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Authors: Moore, Joseph D., Andersen, David E., Cooper, Tom, Duguay, Jeffrey P., Oldenburger, Shaun L., et al.

Source: Wildlife Biology, 2021(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00816>

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Migration phenology and patterns of American woodcock in central North America derived using satellite telemetry

Joseph D. Moore, David E. Andersen, Tom Cooper, Jeffrey P. Duguay, Shaun L. Oldenburger, C. Al Stewart and David G. Krentz

J. D. Moore, Arkansas Cooperative Fish and Wildlife Research Unit, Dept of Biological Sciences, Univ. of Arkansas, Fayetteville, AR, USA, and: Ecological Services, Utah Field Office, U.S. Fish and Wildlife Service, West Valley City, UT, USA. – D. E. Andersen (<https://orcid.org/0000-0001-9535-3404>), U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, Dept of Fisheries, Wildlife and Conservation Biology, Univ. of Minnesota, St. Paul, MN, USA. – T. Cooper, Migratory Bird Program, U.S. Fish and Wildlife Service, Bloomington, MN, USA. – J. P. Duguay, Louisiana Dept of Wildlife and Fisheries, Baton Rouge, LA, USA. – S. L. Oldenburger, Texas Parks and Wildlife Dept, Austin, TX, USA. – C. A. Stewart, Michigan Dept of Natural Resources, Lansing, MI, USA. – D. G. Krentz (<https://orcid.org/0000-0002-5661-4541>) ✉ (krentz@uark.edu), U. S. Geological Survey, Arkansas Cooperative Fish and Wildlife Research Unit, Dept of Biological Sciences, Univ. of Arkansas, Fayetteville, AR, USA.

American woodcock *Scolopax minor* (hereafter woodcock) migration ecology is poorly understood, but has implications for population ecology and management, especially related to harvest. To describe woodcock migration patterns and phenology, we captured and equipped 73 woodcock with satellite tracking devices in the Central Management Region (analogous to the Mississippi Flyway) of North America and documented migration paths of 60 individual woodcock and 87 autumn or spring woodcock migrations during 2014–2016. Woodcock migration at the scale of the Central Management Region was more synchronous in spring than in autumn, but unlike most other migratory birds, average duration of autumn migration (31 days) was shorter than duration of spring migration (53 days). This difference in migration duration resulted from woodcock making more close-together migratory stopovers during spring migration, not because woodcock had individual stopovers of longer duration. During autumn migration, the number of days, the number of stopovers, migration end date and net migration displacement were negatively related to initiation date and rate of migration, and the number of stopovers and the net migration displacement were negatively related with migration end date. Spring migration duration, end date, the number of stopovers and net migration displacement were negatively related to migration rate and initiation date was positively related to migration rate, suggesting that woodcock that initiated spring migration later had faster migration rates. Juvenile female woodcock began spring migration later than adult female woodcock. Our results provide a basis for comparing current harvest seasons with presence of migrating woodcock during autumn and provide insight into differential harvest of migratory versus local woodcock on breeding areas.

Keywords: American woodcock, migration phenology, satellite telemetry, *Scolopax minor*

American woodcock *Scolopax minor* (hereafter woodcock) occur throughout much of the forested portions of central and eastern North America and are managed on the basis of a Central and an Eastern Management Region (Seamans and Rau 2019; Fig. 1). Woodcock breeding ecology and to a lesser extent, wintering ecology, have been studied (Straw et al. 1994, Krentz et al. 2019, McAuley et al. 2020) previously. However, information about woodcock migration ecology, including phenology (i.e. seasonal occur-

rence of migration and related behavior) is generally lacking and has been identified as a high-priority information need (Case and Sanders 2010). Information about woodcock migration is useful from a management perspective (e.g. in making management decisions related to harvest seasons) and an ecological perspective (e.g. better understanding potential limiting factors related to migration in a short-distance migrant).

Understanding woodcock migration has been hindered by limitations of existing technology, although there have been several efforts to assess migration by marking woodcock with very high frequency (VHF) transmitters (Myatt and Krentz 2007b), using band returns (Myatt and Krentz 2007a), and via assessing stable isotopes (Sul-lins et al. 2016) and genetics (Rhymer et al. 2005). Those

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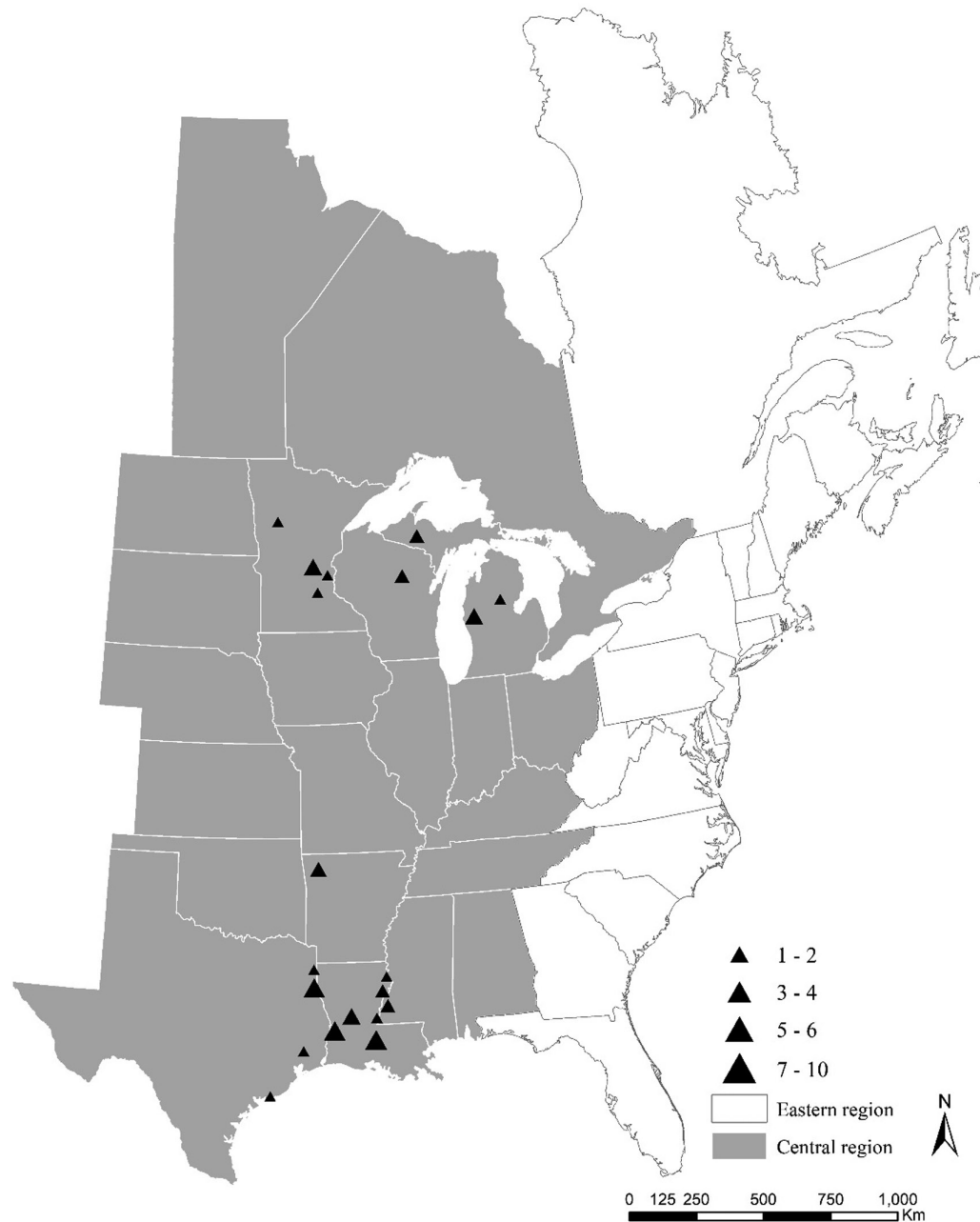


Figure 1. Central (gray) and Eastern (white) Management Regions for American woodcock in North America as designated by the United States Fish and Wildlife Service and the Canadian Wildlife Service. Also included are the numbers of woodcock marked and locations where those woodcock were marked.

assessments were limited by short distances over which it was possible to receive signals (VHF transmitters); low numbers of band recoveries, and biases associated with where and how bands are recovered (Moore and Krementz 2017, Moore et al. 2019a, b); and an inability to monitor individual movements (stable isotopes and genetics). More recently, satellite-based tracking devices have been scaled-down to a size appropriate for birds the size of woodcock and provide resolution of resulting location data sufficient to investigate migration ecology. To date, such devices have primarily been deployed in migration studies of large birds (e.g. sandhill cranes *Antigone canadensis*; Fronczak et al. 2017) and on large birds that undergo long-distance migration (e.g. white-fronted geese *Anser albifrons*; Fox et al. 2003). Recent studies

on Eurasian woodcock *Scolopax rusticola* have demonstrated that smaller long-range migrants are also capable of carrying satellite-based tracking devices during migration (Hoodless and Heward 2019). These studies suggested that the migration phenology and patterns in American woodcock could be studied using similar methods.

Woodcock use stopover sites during autumn migration, evidenced by they occur in relatively high abundance during autumn in areas where they do not breed or breed at low densities (Myatt and Krementz 2007a, b). Juvenile and adult woodcock also exhibit differential migration patterns, likely due to naiveté of juveniles compared to adults (Myatt and Krementz 2007a, b, Meunier et al. 2008). Beyond that basic understanding of woodcock migration, however, there is

relatively little known about woodcock migration phenology and patterns. To address the lack of information regarding woodcock migration phenology and patterns, our objectives were to descriptively quantify attributes of woodcock migration ecology such as phenology and migration duration, characterize use of stopover sites during spring and autumn migration, and evaluate sex and age related to patterns in woodcock migration.

Methods

Study area

We studied woodcock in the northern and southern portions of the Central Management Region within the United States (Fig. 1) to sample woodcock associated with that management region. We captured woodcock during breeding and wintering periods (except for one woodcock captured in northwestern Arkansas during presumed northward migration; Fig. 1) at 20 different sites between September 2013 and February 2016 (Supporting information). In addition to woodcock capture sites, our study area included the locations to which marked woodcock migrated and the areas between wintering and breeding sites, including portions of Canada and the Eastern Management Region (Seamans and Rau 2019). Sullins et al. (2016) provided a more complete description of our study area.

Capture and marking

We captured woodcock between September 2013 and February 2016 using spotlights and hand-held nets at night while on foot and from all-terrain vehicles (Rieffenberger and Kletzly 1967), with mistnets to intercept woodcock flying between daytime and roosting locations during the crepuscular period (McAuley et al. 1993), and with a hand-held net and a trained pointing dog during daylight. We banded all captured woodcock with a United States Geological Survey Bird Banding Lab 3A aluminum band. Before we attached transmitters to woodcock, we tested this technology by affixing satellite-based tracking devices to six woodcock between September 2013 and March 2014. We did so to assess the ability of woodcock to carry these devices and for these devices to produce location data useful for assessing migration phenology and patterns. Based on the success of our initial assessment (Moore et al. unpubl.), we captured and deployed 67 additional platform transmitting terminals (PTTs) on woodcock representing the population that breeds and winters in the Central Management Region. Therefore, our sample included 73 tracked woodcock. We attached PTTs using a modified thigh harness where the PTT rested on the lower back, secured by loops over each leg (Rappole and Tipton 1991, Streby et al. 2015). We constructed PTT harnesses with two strands of 0.7-mm Stretch Magic elastic plastic cord threaded through Tygon tubing (Hughes et al. 1994) that were crimped with aluminum rings to attachment points on the PTT. The PTT mass did not exceed 5% of the individual's body mass (we received an exception from the United States Geological Survey Bird Banding Laboratory to exceed the usual 3% body mass restriction).

We captured and equipped woodcock with PTTs as close to the initiation of spring or autumn migration as feasible to reduce the risk of mortality or transmitter failure before migration. Before spring migration, we captured woodcock ($n = 51$) between 5 January and 16 February (except for one woodcock captured in Arkansas on 10 March 2014). Before autumn migration, we captured woodcock ($n = 22$) between 18 September and 3 November. We measured body mass using a spring scale (g) and determined age (hatch year, second year or after second year) and sex of captured woodcock based on plumage and morphological characteristics (Martin 1964). During spring, we considered after-hatch-year woodcock to be juveniles and after-second-year woodcock to be adults. During autumn, we considered hatch-year woodcock to be juveniles, and after-hatch-year and after-second-year woodcock to be adults. We performed this study under protocols approved by 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.

Woodcock locations

We equipped woodcock with one of three types of PTTs during our study: a 9.5-g PTT, a 5-g PTT and a 4.9-g GPS PTT and assumed no difference in effects of PTTs on long-distance movement based on our initial assessments of the heaviest of these devices (i.e. woodcock equipped with 9.5-g PTTs migrated to wintering areas and returned to breeding areas). We were unable to assess the potential influence on woodcock migration of different PTT weights because PTT weight was confounded with sex (we did not deploy each tag type on both sexes), location (we did not deploy all tag types at each location) and year (we did not deploy all tag types each year). The 9.5-g and 5-g PTTs (Microwave Telemetry, Columbia, MD, USA) 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, MD) estimated woodcock locations using the Doppler shift of transmissions originating from the PTTs (Argos 2016). Associated with each location was a class designation that provided estimated spatial error or indicated that Argos was unable to estimate spatial error. Reported location errors were between 250 and 1500 m (Argos 2016). These PTTs had auxiliary sensors that provided information on temperature, voltage and activity (i.e. documented whether the PTT physically moved). We censored location data from PTTs when auxiliary sensors indicated that the tag was no longer moving and the temperature had dropped to ambient, or at the last location prior to absence of additional locations (i.e. a PTT no longer transmitted location data). The battery powered 4.9-g global positioning systems (GPS) PTTs (Lotek Wireless, Newmarket, Ontario, Canada) had only enough charge to collect 30 GPS locations along one migration path. Before deployment, we programmed the times and dates these 30 GPS locations would be collected. After collecting the GPS locations, the tag attempted to transmit 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 to satellites. In autumn 2015, we

programmed GPS PTTs to record one location every three days between 18 October and 19 January. In spring 2016, we programmed GPS PTTs to record one location 24 January, one location 31 January, a location every three days from 7 February to 1 May, and a final location on 8 May. We deployed 9.5-g PTTs only on females with mass > 200 g. We deployed 5-g PTTs and 4.9-g GPS PTTs on males and females with mass > 150 g.

Classifying stopovers, wintering sites and breeding-period sites

We identified stopover, wintering and breeding-period sites based on location data from PTTs. We used the *Movebank* tracking data map (Kranstauber et al. 2011, Wikelski and Kays 2016) to identify clusters of locations for each individual and to classify clusters as migratory stopover, wintering-period or breeding-period sites. We mitigated the influence of implausible Argos locations by using clusters of ≥ 2 successive Argos locations for each individual to define stopover sites (Douglas et al. 2012). Because woodcock migrate nocturnally (Meunier et al. 2008), we classified clusters of ≥ 2 successive nocturnal GPS PTT locations (taken every three days) as stopover sites and a single diurnal GPS PTT location to identify a stopover site. We used location proximity, time lag between locations, and Argos location class to determine whether locations were clustered under the assumption that spatial and temporal autocorrelation confirm the validity of the location (Douglas et al. 2012). We defined the first wintering site as a site where a woodcock remained for > 25 days and had no further movement > 50 km southward. We defined subsequent sites as wintering sites until northward movement > 25 km began. We defined the first breeding-period site as a site where a woodcock remained for > 25 days and had no further movement > 50 km northward. We defined subsequent sites as breeding-period sites until southward movement > 25 km began. We classified sites used by woodcock between breeding-period and wintering-period sites as migratory stopover sites. We determined the coordinates of each stopover site by taking the median center of all locations within the cluster (Arizaga et al. 2014).

Timing of woodcock movements

We 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-period site and the first migratory location (Arizaga et al. 2014, Olson et al. 2014). We determined the date of arrival at a breeding-period or wintering-period site by using the median date between the last known migratory location and the first location at a breeding-period or wintering-period site. We 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). We determined the duration of migration as the period between the date of migration initiation and the arrival date and we excluded migration durations where the amount of uncertainty (i.e. the potential error in the estimate of the number of days during migration) in migration duration was > 10 days. We determined the number of days

spent at a stopover site as the period between the first and last locations recorded at that site. Because PTTs typically had 48–72 h off-duty cycles and because PTTs sometimes failed to upload locations, the number of days at each stopover site represents a minimum number of days. In addition, there may have been stopover sites that we were not able to identify or account for if a woodcock stopped at a location for a short period during an off-duty cycle. Therefore, the number of stopover sites identified is a minimum.

Distances moved during migration

We estimated the distance traveled during autumn migration as the sum of the great-circle distances (the shortest distance between two points along the surface of a sphere) between the last breeding-period site, all known stopover sites and the first wintering-period site. We similarly determined the distance traveled during spring migration as the sum of the great-circle distances between the last wintering-period site, all known stopover sites and the first breeding-period site. The migration distance represents a minimum possible distance because each woodcock may have had more stopovers than we were able to identify because woodcock did not necessarily make direct movements between transmitter-derived locations. We determined the net displacement during autumn migration as the great-circle distance between the last breeding-period site and the first wintering-period site and during spring migration as the great-circle distance between the last wintering-period site and the first breeding-period site. We determined the rate of migration by dividing the net displacement by the duration of migration (i.e. the estimated number of days of migration). We excluded estimates of migration distance, net displacement, rate of migration and the number of stopover sites from analysis if we were unable to document a complete migration path (i.e. if a woodcock had an undetermined origin or final destination due to mortality or PTT failure). We used the first instance of each spring and autumn migration metric for each individual in our analysis to avoid pseudoreplication. Because we were not able to calculate all metrics for each bird each season (i.e. if we did not have the date of arrival at a breeding season site we could not calculate arrival date, migration rate or migration duration for that individual that season), we used the first year that information was available.

Data analyses

We assessed differences between spring and autumn patterns in migration duration, number of stopovers during migration, net displacement between the start and end of migration, stopover duration and the distance between stopovers based on 95% confidence intervals around means (i.e. we used non-overlapping 95% confidence intervals to indicate differences in woodcock migration metrics). We also estimated the migration initiation date and migration end date. To assess the influence of age and sex on woodcock migration (depending on available sample sizes, see below), we first used program JMP ver. 15.2 to conduct a principal component analysis (PCA) to evaluate factors related to spring migration and to autumn migration. We opted to use a PCA because we had a large number of variables to

evaluate relative to our sample sizes and to avoid making type I errors associated with conducting multiple univariate comparisons. We evaluated spring and autumn migration separately based on individuals for which we had data for ≥ 3 variables during each period. For autumn migration, because we tracked so few males and only three had complete migration records, we evaluated only females ($n=13$) whereas for spring migration, we evaluated males ($n=8$) and females ($n=33$) together and females alone. We evaluated the following variables in our PCAs: the start and end dates of migration, duration (number of days), net displacement, the number of stopovers during migration and the rate of migration. Because there was a large absolute difference in the magnitude of the variables in the PCAs, we first standardized all variables to have a mean of zero and standard deviation of 1. We then considered the first 2 resulting principal components and used these principal components in a nominal logistic regression to evaluate whether there were differences in migration based on age (juvenile versus adult). In the instances where there was a relationship between the first and/or second principal component and age (evaluated using a whole-model χ^2 test followed by χ^2 tests of parameter estimates for each principal component in JMP), we assessed which variables were most associated with sex based on the partial contributions of variables (i.e. loadings) to principal components.

Temporal distribution of migrating woodcock

To describe the distribution of woodcock through time during autumn and spring migration, we derived a subset of all locations that consisted of a single location/transmitter duty cycle using the Douglas–Argos filter (Douglas et al. 2012). For autumn migration we further filtered this dataset to include only the last known breeding-period location (because the earliest recorded autumn migration was on 14 October, we removed the breeding period location if it was before 1 October), all autumn locations, and the first wintering-period location for each individual. For spring migration, we filtered the dataset to include only the last known wintering-period location, all spring locations and the first breeding-period location for each individual. For each migration season, we fitted a smoothed line using local polynomial regression fitting on latitude versus date using the loess function in R (<www.r-project.org>) with the default smoothing parameter of 0.75.

Results

We deployed PTTs on 53 females (25 adults, 28 juveniles) and 20 males (8 adults, 12 juveniles, Supporting information) using 42 9.5-g PTTs, 10 5-g PTTs and 21 4.9-g GPS PTTs (Supporting information). We captured 22 of these woodcock before the start of autumn migration in Michigan ($n=11$), Minnesota ($n=8$) and Wisconsin ($n=3$); we captured 50 of these woodcock before the start of spring migration in Louisiana ($n=36$) and Texas ($n=14$); and we captured one woodcock during spring migration in Arkansas, USA. We monitored woodcock during autumn migration in 2013, 2014 and 2015 and we monitored woodcock

during spring migration in 2014, 2015 and 2016. Though our PTTs had off periods of 48 h, 72 h or one week, gaps between estimated locations occurred that were longer than off-periods. A possible cause of these gaps was that the thick cover used by woodcock prevented the solar-powered PTTs from charging or prevented PTTs from successfully transmitting or receiving messages from a satellite. We monitored the migration paths of 60 individual woodcock (Fig. 2) and documented 67 complete migrations (migrations for which both the breeding-period and wintering-period sites were known) and 20 partial migrations (some migration data but the migratory origin and/or destination were unknown, Supporting information). We censored 13 woodcock because no migration data were recovered from their PTTs.

Autumn migration

During 2013–2015, we documented the autumn migration paths of 30 individual woodcock; 26 females (16 adults, 10 juveniles) and 4 males (1 adult, 3 juveniles; Supporting information). We monitored all woodcock during one season, except for one woodcock that we monitored in 2013 and 2014, for 31 migration paths (Fig. 2), which included 23 complete migration paths and 8 partial migration paths. Because we censored 3 woodcock marked with PTTs in the autumn before initiating autumn migration and we received migration data from 11 woodcock captured during the winter, autumn migration data were from two groups: woodcock tagged in Michigan, USA ($n=8$), Minnesota, USA ($n=8$) and Wisconsin, USA ($n=3$) before autumn migration and the autumn migrations of woodcock tagged during winter in Texas, USA ($n=3$) and Louisiana, USA ($n=8$) that migrated in spring to Maine, USA ($n=1$), New Brunswick, Canada ($n=1$), New York, USA ($n=1$), Ontario, Canada ($n=3$), Quebec, Canada ($n=1$), Vermont, USA ($n=2$) and Wisconsin, USA ($n=2$).

Slightly more than 50% (50.8%) of the variation in the data were explained by the first principal component derived from the number of days, number of stopovers, migration end date and net displacement, all of which were negatively related to initiation date and rate of migration (Fig. 3, Supporting information). There was not a statistically significant relationship between the first principal component and age for only females, based on logistic regression ($\chi^2=0.02$, $df=1$, $p=0.88$). The second principal component explained 25.9% of the total variation and was derived from the number of stopovers and net displacement, both of which were negatively associated with migration end date (i.e. woodcock with higher numbers of stopovers and longer migration distances ended migration later). There was not a statistically significant relationship between the second principal component and age for only females, based on logistic regression ($\chi^2=1.73$, $df=1$, $p=0.19$).

Spring migration

During 2014–2016, we monitored spring migration paths of 48 individual woodcock; 36 females (16 adults, 20 juveniles) and 12 males (4 adults, 8 juveniles; Supporting information). We monitored 40 woodcock during 1 spring migration and 8 woodcock during 2 spring migrations for

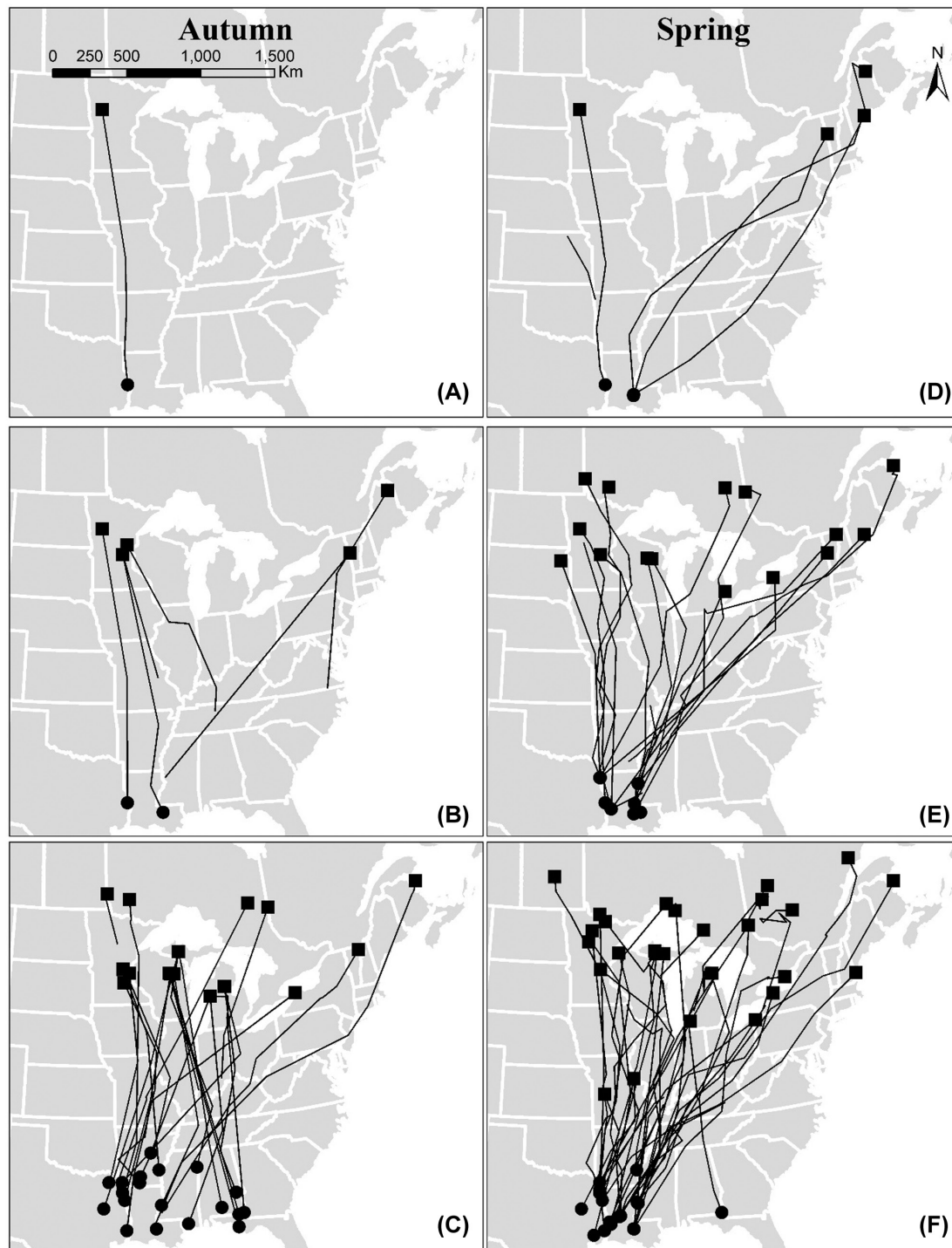


Figure 2. Migration routes of American woodcock ($n=60$) captured in the Central Management Region in North America tracked during autumn migration 2013 (A), 2014 (B) and 2015 (C) and during spring migration 2014 (D), 2015 (E) and 2016 (F). We monitored one woodcock during 2 autumn migrations, 8 woodcock during 2 spring migrations and 18 woodcock during both autumn and spring migrations. Squares represent breeding-period sites and circles represent wintering-period sites.

56 migration paths (Fig. 2), which included 44 complete migration paths and 12 partial migration paths. Because 10 woodcock tagged in winter were censored before initiating spring migration and we received migration data from 11 woodcock captured during autumn, spring migration paths were from two groups: woodcock tagged in Arkansas, USA ($n=1$), Louisiana, USA ($n=31$) and Texas, USA

($n=9$) and the spring migrations of woodcock tagged during the autumn in Michigan, USA ($n=3$) and Minnesota, USA ($n=4$) that had migrated to Alabama, USA ($n=1$), Arkansas, USA ($n=1$), Louisiana, USA ($n=1$) and Texas, USA ($n=4$).

The first principal component in our evaluation of spring migration data from both males and females explained

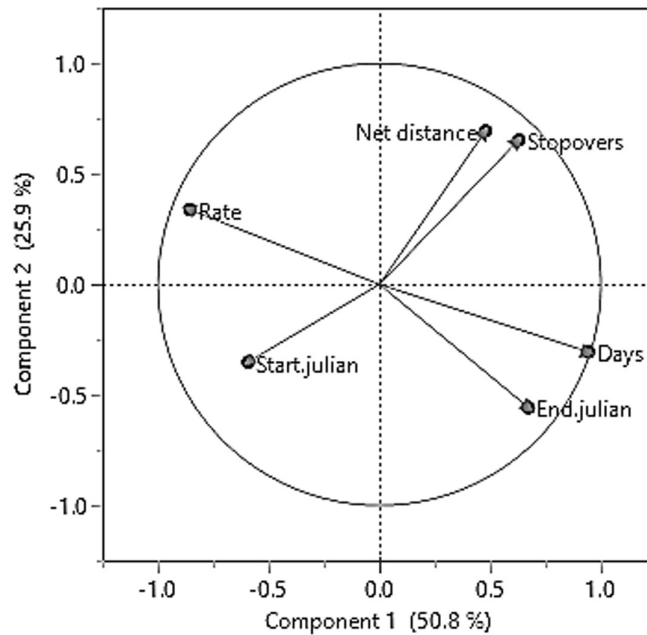


Figure 3. Principal components 1 and 2 plotted for autumn-migrating American woodcock females (13 adults, 6 juveniles) captured in the Central Management Region of North America. Variables analyzed are net displacement (Net distance), number of stopovers (Stopovers), migration duration (Days), date migration began (Start.julian), date migration ended (End.julian) and migration rate (Rate).

58.1% of variation and 58.3% of variation using data only from females, and was derived from the covariates migration duration, end date, the number of stopover sites and net displacement, all of which were negatively related to migration rate (Fig. 4, Supporting information). There was not a statistically significant relationship between the first principal component and age for either males and females or only females, based on logistic regression (both p s > 0.05 for χ^2 tests of parameter estimates). The second principal component explained 19.6% of the total variation (females and males combined) and 19.3% of total variation (females

only) and initiation date was positively related to migration rate, suggesting that woodcock that initiated spring migration later had faster migration rates. The second principal component was related to age during the spring for males and females combined ($\chi^2=8.254$, $df=1$, $p=0.004$) and for only females ($\chi^2=4.847$, $df=1$, $p=0.03$) and was dominated by initiation date for females and males combined (loading=0.738; Supporting information) and only females (loading=0.759; Supporting information), indicating that juvenile woodcock began migration later than adult woodcock (about one day later).

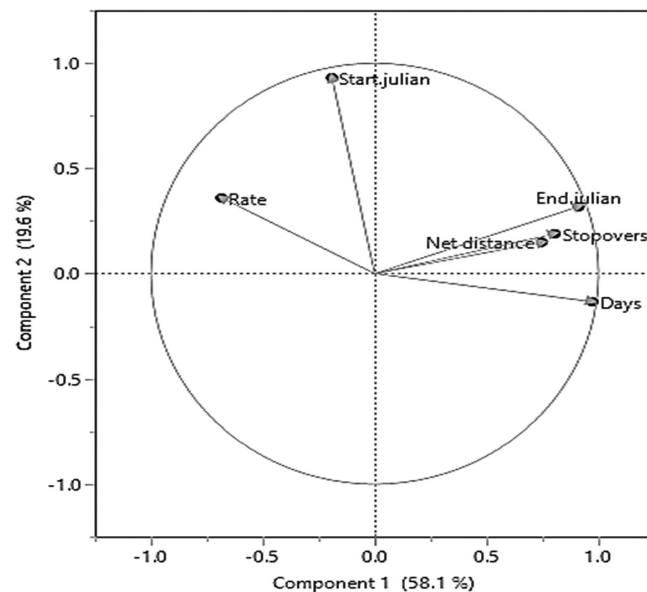


Figure 4. Principal components 1 and 2 plotted for male ($n=9$) and female ($n=33$) spring-migrating American woodcock captured in the Central Management Region of North America. Variables analyzed are net displacement (Net distance), number of stopovers (Stopovers), migration duration (Days), date migration began (Start.julian), date migration ended (End.julian) and migration rate (Rate).

Differences between autumn and spring migration

Based on 95% confidence intervals, woodcock in autumn had a shorter migration duration, made fewer stopovers, migrated at a faster rate, had a longer distance between stopover sites, and had a shorter minimum distance traveled (Table 1, 2) than woodcock during spring migration. There was no difference in net displacement or stopover duration based on 95% confidence intervals between autumn and spring migration. During autumn migration (Table 1, Fig. 5), marked woodcock exhibited most southward movement beginning in November and arrived at wintering areas by early December. During spring migration (Table 2, Fig. 6), marked woodcock exhibited northward movement beginning in late February and woodcock arrived on the most northerly breeding areas in May.

Discussion

We provide comprehensive information about migration phenology and movements of American woodcock for the Central Management Region in North America and present the first descriptions of complete autumn and spring migrations of American woodcock. The mean autumn departure date of 3 November we observed was similar to the date of 28 October observed by Meunier et al. (2008), the peak departure taking place in the first week of November by Sepik and Derleth (1993; in the Eastern Management Region), and by Myatt and Kremetz (2007a). Although the median stopover duration in spring and autumn migration was 3 days, stopover duration was highly variable within seasons. Time at stopovers lasted as long as 28 days in autumn and as long as 43 days in the spring. This pattern of primarily shorter stopover duration, intermixed with extended stopover duration is similar to the minimum stopover durations ($n=22$) between 1 and 14 days observed by Myatt and Kremetz (2007b) using aerial telemetry and VHF transmitters. The extended stopover duration during spring migration may have resulted from nesting attempts during migration or spring weather conditions that hindered northward movement (Taylor and Stutchbury 2016). Spring migration was longer in duration than autumn migration, likely at least

in part because woodcock stopped more frequently during spring migration than during autumn migration, and not because woodcock stayed at individual stopover sites longer in the spring. Some variation between autumn and spring migration may be explained because our autumn sampling site locations are all in the north-central United States whereas many woodcock captured during the winter migrated to the northeastern United States and adjacent southern Canada. However, we accounted for this influence by analyzing the return autumn migration of woodcock captured during the winter and there was no difference in net displacement between seasons based on 95% confidence intervals.

The migration pattern we observed is different than migration patterns in the majority of bird species that have been studied, which exhibit shorter duration spring migration (Nilsson et al. 2013). Earlier spring migration in many migratory birds is thought to confer increased fitness in that individuals that arrive sooner on breeding areas tend to have higher reproductive output (Kokko 1999, Moore et al. 2005). Piersma (1987), who worked on Arctic breeding shorebirds, described hop, skip and jump migration strategies based on whether an individual completes migration in a series of short flights with many stopovers (e.g. 10, hop strategy), traverses the same migration distance with fewer stopovers (e.g. 5, skip strategy), or traverses the same migration distance with long flights between infrequent (e.g. 1 or 2, jump strategy) stopovers. Piersma (1987) hypothesized that which of the three strategies was employed was dependent on a number of interrelated factors including food availability, foraging activity, staging time, and how fast individuals accumulate fat reserves. Short hops may be energetically favorable when there are high metabolic costs of transporting large amounts of fat to fuel longer flights (Piersma 1987) and when resources are broadly but not predictably available at fine spatial scales. Hops also allow migrants to assess environmental and phenological conditions during migration, and therefore adjust their migration rate to arrive at their destinations when environmental conditions are conducive to attracting mates and breeding (Taylor and Stutchbury 2016). Jumps may be advantageous when there are a limited number of high quality foraging (stopover) sites along

Table 1. 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 wintering-period sites and breeding-period sites), stopover duration, and distance between stopover sites for American woodcock monitored during autumn migration in the Central Management Region in North America in 2013, 2014 and 2015. Sample size (n) equals the number of individuals for which we had data to calculate the parameter except for sample sizes of stopover duration and distance between sites where additional sample sizes were added for clarification.

Parameter	Mean	SE	95% CI		Median	Min	Max	n
			Lower	Upper				
Departure	3 Nov	2.0	30 Oct	7 Nov	4 Nov	14 Oct	21 Nov	21
Arrival	6 Dec	3.8	28 Nov	14 Dec	3 Dec	21 Nov	9 Jan	17
Duration (days)	31.2	4.0	22.7	39.7	32	9	68	17
Number of stopovers	2.4	0.4	1.5	3.3	2	0	9	22
Rate (km day ⁻¹)	69.1	9.4	49.3	88.9	62.1	24.7	146.9	17
Minimum distance (km)	1669	83	1496.3	1842.3	1622	1097	3094	22
Net displacement (km)	1612	81	1444.2	1779.5	1539	1097	2958	22
Stopover duration (days)	5.1	0.7	3.7	6.9	3	1	28	68 stopovers, 27 individuals
Distance between sites (km)	456	40	377.0	535.1	359	9	1987	93 segments, 27 individuals

Table 2. 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 wintering-period sites and breeding-period sites), stopover duration and distance between stopover sites for American woodcock monitored during spring migration in the Central Management Region in North America in 2014, 2015 and 2016. Sample size (n) equals the number of individuals for which we had data to calculate the parameter except for sample sizes of stopover duration and distance between sites where additional samples sizes were added for clarification.

Parameter	Mean	SE	95% CI		Median	Min	Max	n
			Lower	Upper				
Departure	22 Feb	1.6	19 Feb	26 Feb	19 Feb	1 Feb	16 Mar	40
Arrival	17 Apr	3.6	9 Apr	24 Apr	18 Apr	8 Mar	25 May	37
Duration (days)	53.2	3.8	45.6	60.8	51	16	91	37
Number of stopovers	6.0	0.6	4.8	7.2	6	0	18	40
Rate (km day ⁻¹)	41.4	2.9	35.6	47.2	35.6	21.8	97.4	37
Minimum distance (km)	2069	87	1893	2245	2049	666	3341	40
Net displacement (km)	1898	71	1754	2041	1907	621	2959	40
Stopover duration (days)	5.9	0.5	5.0	6.9	3	1	43	254 stopovers, 42 individuals
Distance between sites (km)	301	15	272.4	330.3	250.1	7	1782	302 segments, 43 individuals

migration routes (Piersma 1987). Woodcock we monitored used more migratory stopover sites during spring migration (median = 6, max. = 18) than during autumn migration (median = 2, max. = 9) and appeared to exhibit a hopping migration strategy during the spring and either a hopping or skipping migration strategy during autumn migration. Woodcock in our marked sample began to arrive at their breeding-period sites as early as March and April, when winter conditions may persist. Thus, early initiation of a spring migration hopping strategy can have costs as foraging conditions can be difficult if arrival on the breeding grounds occurs during harsh environmental conditions (Dwyer et al. 1988). Woodcock may be able to respond to unfavorable conditions during spring migration by lingering at stopover sites when they encounter winter-like conditions, which may explain our observation of slower migration rate and higher number of stopover sites used by woodcock during spring migration than during autumn migration. Because woodcock depart wintering areas when breeding areas are generally experiencing harsh environmental conditions and deploy an energetically favorable hopping strategy during spring migration, they may arrive

at breeding-period sites as early as is feasible and with sufficient energy reserves to support courtship and breeding activities.

Our description of American woodcock annual movements provides insight into migration ecology of a short-distance migrant, and suggests that woodcock migration, especially in spring, differs from that of many other migratory birds (Colwell 2010). Woodcock appear to move deliberately during spring migration, potentially assessing local environmental conditions to time of arrival on breeding areas when conditions are conducive to attracting mates and breeding. From a management perspective, our observations of how woodcock are distributed spatially and temporally during autumn migration could be used to assess current harvest strategies. Woodcock in North America are managed cooperatively among states and provinces, with hunting seasons that vary by jurisdiction (i.e. states and provinces) within a larger, Management Region-wide framework. Comparing when and where woodcock occur during autumn to current hunting seasons, at both the scales of the Central Management Region and individual states and provinces, could provide insight into how well current hunting seasons

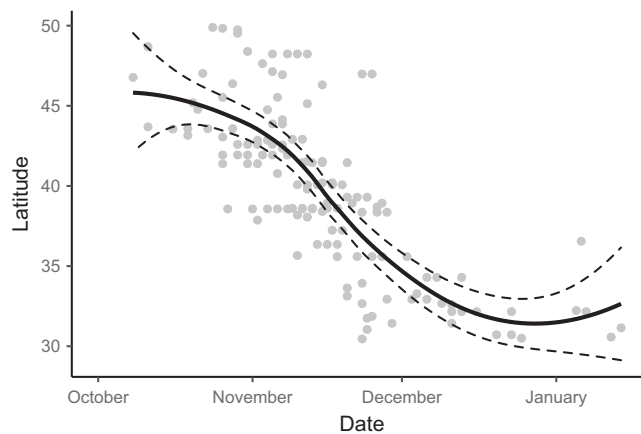


Figure 5. Latitude during autumn migration 2013, 2014 and 2015 of American woodcock (n = 48) captured in the Central Management Region of North America and monitored with platform transmitting terminals (PTTs) using one location/duty cycle (one 10-hour period every four days for Doppler PTTs or single locations on individual days for global positioning system PTTs, n = 136). Locations included the last location at a breeding-period site, all locations at autumn-migration stopover sites and the first location at a wintering-period site. We fitted a smoothed (solid) line to the data using local polynomial regression fitting. The dotted lines represent the 95% confidence interval.

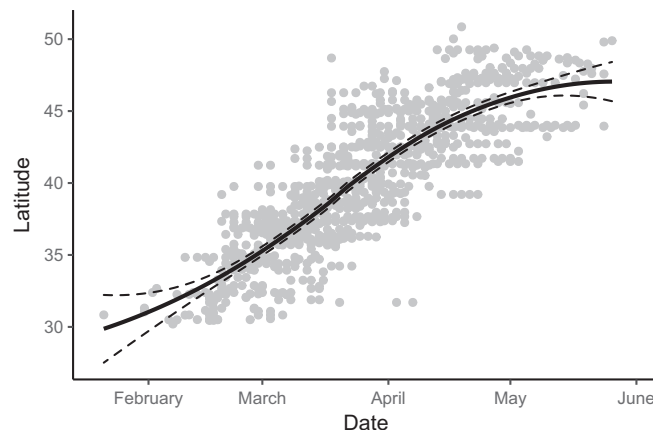


Figure 6. Latitude during spring migration 2014, 2015 and 2016 of American woodcock ($n=48$) captured in the Central Management Region of North America tracked with platform transmitting terminals (PTTs) using one location/duty cycle (one 10-hour period every four days for Doppler PTTs or single locations on individual days for global positioning system PTTs, $n=823$). Locations included the last location at a wintering-period site, all locations at spring-migration stopover sites and the first location at a breeding-period site. We fitted a smoothed (solid) line to the data using local polynomial regression fitting. The dotted lines represent the 95% confidence interval.

align with presence, and potential harvest mortality risk, of migrating woodcock. Finally, our observations of the spatial and temporal distribution of woodcock migration stopover sites could help guide conservation during that portion of their annual cycle.

Acknowledgements – We thank all of the people who helped us capture and mark woodcock including: A. P. Weik, E. A. Moore, J. M. Mueller, V. S. Neace, R. C. Deroche, J. M. Hammill, S. M. Peterson, A. C. Dailey, D. F. Locascio, W. L. Brininger, A. R. Hewitt, S. G. Zodrow, A. R. Forbes, K. O. Daly, G. L. Kemper, N. M. Hill, D. W. Wolfson, M. E. Tuma, G. R. Kramer, M. W. Olinde, T. L. Edwards, G. J. Byker, C. E. Sebright and C. J. Cahill. We thank D. M. Keppie, D. S. Sullins, K. T. Vierling, J. W. Connelly and P. R. Krausman.

Funding – This research was funded by the United States Fish and Wildlife Service Webless Migratory Game Bird Program, the Arkansas Cooperative Fish and Wildlife Research Unit (Grant/Cooperative Agreement Number G15AC00258 from the United States Geological Survey), the Minnesota Cooperative Fish and Wildlife Research Unit, the Louisiana Department of Wildlife and Fisheries, the Texas Parks and Wildlife Department, the Hal and Jean Glassen Memorial Foundation, the Ruffed Grouse Society and American Woodcock Society, the University of Arkansas, the University of Minnesota and Woodcock Limited.

Author contributions – JDM and DGK contributed to all aspects of the study. DEA contributed to field aspects during the pre-season capture period and to the study design, analyses, interpretation and manuscript preparation. TC contributed to acquisition of funding, field aspects during both the pre- and post-season capture periods, the study design, interpretation and manuscript preparation. JPD and SLO contributed to acquisition of funding, field aspects during the post-season capture periods, interpretation and manuscript preparation. CAS contributed to acquisition of funding, field aspects during the pre- and post-season capture periods, the study design, interpretation and manuscript preparation.

Conflicts of interest – Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the United States Government or the University of Minnesota. The findings and conclusions in this article do not necessarily represent the views of the United States Fish and Wildlife Service.

Permits – We performed this study under protocols approved by the Institutional Animal Care and Use Committee (IACUC) at the

University of Arkansas, protocol no. 15011, and the IACUC at the University of Minnesota, protocol no. #1408-31777A.

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