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Industrial agricultural and woody encroachment associated with American Woodcock habitat selection in an altered grassland ecosystem

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Abstract

Animal distributions continue to undergo dramatic shifts in response to environmental change as many ecosystems become altered or transition away from their historic states. The North American Great Plains was historically a vast prairie ecosystem that has been heavily altered into a patchwork of remnant grasslands, industrial agriculture, and tracts invaded by woody vegetation. We studied the habitat selection of a forest-dwelling bird, the American Woodcock (*Scolopax minor* J. F. Gmelin, 1789), at the westward periphery of the species' range to determine how this species uses resources in this modified landscape. During the migratory and breeding season (March–May), woodcock tracked using GPS transmitters in Nebraska selected areas with higher proportions of young forest and forests with moist soils, exhibiting similar selection to birds occupying core areas of their range in eastern North America. During the summer, woodcock routinely used (46% of diurnal points) irrigated agricultural fields during the day, which was unexpected for a species that is known to summer in forest-dominated ecosystems. Our study provides evidence for flexible and atypical woodcock habitat selection at the edge of their range. These results add to the growing body of evidence pointing to regional shifts in avian community structure and further underscore the threats of agricultural conversion and woody encroachment to the Great Plains.

Key words: American Woodcock, *Scolopax minor* J. F. Gmelin, 1789, Great Plains, agriculture fields, range periphery, woody encroachment

Introduction

Human activity is causing unprecedented environmental changes across the globe (Nelson et al. 2006). Many species' distributions have and continue to undergo range shifts because of and in response to environmental change (Lord and Whitlatch 2015). Typically, anthropogenic changes are associated with range contractions, as the removal or degradation of key habitats or large-scale shifts in climate often result in resource limitations and eventual range and population loss (Jetz et al. 2007; Okes et al. 2008; Stevens and Conway 2020). Although rapid environmental change poses a substantial challenge to conservation (Lee and Jetz 2008), subsequent distributional shifts also present opportunities to study how pioneering species colonize new areas and how they use available, and potentially unconventional resources (Livezy 2009; Ehrlén and Morris 2015; Fitzgerald et al. 2018). Environmental changes may also facilitate range expansions if modifications make previously unsuitable habitat suitable (Hitch and Leberg 2007; Veech et al. 2011).

The North American Great Plains was once a vast expanse of prairie that has been heavily altered since settlement by European Americans (Engle et al. 2008; Fogarty et al. 2020). This biome is now fragmented into a patchwork of remaining and replanted prairie, industrial agriculture, and tracts that have been invaded by woody vegetation (Briggs et al. 2002, 2005; Van Auken 2009; Twidwell et al. 2013). Here, several bird species have recently undergone distributional change. The anthropogenic changes that have occurred in the Great Plains have contributed to ongoing declines of many grassland bird species (Grant et al. 2004; Askins et al. 2007; Roberts et al. 2022). While grassland obligates have declined in the region, many generalists and woodland species have concomitantly expanded their ranges (Coppedge et al. 2001), including Red-bellied Woodpecker (*Melanerpes carolinus* (Linnaeus, 1758); Kirchman and Schneider 2014) and Barred Owl (*Strix varia* Barton, 1799; Livezy 2009).

The American Woodcock (*Scolopax minor* J. F. Gmelin, 1789; hereafter woodcock) is a migratory forest-dwelling shorebird that has declined over much of its range and these declines are typically attributed to habitat loss (McAuley et al. 2005; Kelley et al. 2008; Seamans and Rau 2019). The woodcock's core range includes forested ecosystems of the eastern US and Canada. Breeding habitat includes early-successional habitats, mature forests, and open areas located in close proximity to each other (McAuley et al. 2020). Young, upland forest is used for nesting sites and diurnal cover, and breeding display grounds are usually located near these areas (Gutzwiller et al. 1983; McAuley et al. 1996; Dessecker and McAuley 2001). Forests with moist soils and ample cover provide safe diurnal feeding locations (Masse et al. 2013; McAuley et al. 2020). Multiple studies have also identified open fields and clearings as important for woodcock, as these areas provide nocturnal roosting sites across all seasons as well as display grounds during the breeding season (Krementz et al. 2014; Masse et al. 2014; Allen et al. 2020).

Although woodcock habitat use and selection has been studied extensively in core portions of its range, these aspects of its life history have not been studied in the Great Plains. We studied the habitat selection of woodcock at the westward periphery of their range to determine what resources a forest-dwelling species uses in a landscape dominated by dwindling native prairies, large-scale row crop agriculture and expanding woody vegetation. We primarily focused on examining woodcock selection of agriculture and grasslands, as both habitats exist in much larger quantities in the Great Plains relative to eastern North America. We also compared seasonal differences between habitat use in grasslands and agricultural fields by tracking individual woodcock at both spring locations and throughout the post-breeding period into summer. By doing so, we provide important information about the ongoing habitat changes within the Great Plains and about the woodcock's ability to adapt to novel environments, particularly in recently altered and transitioning ecosystems.

Materials and methods

Study area

Our study area included multiple sites in eastern and central Nebraska (Fig. 1). Historically, the locations and areas around our study sites were open prairie (Kaul and Rolfsmeier 1993) and outside the known range of woodcock at the time of European settlement (Bruner et al. 1904). Woodcock appear to have not significantly expanded their range in Nebraska until about the 1970s (Lingle 1981; Jorgensen and Brenner 2023 in press). Eastern-most trapping sites included four different State Wildlife Management Areas (WMAs) near Lincoln, Nebraska, as well as WMAs farther north near the Elkhorn and Platte rivers. Our western-most trapping location was at Calamus Reservoir WMA (41°55′′25′N, 99°19′′10′W), situated within the eastern edge of the Nebraska Sandhills (Fig. 1).

Capture and GPS tags

We used existing knowledge or surveys to identify specific locations where woodcock were displaying and used mist nests to capture birds in early spring (March–early April). Sex was determined using various morphological measurements and age was determined using plumage characteristics of the wings (Martin 1964). We used Lotek Pinpoint Argos GPS tags (model Pinpoint Argos 75 for males at ~4 g, model Pinpoint Argos 120 at ~6 g for females; Lotek Wireless, Newmarket, ON, Canada) for tracking woodcock. We outfitted birds with satellite transmitters using a modified leg-loop harness (Rappole and Tipton 1991) with 0.7 mm elastic chord (Stretch Magic® Pepperell Braiding Co., Pepperell, MA) threaded through Tygon tubing (Saint Gobain, Courbevoie, France) and secured using small metal crimps (Moore et al. 2019). Tags were programmed with variable duty cycles within certain parameters each season, and location data was high-quality (±10 m) and remotely transmitted and downloaded via the Argos system (CLS America 2016). During spring (March–late May), GPS fixes were scheduled between 22–48 h, usually targeting a different hour in each day to capture diurnal and nocturnal use, or in the case of actively migrating birds, their flight path. In the summer months (June–August), fixes were more spaced out to maximize battery life, ranging from 2.5- to 5-day duty cycles also targeting different hours between fixes to maximize both diurnal and nocturnal habitat use. All capture, handling, and transmitter deployment was authorized under USGS Federal Bird Banding Permit (20259) and State of Nebraska scientific permit (1304).

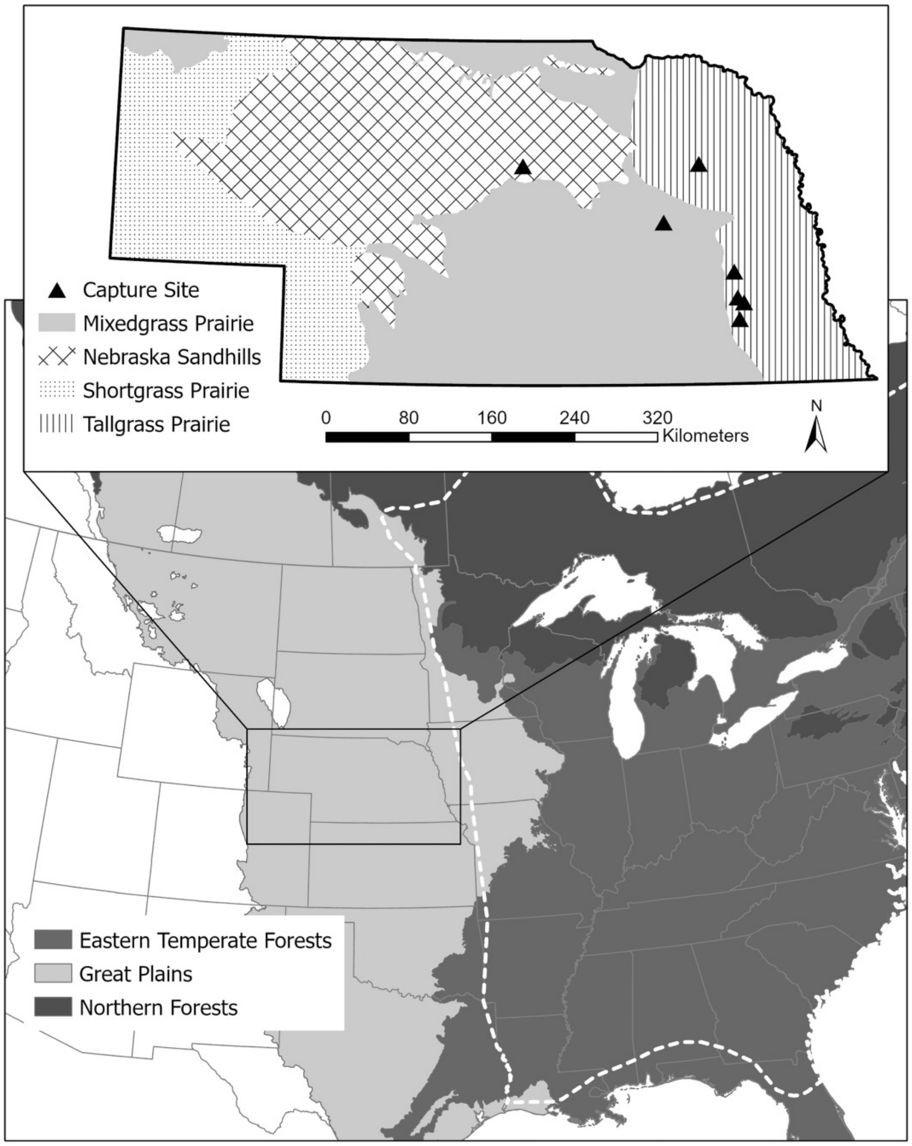
Resource selection function analysis

We developed basic resource selection functions (RSFs) for all woodcock in Nebraska during spring using 200 point locations collected from capture to departure in 2021 and 2022. For birds that remained in the state throughout the summer, we delineated this spring period from 7 March–7 May, which includes multiple overlapping life stages of migration, stopover, and courtship/breeding. Any bird that was in Nebraska after 7 May in either year remained in the state for the rest of the summer. Lastly, all summering birds were male, and male woodcock do not participate in incubation or brood-rearing. Thus, their movements were not influenced by young or a nest.

We developed RSFs following the methodology and recommendations of Manly et al. (2002) and Johnson et al. (2006). This framework has been used in multiple recent studies on woodcock to create probability of use maps, refine target management locations, and compare habitat selection across different seasons (Masse et al. 2014, 2019; Allen et al. 2020). We defined "used" locations as the GPS locations for tagged woodcock in Nebraska. To determine habitat "available" to a woodcock, we grouped individuals based on capture sites and created composite home ranges using 95% kernel density estimation using the *adehabitatHR* package in program R (Calenge 2006). The smallest area we considered available to birds on migration was the WMA in which they were captured (min size = 120 ha). If the estimated composite home range exceeded this size, we used that total area to delineate "available" habitat. We then created random points within these areas ($n = 1169$) that were >50 m apart, and we measured proportional land cover with the same covariates and scales as the "used" woodcock GPS locations.

Woodcock outfitted with satellite transmitters are known to travel large distances over relatively short periods during spring migration (Moore et al. 2019). Thus, very large areas (e.g., entire states) could be considered "available" to a migrating bird. This approach has been taken on a slightly

Fig. 1. Capture locations for American Woodcock (*Scolopax minor*) within Nebraska relative to the dominant historic grassland ecoregions within the state. The extent of the core range of American Woodcock as depicted by Kelley et al. (2008) is drawn as a dashed white line within the dominant continental ecoregions of interest (CEC 1997). Map projection: NAD 1983 UTM Zone 14N. Map imaging: ESRI, U.S. EPA and GIS User Community.



smaller scale (county-level) for woodcock fall migration and wintering selection decisions in New Jersey (Allen et al. 2020). However, birds caught as part of our study during migration did not use multiple sites within the state while in Nebraska. Additionally, historical data and counts from scouting surveys all indicate that woodcock numbers in Nebraska are consistent but relatively low compared to the core range, and thus distribution is likely concentrated around small areas with suitable habitat and not evenly distributed across the state.

Model parameters

We simplified statewide land cover data (Bishop et al. 2009) into the following classifications: agriculture, grasslands, Sandhills prairie, young forest/shrub, deciduous or mixed upland forest, wetland forests, human development (roads and structures), and wetlands using ArcGIS Pro (ESRI 2021; version 2.8). The Sandhills are a distinct dune-stabilized prairie ecosystem and the largest intact grassland remaining in North America (Loope and Swinehart 2000). In our land cover dataset, "agriculture" represents industrialized center pivot irrigated row crop production, predominately soybean (*Glycine max* (L.) Merr.) and corn (*Zea mays* L.) with very small proportions of wheat or other crops. Agriculture fields in our system are generally not fallow during summer. Grasslands in our study includes native and restored tall- and mixed-grass prairies, pasture, and some seasonally wet meadows.

We examined habitat variables at two different scales by measuring proportional land cover within 300 m radius of a bird's location and within a 1000 m radius of a bird's location. The average distance moved by woodcock in Nebraska between successive points was typically ~250 m, and 1000 m generally encompasses a larger, landscape-level composition of habitat relevant to woodcock (Kramer et al. 2019). We then optimized the scale for each land cover type by building competing models at each distance (Allen et al. 2020) and used Akaike's information criteria corrected ($\mathrm{AIC_c}$) for small sample sizes to test which scale had the better fit (Burnham and Anderson 2002). For subsequent model development, we then considered only the best-performing scale for each land cover type.

To examine woodcock habitat selection at the periphery of the woodcock range, we initially considered models that include grasslands, Sandhills prairie, and agricultural cover, as these land cover types are both predominate within eastern and central Nebraska and exist at much larger proportions on the landscape in our study area relative to the core of the woodcock range. Our main objective was to determine the influence of atypical habitats at range periphery on woodcock selection. Thus, we were most concerned with modeling the effects from regionally specific land cover and not attempting to use these models to create a predictive map of woodcock use in the state.

Sandhills prairies were found at relatively small proportions (mean < 0.06) within the study sites at both scales (300 and 1000 m), so we eliminated this land cover from model consideration. To reduce model complexity given our low sample size, we then restrained our models to three land cover types, with eligible models, including agriculture, grasslands, and one additional relevant land cover type. We tested woodcock selection using a binomial logistic regression mixed-effect modeling format. We treated site as a random intercept for all models to account for imbalances in the number of individuals tracked at each site (Gillies et al. 2006; Allen et al. 2020) and to account for the variation in the length of stay during spring for birds in our study (see Brenner and Jorgensen 2023). We evaluated our highest-rated RSF model (lowest $\mathrm{AIC_c}$ score) models using k-fold cross validation (Boyce et al. 2002). We used three-fold cross validation by randomly dividing birds into three groups of five and using two thirds of the data to re-estimate coefficients from our best models. We then generated predicted RSF values using the withheld subset and assigned these values into 10 equal-area bins from low to high relative probability of use and repeated the process withholding a different bin for testing in each iteration. We used Spearman's rank correlations (r_S) on the mean frequency of predicted locations within each RSF bin to assess the robustness of our top models (Boyce et al. 2002; Holbrook et al. 2017).

Diurnal versus nocturnal field use

Woodcock use different habitat during the daytime versus overnight periods. Diurnal habitat typically includes young forests or scrub areas for nesting and cover during the breeding season and forests with moist soils for feeding during other seasons (Gregg and Hale 1977; McAuley et al. 1993; Masse et al. 2014; Daly et al. 2019). Nocturnal habitat during all seasons typically includes a field or forest opening for display flights and roosting (Sheldon 1967; McAuley et al. 2020). We examined all summer (8 May–1 September) locations that were in agricultural fields to determine the predominate time of day these areas were used. We also compared all diurnal and nocturnal summer locations that were in grasslands. We defined nocturnal use as 30 min after sundown to 30 min before sunrise. We used a chi-squared test (χ^2) to compare the proportion of diurnal and nocturnal points in agricultural fields and diurnal versus nocturnal use of grasslands. All locations classified as agriculture used by Nebraska woodcock during this study were surveyed to assess crop and confirm the field was actively irrigated.

Table 1. Standardized coefficient estimates with 95% upper (UCI) and lower (LCI) confidence interval from best-supported resource selection models for American Woodcock (*Scolopax minor*) in Nebraska in spring (7 March–7 May) 2021–2022.

	ß	LCI	UCI
Grassland (300 m)	0.60	0.41	0.80
Scrub/young forest (300 m)	0.58	0.42	0.76
Agriculture (1000 m)	−0.98	−1.30	−0.68
Wet forest (1000 m)	0.86	0.64	1.08
Agriculture (1000 m)	−0.43	−0.75	−0.12
Grassland (300 m)	0.79	0.59	1.01

Note: Land cover predictors are listed with their optimized extent (300 or 1000 m).

We divided the summer period into four blocks containing an equal number of GPS locations moving from early in the summer to end of summer to determine whether diurnal agricultural field use shifted over time. We examined the proportion of individual diurnal locations within grassland and agriculture across the summer using generalized linear models (GLMs) logistic regression. We delineated the summer as early season (8 May–26 May), mid-summer (27 May–17 July), late summer (18 July–12 Aug), and end of season (13 Aug–1 Sep). All statistical testing was done in program R (R Core Team 2021).

Results

We captured 15 woodcock, 5 between 8 March and 15 April 2021 and 10 between 14 March and 4 April 2022. We captured 13 males, 5 of which were second-year (SY) and 8 of which were after second-year (ASY). Two of the woodcock we captured were SY females. Four ASY male woodcock remained in Nebraska during spring and summer. The 11 birds that left Nebraska in spring all terminated their migrations in forested regions of northern Minnesota ($n = 4$), Manitoba ($n = 6$), and Ontario ($n = 1$; see Brenner and Jorgensen 2023).

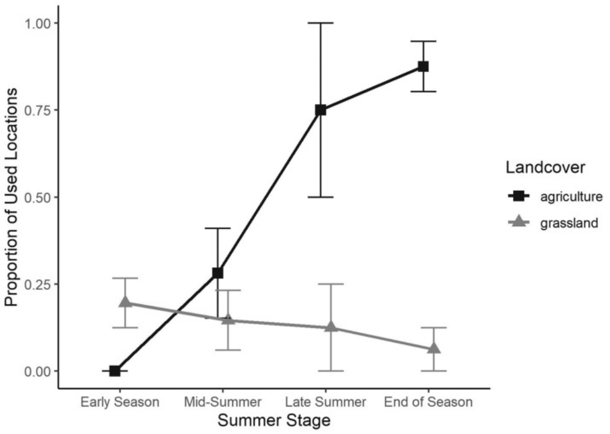
Our top mixed-scale RSF model indicated that during spring, woodcock in Nebraska selected areas with higher amounts of young forest and grassland within a 300 m extent, while higher proportions of agriculture within 1000 m had a negative effect on probability of use (Table 1). The next best-performing model ($\Delta\mathrm{AIC_c} = 2.6$, $w_i = 0.21$) also indicated that woodcock avoided areas with higher proportional coverage of agriculture within 1000 m and selected areas with

Table 2. Candidate mixed-scale RSF models for American Woodcock (*Scolopax minor*) in Nebraska.

	AIC	ΔAIC_c	w_i
Ag (1000 m), Grass (300 m), YF (300 m)	924.1	–	0.79
Ag (1000 m), Grass (300 m), WetFor (1000 m)	–	2.6	0.21
Ag (1000 m), Grass (300 m), Wetland (1000 m)	–	45.9	<0.01
Ag (1000 m), Grass (300 m), Upwoods (1000 m)	–	48.8	<0.01
Ag (1000 m), Grass (300 m), Developed (1000 m)	–	54.3	<0.01
Ag (1000 m), Grass (300 m)	–	60.7	<0.01
Null	–	187.5	<0.01

Note: Land cover variables include Ag (agriculture), Developed (developed), Grass (grassland), Upwoods (Upland woodland), WetFor (mixed forest with moist soil), Wetland (wetlands), and YF (young forest/scrub). AIC_c is Akaike's information criteria corrected.

Fig. 2. Average diurnal woodcock locations in grasslands (gray triangles) and irrigated agriculture (black squares) per bird from early season (8 May–26 May), mid-summer (27 May–17 July), and late summer (18 July–12 August) to the end of season (13 August–1 September). Mean values are displayed as proportion of points ± standard error.



higher proportional cover of grassland within 300 m and wetland forests within 1000 m (Table 1). All other predictors and models we tested lacked adequate support ($\Delta\text{AIC}_c > 3$, $w_i \leq 0.01$, Table 2). Our *k*-fold cross validation revealed the highest-ranking spring RSF models, including young forest cover within 300 m ($r_S = 0.78$, $p = 0.007$) and wetland forest cover within 1000 m ($r_S = 0.85$, $p = 0.002$), each had moderate Spearman's rank correlations and adequate predictive performance.

Of the 72 diurnal woodcock GPS locations in Nebraska during the summer, 33 occurred in irrigated agriculture fields and 10 occurred in grasslands. Of the 42 nocturnal woodcock locations in Nebraska during the summer, 10 occurred in agricultural fields and 24 occurred in grasslands. There was a higher proportion of diurnal points (46%) in irrigated agricultural fields compared to the proportion of nocturnal points (24%) in irrigated agricultural fields ($\chi_1^2 = 4.58$, $p < 0.05$). Nocturnal use of grassland cover (67%) was higher for woodcock in the summer ($\chi_1^2 = 30.91$, $p < 0.05$) than diurnal use of grassland cover (13.9%). Diurnal grassland use did not differ over the summer ($ß = 0.15 \pm 0.38$, $p = 0.69$), but diurnal agricultural field use increased with later dates from mid-summer to the end of the season ($ß = 1.78 \pm 0.63$, $p = 0.002$; Fig. 2). One woodcock had four nocturnal locations, presumably roost sites, in a Sandhills prairie over the course of the summer, and all individuals had diurnal locations within agricultural fields during the summer.

Discussion

Woodcock habitat selection in Nebraska during spring (March–early May) appears analogous to habitat selection in the core of their range, namely, birds selected areas with higher amounts of young forests with nearby open areas (in this study, grasslands) and forests with moist soils (Table 1). However, woodcock habitat selection in summer was not only different to spring selection in the state but also different from the habitat selection of woodcock in the core range during summer. Specifically, woodcock in Nebraska had a higher than expected use of irrigated agricultural fields during the day, as well as documented use of a regionally unique habitat (Sandhills prairies) for roosting. While these findings are based on a relatively small number of male individuals ($n = 4$), the high proportion (46%) of summer diurnal use of industrial agriculture fields and extreme western location of these birds relative to their core range is notable. This is not only counter to typical diurnal habitat use in their core range but also different to the other 11 woodcock tracked for this study that summered in forested locations farther north.

Nocturnal use of a variety of agricultural fields has been documented for woodcock on migratory, summering, and wintering grounds (Blackman et al. 2013; Masse et al. 2013; Krementz et al. 2014; Graham et al. 2022). However, the extensive diurnal use of actively irrigated agricultural fields during the summer months contrasts with typical diurnal use observed in woodcock studies during summer, migratory, and wintering periods (Krementz and Pendleton 1994; Masse et al. 2014; Elizondo et al. 2019; Allen et al. 2020). Woodcock in our study used these fields primarily from June–August (Fig. 2), which is peak growing season in Nebraska for industrialized row crops such as soy and corn.

We suspect diurnal use of center-pivot irrigated agricultural fields in Nebraska is related to soil moisture. Woodcock will move large distances to forage in areas with higher earthworm abundance and soil moisture (Doherty et al. 2010; Masse et al. 2013). In dry soil environments, earthworms retreat to deeper soil layers (Onrust et al. 2019), which makes probing and foraging on this prey less efficient. In addition, northeastern Nebraska was experiencing drought conditions in the latter part of 2021 and most of 2022 (US Drought Monitor, University of Nebraska–Lincoln, NE, USA). Thus, higher soil moisture, particularly near the surface, was almost certainly within irrigated agricultural fields compared to the nearby grasslands, woodlands, or other areas during this study.

Windbreak plantings and shrubby areas were present and available to the birds if vegetative structure was the most important resource for selection. However, these fragmented, small woody tracts are generally preferred over agricultural fields by common mammalian predators that reside in agricultural landscapes (Gehring and Swihart 2003; Salek et al. 2010). Woody tracts near irrigated crop fields in Nebraska could increase diurnal predation risk for woodcock (Masse et al. 2013), thus discouraging the use of this locally available woody cover. Further study on woodcock diurnal habitat selection in other areas where row crop agriculture exists in relatively high abundance is needed to determine whether agriculture is used more frequently than previously understood and not just at the extreme western periphery in Nebraska.

The atypical selection behaviors of woodcock in Nebraska also demonstrate the ability of this species to rapidly assess landscapes, adapt to new environments, and exploit novel resources. The strong use of young forests for woodcock nesting likely facilitated the species' ability to disperse and rapidly adapt to changing or novel environments. Young forest is by its nature ephemeral and will shift in relatively short timespans through disappearance (growth to mature forest) or sudden appearance (natural disturbance event, field regeneration, or active forest management). In the case of Nebraska woodcock, the continual woody encroachment into native prairie ecosystems provides the prerequisite young forest habitat for woodcock to occupy an ecosystem in transition.

The apparent expansion of woodcock into Nebraska aligns with previously identified range expansions of both forested and synanthropic birds in the region. Barred Owls expanded into the Great Plains as available forested land increased in modified prairies (Livezey 2009). Increased agricultural landscapes and other human-modified habitats facilitated Great-tailed Grackle (*Quiscalus mexicanus* (Gmelin, 1788)) expansion into the Great Plains (Wehtje 2003), and woodcock also appear to utilize these habitats to a larger-than-expected degree. Lastly, the observed habitat selection behaviors of a forest-obligate species like woodcock complement the inversely shifting range and habitat avoidance of nearby grassland obligates like the Greater Prairie Chicken (*Tympanuchus cupido* (Linnaeus, 1758)) in response to woody encroachment and agricultural conversion (McNew et al. 2012; Roberts et al. 2022).

Grassland conversion to agriculture and continual woody encroachment are the two biggest threats and drivers of grassland loss in the Great Plains (Briggs et al. 2005). The fact that woodcock, even in small numbers, can exploit both agriculture in summer and increased woody vegetation in spring is further evidence that a large shift in both ecosystem functionality and avian community structure has occurred in central and eastern Nebraska. Species at the edge of their range and in atypical environments can be important indicators of ecosystem transitions, and this study offers unique data to support our understanding of the various effects of grassland loss in the Great Plains. Further research on woodcock and other pioneering species in transitional environments should be used as additional tools to track future ecosystem changes as land use and climate pressures continue apace in the 21st century.

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Data availability

Data generated or analyzed during this study are available from the authors upon reasonable request.

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Investigation: SJB, JGJ
Methodology: SJB
Project administration: JGJ
Writing – original draft: SJB, JGJ

Competing interests

The authors declare no competing interests.

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