The Journal of Wildlife Management 83(7):1617–1627; 2019; DOI: 10.1002/jwmg.21741

Note

Migratory Connectivity of American Woodcock Derived Using Satellite Telemetry

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ABSTRACT American woodcock (*Scolopax minor*; woodcock) migratory connectivity (i.e., association between breeding and wintering areas) is largely unknown, even though current woodcock management is predicated on such associations. Woodcock are currently managed in the Eastern and Central management regions in the United States with the boundary between management regions analogous to the boundary between the Atlantic and Mississippi flyways, based largely on analysis of band returns from hunters. Factors during migration influence survival and fitness, and existing data derived from banding and very high frequency telemetry provide only coarse-scale information to assess factors influencing woodcock migratory movement patterns and behavior. To assess whether current management-region boundaries correspond with woodcock migratory connectivity in the Central Management Region and to describe migration patterns with higher resolution than has been previously possible, we deployed satellite transmitters on 73 woodcock (25 adult and 28 juvenile females, and 8 adult and 12 juvenile males) and recorded 87 autumn or spring migration paths from 2014 to 2016. Marked woodcock used 2 primary migrations routes: a Western Route and a Central Route. The Western Route ran north-south, connecting the breeding and wintering grounds within 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 in both the Eastern Management Region and Central Management Region and woodcock following this route migrated through the area between the Appalachian Mountains and the Mississippi Alluvial Valley in western Tennessee during autumn and spring. Two of 17 woodcock captured associated with breeding areas in Michigan, Wisconsin, or Minnesota migrated to wintering sites in the Eastern Management Region and 12 marked woodcock captured on wintering areas in Texas and Louisiana migrated to breeding sites in the Eastern Management Region. Woodcock that used the Western Route exhibited high concentrations of stopovers during spring in the Arkansas Ozark Mountains and northern Missouri, and along the Mississippi River on the border between Wisconsin and Minnesota, and autumn concentrations of stopovers in southwestern Iowa, central Missouri, the Arkansas portion of the Ozark Mountains, and around the junction of Texas, Louisiana, Oklahoma, and Arkansas. Woodcock that used the Central Route exhibited high concentrations of stopovers during spring in northern Mississippi through western Tennessee, western Kentucky, and the Missouri Bootheel, and autumn concentrations of stopovers in northern Illinois, southwestern Ohio, and the portions of Kentucky and Tennessee west of the Appalachian Mountains. We suggest that current management of woodcock based on 2 management regions may not be consistent with the apparent lack of strong migratory connectivity we observed. Our results also suggest where management of migration habitat might be most beneficial to woodcock. © 2019 The Wildlife Society.

KEY WORDS American woodcock, migratory connectivity, satellite telemetry, *Scolopax minor*.

Received: 19 December 2018; Accepted: 2 June 2019

The time, energy, and risks associated with migration between breeding and winter areas are critical for migratory birds (Alerstam and Lindström 1990, Colwell 2010). The migratory connectivity of American woodcock (*Scolopax*

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minor; woodcock) is poorly understood (Case and Sanders 2010). Migratory connectivity is defined as "the movement of individuals between summer and winter populations, including immediate stopover sites" (Webster et al. 2002:77). Knowing migratory connectivity is important to understanding the movement of individuals between 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, Kramer et al. 2018). For woodcock, understanding migratory connectivity is important because woodcock populations in most portions of their breeding distribution have experienced population declines since the initiation of a standardized population survey in 1968 (Seamans and Rau 2016). Furthermore, woodcock are currently managed based on the assumption of strong migratory connectivity, and different harvest regulations have been applied to different geographic regions based on this assumption. By understanding annual movements, managers can better focus conservation efforts and determine factors that may be limiting woodcock populations.

Woodcock migration has been studied using band returns from hunters (Glasgow 1958, Sheldon 1967, Coon et al. 1977), radio-telemetry (Krementz et al. 1994, Myatt and Krementz 2007, Meunier et al. 2008), phylogenetics (Rhymer et al. 2005), and stable isotopes (Sullins et al. 2016). These studies provided insight into woodcock migration; however, they were limited by focusing on a single geographic area, being unable to provide information on >1 relocation per individual, or only allowing inference at coarse temporal (phylogenetics) or spatial (stable isotopes) scales.

Based primarily on data derived from band returns, woodcock are managed by the United States Fish and Wildlife Service and Canadian Wildlife Service in 2 management regions, Central and Eastern, with presumed low rates of exchange of individuals between regions (Coon et al. 1977, Owen et al. 1977). Also based on band returns, Glasgow (1958) and Sheldon (1967) proposed 3 primary woodcock migration routes: Western, Central, and Atlantic (Fig. 1). Glasgow's proposed Western route starts in East Texas and Louisiana. During northward migration along the Western Route, woodcock use disparate pathways through Arkansas and Missouri before converging on and following the Mississippi River. Woodcock using this route then diverge towards their breeding-period sites in Minnesota and Wisconsin. Glasgow (1958) described the Central route as starting in 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 (1958) described additional spurs on this route as crossing New York to breeding sites in New England and the Maritime Provinces of Canada and as crossing Illinois and Ohio to breeding-period sites in Michigan. Glasgow's (1958) Atlantic Route runs through the area between the Appalachian Mountains and the Atlantic Coast, connecting the southeastern states from Mississippi to Florida to New England and the eastern Canadian provinces.

Until recently, it has not been possible to clearly assess migratory connectivity in woodcock or evaluate how well currently defined management regions reflect woodcock population affiliation (i.e., whether individual woodcock associate with a single management region). Advances in the miniaturization of satellite transmitters, or platform transmitter terminals (PTTs), now allow remote tracking of woodcock, providing a means to evaluate current woodcock migratory connectivity, affiliation with management region, and migration routes. Our objective was to describe spring and autumn migration routes and stopover regions used by woodcock in the Central Management Region.

STUDY AREA

Woodcock are found throughout much of eastern North America and are managed based on an Eastern and a Central management region (Seamans and Rau 2016). Management region boundaries are analogous to those of the Atlantic and Mississippi flyways, with the eastern part of the Central Flyway included in the Central Management Region (Fig. 2). We designed our study to represent woodcock associated with the Central Management Region, which was the approximate geographic extent of our study area. However, we expanded the geographic extent of our study area to include portions of the Eastern Management Region because some woodcock that we captured and marked with satellite transmitters migrated to that region. See Sullins et al. (2016) for a complete description of our study area. We conducted this study from September 2013 to June 2016.

METHODS

Capture and Transmitters

We captured woodcock within the United States portion of the Central Management Region during the breeding and wintering periods except for 1 woodcock captured in northwestern Arkansas (Fig. 2) during presumed northward migration. We captured woodcock at 20 different sites throughout Arkansas, Louisiana, Michigan, Minnesota, Texas, and Wisconsin between September 2013 and February 2016 (Table S1, available online in Supporting Information). To represent woodcock across the breeding-period and wintering distribution within the Central Management Region, we captured woodcock across the northern and southern portion of the Central Management Region within the United States and chose specific capture sites that would facilitate woodcock capture. We trapped 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), mistnets during the crepuscular period (McAuley et al. 1993), and captured 1 woodcock with a handheld-net and a trained pointing dog during daylight. We tagged woodcock as close to the initiation of spring or autumn migration as possible to reduce the risk of mortality or transmitter failure before migration began. Before spring migration, we captured woodcock between 5 January and 16

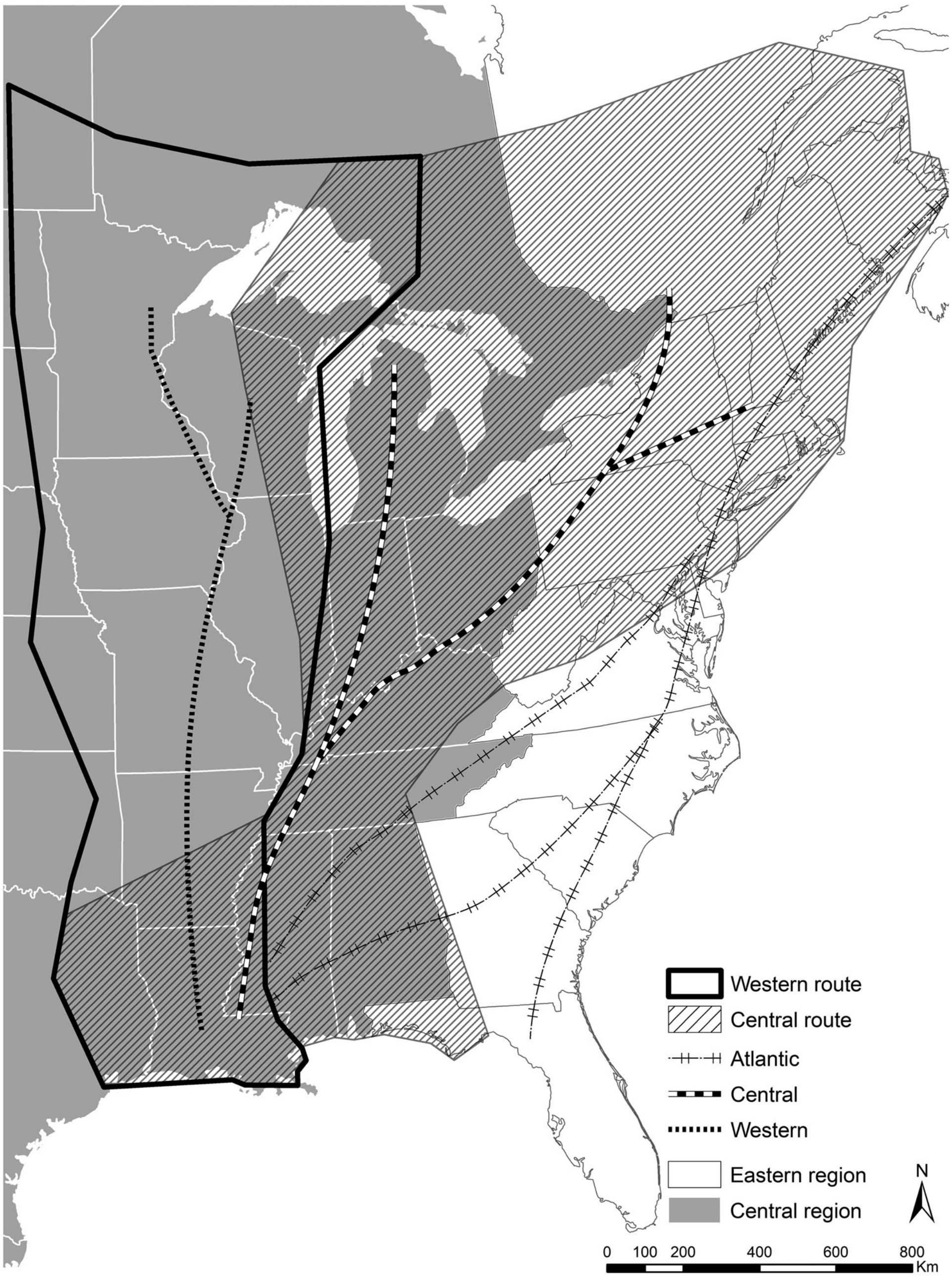

Figure 1. Hypothesized Western (black outline) and Central (crosshatch) migration routes derived from locations of monitored American woodcock captured in the Central Management Region (2013–2016) along with Glasgow's (1958) hypothesized Western, Central, and Atlantic migration routes of American woodcock overlaid on current (2019) Eastern and Central Management Regions.

February (except for 1 woodcock captured in Arkansas on 10 Mar 2014). Before autumn migration, we captured woodcock between 18 September and 3 November. We recorded the body mass and determined age and sex of captured woodcock (Martin 1964). We banded all captured woodcock with a United States Geological Survey (USGS) band. We attached satellite transmitters 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 2 strands of 0.7-mm Stretch Magic® elastic plastic cord (Pepperell Braiding Company, Pepperell, MA, USA) threaded through Tygon tubing (Saint Gobain, Courbevoie, France; Hughes et al. 1994) that were crimped with metal rings to attachment points on the transmitter. We performed this study under protocols approved by the Institutional Animal Care and Use Committee at the University of Arkansas (protocol 15011) and the University of Minnesota (protocol 1408-31777A).

We equipped woodcock with 3 types of PTTs: a 9.5-g PTT, a 5-g PTT, and a 4.9-g global positioning system (GPS) PTT. 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, Landover, MD, USA) estimated woodcock

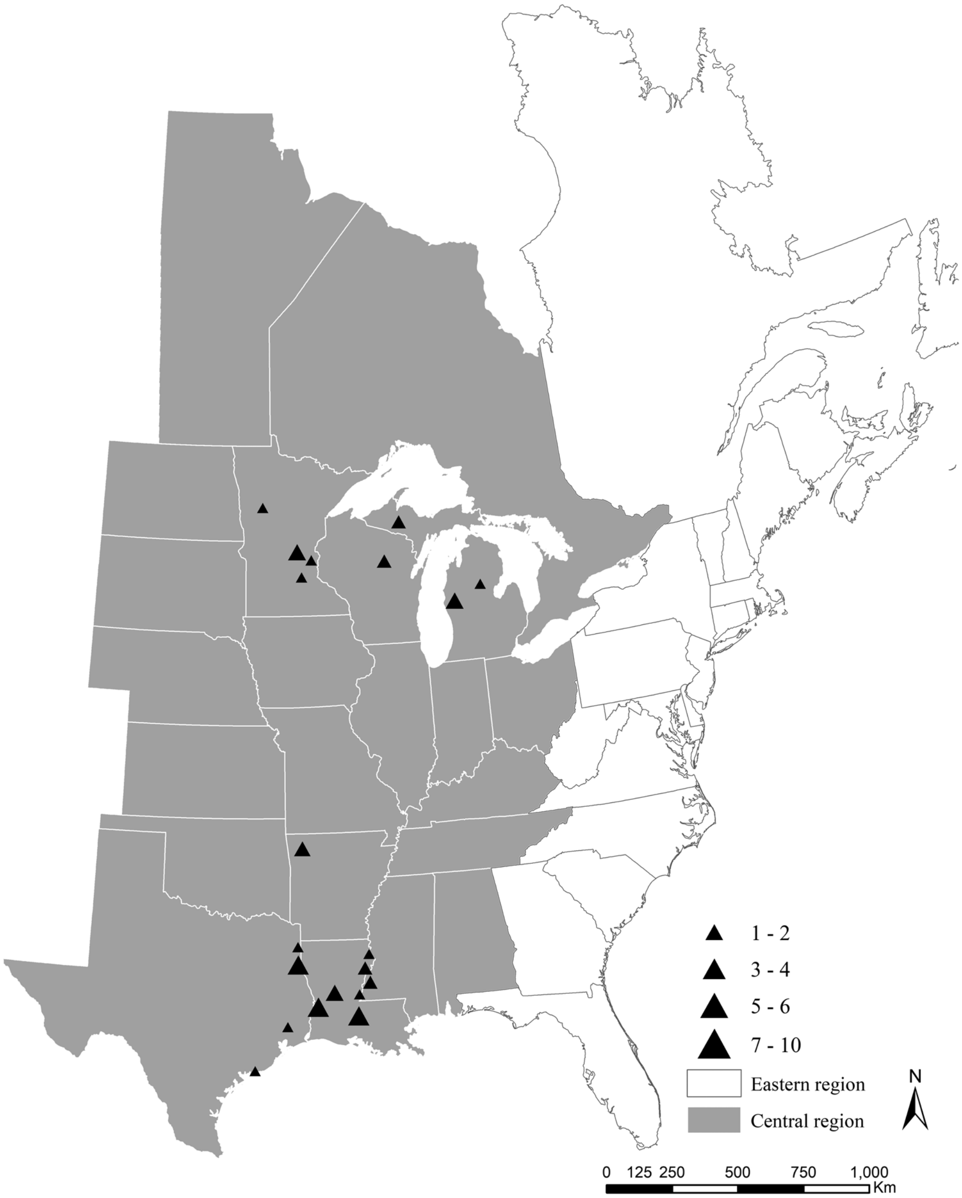

Figure 2. American woodcock capture sites from 2013 to 2015. The size of the triangle represents the number of woodcock captured and outfitted with a platform transmitter terminal. Overlapping symbols were jittered. States and provinces filled in gray are part of the Central Management Region. States and provinces filled with white are part of the Eastern Management Region.

locations using the Doppler shift of transmissions originating from the PTTs (Argos 2016). A class designation that provided estimated error was associated with each location. Reported location errors were between 250 m and 1,500 m or there was no error estimation (Argos 2016). The PTTs had auxiliary sensors that provided information on temperature, voltage, and activity (i.e., 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 when we stopped receiving messages. The battery powered 4.9-g GPS PTTs (Lotek Wireless, Newmarket, Ontario, Canada) had only enough charge to collect 30 GPS locations along 1 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 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 to the satellites. In autumn 2015, we programmed GPS transmitters to record 1 location every 3 days between 18 October and 19 January. In spring 2016, we programmed 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 estimated locations. 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 (we received an exception from the USGS Bird Banding Laboratory to exceed the usual 3% body mass restriction). We deployed 9.5-g PTTs only on females weighing >200 g. We deployed 5-g PTTs and 4.9-g GPS PTTs on males and females weighing >150 g.

We used the Movebank tracking data map (Kranstauber et al. 2011, Wikelski and Kays 2016) to identify clusters of locations and to classify clusters as migratory stopovers, wintering sites, or breeding sites. We eliminated implausible Argos locations using location proximity, time lag between locations, and Argos location class under the assumption spatial and temporal autocorrelation confirm the validity of the location (Douglas et al. 2012:6). For Argos locations, we used clusters of ≥2 successive Argos locations to define stopover sites (Douglas et al. 2012). The GPS locations had reduced error compared to the Doppler-shift-based Argos locations; therefore, a single diurnal GPS location was enough to identify a stopover site. Because woodcock migrate nocturnally, clusters of ≥2 successive nocturnal GPS locations (taken every 3 days) were necessary to confirm a stopover. 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 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 sites until southward movement >25 km began. We classified sites between breeding and wintering sites as migratory stopovers. We determined the coordinates of each stopover by taking the median center (i.e., a central point that minimizes the total distance to all other points in the cluster) of all locations within the cluster (Arizaga et al. 2014).

High-Density Stopover Regions

We visualized geographic areas with high densities of migratory stopovers using the kernel density tool in ArcMap 10.3 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA). We used a search radius of 150 km and a grid size of 10 × 10 km that balanced between under-smoothing and over-smoothing while recognizing the limitations in choosing the best smoothing parameter value (Schuler et al. 2014). We 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. To avoid pseudoreplication, we included stopover sites from only 1 migration season per individual into each kernel density estimate. We used natural breaks (Jenks 1967) to classify and symbolize each kernel density estimate into 5 categories based on stopover density.

Migration Routes

We visualized migration routes (i.e., collections of concentrated migration paths) using the line density tool in ArcMap 10.3 (ESRI). We used a search radius of 75 km and a grid size of 10 × 10 km. We created separate line density estimates for autumn migration, spring migration, and for spring and autumn migration combined. For autumn migration, we included autumn migration paths only from woodcock captured during the breeding period. For spring migration, we included spring migration paths only from woodcock captured during the wintering period. To avoid pseudoreplication, we included stopover sites from only 1 migration season per individual into each density estimate. We used natural breaks (Jenks 1967) to classify and symbolize each line density estimate into 5 categories based on path density. To assess whether individual woodcock used similar routes between years, we visually compared subsequent autumn or spring migrations paths from individuals monitored for multiple autumn ($n = 1$) and spring ($n = 7$) migrations.

RESULTS

We tagged 73 woodcock and deployed transmitters on 25 adult and 28 juvenile females, and 8 adult and 12 juvenile males; Table S1) using 42 9.5-g PTTs, 10 5-g PTTs, and 21 4.9-g GPS PTTs (Table S2, available online in Supporting Information). Before the start of autumn migration, we captured 11 woodcock in Michigan, 8 in Minnesota, and 3 in Wisconsin. Before the start of spring migration, we captured 36 woodcock in Louisiana and 14 in Texas; during spring migration we captured 1 woodcock in Arkansas. We monitored woodcock during autumn migration in 2013, 2014, and 2015 and we monitored woodcock during spring migration in 2014, 2015, and 2016. We censored 13 woodcock because we did not recover migration data from their PTTs. We monitored the migration paths of 60 individual woodcock (Fig. 3) and documented 67 complete migrations (migrations in which the breeding and wintering sites were known) and 20 partial migrations (the migratory origin or destination were unknown; Table S3, available online in Supporting Information).

Autumn Migration

During 2013–2015, we documented the autumn migration paths of 30 woodcock: 26 females (16 adult, 10 juvenile) and 4 males (1 adult, 3 juvenile; Table S3). We monitored all woodcock during 1 season, except for 1 woodcock that we monitored in 2013 and 2014, for 31 migration paths (Fig. 3), which included 23 complete migration paths and 8 partial migration paths. We censored 3 woodcock tagged before they initiated autumn migration with an unknown fate because we stopped receiving locations from the transmitters. We received migration data from 11 woodcock captured during winter. Thus, autumn migration data were from woodcock tagged in Michigan ($n = 8$), Minnesota ($n = 8$), and Wisconsin ($n = 3$) before autumn migration and the autumn migrations of woodcock tagged during the winter in Texas ($n = 3$) and Louisiana ($n = 8$) that 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 ($n = 2$).

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 ($n = 3$). We censored 2 woodcock

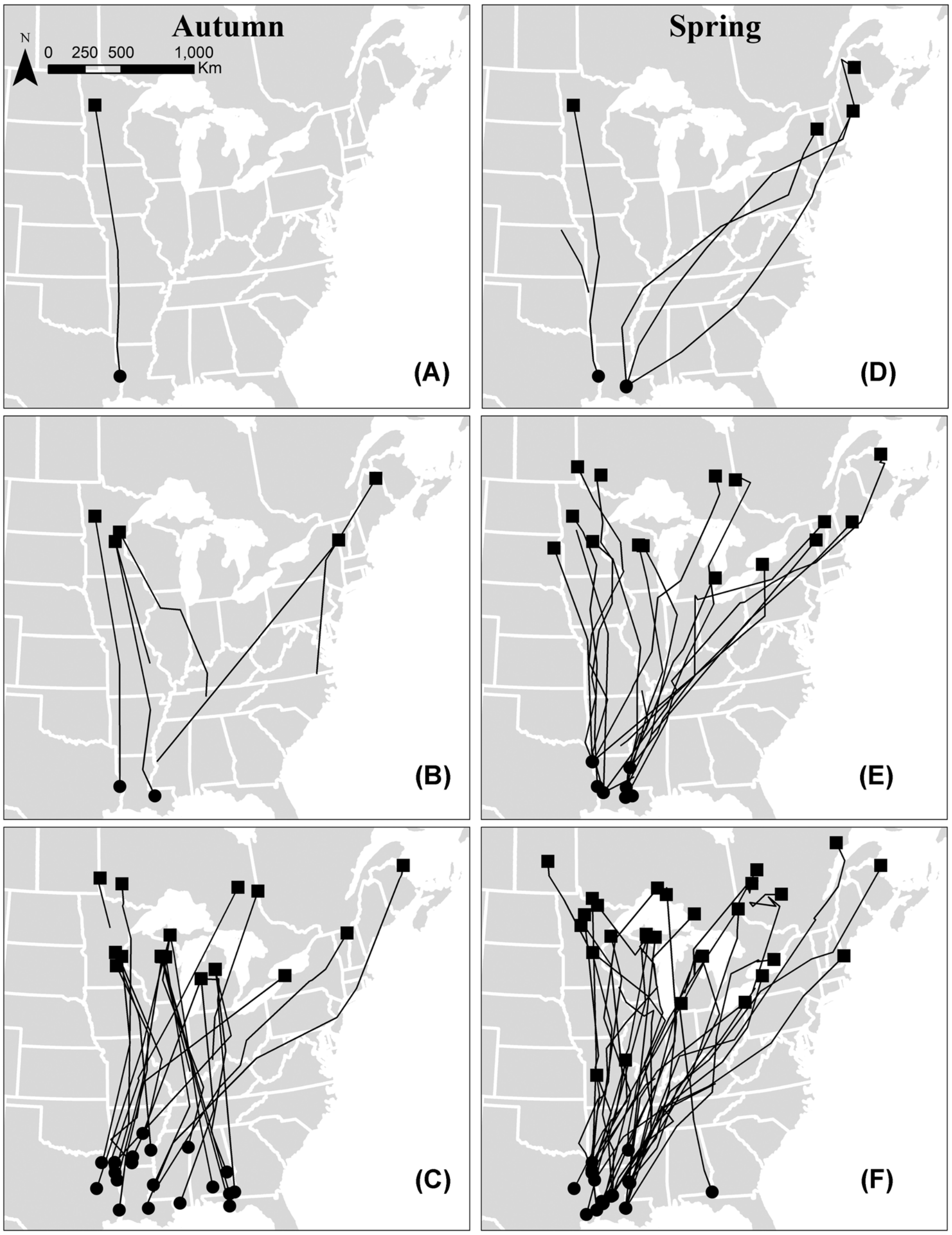

Figure 3. The spring and autumn migration routes of American woodcock (n = 60) tracked during autumn migration 2013 (A), 2014 (B), and 2015 (C) and during spring migration 2014 (D), 2015 (E), and 2016 (F). We monitored 1 woodcock during 2 autumn migrations, 8 woodcock during 2 spring migrations, and 18 woodcock during autumn and spring migrations. Squares represent breeding-period sites, and circles represent winter sites.

captured in Minnesota (unknown fate) during autumn migration after they reached locations in Missouri and Tennessee. Woodcock captured in Wisconsin and a nearby site in the Upper Peninsula of Michigan with complete autumn 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 before autumn 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 captured in the Central Management Region migrated to winter sites in the Central Management Region and 2 woodcock migrated to winter sites in the Eastern Management Region (Table 1).

We recorded 2 years of winter-site locations for 6 woodcock. 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 km and 100 km apart between years (Table S4, available online ins Supporting Information).

Woodcock breeding in the Central Management Region showed 2 primary autumn migration routes: a Western and a Central Route (Figs. 1 and 4; Table 1). Woodcock that used the Western Route moved south to Arkansas, Louisiana, and Texas with main stopover regions (Fig. 4) in southwestern

Iowa, central Missouri, the Arkansas portion of the Ozark Mountains, and depending on winter destination, the northeastern 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 portions of Kentucky and Tennessee west of the Appalachian Mountains.

Spring Migration

During 2014–2016, we monitored spring migration paths of 48 individual woodcock: 36 females (16 adult, 20 juvenile) and 12 males (4 adult, 8 juvenile; Table S1). We monitored 40 woodcock during 1 spring migration and 8 woodcock during 2 spring migrations for 56 (44 complete and 12 partial) migration paths (Fig. 3). We censored 10 woodcock tagged in the winter before they initiated spring migration with an unknown fate because we stopped receiving locations from the transmitter. We received migration data from 11 woodcock captured during the autumn. Thus, spring migration paths were from woodcock tagged in Arkansas ($n = 1$), Louisiana ($n = 31$), and Texas ($n = 9$) and the spring migrations of woodcock tagged during the autumn in Michigan ($n = 3$) and Minnesota ($n = 4$) that had migrated to Alabama ($n = 1$), Arkansas ($n = 1$), Louisiana ($n = 1$), and Texas ($n = 4$).

Nine woodcock captured in Texas had complete migration paths and most of these woodcock ($n = 7$) migrated north 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 the woodcock with complete migration paths migrated generally north 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 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 ($n = 1$). Fourteen of the 18 woodcock captured in the MAV migrated through western Mississippi into Tennessee before reaching their breeding sites. Of the remaining 4 woodcock, 1 migrated along the east side of the Appalachian Mountains to a breeding 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. Overall, 21 woodcock captured in the winter migrated during spring to breeding sites in the Central Management Region and 12 woodcock migrated to breeding sites in the Eastern Management Region (Table 1). Eight of 9 woodcock captured in Texas migrated to breeding sites in the Central Management Region, whereas just over half of woodcock captured in Louisiana (13 of 24) remained in the Central Management Region. Fifteen of 33 woodcock captured in Texas or Louisiana migrated to breeding sites in Canada.

We had 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 (captured as second-year female in Louisiana in Jan) that used different migration paths between years migrated from Louisiana to Maine on the east side of the Appalachian

Table 1. The migration route used and the destination management region of American woodcock, captured within the Central Management Region, USA, and monitored with platform transmitter terminals 2013–2016.

	Autumn migration[a]				Spring migration[b]			
	Male		Female		Male		Female	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
Migration route								
Western Route	0	0	4	7	3	1	6	4
Central Route	0	0	2	4	4	2	8	7
Atlantic Route	0	0	0	0	0	0	1	0
Destination region								
Central region	0	1	6	8	4	2	9	6
Eastern region	0	0	0	2	2	1	5	4

[a] Autumn migration information is from woodcock captured in Minnesota, Michigan, and Wisconsin.
[b] Spring migration information is from woodcock captured in Arkansas, Louisiana, and Texas.
For migrating woodcock, we documented a Western Route and a Central Route through the Central Management Region and documented a higher proportion of marked woodcock that migrated from wintering sites in the Central Management Region to breeding sites in the Eastern Management Region. This crossover between management regions suggests lower migratory connectivity than previously estimated based on band returns and raises questions about the need for managing woodcock in separate management regions.

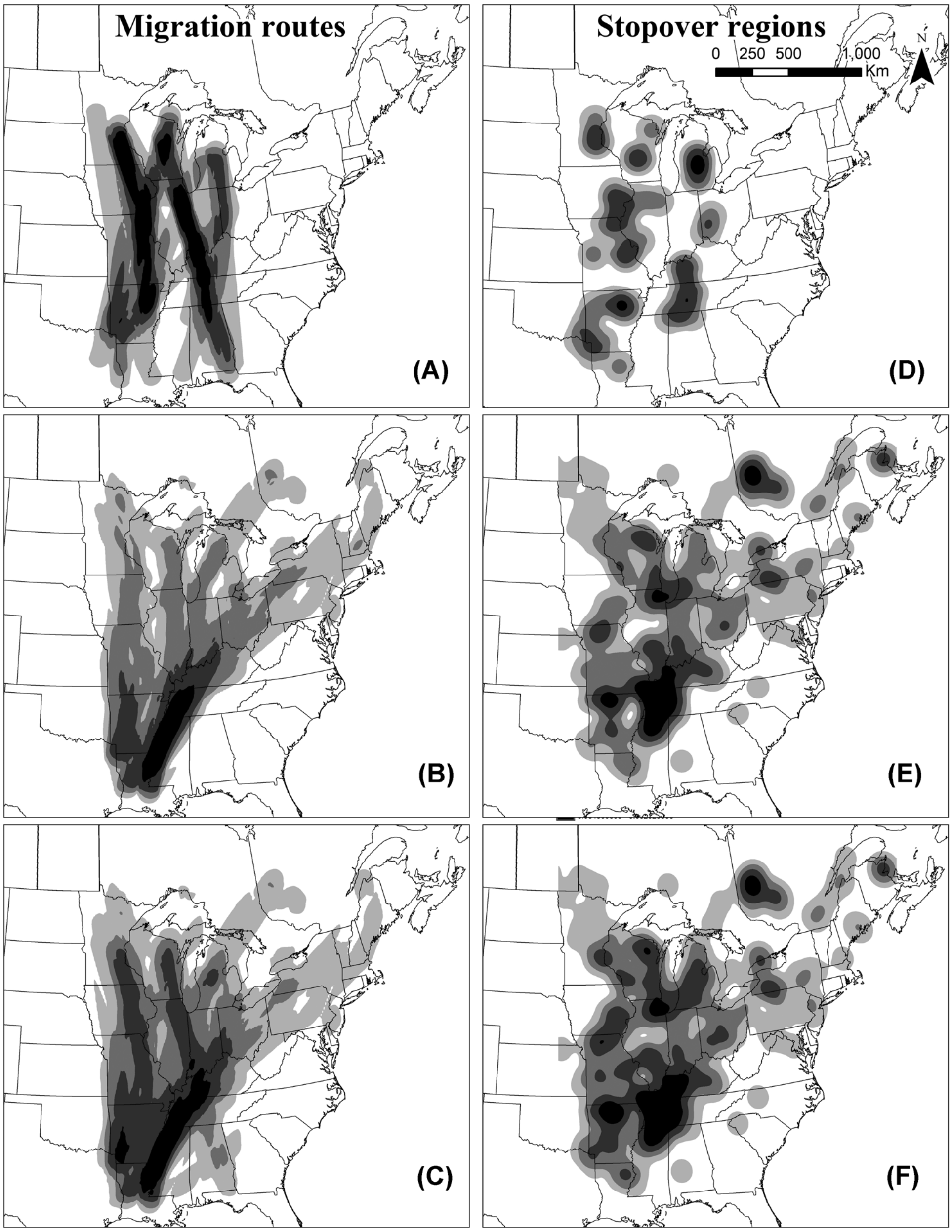

Figure 4. Migration routes and stopover regions of American woodcock, captured within the Central Management Region, and monitored with platform transmitter terminals. Autumn migration routes (A), spring migration routes (B), and an aggregate of autumn and spring migration routes (C) were visualized 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.

Mountains during spring 2014, had no recorded locations in the following autumn and winter, and then migrated from Louisiana to Maine on the west side of the Appalachian Mountains during spring 2015. We documented 2 years of breeding sites for 11 woodcock. Six of these woodcock had centers of their breeding sites <1.5 km apart between years. One woodcock had successive breeding sites approximately 25 km apart between years and 3 had successive breeding sites that were between 200 km and 1,000 km apart between years (Table S4). The 3 woodcock with breeding sites >200 km apart were captured in October in Minnesota or Michigan. It is possible that the capture sites for these birds were not breeding sites but were instead autumn migratory stopovers.

We observed 2 primary migration routes north from sites in Texas and Louisiana (Figs. 1 and 4): a Western Route and a Central Route (Table 1). The Western Route went north from Texas and Louisiana through Arkansas and Missouri before ending at breeding-period sites west of Lake Michigan. A primary 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 Ozark Mountains and in northern Missouri (Fig. 4). 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 Missouri Bootheel, with a lower density of stopover sites extending north into southern Illinois and southern Indiana. Other areas with high stopover-site density included northeastern Wisconsin, along the southern shoreline of Lake Michigan (with the highest density near Chicago, Illinois), the northern portion of Michigan's Lower Peninsula, and along the western half of the border between New York and Pennsylvania.

DISCUSSION

We observed strong migratory connectivity where woodcock breeding in the Central Management Region moved to winter sites in the Central Management Region; however, woodcock tagged during the winter in the Central Management Region migrated to breeding sites in the Eastern and Central management regions. Our observed connectivity between woodcock wintering within the Central Management Region and breeding throughout the Central and Eastern management regions contradicts pre-season band return analyses showing <5% crossover between regions (Coon et al. 1977), but Coon et al. (1977) included all direct and indirect recoveries regardless of whether woodcock were harvested during migration or on the winter grounds. Our results are consistent with an analysis of woodcock band returns using a subset of band returns representing complete migrations between the breeding and wintering grounds (Moore and Krementz 2017). Coon et al. (1977) results were used as the biological justification for managing woodcock as 2 populations. 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 and more recently for blue-winged warblers (*Vermivora cyanoptera*) and western-breeding golden-winged warblers (*V. chrysoptera*; Kramer et al. 2018).

Woodcock we monitored in the Central Management Region followed migration routes similar to the Western and Central Routes described by Glasgow (1958) and Sheldon (1967). Woodcock captured in Texas and Louisiana (west of the MAV) tended to follow the Western Route to breeding sites in Minnesota, Wisconsin, and Michigan's Upper Peninsula (Fig. 3). Similar to Glasgow's Western Route, we observed diffuse movement through Iowa, with many woodcock continuing farther north to breeding sites in Ontario and Manitoba (Fig. 3). Monitoring woodcock captured on the wintering grounds enabled us to document this northern extension of the Western Route (Fig. 4). The high proportion of woodcock in our sample that migrated to breeding 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.

Myatt and Krementz (2007) proposed a route similar to Glasgow's Western Route based on observations made using aerial radio-telemetry of woodcock marked with very high frequency transmitters before southward migration from Minnesota, Wisconsin, and the Upper Peninsula of Michigan. As an addition to this route, they proposed a Mississippi Route that branched south from the Western Route in the Missouri Bootheel and followed the eastern edge of the MAV into Mississippi. We observed limited use of this proposed route during spring migration. In addition, we observed a migration route oriented southeast from Wisconsin and the Upper Peninsula of Michigan to the portion of Tennessee between the MAV and the Appalachian Mountains and then spread to wintering sites extending from Louisiana to Florida. Both sections of this route (WI to TN, and TN to AL and FL) were previously undescribed; these movements seem to be along an extension of Glasgow's Central Route.

We documented extensive use of the Central Route by woodcock captured in the MAV, and we documented use of the Central Route to a lesser extent by woodcock captured in Texas and in Louisiana west of the MAV. We 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 and Kentucky serving as an important migratory corridor for woodcock using this route. This route connects woodcock populations that winter in the Central Management Region to breeding-period populations in both the Central and Eastern management regions. Based on the tagged woodcock we monitored, we documented a broader Central Route (Fig. 1) than previously described.

By capturing woodcock in the Central Management Region, our sample did not include woodcock likely to use Glasgow's Atlantic Route, which runs in the area between the Appalachian Mountains and the Atlantic Coast. We 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. 3). It is likely that many woodcock captured during the breeding or wintering period in the Eastern Management Region would use a route similar to Glasgow's Atlantic Route; however, it is not currently known whether the connectivity we observed within the Central Management Region is present in the Eastern Management Region.

The 377 migratory stopovers we identified in our study were widely distributed throughout eastern North America but not distributed randomly. There were regions with a higher density of migratory stopovers (Fig. 4), 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 a barrier to movement or by woodcock following rivers or other natural features during migration (Hutto 1985). For example, an area in northern Mississippi (Fig. 4) with high stopover density is approximately 300–400 km from our capture sites in Louisiana (Fig. 2). This stopover region extends into western Tennessee and western 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 over. Additional examples of major stopover regions that may be because of 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 the Western and Central Routes there are high stopover densities in more forested regions such as northwestern Arkansas. In contrast, we observed low stopover densities in agriculturally dominated regions such as the Arkansas, Louisiana, Iowa, and Mississippi portion of the MAV, central Illinois, and Iowa (Myatt and Krementz 2007). The potentially limited stopover habitat in the MAV may explain the eastern boundary of the narrow portion of the hourglass-shaped Central Route in Tennessee (Fig. 4). Additional analysis of landscape-level factors that influence migratory stopover location may show that woodcock would make stopovers during migration in the low stopover density regions if suitable habitat became available.

MANAGEMENT IMPLICATIONS

Our observations call into question whether there is biological justification for managing woodcock in only 2 management regions. We identified areas with high stopover concentrations during spring and autumn migration of woodcock migrating along the Western and Central Routes, and these are likely the areas where managing migration habitat is most beneficial to woodcock. Identification of these areas and when they are used by woodcock can help prioritize when and where to target conservation efforts to benefit woodcock during migration and where to target future research to better understand habitat requirements and factors that influence survival during migration.

ACKNOWLEDGMENTS

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the United States Fish and Wildlife Service. 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 project described in this publication was supported by Grant/Cooperative Agreement Number G15AC00258 from the USGS.

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. Bringer, A. R. Hewitt, S. G. Zodrow, A. R. Forbes, K. O. Daly, G. L. Kemper, N. M. Hill, D. W. Wolfsom, M. E. Tuma, G. R. Kramer, M. W. Olinde, T. L. Edwards, G. J. Byker, C. E. Sebright, and C. J. Cahill. We thank E. B. Webb for reviewing an early version of our manuscript. This research was funded by the United States Fish and Wildlife Service Webless Migratory Game Bird Program, the USGS Arkansas Cooperative Fish and Wildlife Research Unit, the USGS 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.

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Associate Editor: Adam Janke.

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