumn migration routes (A), spring migration routes (B), and an aggregate of autumn and spring migration routes (C) were visualized using line density. Autumn stopover regions (D), spring stopover regions (E), and an aggregate of autumn and spring stopover regions were visualized using a kernel density estimate. The line and kernel density surfaces are categorized into 5 classes, with darker classes having a higher density of migration paths or stopovers.

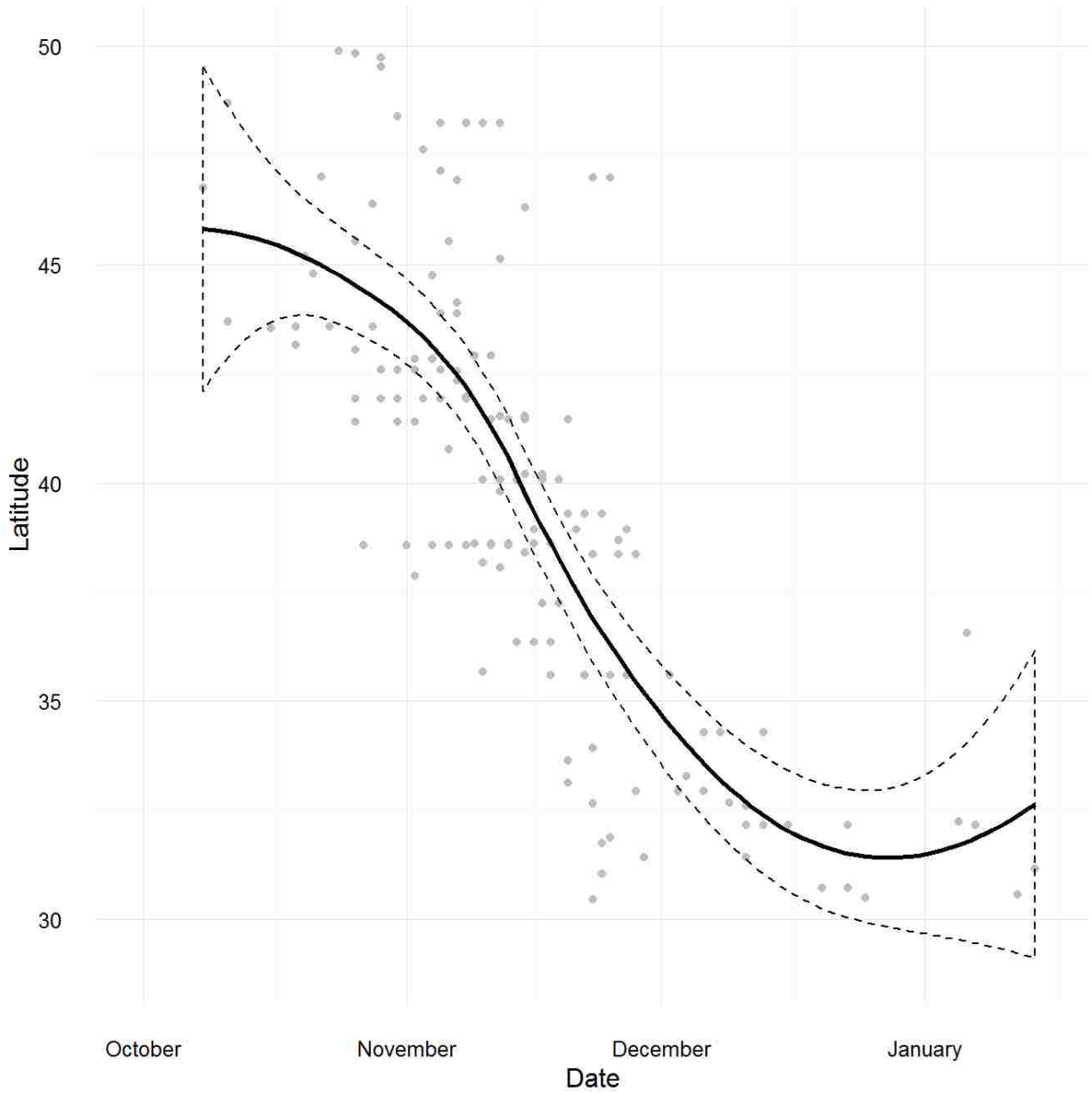


Figure 4. Scatterplot of latitude during autumn migration of American woodcock monitored with PTTs using 1 location per duty cycle. The locations included are; the last location at a breeding-period site, all locations at autumn stopover sites, and the first location at a winter site. A smoothed (solid) line is fit to the data using local polynomial regression fitting. The dotted lines represent the 95% confidence interval.

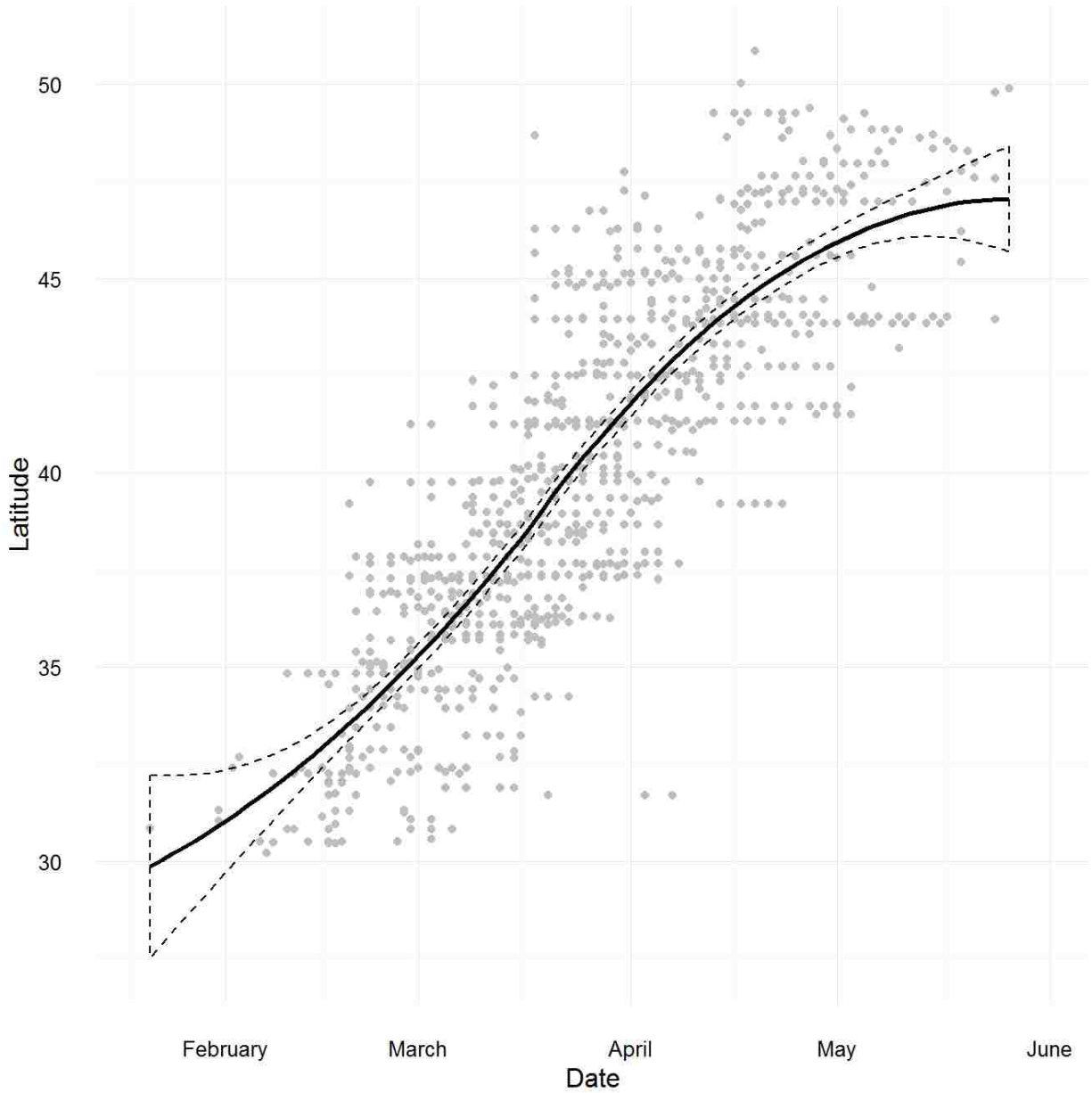


Figure 5. Scatterplot of latitude during spring migration of woodcock tracked with PTTs using 1 location per duty cycle. The locations included are; the last location at a winter site, all locations at spring stopover sites, and the first location at a breeding-period site. A smoothed (solid) line is fit to the data using local polynomial regression fitting. The dotted lines represent the 95% confidence interval.

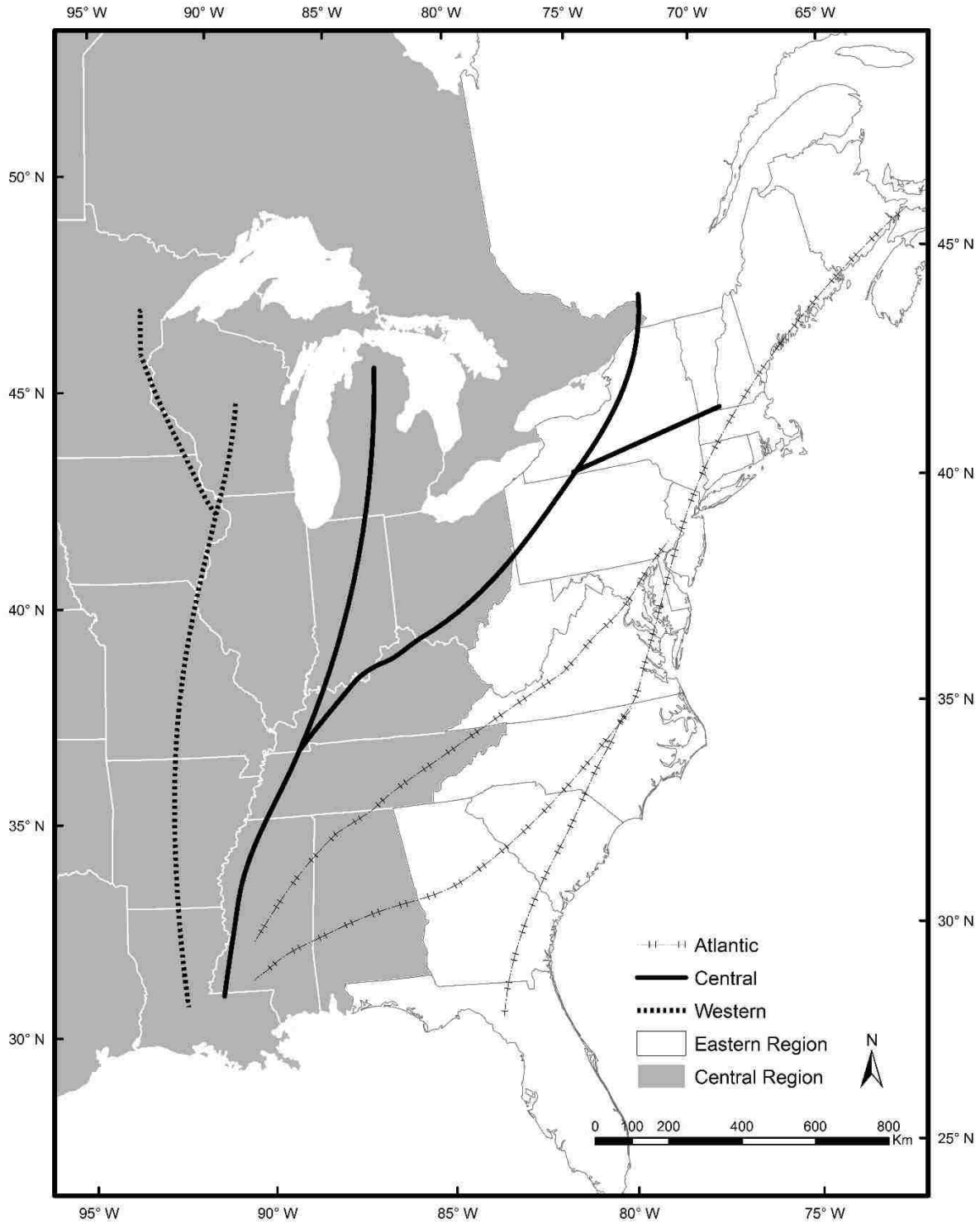


Figure 6. Glasgow's (1958) hypothesized migration routes of American woodcock overlaid on current Eastern and Central American woodcock Management Regions.

CONCLUSION

Improving the understanding of American woodcock (*Scolopax minor*, hereafter woodcock) migration has been identified as a priority information need for woodcock management. Woodcock band return records are an important long-term dataset that have been used to infer migration routes and to establish management regions (Glasgow 1958, Sheldon 1967, Coon et al. 1977). I analyzed band return records to determine the extent of crossover between management regions and to describe woodcock migratory connectivity. I found that the criteria used to determine which band return records to include in the analysis greatly affects the estimated amount of crossover between management regions. My results of 17.9% crossover between regions using raw counts showed more crossover than the < 5% crossover found by Coon et al. (1977). This is most likely because my dataset only included woodcock that had completed migration instead of including woodcock that had yet to initiate migration or were harvested early in migration before they had an opportunity to cross between management regions. Most of this crossover was between the breeding grounds of the Eastern Region and the wintering grounds of the Central Region. Using the division coefficient, I found that a higher proportion of the banded woodcock population may have crossed from the Eastern Region to the Central Region during autumn migration than was suggested by the raw counts alone (division coefficient; 0.54, 95% CI: 0.35-0.78). Further analyzing the data using kernel density estimates, *pam* clustering, linear models, and the Mantel test supported the results using raw counts and the division coefficient, and provided additional insight into the nature of woodcock migration. These methods demonstrated that during autumn migration woodcock from the Central Region largely migrate to destinations throughout the Central Region, whereas woodcock from the Eastern Region migrate to destinations across the wintering range and mix with individuals from the Central Region.

Between September 2013 and February 2016, I deployed 75 satellite transmitters on woodcock at sites on their breeding and wintering grounds, focusing on the United States portion of the Central Region. This was the first study to track woodcock using satellite transmitters. I successfully tracked the migration paths of 61 woodcock and documented 88 woodcock migrations. I observed two primary migration routes used by woodcock in the Central Region and identified geographic regions with a high stopover density along these routes. During spring migration, many woodcock (36%, $n = 12$) migrated from the Central Region to the Eastern Region, complementing my findings using band return data. Using satellite transmitters, I documented the start date of migration, end date of migration, net displacement, the rate of migration, and the number of stopovers for fall and spring migration.

High stopover density regions along migration routes may represent areas that are important for migrating woodcock and low stopover density regions may represent areas where appropriate management may make habitat available for migrating woodcock. Managers should consider these regions when making land management and acquisition plans for migrating woodcock. Documenting woodcock migration routes provides an improved understanding of the connection between woodcock populations on the breeding and wintering grounds. I observed a higher than expected proportion of woodcock travel from the Central Management Region to the Eastern Management Region during spring migration, raising questions about the biological basis of managing woodcock as 2 separate populations. Managers can use the observed dates of autumn migration initiation and arrival on winter grounds along with the scatterplot showing the latitude and date that tagged woodcock made migratory stopovers during migration to identify the periods in which woodcock migrate through individual states and the periods in which both migrating woodcock and woodcock yet to initiate migration are present. Depending on

management goals, states can use these data to choose woodcock season dates within the framework established by the U.S. Fish and Wildlife Service to maximize the likelihood of woodcock being present or to minimize harvest on the local population.

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Sheldon, W. G. 1967. Book of the American woodcock.

APPENDIX A: Research Compliance Protocol Letter



UNIVERSITY OF
ARKANSAS

Office of Research Compliance

MEMORANDUM

TO: Dr. David Kremetz

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee (IACUC)

DATE: November 7, 2014

SUBJECT: IACUC APPROVAL
Expiration date: November 8, 2016

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your to protocol 15011 *Migration Ecology of American Woodcock*

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond November 8, 2016, you must submit a modification or new protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian