Brenner, S. J., and J. G. Jorgensen. 2026. Wood-warblers of the prairie: nonbreeding distribution and migratory routes of Ovenbirds breeding at range periphery in the Great Plains. Journal of Field Ornithology 97(1):7. https://doi.org/10.5751/JFO-00777-970107

Avian Behavior, Ecology, and Evolution

Wood-warblers of the prairie: nonbreeding distribution and migratory routes of Ovenbirds breeding at range periphery in the Great Plains

Reinitas de la pradera: distribución no reproductiva y rutas migratorias de individuos de *Seiurus aurocapilla* que se reproducen en la periferia de su distribución en las Grandes Llanuras

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ABSTRACT. There is limited information on migratory ecology, nonbreeding grounds, and return rates from populations at distributional limits of species' ranges. Assuming uniform ecology from core areas to range periphery may limit understanding of potential migratory routes, nonbreeding distribution, and connectivity, complicating conservation actions and assessing species-level management. We tracked a relatively well-studied Nearctic-Neotropical migratory wood-warbler, the Ovenbird (*Seiurus aurocapilla*), breeding in atypical habitats at their distributional limit in northwestern Nebraska. Individuals wintered in northwestern Mexico and migrated through the southwestern U.S., western and central Great Plains. Compared to previous studies of birds breeding in core range, the migration routes and nonbreeding areas used by western Nebraska Ovenbirds also represent the seasonal distributional limits for this species. Despite a small sample size, male return rates were also relatively high and comparable to populations breeding in large, contiguous forest regions of the core range. Overall, this study adds novel data from range periphery for a well-studied species, further reinforcing the importance of full annual cycle data and studying birds across all parts of their distribution.

RESUMEN. Existe información limitada sobre la ecología migratoria, las áreas no reproductivas y las tasas de retorno de poblaciones ubicadas en los límites del área de distribución de las especies. Asumir que la ecología es uniforme desde las áreas núcleo hasta la periferia de la distribución puede limitar la comprensión de las rutas migratorias potenciales, la distribución no reproductiva y la conectividad, lo que complica las acciones de conservación y las evaluaciones de manejo a nivel de especie. Seguimos individuos de una especie de reinita migratoria neártica-neotropical relativamente bien estudiada, *Seiurus aurocapilla*, que se reproducen en hábitats atípicos en el límite de su distribución en el noroeste de Nebraska. Los individuos invernaron en el noroeste de México y migraron a través del suroeste de Estados Unidos y de las Grandes Llanuras occidentales y centrales. En comparación con estudios previos de individuos que se reproducen en el área núcleo de la distribución, las rutas migratorias y las áreas no reproductivas utilizadas por los individuos del oeste de Nebraska también representan los límites estacionales de distribución de esta especie. A pesar del reducido tamaño de muestra, las tasas de retorno de los machos fueron relativamente altas y comparables a las de poblaciones que se reproducen en grandes regiones forestales continuas del área núcleo. En conjunto, este estudio aporta datos novedosos provenientes de la periferia de la distribución para una especie bien estudiada, reforzando la importancia de contar con información del ciclo anual completo y de estudiar las aves en todas las partes de su distribución.

Key Words: *annual cycle; Great Plains; range periphery; warbler migration*

INTRODUCTION

Migratory ecology of wide-ranging species in isolated or peripheral populations or at distributional limits is often overlooked. Population occupancy is generally lower than in the core range and decreases near the distributional limit (Gaston 2003, Pironon et al. 2017), and this can present challenges for researchers. However, individuals from edge-of-range populations may also exhibit different behaviors than conspecifics in core populations, such as occupying atypical habitats and landscapes (Brenner and Jorgensen 2023), or exhibit differing migration phenology (Olson et al. 2014). Although geographic proximity or isolation to a core range can determine whether functionally different populations exist across a given species' distribution, genetic isolation (Eckert et al. 2008) or divergent migratory ecology (DeLuca et al. 2019, Sharp et al. 2023) may also characterize and influence range-edge dynamics. Thus, assuming uniform ecology in populations across a species' distributions from the core to the limits may obscure important differences that may have conservation implications (Telleria et al. 2021, Lewis et al. 2023). Yet, limited studies have focused on the annual-cycle ecology of many birds breeding at the periphery across migratory species.

Ovenbirds (*Seiurus aurocapilla*) are migratory wood-warblers that breed in continuous forest biomes from eastern and north-central North America, including boreal regions of Canada. Ovenbirds nonbreeding range includes central and southern Mexico, Central America, northern South America, the Caribbean and peninsular Florida, USA (Porneluzi et al. 2020). Away from these major forest biomes in North America, Ovenbirds also breed in mostly disjunct patches within the Great Plains and eastern Rocky Mountain states from northern Nebraska to Montana and North Dakota (Porneluzi et al. 2020). These relatively small and isolated woodland habitats were formerly part of a larger forest biome that encompassed this region following the last glacial period

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(Kaul et al. 1988), but are now separated by extensive areas of grasslands, which are presently intermixed with agriculture. These habitats are inhospitable to Ovenbirds and the overall landscape habitat matrix is different than the continuous forest biomes of eastern and northern-central North America that constitute the majority of the species' range.

The migratory ecology and connectivity of Ovenbirds has been relatively well-studied compared to other Neotropical wood-warblers. Birds have been tracked using light-level geolocators in core breeding and nonbreeding ranges, and previous studies have quantified and established strong migratory connectivity within this species (Hallworth et al. 2015) and examined genetic relationships between populations with differing connectivity (Haché et al. 2017). We studied the migration ecology of Ovenbirds breeding in northwestern Nebraska, USA to determine the nonbreeding area and general migration routes of populations at the range-periphery. We also examined the apparent return rates of Ovenbirds that occupy the isolated pockets of ponderosa pine (*Pinus ponderosa*) forest in the Great Plains and mountain foothills of the west at relatively low densities.

METHODS

Study area

We studied Ovenbirds at Gilbert-Baker and Anderson Bridge Wildlife Management Areas (WMAs) in northwestern Nebraska at the western limits of the species' distribution and their southern periphery in the Great Plains. Sites were located along the Niobrara River valley in the north-central part of the state and in the Pine Ridge in the Nebraska panhandle (Fig. 1). Ovenbirds breed in mixed-deciduous forest stands in riparian corridors within ponderosa pine occupying slopes. Both of these pine-forest systems are isolated from the core breeding regions of the forested Midwestern United States, including the outlying pockets of deciduous woodlands along the Missouri River in Nebraska and South Dakota by at least 250 km. The eastern extent of the Pine Ridge and western reaches of the forested Niobrara River valley are also isolated from each other by ~120 km, and are isolated from similar habitats that may host breeding Ovenbirds in southern South Dakota (~40–60 km) and from the foothills of the outlying Laramie Mountains of Wyoming by ~80 km (Fig. 1).

The floral community of the Niobrara Valley, and to a lesser extent the Pine Ridge, contains several eastern deciduous and boreal species despite being isolated within the arid grasslands of the western Great Plains (Kaul et al. 1988). These forest communities are likely remnant from the last glacial maximum and subsequently isolated after glacial retreat. Modern avian communities also include species usually associated with both eastern and western forest biomes (Ducey 1989), as well as contact zones of a handful of east-west sister species pairs (Swenk 1936, Sibley and Short 1959, Manthey and Robbins 2025). Given that the Niobrara Valley and Pine Ridge act as a refugia for plant communities, it is likely that certain species in the modern avian community within these regions represent remnant populations now isolated from conspecifics that breed in boreal, eastern, and western forests (Rolfsmeier and Steinhauer 2010).

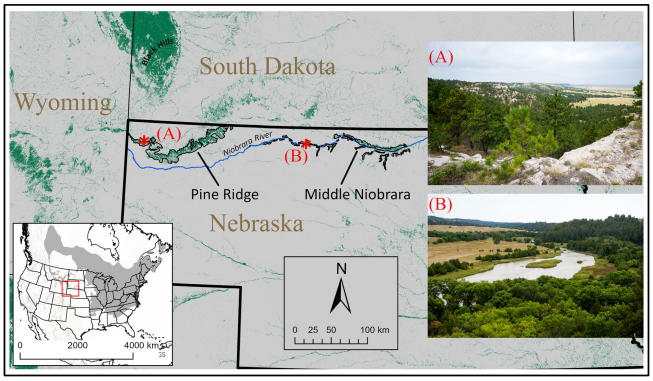


Fig. 1. Location of Gilbert-Baker Wildlife Management Area (A) in the Pine Ridge ecoregion and location of Anderson Bridge Wildlife Management Area (B) in the Middle Niobrara ecoregion in the broader Great Plains. Graphic shows the regional distribution and extent of woodland or forest landcover (green). Inset includes species-level breeding distribution in translucent gray, adapted from Porneluzi et al. (2020). Photographs show respective habitats at each site. Photo credit: Nebraskaland Magazine/Nebraska Game and Parks Commission.

The Pine Ridge is a high (300 m) escarpment created by erosion from the White River (Condra 1914). It extends from approximately east to west in northwestern Nebraska and continues into eastern Wyoming. North and east facing slopes are dominated by ponderosa pine forest and deciduous vegetation is found along streams that feed into the White River. Gilbert-Baker WMA covers 1026 ha in Sioux County and is located at the western edge of the Pine Ridge. This site is dominated by pine parkland savanna, with dense deciduous understory present in < 10% of the total area.

The Niobrara River flows in a relatively narrow (< 1 km) incised valley that is approximately 100 m below the surrounding upland prairies (Condra 1914). The middle portion of the valley in north-central Nebraska is often referred to as a "biological crossroads" because of a diverse plant community that has representation of plants found in eastern deciduous, Rocky Mountain and northern boreal woodlands (Schneider et al. 2011). Anderson Bridge WMA is 62 ha and is located at the western extent of the middle Niobrara River valley in central Cherry County at the northern edge of the Nebraska Sandhills. Anderson Bridge is located at the western extent of the Ovenbird's breeding range in the Niobrara River valley (Silcock and Jorgensen 2025), as woodland habitat becomes increasingly fragmented and decreases in extent west of there. Ovenbirds within these systems occur at relatively low breeding densities (8–15 breeding pairs per site; Brenner *unpublished data*), but have been present within these regions since early ornithological records began in the western parts of the state (Ford 1959, Rosche 1982).

Geolocator tagging and bird capture

We captured birds (n = 13) using mist nets placed over conspecific audio playback within territories of singing males. Birds that received new light-level geolocators and color bands were aged as

either second-year (SY) or after-second-year (ASY), measured, and banded with USGS metal bands and 1–3 unique plastic color band combinations. We affixed geolocators (Lotek UK Ltd. model ML6540, 2 min sampling regime) using a modified leg-loop harness (Rappole and Tipton 1991) made from 0.5 mm Stretch Magic® jewelry thread during May and early June of 2023 and 2024 (mass with harness ~0.51 g, 2.6–2.9% male Ovenbird mass). We returned to capture sites in 2024 and 2025 to search for banded birds and targeted returning males for recapture. Once recaptured, we removed geolocators from these individuals and released all birds where captured.

Geolocator analysis

We used Program R (R Core team 2024) for all data analysis. We used the TwGeos package (Wotherspoon et al. 2016) to identify sunrise and sunset transitions from recovered tags using a light threshold value of 1.5. We used the FLightR package (Rakhimberdiev and Saveliev 2015) to approximate locations and movements using a basic behavioral and land mask, restricting stationary periods to locations < 25 km from land but allowing for single overnight flights ≤ 1200 km, and a calibration period from the day after capture to 31 July. Obvious location errors based on season or nonsensical movements during migration were removed from analysis, as were location estimates within 10 days of autumn and spring equinox dates, as these are often subject to error (Hallworth et al. 2015).

Data from all recovered tags (n = 6) demonstrated highly variable shading from approximately the last week of July through end of August. We suspect this was due to bird behavior and/or sensor obstruction during molt. Most tags also demonstrated variable shading during autumn (September–November), which may be due to the monsoon season of west Mexico and north tropics, which can also lead to unreliable location estimates, particularly latitudinal readings (Delmore et al. 2012, Kramer et al. 2017). Given the apparent breeding and molt timing for birds in our study and known autumn migration period for Ovenbirds overlapping with the fall equinox period (Hallworth et al. 2015), we did not attempt to estimate fall stopover locations.

We generally followed the methods described by Kramer et al. (2018) and Delancey et al. (2020) to estimate Ovenbird nonbreeding areas using likelihood surfaces produced by FLightR from 01 December to 28 February. We included estimated likelihood surfaces outside of this time frame in cases of extreme tag shading and if longitudinal estimates did not shift > 1 from the last reliable reading of the nonbreeding period, indicating a bird did not initiate migration. We identified the most probable nonbreeding location for each bird by averaging all spatial likelihood surfaces (of ~0.5° x 0.5° cells) across the eligible nonbreeding periods. We created a probability density distribution for each individual bird and then averaged the density distributions for all individuals to produce a single nonbreeding probability surface for all Ovenbirds in our study (Kramer et al 2018, Lewis et al. 2023). We added a 300 km buffer northwest from central Sinaloa, Mexico, and a 100 km buffer eastward from existing nonbreeding distribution maps for the species (Porneluzi 2020, BirdLife International 2021) and constrained our nonbreeding location estimates to these regions to reduce the impact of outliers. We also included southern Baja California within our buffered nonbreeding distribution. We increased the potential wintering area to accommodate reasonable location estimates that may fall outside popular range map extents (Kramer et al. 2017), which may be expected from birds that breed at the very edge of the distributional limit, such as Ovenbirds in Nebraska.

We considered a bird to have initiated spring migration and identified stopovers if position shifted by more than 2 degrees longitude or 3 degrees latitude for a period > 2 days after 01 March. We estimated spring stopover locations per individual by averaging median and 50% CI location estimates that fell under our movement criteria (Raybuck et al. 2022). Because we did not estimate locations within 10 days of the equinoxes, it is possible that spring migration began during this period but went undetected, and we could miss smaller scale movements or brief stopovers (< 2 days) using our methodology. However, our main goal was to describe the overall pace and most likely regional routes for spring migration in western Nebraska Ovenbirds, and not define exact stopover locales.

RESULTS

We deployed 13 geolocators on male Ovenbirds from 2023 (n = 8) to 2024 (n = 5). Three ASY and one SY males were captured at Gilbert-Baker WMA in 2023. One ASY and three SY males were captured at Anderson Bridge WMA in 2023, and three different ASY and two SY males were captured at Anderson Bridge in 2024. We recaptured five marked Ovenbirds and recovered four geolocators in 2024 (n = 3 at Gilbert-Baker WMA, n = 2 at Anderson Bridge WMA). One of these units stopped collecting data in December and only provided data to estimate nonbreeding location. One bird at Anderson Bridge was recaptured without its geolocator. In 2025, we recaptured 2 Ovenbirds marked in 2024 at Anderson Bridge WMA. One unit stopped collecting data in mid-September and the second unit did not collect useable data for any movement analysis. Five of seven males originally banded as ASY returned at least in the year following initial capture, with two of six SY males returning. In 2025 we were able to visually confirm the third-year return of four of eight birds originally banded in 2023; three males at Gilbert-Baker WMA and one male banded at Anderson Bridge WMA.

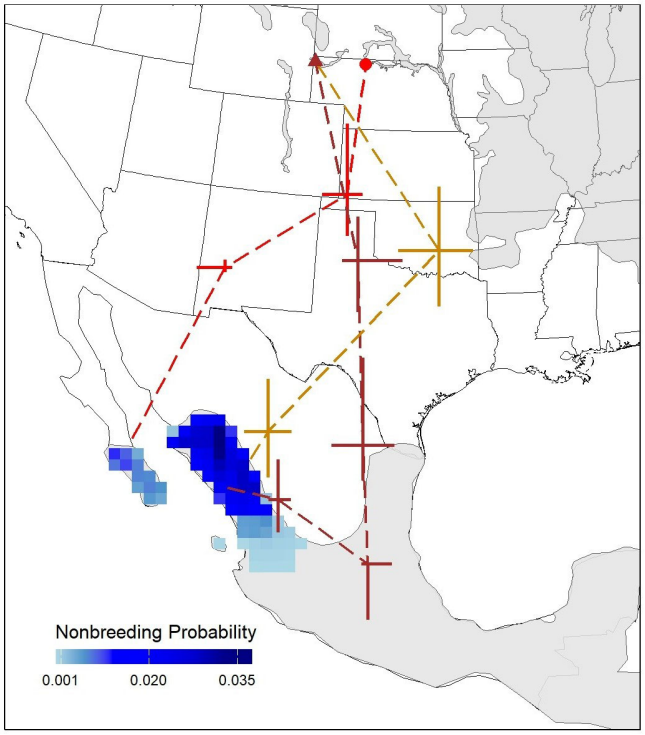
Across both breeding sites in Nebraska, male Ovenbirds wintered along the coastal and Sierra Madre Occidental region of northwestern Mexico, generally between ~103° W and ~110° W, and ~21° N and ~27° N (Fig. 2). Longitudinal estimates in early and late winter (November and March) indicate possible use of Baja California during the wintering period.

Average spring migration initiation date was 10 April (range: 01 April–27 April). Birds used a minimum of two to four stopovers during spring migration in 2024, with median stopover locations occurring in central Mexico, the American Southwest, and in the central Great Plains between Kansas and Texas (Fig. 2). Spring stopover durations were variable per individual, with averages of 11.5 days (10–13 days; red colors Fig. 2), six days (10, 8, 3, and 3 days; brown colors Fig. 2), and five days (6 and 4 days; orange colors Fig. 2). Estimated return dates to breeding grounds ranged from 07 May–17 May in 2024.

DISCUSSION

We identified nonbreeding regions and the general timing and routes of migrations for a well-studied species from its breeding range periphery in Nebraska. The highest-probability nonbreeding grounds for Ovenbirds breeding in northern

Fig. 2. Nonbreeding probability of occurrence (dark blue = highest probabilities) and estimated spring migration stopover locations for Ovenbirds (*Seiurus aurocapilla*) breeding in northern Nebraska (n = 4). Solid lines represent 50% credible intervals for individual stopover locations for Ovenbirds (n = 3) with complete spring migration data in 2024. Translucent gray represents species-level breeding distribution and solid gray delineating buffered nonbreeding distribution, adapted from Porneluzi et al. (2020). Dashed lines connecting stopover locations do not necessarily represent the migration path of individual birds.



Nebraska is also at the nonbreeding range limit for this species in northwest Mexico. Migrating birds likely used Baja California and the southwestern U.S., regions previously not considered frequently used by this species during any season. However, our results comport with dozens of documented records (eBird 2021) of Ovenbirds from southern Sonora and northern Sinaloa, the Southwest U.S., and Baja California during winter and migration, typically in pine-oak mountain foothills, along river valleys and in developed areas featuring limited vegetation that are otherwise surrounded by desert. Additionally, the Gulf of California (GOC) is ~200 km at its widest point, and although open water crossings are potentially hazardous to any small landbird, eastern and northern breeding populations of this species typically cross the Gulf of Mexico (GOM) in spring, which entails a > 1000 km nonstop flight over open ocean (Hallworth et al. 2015). Thus, the GOC is likely a lesser barrier for Ovenbird movements than the GOM barrier encountered by most central and eastern breeding Ovenbirds wintering in southern Mexico, Central America, or the Caribbean islands.

Haché et al. (2017) found strong genetic isolation in Ovenbirds breeding in the Cypress Hills of southern Alberta/Saskatchewan, supporting the identification of this population being the northern extent of the subspecies *S. a. cinereus*. The Cypress Hills is also an isolated forest ecoregion in the northern Great Plains (Newsome and Dix 1968). Ovenbirds breeding in western Nebraska share similar nonbreeding grounds (western Mexico) and breeding habitat (i.e., isolated forests within prairie landscapes) as the Cypress Hills population, and the only specimen record for the Pine Ridge area of Nebraska was also identified as *S. a. cinereus* in 1957 (Ford 1959). We suggest that Ovenbirds breeding in the Pine Ridge and western reaches of the Niobrara Valley in Nebraska likely represent the southern limit of this subspecies' breeding range. Highest probability nonbreeding locations were also the most northerly compared to the nonbreeding grounds of other tracked Ovenbirds, further supporting the proposed leapfrog migration strategy in Ovenbirds (Hallworth 2015, Haché 2017).

Throughout their core breeding range, Ovenbirds have higher nest success in large, contiguous tracts of forest (Burke and Nol 2000), have lower territory densities closer to forest edge (Langlois et al. 2023), and have lower adult male return rates in fragmented forests (Bayne and Hobson 2002, Porneluzi 2003). In northwestern Nebraska, all breeding sites for Ovenbirds are relatively small, unevenly distributed and patchy within narrow habitat corridors, and surrounded by prairie. Every male we tracked for this study was captured on territory at locations < 450 m from forest edge in all directions, and many territories were within 25–100 m of a substantial edge feature (grassland, river corridor, or developed road; Fig. 1). Although use of forest edge within successful territories has been documented in the core Ovenbird range (Mazerolle and Hobson 2003), the return rates for Nebraska Ovenbirds were comparable to birds breeding in large, contiguous habitats throughout their core range (Burke and Nol 2001, Bayne and Hobson 2002). Our anecdotal observations of marked birds indicate successful pairing and reproduction across multiple years (Brenner and Jorgensen, *personal observation*), which could explain the relatively high return rate (> 50%) of males in our region (Porneluzi 2003). Likewise, Ovenbirds may also return to northwestern Nebraska at high rates because of the isolation and limited availability of suitable forest habitat at the range periphery. Ultimately, Ovenbirds breeding in the Great Plains that also spend the nonbreeding and migratory periods at range periphery appear to have comparable return rates to Ovenbirds within the core of the species' distribution.

Future work on Ovenbirds and other Neotropical warblers in the Great Plains could compare breeding success as well as breeding and nonbreeding habitat quality to populations from the core range. Additionally, there could be impacts on return rates and survival because of a predominately overland migratory route for Nebraska Ovenbirds compared to populations from the core range crossing a major ecological barrier. Overall, future migration studies should consider the movements and migratory ecology of bird populations both within the core and at the range edge/distributional limits. This will enhance understanding of any species across all parts of its breeding, migratory, and wintering range and help identify both conservation challenges and opportunities throughout the annual cycle.

Acknowledgments:

We thank Olivia DaRugna for her assistance in the field, Rick Arnold, Hunter Bailey, Tom Krolikowski, and the Management division of Nebraska Game and Parks Commission, and Kent Fricke and Leslie Hershberger. This work was funded by the Nebraska State Wildlife Grant program, the Nebraska Wildlife Conservation Fund and Audubon Great Plains. We report no conflict of interests. All handling and care of birds was operated under appropriate state of Nebraska scientific permits and authorization from the Federal Bird Banding Lab (Permit # 20259).

Data Availability:

Data is available on Movebank, under study title: "Nebraska Ovenbird Migration Ecology": https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study7967250459.

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