An experimental study of woody avoidance in Grasshopper sparrows (*Ammodramus savannarum*)

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Abstract

Woody encroachment alters and fragments native prairies, and it is a major driver in global grassland loss and declines in the bird that depend on them. The presence of woody plants can increase nest predation risk, and many grassland birds appear to strongly avoid trees by altering their space use in the presence of woody plants. To understand why woody avoidance occurs in grassland birds, I hypothesized the behavior is driven by either by an innate fear shaped by an evolutionary history of elevated risk, or by current experience of predators encountered in encroached areas. To distinguish between these mechanisms, I experimentally manipulated woody plant presence and simulated predator risk. I used radio transmitters to track a common grassland songbird, the Grasshopper Sparrow (*Ammodramus savannarum*), in the Flint Hills of eastern Kansas, comparing unmanipulated periods as controls, after the introduction of experimentally placed trees, after the introduction of a decoy predator, and during a combination of trees and the predator decoy. Treatments were located around each sparrow's territory center, and each bird was compared to its own control period. I measured the distance of each sparrow's location to the center of its territory, its daily home range estimates, and the number of location estimates between 6-10 AM. Sparrows moved ~11 meters closer to the territory center during the predator treatment ($p < 0.0001$), ~4 meters closer during the tree treatment ($p < 0.0001$), and moved ~5 meters further away during the combination of the predator and tree ($p = 0.0002$). The home range area did not change over any of the treatments. The number of location estimates decreased during the cedar-only treatment ($p < 0.0001$) and the combined cedar-decoy shrike treatment ($p < 0.0001$), suggesting sparrows decrease their movements or hide during the treatments with trees. These results suggest that avoidance of woody plants are not due to elevated perceived predation risk but rather, due to an innate fear of woody plants themselves.

Management should thus focus on the removal of encroaching woody plants rather than targeting the predators that may come with them. This study provides insights into the behavioral mechanisms leading to habitat selection in the face of a dire anthropogenic threat to Great Plains grassland-dependent birds.

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Chapter 1 - Drivers of woody avoidance in Grasshopper Sparrows (*Ammodramus savannarum*)

Introduction

An estimated 26% of the Earth's land surface is covered in grasslands (Foley et al. 2011). Yet, despite making up a large portion of the terrestrial surface, many grasslands are unprotected and are threatened due to habitat loss (Hoekstra et al. 2005). As a result, the populations of grassland-dependent flora and fauna are quickly declining (Weiner et al. 2011, Wesche et al. 2012, Seibold et al. 2019). The destruction of grasslands has been particularly detrimental to wildlife and is considered one of the largest drivers of the steep declines in grassland bird populations (Knopf 1994, Stanton et al. 2018). Human-mitigated landscape changes, such as agricultural intensification and urbanization, have fragmented and degraded remaining patches of habitat, severely impacting grassland bird populations (Mineau and Whiteside 2013, Mclaughlin et al. 2014, Douglas et al. 2023). One such form of landscape change, woody encroachment, threatens grasslands globally (Myers-Smith et al. 2011, Murphy et al. 2014, Archer et al. 2017). In recent decades, climate change, fire suppression, over-grazing, and anthropogenic landscape changes have increasingly promoted the growth and spread of woody plants further threatening grasslands around the globe (Grover and Musick 1990, Briggs et al. 2005, Bond and Midgley 2012, Ratajczak et al. 2014).

Woody encroachment has contributed to the loss and degradation of native grasslands at rates equal to or sometimes surpassing agricultural conversion (Bakker 2003, Graves et al. 2010,

Morford et al. 2022). Globally, woody encroachment threatens grasslands and the birds that rely on them (Stevens et al. 2017). In South Africa, woody plant encroachment has disproportionately affected savanna-associated species (Sirami et al. 2009). In other parts of southern Africa, the abundance of 18% of bird species decreased due to woody encroachment, and encroaching woody plants caused the local extinctions of several grassland obligate, ground-nesting, and invertivorous birds (White et al. 2024). In arid the grasslands of North America's desert southwest, the distribution of most grassland birds decreased in response to encroaching Velvet mesquite (*Prosopis velutina*; Boggie et al. 2017, Andersen and Steidl 2019). Far from low lying desert, the spread of woody plants has also affected high-elevation sage brush-associated species such as the Greater sage-grouse (*Centrocercus urophasianus*) which prefers sites with ≤4% conifer cover (*Juniperus occidentalis*; Coates et al. 2017).

There lies a clear pattern of woody plant driven declines in grassland birds across the globe, and a pattern of woody plant avoidance in some grassland obligate birds. Ultimately low tolerance of woody plants exhibited by grassland birds may be driven in large part by high predation rates in wooded habitats and edges. For example, nest predation rates are greater in woody encroached grasslands (Bergin et al. 2000, Johnson and Temple 2016, Davis et al. 2019). One way in which woody plants facilitate increased predation rates is by serving as a vantage point for sit-and-wait predators. Avian predators, such as species of Corvidae (Møller 1989, Söderström et al. 1998), hawks (Preston and Bean 2024), and shrikes (Yosef and Grubb 1992, Yosef 2020) use elevated perches to hunt in open grasslands where they may not otherwise hunt (Ratti and Reese 1988, Söderström et al. 1998). Woody plants can also increase predation rates by providing cover for non-avian shrub predators; populations of snakes and both mid-sized and small mammal

carnivores can increase with the spread of woody plants (Blaum et al. 2007, Klug et al. 2010, Dijak and Thompson 2016). For example, in southern Texas, snake nest predation increased by 6.7% for every 10% increase in shrub cover (Davis et al. 2019).

Increases in predator abundance due to woody plants can have several adverse effects on grassland birds that can further contribute to avoidance. When predators are more abundant, prey species spend more time being vigilant, and consequently, they spend less time eating (Zanette and Clinchy 2019). Interactions with predators can alter prey space-use. After hearing a lion's roar, African wild dog (*Lycaon pictus*; a subordinate predator to the Africa lion; *Panthera leo*) will move several kilometers away if they hear a lion's roar (Gallagher et al. 2017). Additionally, they will consistently avoid areas heavily used by lions (Creel and Creel 1996). Another study aimed to determine the effectiveness of trained hawks as a deterrent of golf course geese. At golf courses with hawk treatments, the time geese spent vigilant increased by 76% and their abundance decreased by 73% (Atkins et al. 2017). Woody-mediated predator increases may create a landscape of fear: a spatial pattern describing how animals alter their behavior based on perceived predation risk (Laundré et al. 2001). Increases in predation risk may cause fearful prey species to stay more vigilant, eat less, and alter their space use by avoiding risky areas (Gallagher et al. 2017, Zanette and Clinchy 2019). However, despite links between woody avoidance and predation risk, the mechanisms driving this behavior in grassland birds remains poorly understood.

The reasons for avoidance of woody plants by grassland-obligate taxa may result from one of two potential mechanisms: the current predation risk and innate fear hypotheses. One

explanation is that avoidance may be driven by a current predation risk elevated by frequently observed predators. Because predator presence is often greater in wooded, shrubby, or edge habitats (Winter et al. 2000, Renfrew et al. 2005), birds likely encounter predators most often around woody plants than in open grasslands and avoid those areas to minimize immediate risks. Alternatively, birds may have an innate fear developed over an evolutionary history of elevated risk; thus, avoidance may occur even when birds rarely encounter predators in current contexts. Consistent with this idea, Lesser prairie-chickens (*Tympanuchus pallidicinctus*) avoid tall objects such as utility lines, buildings, and other anthropogenic structures (Lautenbach et al. 2017, Plumb et al. 2019, Sullins et al. 2019). Lesser prairie-chickens will avoid trees up to one kilometer away, a distance likely too far for the chicken to detect a predator from and would therefore indicate avoidance was occurring because of the structure–not an observable predator. Other grassland birds may anticipate high nest predation rates in woodier areas and are thus fearful due to the threats woody plants may pose to an individual's future reproductive success. These alternative explanations may explain how individual grassland birds respond to woody encroachment–an important aspect of their ecology to understand given the threats that face them today.

Understanding the mechanism driving woody avoidance in grassland birds is crucial because of the rapid decline of these birds globally. In Europe, a variety of factors are at fault for the declines documented in grassland-dependent birds (Donald et al. 2006, Wretenberg et al. 2006, Heldbjerg et al. 2018, Bowler et al. 2019), while in South America and Asia, significant proportions of native grassland birds are designated as globally threatened or near-threatened (BirdLife International 2003, Azpiroz et al. 2012). In North America, approximately 53% of the

continent's grassland bird population has disappeared since 1970 contributing to a total loss of 720 million birds (Rosenberg et al. 2019). North American temperate-breeding grassland birds are among the fastest declining species of landbird on the continent (Berlanga et al. 2010). In the southern and central Great Plains, woody encroachment ranks among one of the most pressing issues and has been a particular challenge in tallgrass prairies (With et al. 2008). Most of world's remaining tallgrass prairies lie on privately owned rangeland in the Flint Hills where current land management practices facilitate woody plant encroachment (Samson et al. 1994, Briggs et al. 2002). As much as 56% of the Flint Hill's remaining tallgrass prairie is susceptible to woody plant encroachment (Ratajczak et al. 2016), further highlighting the threat this form of grassland loss poses to the Flint Hills. The loss of prairie in the region has already negatively affected grassland bird populations (With et al. 2008).

Like many other grassland birds, Grasshopper sparrows (*Ammodramus savannarum*) in tallgrass prairies avoid areas where woody plants are present, and have undergone rapid population declines (Ruth 2015, Silber et al. 2024). The negative effects of woody vegetation on Grasshopper sparrow occupancy(Smith 1963, Wiens 1969, Bakker et al. 2002, Herse et al. 2017), abundance (Arnold and Higgins 1986, Helzer 1996, O'Leary and Nyberg 2000, Refnew 2002), and nest success (Johnson and Temple 1990, Refnew 2002, Graves et al. 2010) are well documented. The territories of Grasshopper sparrows comprise less than 3% shrub and 1% tree cover. In tallgrass prairies, territory centroids averaged 27.2 m away from the nearest shrub and 75.5 m away from the nearest tree (Silber et al. 2024). In sum, Grasshopper sparrows have both a low tolerance of woody plants and that small increases in woody plant cover can substantially degrade otherwise high-quality habitat.

The objective of this study was to distinguish between the current predation risk and innate fear hypotheses to explain patterns of woody plant avoidance documented in Grasshopper Sparrows. I experimentally manipulated woody plant presence and perceived predator presence on the territories of radio-tagged male Grasshopper sparrows, estimating the responses of sparrows via changes in behavior and movement. Treatments included manipulating tree presence, predator presence, the presence of both trees and predators simultaneously. All treatments were compared to individual-level pre-treatment control periods in each sparrow. The current predation risk hypothesis predicted no difference between the control and tree treatments and that (*Prediction 1a*) sparrows would move further away when presented with the decoy predator during the treatments that include predator-only or combination of the predator and trees. Thus, the distances to the territory center would be greater than distances of the sparrows during the control and tree treatments. Likewise, this hypothesis predicted (*Prediction 1b*) the sparrow's home range would decrease when a predator or combined predator+tree treatment was deployed on their territory. Sparrows may also change their space use by attempting to stay more hidden. If the sparrow stays close to the ground and is obscured by vegetation or topography, then the ability for a receiver to detect a tag may be more difficult causing a decrease in the number of location estimates. Thus, I expected (*Prediction 1c*) there would be fewer locations estimated when a predator or combined predator+tree treatment was placed on their territory.

Conversely, under the innate fear hypothesis, I expected results to differ between the control and tree treatments, but not necessarily between the tree and combined predator+tree treatments. This hypothesis predicted (*Prediction 2a*) that the distance between the sparrow and the territory

center would increase when trees are placed on their territory but no difference between the distances during the tree and predator+tree treatments. Likewise, sparrows may seek cover when presented with woody plants, in which case his hypothesis predicted (*Prediction 2b*) that the sparrow's home range would shrink when the trees are placed on their territory. Home range areas would not differ between tree and predator+tree treatments. Under the innate fear hypothesis, I also expected (*Prediction 2c*) there would be fewer locations estimated when trees are placed on the territory but no difference in the number of location estimates between the tree and predator+tree treatments.

Methods

Study Sites and Species

Grasshopper sparrows are a small (~17 g), grassland-dependent member of the Passerellidae (New World sparrow) family that breeds across the United States and southern Canada (Vickery 2020). Grasshopper sparrows breeding over most of North America are migratory, spending their non-breeding seasons along the gulf coast and in Mexico (Vickery 2020). Grasshopper sparrows arrive in Kansas as early as mid-March, and territories are established by males as early as early-April. In the fall, Grasshopper sparrows will depart between August and September for wintering grounds in the southern United States, Mexico, and parts of northern Central America (Vickery 2020). In this species, long-distance movements are not limited to migration periods. Grasshopper sparrows are highly dispersive within and among breeding seasons. In Kansas, half of all territorial males disperse every month, and birds dispersed an average of 695 m and up to ~9 km between breeding attempts (Williams and Boyle 2018). In tallgrass prairies, Grasshopper sparrows prefer to breed in open grasslands that are burned every 1-3 years and grazed at low to

intermediate levels (Powell 2006, 2008). Moderate grazing pressure produces small patches of bare ground that are optimal foraging habitat for Grasshopper sparrows (Powell 2008). Female Grasshopper sparrows use dead grasses to construct a dome-shaped nest set on the ground (Williams and Boyle 2018). Periodic burns can help limit the spread of woody plants while allowing for the accumulation of dead plant material used for nest construction (Frey et al. 2008, With et al. 2008, Graves et al. 2010).

I conducted field work during the peak of the Grasshopper sparrow breeding season from mid-May to the end of July at Konza Prairie Biological Station (KPBS) in 2024 and at Tallgrass Prairie National Preserve (TPNP) in 2025 (Figure 1). The two sites are found in the northern and central Flint Hills of Kansas, with the latter located approximately 44 miles south of the former. KPBS is a Long-Term Ecological Research (LTER) site that is experimentally managed with replicated, factorial combinations of fire return intervals and grazing regime (bison, cattle, or ungrazed). TPNP contains pastures that are leased to ranchers for cattle grazing and are burned every other year. Unlike KPBS, there has been much less woody encroachment both within TPNP and in the surrounding landscape. TPNP was managed as a private ranch until 1996 and is management is designed to minimize woody encroachment. I conducted experiments at TNPP in 2025 to better to isolate the effects of woody vegetation on grassland bird space at a site that had fewer woody plants.

At KPBS, I worked in eight pastures. Five of the pastures were grazed by cattle throughout the growing season, from April through October. Three of the pastures were ungrazed. Fire return intervals differed between the pastures: three watersheds were burned every year, one was

burned every 2 years, and the remaining four were burned every 3 years with burns conducted in March or April. The four 3-year burn pastures were managed using patch-burn grazing with each pasture in a 3-pasture unit being burned in a different year. In 2024, two of the eight pastures were burned. The areas I worked at KPBS were those where Grasshopper sparrows were most common. At TPNP, I worked in two pastures, also managed using patch-burn grazing burned on a two-year rotation. Each pasture was divided into two subunits. In 2025, the western half of both pastures was burned in March. Like KPBS, cattle were present in the pastures throughout the growing season. Like Konza, I selected areas to conduct experiments at TPNP based on the abundances of Grasshopper sparrows.

Tagging

I tagged and included male Grasshopper sparrows in experiments only if they were observed with a female or showed signs of nesting. I determined if the male was paired with a female if I observed the male interacting with another Grasshopper sparrow in a non-aggressive manner, or if I heard the male singing its "warble/alternate" song; a reliable signal of a paired bird (Lohr et al. 2013). I assumed an individual had a nest if I observed a mating event, agitated behavior within the territory, or found a nest within the male's territory. I targeted paired males because unpaired males may be more likely to disperse after capture due to stress induced during the capture process. To relocate males, I marked the location of the male's preferred perch. If the male had more than one preferred perch, I would mark a location roughly equidistant between the perches. I monitored birds over several days to ensure the marked territory center was accurate and to identify whether he was paired.

I caught male sparrows by placing a mist net (12 m x 2.5 m, 32 mm mesh size, Ecotone, Gdynia, Poland) with a speaker playing Grasshopper sparrow songs. I placed speakers in cloth bags to obscure them from view, then turned on and positioned on the ground midway between the ends of the mist net to attract the bird to an area of the net where it may more easily be caught. To avoid unnecessary stress on the birds, I did not capture birds when temperatures exceeded 30°C. I sexed birds using cloacal protuberance (Pyle 1997) and banded birds using United States Geological Survey (USGS)-issued aluminum bands and unique arrangements of colored plastic bands allowing for individual identification from a distance. Additionally, I took routine measurements of each bird, including body mass, to ensure the tag weighed less than 3% of the bird's weight. In 2025, I was granted permission to use tags up to 4% of the bird's body weight.

I used tags compatible with the Motus Wildlife Tracking System, which allowed me to track birds following the experiment during dispersal and migration events. All tags emitted ultra-high frequency (UHF), digitally encoded signals, enabling individual tag identification on a shared frequency. In 2024, I used solar-powered LifeTags (Cellular Tracking Technology [CTT]; ~0.5 g). In 2025, I used LifeTags, PowerTags (CTT; ~0.5 g), and the slightly larger HybridTag (CTT, ~0.65 g). PowerTags are completely battery-powered, so to prolong the battery life PowerTags were set to beep every 50 sec. HybridTags have both an onboard rechargeable battery and a solar panel. Both Life and HybridTags emitted signals every 5 sec and the LifeTag only transmits when the solar panel is lighted, whereas the HybridTags emit signals day and night. The longer beep frequency of PowerTags meant that we obtained fewer location estimates from them. All tags were fitted with an uncoated metal alloy antennae to minimize risks associated with bird entanglements due to plastic-coasted antennae (Hill and Elphick 2011, van Vliet and Stutchbury

2018, Forrest 2022, Benvenuti et al. 2025). I attached tags to the birds using a leg-loop harness design (Rappole and Tipton 1991) with leg loops made of a 0.7 mm diameter "Stretch Magic" crafting cord (Pepperell Braiding Co.) secured by crimping a small metal bead around the ends of the cord, tying a knot and applying superglue to the area.

Automated Radio Telemetry System

I tracked birds using an automated radio telemetry system comprised of V.2 CTT "nodes" receivers. Receiver grids allow researchers to track animals using arrays of stationary receivers (Krull et al. 2018, Paxton et al. 2022, Wallace et al. 2022). Each receiver is equipped with an omnidirectional antenna capable of detecting UHF signals, an 8 GB micro-SD card to store transmission data, a GPS, and a solar panel. I placed receivers atop ~2 m tall aluminum poles erected using rebar pounded into the ground, or, when fences were present, zip-tied to a fence line. I deployed 22 receivers at KPBS and placed them in prominent locations surrounding patches of prairie where I tagged birds. I placed sets of receivers in discrete arrays with individual receivers placed 150-250 meters away from each other. At KPBS, arrays ranged in size from 4-12 receivers, and I moved arrays several times over the season as sparrows occupied patches of prairie in succession. At TPNP, I began by deploying 11 receivers, expanding the grid to include 70 receivers by the end of the season, leaving all receivers in place. TPNP receivers were spaced 160 – 210 m apart in a continuous rectangular grid (Figure 1).

I downloaded detection directly from the receiver's micro-SD card to a laptop computer in the field. In 2024, I downloaded data from each receiver every ~2 weeks, while at TPNP, I downloaded data 1-2 times over the season. Each detection was associated with a date, time, tag

ID, and Received Signal Strength Indicator (RSSI) value, a measure of the detection's signal strength as recorded by the receiver.

Location and Home Range Analysis

I trained a model to use RSSI data to estimate the distance the tag is from the receiver. I first created a calibration dataset; at KPBS, I used methods modified from Paxton et al. (2022), establishing 21 survey points within each array consisting of four receivers. At each point for three minutes, I held a test tag horizontally and ~1.25 m off the ground to mimic the position and orientation of a tag on a sparrow. I recorded the date, tag ID, marked the location on a GPS, and noted the time at the start and end of the three minutes. I calibrated receivers at 21 points located at 0, 10, 25, and 75 m away from each receiver while walking toward a central point in the array. The central point was located 100-125 m from each receiver in the array. I took four more calibration points located between the two lines I walked (Figure 2). At TPNP, I used a new calibration method using location data from a handheld UHF receiver ("Sidekick" CTT; Burcher et al. 2025). The Sidekick connects to a cell phone via Bluetooth using the CTT Mobile app (CTT; v. 1.11). When the Sidekick detects a tag transmission, the date, time, and tag ID are sent to the app triggering the phone to take GPS location. All data is then stored in the phone within a CSV file. This method was faster and more efficiently, allowing the user to cover a larger area more quickly. I fixed the test tag, the Sidekick, and a phone to a cart ~ 1 m off the ground. Over two days I pulled the cart across the receiver grid passing within a meter of every receiver within the grid to ensure all receiver detected the test tag, covering ~18 km (Figure 3).

I isolated detections from the test tag during each survey period and measured the Euclidean distance between the receiver and the survey location. In 2024, I averaged the RSSI values over the 3-minute survey period for each of the receiver within the array. I then fit an exponential decay function for each receiver array at KPBS (n = 8) and TPNP (n =1). This function allowed me to estimate the distance between a tagged bird and each receiver by using RSSI values. I lumped detections from each tag into 1-minute bins to minimize the effect of an outlier detection. At KPBS, I used a filter to remove detections with estimated distances longer than the distance between the two furthest receivers in each array. At TPNP, the filters severely limited the number of location estimates generated from birds with PowerTags. I used trilateration to calculate locations using the distance estimates (Lee and Buehrer 2019, Paxton et al. 2022). Trilateration required that a signal be detected by at least 3 receivers within the 1-minute bins. I used R (v. 4.5.2) and modified trilateration code from Paxton et al. (2022). The estimated distance represents the radius of a circle centered around the receiver–the circumference of the circle representing the range of possible locations. If three or more receivers detect the same signal, the tag's location would be, theoretically, at the intersection of all circles; however, due to a variety of environmental factors, the circles do not always intersect perfectly. Trilateration uses a non-linear least squares model that optimizes the location estimate, even when the circles do not perfectly intersect (Paxton et al. 2022).

I used location data to create home range estimates using autocorrelated kernel density estimates (Flemming et al. 2015), a type of home range estimator. Like the standard kernel density estimate (KDE), ADKEs use an animal's movement data to produce an estimate of its home range. AKDEs utilize continuous-time movement models to model movement processes and

estimate the utilization distribution, allowing for home range estimation. ADKEs account for the sequential nature of animal movements and location uncertainty, resulting in larger but more accurate estimates than other methods of home range estimation (Flemming et al. 2015), such as minimum convex polygons and standard KDE. I chose not to use the other methods because minimum convex polygons were not created for use in animal movement data (Worton 1989), and standard KDEs assume that all estimated locations are independent (Silverman 1986) which is unrealistic due to the autocorrelated nature of an animal's movement data. To create AKDEs, I used the package ctmm (Flemming and Calabrese 2023) in R (v. 4.5.2).

Experimental Design

I assigned every male to one of two treatment groups: (1) the predator group, or (2) the predator+tree group (Figure 4) starting with the first tagged bird of the season in the predator group and alternating assignments subsequently to ensure an equal number of samples and an equal spread of the treatments over the season. Following the ≥2 day post-tagging, I used a handheld radio receiver and resighting efforts to confirm that the male was still present in the area. If the bird remained on his territory, I started a 3-day control period (days 1-3 of the experiment).

On day 4, I deployed a decoy Loggerhead shrike (*Lanius ludovicianus*) on the territories of birds in the predator group (Figure 4). I used a decoy Loggerhead shrike because it is a known predator of Grasshopper sparrows (Leppla and Gordon 1978, Stewart 1990) and can elicit agitated behaviors from breeding sparrows (A. Boyle, personal communication). I attached the decoy shrike to a PVC cap that was slid atop a 1-m tall rebar pole located 20 m north of the

territory center for two, 1-hour periods each day for three consecutive days. The shrike was handmade of felt and accurate in body length and proportions. I deployed the shrike once between 07:00-10:00 and once between 11:00-15:00. I opted to deploy the shrike decoy twice daily for 1-hour intervals instead of continuously to minimize stress on nesting birds. I mounted a speaker playing shrike vocalizations from inside a small, camouflaged cloth bag suspended under the decoy. I downloaded shrike songs and calls from xeno-canto (xeno-canto 2024) from birds recorded in Arizona and California. I created a 1 hr audio track beginning with a 10 sec clip of shrike vocalizations to test the volume. To ensure a standard volume at the start of each deployment, I tested the speaker volume using a phone app (Decibel X:dB Sound Level Meter, 2024), adjusting volume as necessary until shrike vocalizations registered between 80-90 dB at 1 m. After the 10 sec clip at the beginning of the recording, I created a 10-minute silence in the audio track during which I left the territory, followed by 50 minutes of vocalizations. Shrike deployments occurred for the three days following the control period (days 4–6).

For birds in the predator+tree group, I placed three 2 m tall Eastern red cedars (*Juniperus virginiana*) before 10:00 on day 4 (Figure 4). I used cedars because they rapidly encroach on tallgrass prairies, especially in the absence of grazing (Owensby et al. 1973, Briggs et al. 2002). I placed each cedar 20 meters from the designated territory center with one each at the following compass directions: north = 0°, southeast = 120°, and southwest = 240°. I mounted the cedars using wooden tree stands and with additional support of cord wrapped around the trunk and staked to the ground. When cattle pushed the trees over, I reinforced the cedars by zip-tying them to t-posts pounded into the ground. On day 7, I added the shrike decoy to the territories with the trees, mounting the decoy and speaker atop the northern cedar. As with the predator group, I

broadcast shrike vocalizations for two, 1-hour periods each day for three days. After the treatments were finished in both groups, I removed all equipment (e.g. rebar, trees, tree stands, etc.).

Analysis

To create the distance dataset, I measured the Euclidean distance from every estimated location to the coordinates of that bird's territory center. I analyzed the results from the two experimental groups separately. I calculated an AKDE for each bird during each day of the experiment. Thus, birds in the predator group had up to six home range estimates (Figures 5-6), and birds in the predator+tree group had up to nine (Figures 7-9). I created an AKDE if I obtained >30 estimates in a day. In the location analysis, I used locations obtained between 06:00–10:00, the peak hours of Grasshopper sparrow activity, for each day during the control and treatment periods. Using the filtered location data, I created a data frame with the sum of the location estimates for every bird on each day of its control and treatment periods. I checked the data for all three covariates for normality using a Shapiro-Wilk test and by visually inspecting the distribution of the data using histograms.

To improve normality of home range estimates, I *ln*-transformed them before analysis. To determine whether trees or predators reduce home range size (*Predictions 2b and 1b*), I used the R-package *lme4* (Bates et al. 2015), to fit a linear mixed effects model to the home range data to compare treatment levels which accounting for repeated measures (random effect) of individual birds.

I also used a linear mixed effects model to test for differences in the distances between the control and predator treatment (*Prediction 1a*) and for differences between the control and tree treatments (*Prediction 2a*). To test predictions (*1c*) and (*2c*), I used a Poisson generalized linear mixed model to analyze whether tree or predator treatments caused a decrease in the number of locations estimates. In all models, I included site as a covariate to account for differences between years in study location, tag type, background shrub and tree cover, density of territories, and any other factors that could influence home range size and movement behavior. I included individual as a random effect to compare each individual's treatment responses against its initial control period.

To confirm that pre-treatment control periods soon after tagging were truly representative of the bird's day-to-day space use and movements, I compared them to three days following experiments that functioned as a post-treatment control. Many birds did not remain on territories long enough to measure this post-treatment period, however. To compare control and post-treatment control datasets, I fit a linear mixed effects model to the home range area data and a generalized linear mixed model for the location data.

Results

Across both field seasons, I tagged 76 Grasshopper sparrows, of which, 35 remained on their territories long enough to complete full sets of experimental treatments. Of the over half (41) of the tagged birds with which we were unable to complete experiments, one died within 2 days of tagging for unknown reasons (possibly due to stress induced from tagging in combination with a severe thunderstorm the evening after capture). Another bird lost its tag within a week of

capture. Two other birds disappeared, but after 2-3 weeks, they were re-located in different locations without tags. Over both seasons, 37 birds disappeared entirely from the experimental plots: 14 of 35 in 2024 and 23 of 41 in 2025. One bird was removed from all analyses because its daily home range estimates were up to 44 ha which covered most of the study area. A home range this large is almost certainly reflective of a bird that is not holding a consistent territory. Of the remaining 34 birds, each treatment group (predator and predator+tree) and each site (KPBS and TPNP) had 17 birds.

None of the birds that disappeared in 2024 were detected on the wider Motus network. However, in 2025, 12 sparrows were detected at Motus stations between 6-325 km (Appendix Figure 6, 12) from TPNP during June and July. Similar to their migratory movements (Vickery 2020), Motus detections revealed that dispersal movements were occurring nocturnally. The fate of the remaining 21 birds was unknown but likely represent birds that dispersed but were not detected subsequently near a Motus receiver (Table 1).

At KPBS 21 of the 22 receivers worked throughout the season. One receiver failed to record any data. At TPNP, three of the 70 receivers deployed failed to record data. Two of the faulty TPNP receivers were replaced within 1-2 weeks of deployment. The third receiver that failed was one of the last several deployed in the final 2-3 weeks of the season.

Distance to Treatment

Tagged birds were detected ~20,000,000 times over the two field seasons. We obtained 28,860 location estimates from these detections. The dramatic decrease in samples from the total number

of detections to the number of location estimates was due to the 1-minute time binning, the filters used in 2024, and the trilateration method that requires simultaneous signal from 3 receivers to generate a location estimate. There were 12,832 location estimates in the predator group: control (n = 5939) and shrike (n = 6893). In the predator+tree group, there were 16,028 location estimates: control (n = 5020), tree (n = 6486), and predator+tree (n = 4522).

In the predator group, the linear mixed-effects model indicated that the predator treatment affected the sparrow's distance to the treatment location. After accounting for repeated measures of individuals and any site-induced variation, results were not consistent with predictions of either the *current predation risk* hypothesis or the *innate fear* hypothesis. Birds in the predator treatment (t = -12.0 , $p < 0.0001$) averaged 10.8 (± 0.9 SE) meters closer to the territory center than the control (Figure 12). The distances of birds at TPNP (30.5 m ± 41.2 SE, t = 0.7, p = 0.46) did not differ from those at KPBS. Consistent with the *current predation risk* hypothesis, however, birds in the predator+tree group averaged ~4 meters closer to the territory center during the tree treatment (-3.92 m ± 1.15 SE, t = -4.3, $p < 0.0001$), and 5 meters further during the predator+tree treatment (4.78 m ± 1.28 SE, t = 3.7, p = 0.0002) than the control distances (Figure 12). As with the predator group, results from the distance analysis did not differ between KPBS and TPNP (-4.89 m ± 47.4 SE, t = -0.1, p = 0.92).

Home Range Area

In the predator group, I created 38 control and 44 predator daily home range estimates. In the predator+tree group there were 33 control, 37 tree, and 36 predator+tree home range estimates. After back transforming the *ln*-transformed home range data, results from the linear mixed-

effects model indicated the home ranges of sparrows in the predator group at TPNP were 7.1 ha larger (1.96 ± 0.37 SE, $t = 5.3$, $p < 0.0001$) than KPBS, and in the predator+tree group, the home ranges of TPNP birds were 8.2 ha larger at (2.11 ± 0.59 SE, $t = 3.5$, $p = 0.0004$).

Accounting for repeated measures of individuals and any site-induced variation, the area of the home ranges during the predator treatments did not differ from the control (-0.129 ± 0.142 SE, $t = -0.90$, $p = 0.37$; Figure 13). Likewise, in the predator+tree group, home ranges for the tree (0.048 ± 0.102 SE, $t = 0.5$, $p = 0.64$) and predator+tree treatments (0.128 ± 0.106 SE ha, $t = 1.2$, $p = 0.23$) did not differ from the control (Figure 13). The results from the predator and predator+tree groups were not consistent with any predictions made by either the *innate fear* or *current predation risk* hypotheses.

Location Estimates

In the 17 birds of the predator group, there were 43 control days and 48 predator treatment days. The 17 birds of the predator+tree group consisted of 38 control, 45 tree, and 45 predator+tree treatment days. Results from the Poisson generalized linear mixed model indicated that there were 46 location estimates per day during the control (3.82 ± 0.37 SE, $p < 0.0001$). The number of locations for the tree treatment decreased by an average of 5 locations (-0.151 ± 0.035 SE, $p < 0.0001$) and the predator+tree treatment decreased by 10 locations (-0.203 ± 0.31 SE, $p < 0.0001$; Figure 14) consistent with *prediction 2c* of the *innate fear* hypothesis. Birds at the TPNP may have had fewer location estimates than those at KPBS (estimate = -0.98 ± 0.51 SE, $p = 0.057$). For the predator group, the Poisson generalized linear mixed effect model indicated there was no difference in the number of location estimates from birds at TPNP (estimate = 0.18 ± 0.36 SE, p

= 0.62) compared to KPBS. Likewise, there was no difference in the number of location estimates during the predator group (estimate = 0.01 ± 0.03 SE, $p = 0.86$) compared to the control (3.42 ± 0.27 SE, $p < 0.0001$; Figure 14). The model estimated there were 31 location estimates per day during the control. The results show no change in the number of location estimates made during treatments with trees (e.g. tree and predator+tree treatments). These results are not consistent with either hypothesis.

Control vs Post Control

Results from the linear mixed effect model showed post control daily home range areas (1.05 ha ± 0.13 SE, $t = 0.38$, $p = 0.70$) did not differ in size from the control home ranges. Results from the generalized linear mixed effect model indicated there were fewer rather than more post control location estimates (-0.15 ± 0.023 SE, $p < 0.0001$) relative to pre-treatment controls.

Discussion

The results of this study show Grasshopper sparrows respond to the experimental additions of trees, predator models, and the combination of these treatments in ways that were consistent with some of the predictions of each of the *current predation risk* and *innate fear* hypotheses (Figure 15). Contrary to expectation, there was a decrease in the mean distance a bird spent relative to its territory center during both the predator-only and tree-only treatments. Only during the combination of predator and tree manipulations did the mean distance to the territory center increase which I interpret as consistent with the *current predation risk* hypothesis. All models of the home range analysis indicated there was no change in the home range area during any of the experimental treatments (e.g. tree, predator, predator+tree). Results from the location analysis

showed there was no change in the number of locations estimated during the predator treatments, but there was a decrease from the control during the tree and predator+tree treatments. Thus, location results were inconsistent with *Prediction 1c*, but consistent with *Prediction 2c* of the *innate fear* hypothesis.

The distance results were surprising in several ways. Apart from the predator+tree treatment, most of the results were inconsistent with the predictions made. Differences in the distances, although statistically significant, did not differ greatly. The predator+tree treatment was the only instance when the sparrows moved further from the territory center. This may indicate that no one stressor (e.g. trees or predator) but the two in combination causes woody avoidance. That said, the small shifts between treatments may not reflect biologically significance given the large sizes of these Grasshopper sparrows home ranges and the ability of these birds to disperse hundreds of km away from their previous territory. Statistical significance was more easily achieved given the large sample size of the distance dataset. The predator+tree treatment had the smallest distance sample size (4522 distance measurements) of any of the treatments. Additionally, there was minimal change in the distances between the different treatments. Distance model estimates differed, at the most, by 15.6 m between the predator (model estimated mean = -10.8 m) and the predator+tree treatments (model estimated mean = 4.8 m). In terms of Grasshopper sparrow movements, a maximum difference of 15.6 m between the treatment model estimates is not a large difference.

Home range area did not differ among control and treatment periods. The area of a home range can be effected by a variety of intrinsic and extrinsic factors (e.g. habitat quality, Mazerolle and

Hobson 2005, Leonard et al. 2008); the number of neighboring territories (Both and Visser 2000); a male's level of territorial aggressiveness (Naguib et al. 2022); whether an individual is polyterritorial (e.g. holds more than one territory; Luepold et al. 2024); time during the breeding season (Wiens 1973, Aldredge 2009), and body size (Mazerolle and Hobson 2005). Even in Grasshopper sparrows, home range size varies both temporally and spatially. A radiotelemetry study of Grasshopper sparrows in Ontario found that home ranges varied between 0.9 and 5.8 ha (Hannah et al. 2024) while in Florida, home ranges of the resident Florida Grasshopper sparrow (*A. s. floridanus*) varied between 0.5 and 4.8 ha (Delaney et al. 1992). Additionally, home range size may vary across the season. A study in Florida showed that the territory size of Florida Grasshopper sparrow's increased from 1.1 (± 0.29 SE) ha during early nesting stages (e.g. before eggs hatch) to 1.7 (± 0.14 SE) ha in later nesting stages (e.g. after eggs hatch; Aldredge 2009). Even among one-day home range areas, my control period home ranges varied between 0.1 and 22.6 ha (mean = 5.7 ha), and in the predator+tree group, model estimates of the control home ranges differed from the post control by 0.7 ha (mean = 4.9 ha).

My home range estimates were, on average, larger than those reported in previous studies. One study required >15 location estimates to create an AKDE-produced home range (Hannah et al. 2024) whereas I used a cut-off of >30, potentially leading to larger home range estimates because of the larger number of location estimates. This larger number of points is likely to lead to more biologically-realistic estimates, however; estimating home range sizes with fewer than 30 points can created biased home range areas (Seaman et al. 1999). Another study used spot mapping to create their home range estimates (Delaney et al. 1992), a method that may underestimate the true home range size (Forrest 2022).

The home ranges of birds at TPNP were between 7.1-8.2 ha larger than those at KPBS. This difference may be in part due to differences in the amount of available habitat between the sites. TPNP had less shrub cover and thus, more uninterrupted habitat for Grasshopper sparrows than KPBS. Alternatively, this discrepancy may reflect differences in the number of receivers used at the two sites. KPBS had up to 9 receivers deployed in any one grid with grids separated by unmonitored areas, while TPNP had up to 70 receivers covering a much larger area. Thus, if any birds were to wander, the likelihood of being detected was greater than those at KPBS.

While the results from the home range and distance analyses were inconclusive, the results of the location estimate analysis are consistent with the *innate fear* hypothesis. The number of locations estimated was influenced by the presence of the cedars. Grasshopper sparrows may attempt to hide, stay low, and inconspicuous when trees are placed on their territory, similar to the responses of Lesser prairie-chicken (Hagan and Giesen 2020). The presence of a perceived predator, like the decoy shrike, may represent a fleeting threat, and if in a conspicuous location, nearby sparrows may stay more vigilant but will not attempt to hide. The presence of a woody-associated predator does not explain woody avoidance. Woody plants, though not a threat by themselves, elevate predation risk, and sparrows may be more wary of silent and skulky predators attracted by the trees. In the presence of woody plants, Grasshopper sparrows will stay low and hide but do not change their home ranges.

The decoy shrike may have been one limitation in my study. Despite observing agitated behavior in the presence of the shrike decoy, it may not have been realistic enough to for sparrows to

perceive it as a true threat. The proportions and colors of the shrike were correct. However; the decoy could not move, it was made of felt rather than feathers, and it may not have reflected in the same spectra as a real Loggerhead Shrike (including in ultra violet (UV) visible to many birds; Huth and Burkhardt 1972, Honkavaara et al. 2002), A future project could address this limitation by creating a UV light accurate shrike replica. Unfortunately, doing so would be quite challenging; a real Loggerhead shrike specimen would be unsuited for such a study due to the fragility of bird specimens and the environmental conditions (rain, hail, wind) of the tallgrass prairies.

Results from this study suggest that the presence of predators does not play a direct role in woody avoidance by grassland species. Instead, avoidance behaviors may be driven by an innate fear of woody plants. The high nest predation rates and diversity of predators within wooded and edge habitats likely continue to contribute to avoidance behaviors although not directly. Avoidance of woody plants due to innate fear may play a role in explaining global declines in grassland birds, even in protected areas (With et al. 2008). Despite the prevalence of this behavior, the mechanism driving woody avoidance has long been unknown. Using a novel experimental design, the results of this study indicate woody avoidance in grassland birds suggest that avoidance may occur regardless of whether the predators follow the plants into the prairie.

Grasslands and the birds that depend on them are continuing to disappear around the world. As a driver of grassland loss, woody plant encroachment presents a major issue to grassland birds. Results from this study may indicate that woody avoidance is the result of an innate fear of

shrubs and trees. Thus, combatting encroachment via the targeted removal of invading woody plants may present a straightforward solution to mitigating grassland bird declines. These results further highlight the effects woody plants have on grassland birds and the importance of implementing land management practices to combat woody encroachment globally.

Figures

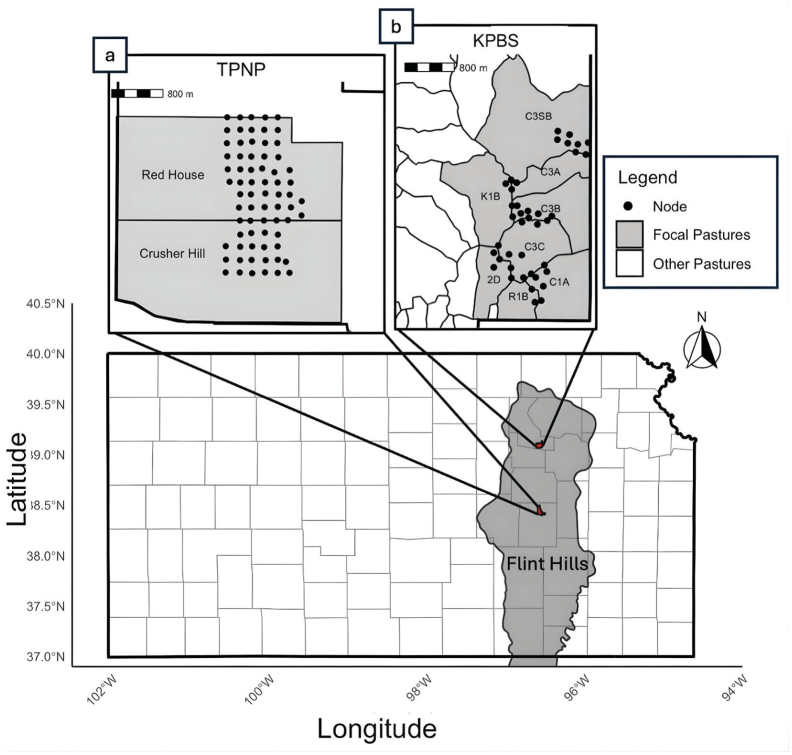


Figure 1. Map is of Kansas with the Flint Hills ecoregion in gray showing the two sites in this study. (a) Map inset study site within Tallgrass Prairie National Preserve (TPNP). (b) Map inset of study site within Konza Prairie Biological Station (KPBS). Study areas at both sites are in gray-highlighted pastures with labels. Receivers (nodes) are designated with black dots.

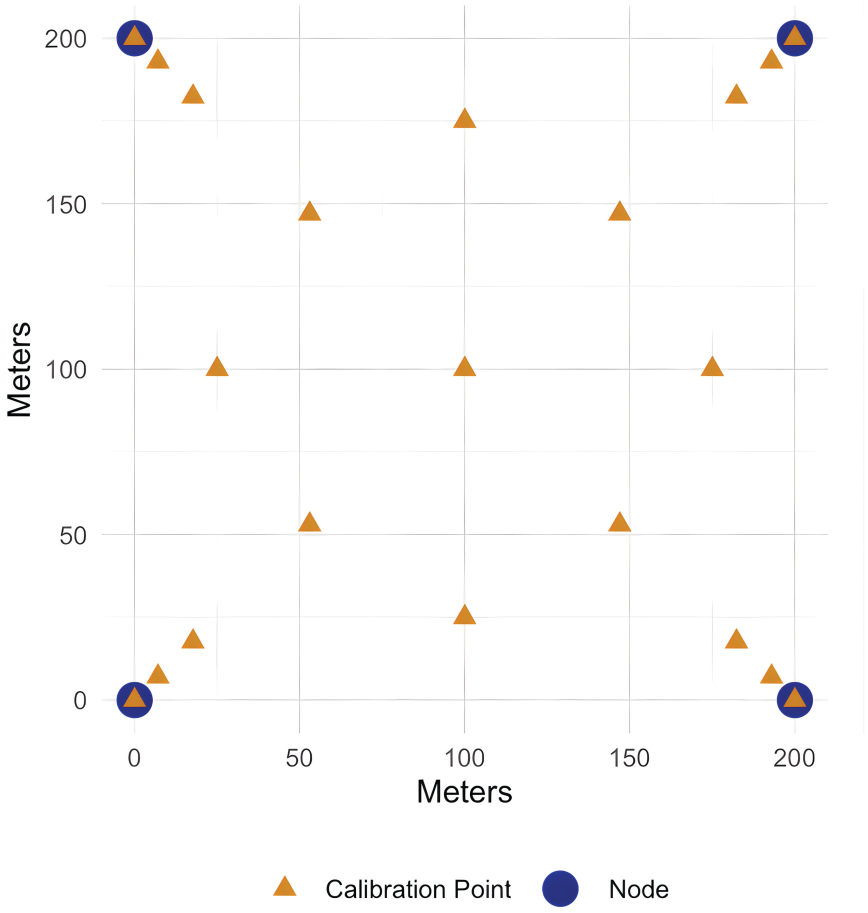


Figure 2. Graphical demonstration of method used to calibrate a signal strength to distance model at KPBS. Each grid of four receivers called nodes (dark blue circles) and consists of 21 calibration points (lighter orange triangles).

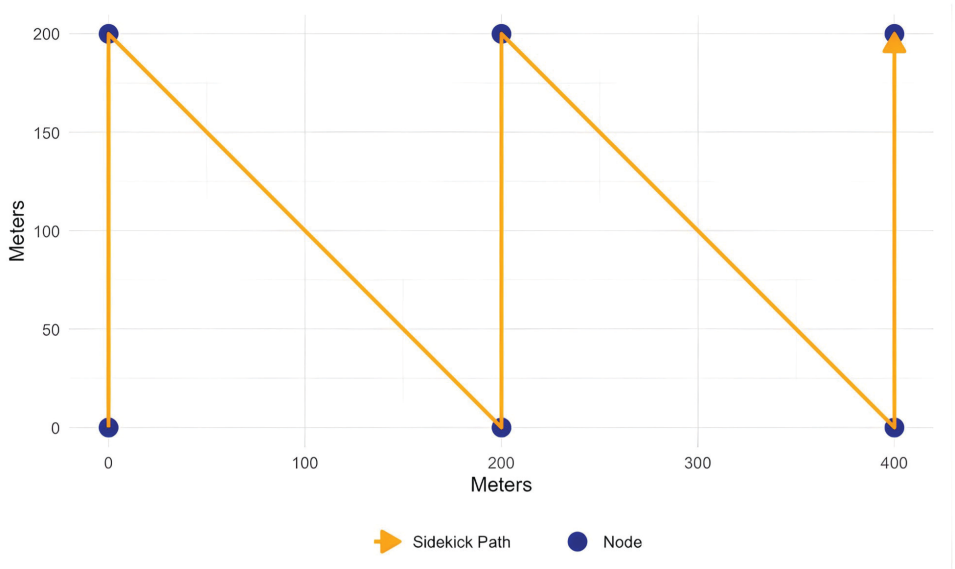


Figure 3. Graphical representation method used to calibrate a signal strength to distance model at TPNP. This figure shows the path taken (lighter orange arrow) while walking with the Sidekick (handheld radio receiver). The path passes by each receiver (dark blue circles) and the center of a grid of four receivers.

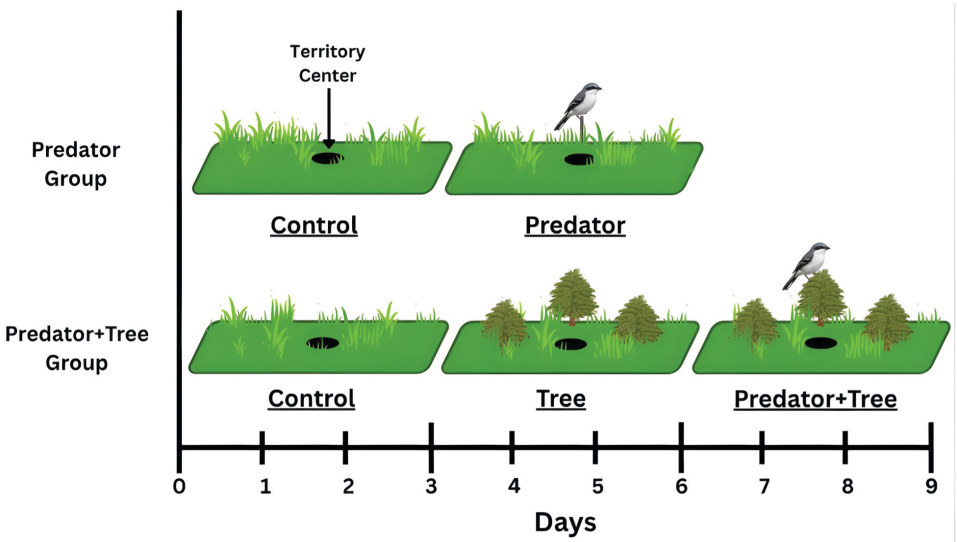


Figure 4. Experimental design for both predator and predator+tree treatment groups. The black dot represents the territory center–a previously marked GPS location that allowed me to relocate the bird and was the point at which the treatments were centered around. The predator group begins with a 3-day control period followed by a 3-day predator treatment featuring a decoy Loggerhead shrike deployed 20 m north of the territory center. The predator+tree group also begins with a 3 day control period followed by a 3 day tree period containing three 2-m tall Eastern red cedars placed 20 m from the territory center at 0°, 120°, and 240°. The tree treatment is followed by a 3-day predator+tree treatment that combines the trees with the predator. The decoy shrike is deployed on the northernmost cedar.

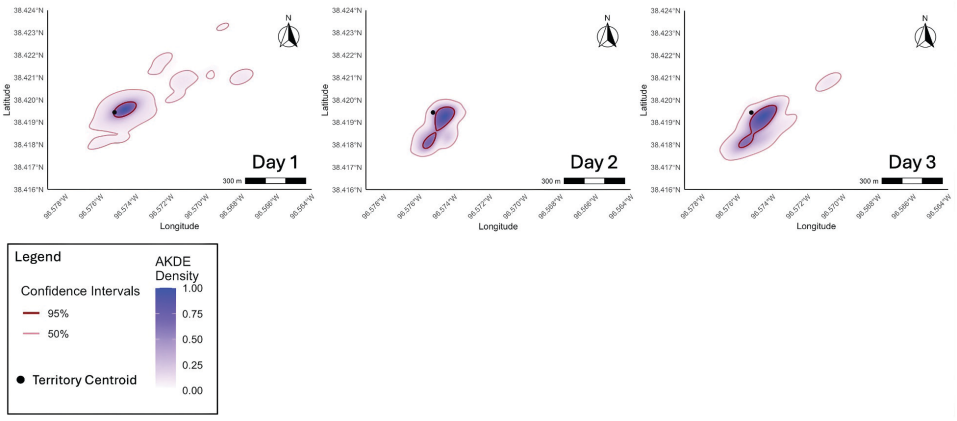


Figure 5. An example series of autocorrelated kernel density estimates (AKDE) from the predator group showing three days of the control period: days 1-3 from left to right. The density

function is represented by the intensity of blue. The darker the shade of blue the greater the likelihood of encountering the tagged sparrow. 50% (light orange line) and 95% (dark blue line) confidence intervals are represented by the contour lines. The territory center is represented by the black dot on each AKDE plot. The predator decoy during the predator treatment (days 4-6) will be located 20 m north of this location.

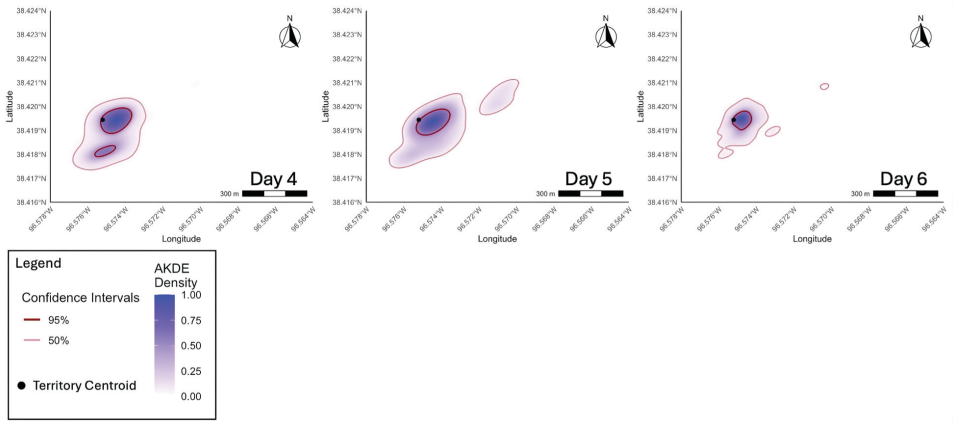


Figure 6. An example series of autocorrelated kernel density estimates (AKDE) from the predator group showing three days of the predator treatment: days 4-6 from left to right. The density function is represented by the intensity of blue. The darker the shade of blue the greater the likelihood of encountering the tagged sparrow. 50% (light orange line) and 95% (dark blue line) confidence intervals are represented by the contour lines. The territory center is represented by the black dot on each AKDE plot. The predator decoy is located 20 m north of this location.

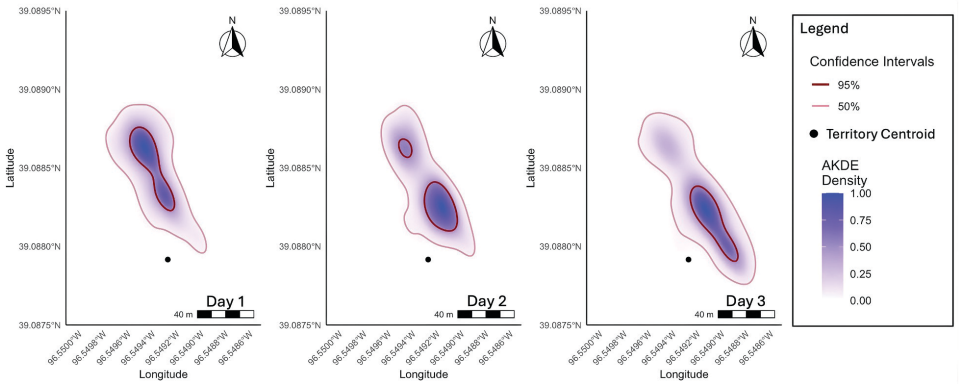


Figure 7. An example series of autocorrelated kernel density estimates (AKDE) from the predator+tree group showing three days of the control period: days 1-3 from left to right. The density function is represented by the intensity of blue. The darker the shade of blue the greater the likelihood of encountering the tagged sparrow. 50% (light orange line) and 95% (dark blue line) confidence intervals are represented by the contour lines. The territory center is represented by the black dot on each AKDE plot. The treatments during the tree and predator+tree treatments will be located 20 m of this location.

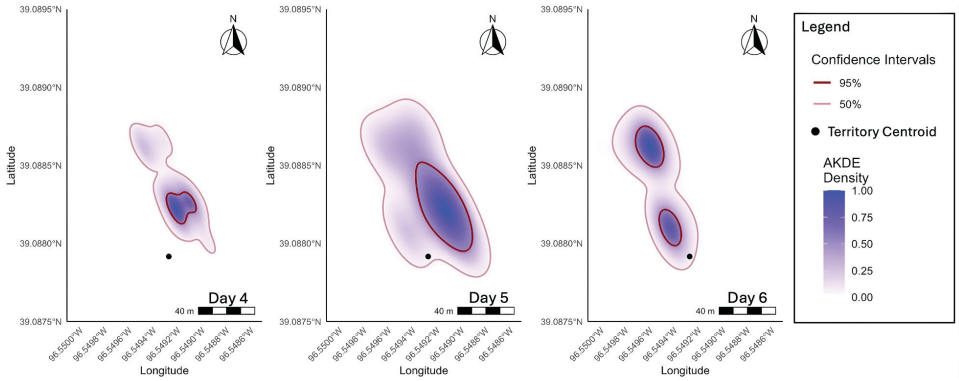


Figure 8. An example series of autocorrelated kernel density estimates (AKDE) from the predator+tree group showing three days of the tree treatment: days 4-6 from left to right. The density function is represented by the intensity of blue. The darker the shade of blue the greater the likelihood of encountering the tagged sparrow. 50% (light orange line) and 95% (dark blue line) confidence intervals are represented by the contour lines. The territory center is represented by the black dot on each AKDE plot. Three Eastern red cedars (*Juniperus virginana*) were placed 20 m away from territory center. Each was placed in a fixed direction (0°, 120°, and 240°) away from the territory center.

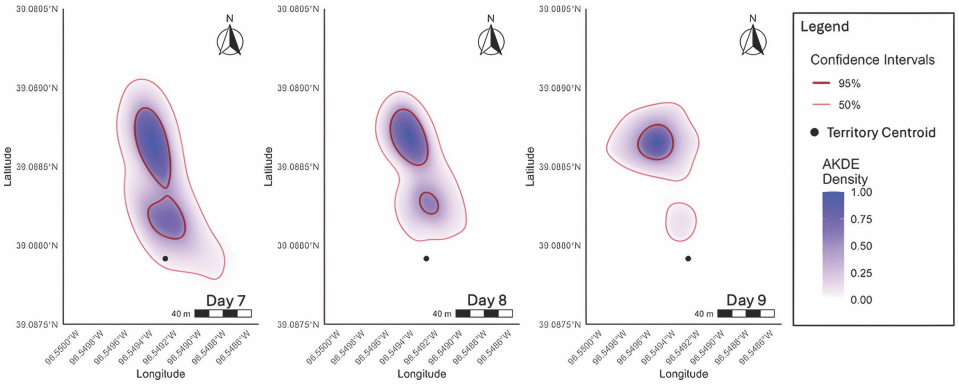


Figure 9. An example series of autocorrelated kernel density estimates (AKDE) from the predator+tree group showing three days of the predator+tree treatment: days 7-9 from left to right. The density function is represented by the intensity of blue. The darker the shade of blue the greater the likelihood of encountering the tagged sparrow. 50% (light orange line) and 95% (dark blue line) confidence intervals are represented by the contour lines. The territory center is represented by the black dot on each AKDE plot. A decoy predator was placed on the northernmost cedar over this three-day period.

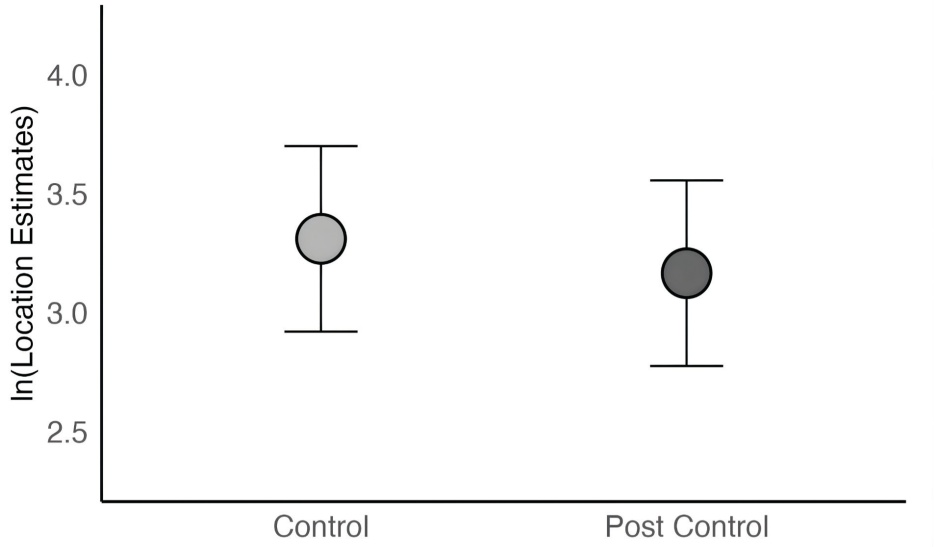


Figure 10. Model-estimated mean *ln*-transformed number of location estimates (± SE) for tagged Grasshopper sparrows during control and post-control treatments. Estimates were obtained from a generalized linear mixed model while accounting for individual and site variation.

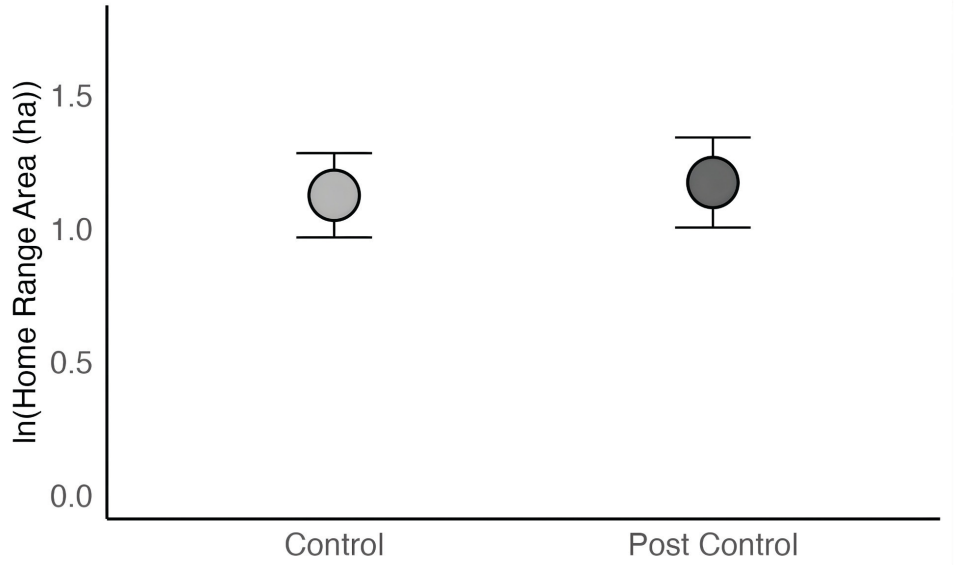


Figure 11. Model-estimated mean *ln*-transformed home range area (± SE) for tagged Grasshopper sparrows during control and post-control treatments. Estimates were obtained from a generalized linear mixed model while accounting for individual and site variation.

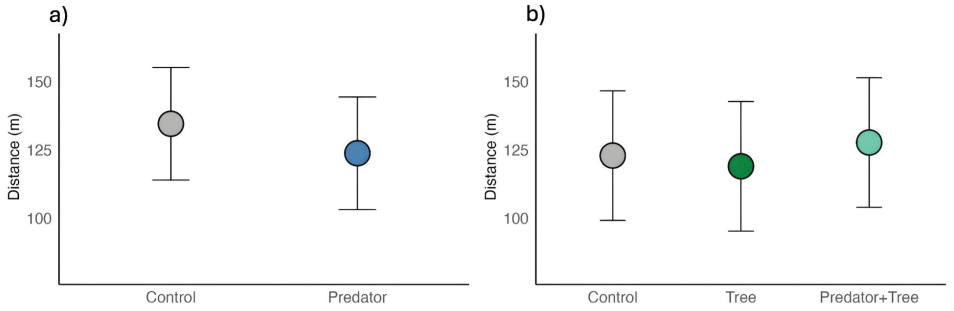


Figure 12. Model-estimated mean distance estimates (± 95% SE) for tagged Grasshopper sparrows in the (a) Predator group and (b) Predator+Tree group. Estimates were obtained from a linear mixed-effects model while accounting for individual and site variation.

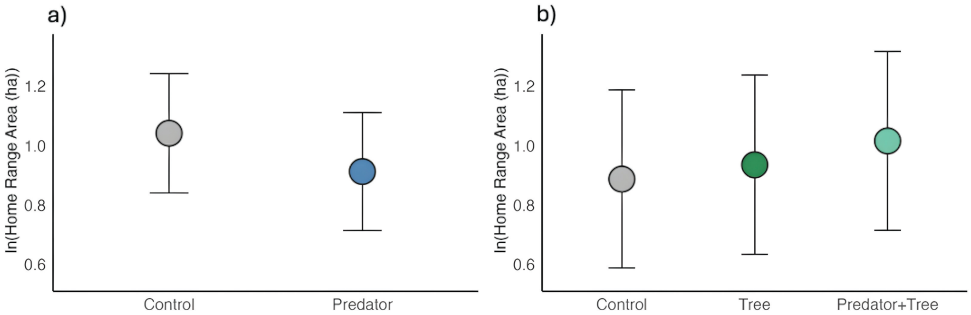


Figure 13. Model-estimated mean *ln*-transformed home range area estimates (± SE) for tagged Grasshopper sparrows in the (a) Predator group and (b) Predator+Tree group. Estimates were obtained from a linear mixed-effects model while accounting for individual and site variation.

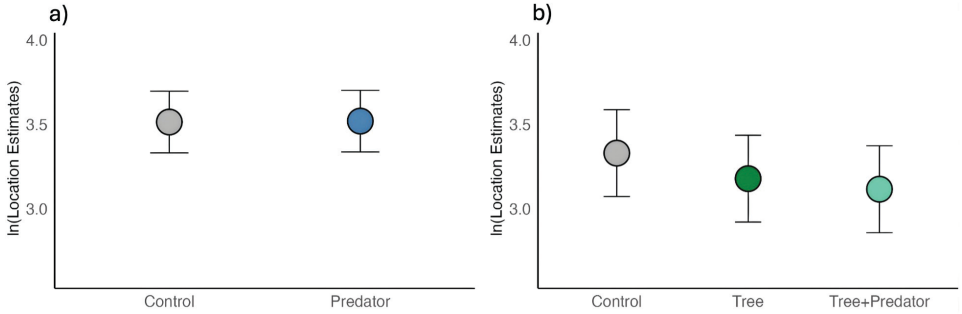


Figure 14. Model-estimated mean *ln*-transformed number of location estimates (± SE) for tagged Grasshopper sparrows in the (a) Predator group and (b) Predator+Tree group. Estimates were obtained from a generalized linear mixed model while accounting for individual and site variation.

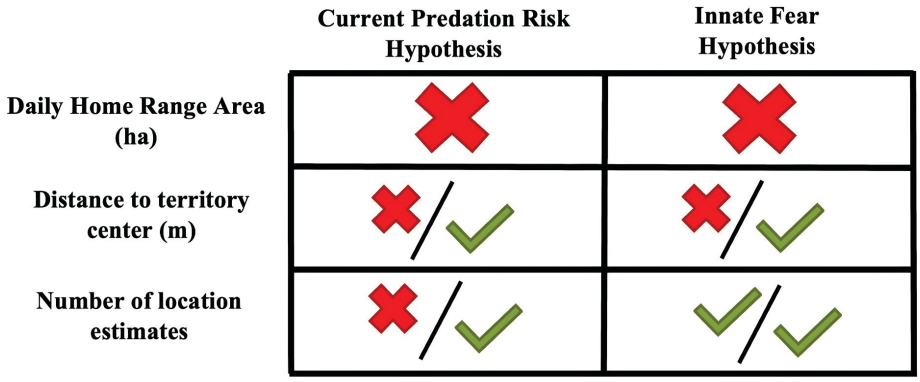


Figure 15. Figure showing whether the data supported or failed to support hypothesis. Red 'X's represent results that failed to support a hypothesis. Green check marks represent results that supported a hypothesis. Under the current predation risk hypothesis column, there are two symbols in the distance to territory center (m) and number of location estimates rows. The left symbol represents results of the predator treatment and the right symbol represents results of the predator+tree treatment. Under the innate fear hypothesis column there are also two symbols on the distance to territory center (m) and number of location estimates rows. Here, the left symbol represents the results under the tree treatment and the right symbol represents results under the predator+tree treatment.

Tables

Table 1: All birds tagged across both field seasons including birds that did not have a treatment deployed on their territory.

Site	Tag ID	Tag Type	Capture Date	Treatment	Dispersal Date	Motus (Y/N)	Appendix Figure
KPBS	52614B4C	LifeTag	5/22/24		5/22/24		
KPBS	2A1E341E	LifeTag	5/22/24	Predator	6/8/24		
KPBS	4B330766	LifeTag	5/22/24		5/28/24		
KPBS	071E1E4C	LifeTag	5/22/24		5/27/24		
KPBS	1E662D07	LifeTag	6/1/24		11/22/24		
KPBS	522A2A78	LifeTag	6/3/24		6/3/24		
KPBS	522A331E	LifeTag	6/3/24		6/3/24		
KPBS	4C2A4B2D	LifeTag	6/4/24	Predator +Tree	6/17/24		
KPBS	7.83E+82	LifeTag	6/7/24	Predator +Tree	7/13/24		
KPBS	7336666	LifeTag	6/8/24	Predator	7/18/24		

KPBS	78335219	LifeTag	6/8/24	Predator	6/14/24		
KPBS	1E525519	LifeTag	6/13/24		6/18/24		
KPBS	6161782A	LifeTag	6/13/24	Predator +Tree	7/21/24		
KPBS	4C4C1E4C	LifeTag	6/15/24		9/4/24		
KPBS	1E526607	LifeTag	6/15/24	Predator	7/25/24		
KPBS	7196607	LifeTag	6/22/24	Predator	9/24/24		
KPBS	194B192A	LifeTag	6/22/24	Predator +Tree	8/12/24		
KPBS	55614C61	LifeTag	6/22/24	Predator	11/27/24		
KPBS	07554B19	LifeTag	6/22/24	Predator +Tree	8/15/24		
KPBS	34196633	LifeTag	7/2/24		7/2/24		
KPBS	4B4C4C34	LifeTag	7/2/24		7/19/24		
KPBS	552D3433	LifeTag	7/2/24		7/3/24		
KPBS	1E2A341E	LifeTag	7/2/24	Predator	10/6/24		
KPBS	33194B2A	LifeTag	7/8/24	Predator	7/29/24		
KPBS	2A55071E	LifeTag	7/8/24	Predator +Tree	7/31/24		
KPBS	34555555	LifeTag	7/8/24	Predator +Tree	8/28/24		
KPBS	1E78614B	LifeTag	7/9/24		7/10/24		
KPBS	34076152	LifeTag	7/12/24	Predator +Tree	10/12/24		
KPBS	1E4B6655	LifeTag	7/15/24		9/30/24		
KPBS	784C332D	LifeTag	7/17/24	Predator +Tree	10/13/24		
KPBS	782D0734	LifeTag	7/19/24		8/26/24		
KPBS	4B2D4B1D	LifeTag	7/19/24		7/19/24		
KPBS	6.13E+11	LifeTag	7/23/24		8/11/24		
KPBS	524B3307	LifeTag	7/23/24		9/27/24		
KPBS	55195533	LifeTag	7/23/24		7/23/24		
TPNP	7866552D	LifeTag	5/14/25	Predator +Tree	5/30/25		
TPNP	2A2D6161	LifeTag	5/14/25	Predator	5/31/25		
TPNP	521E2D61	HybridTag	5/21/25		5/21/25		
TPNP	52344B78	LifeTag	5/21/25	Predator	7/30/25		
TPNP	664B661E	LifeTag	5/22/25		6/1/25		
TPNP	34665266	PowerTag	5/23/25		6/1/25	Y	A.11
TPNP	664B1961	PowerTag	5/30/25		6/1/25	Y	A.5

TPNP	1E2A2A1E	PowerTag	5/30/25	Predator	6/12/25	Y	A.7
TPNP	52666119	PowerTag	5/30/25	Predator +Tree	6/16/25	Y	A.6
TPNP	522D2D07	HybridTag	6/2/25		6/4/25	Y	A.8
TPNP	1E071E55	PowerTag	6/2/25		6/3/25		
TPNP	61333334	HybridTag	6/8/25		6/10/25	Y	A.4
TPNP	33524B19	HybridTag	6/10/25	Predator	7/12/25		
TPNP	662A4C78	HybridTag	6/10/25	Predator	7/30/25		
TPNP	1E074B66	HybridTag	6/11/25	Predator +Tree	6/28/25		
TPNP	192A2A78	HybridTag	6/11/25		6/11/25		
TPNP	19192D78	HybridTag	6/15/25		6/17/25	Y	A.2
TPNP	61524C4C	PowerTag	6/15/25		6/16/25		
TPNP	2D661E4C	HybridTag	6/19/25	Predator +Tree	7/1/25	Y	A.1
TPNP	52346166	HybridTag	6/19/25	Predator	7/21/25		
TPNP	19551978	PowerTag	6/19/25		6/21/25		
TPNP	19664C1E	HybridTag	6/25/25	Predator +Tree	7/31/25	Y	A.10
TPNP	2A334C78	HybridTag	6/25/25	Predator	7/22/25	Y	
TPNP	3352784B	PowerTag	6/25/25	Predator	7/31/25		
TPNP	1E4C2A33	PowerTag	7/1/25	Predator +Tree	7/27/25		
TPNP	522D5566	HybridTag	7/1/25		7/7/25	Y	A.3
TPNP	2D522A52	PowerTag	7/1/25	Predator +Tree	7/29/25		
TPNP	2D2A4C61	PowerTag	7/1/25		7/4/25	Y	A.9
TPNP	55556666	HybridTag	7/1/25		7/1/25		
TPNP	2D4B2A2A	HybridTag	7/1/25	Predator +Tree	7/31/25	Y	
TPNP	55615519	PowerTag	7/8/25	Predator +Tree	7/31/25		
TPNP	33192D78	LifeTag	7/8/25		7/8/25		
TPNP	78664C4B	PowerTag	7/8/25		7/31/25		
TPNP	1E347834	HybridTag	7/8/25	Predator	7/31/25		
TPNP	7330778	HybridTag	7/8/25		7/30/25		
TPNP	0707332D	PowerTag	7/12/25		7/31/25		
TPNP	074B4B4B	PowerTag	7/12/25		7/23/25	Y	A.12
TPNP	2A4B2A1E	PowerTag	7/12/25		7/30/25		
TPNP	55782A34	HybridTag	7/22/25		7/31/25		

TPNP	33344B19	PowerTag	7/22/25		7/24/25		
TPNP	4C190707	HybridTag	7/22/25		7/31/25		
TPNP	5507344B	HybridTag	7/28/25		7/28/25	Y	
TPNP	4C55552A	HybridTag	7/29/25		7/29/25		
TPNP	4C52662D	HybridTag	7/29/25		7/29/25		
TPNP	074B6633	HybridTag	7/30/25		7/30/25		
TPNP	78193320	PowerTag	8/1/25		8/1/25		
TPNP	3466334B	PowerTag	8/1/25		8/1/25		

References

Aldredge, J. N. 2009. Factors affecting breeding territory size and placement of the Florida grasshopper sparrow (*Ammodaramus savannarum floridanus*). University of Central Florida.

Andersen, E. M., and R. J. Steidl. 2019. Woody plant encroachment restructures bird communities in semiarid grasslands. Biological Conservation 240:108276.

Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S. R. Woods. 2017. Woody plant encroachment: causes and consequences. In Rangeland systems: Processes, management and challenges. Cham: Springer International Publishing.

Arnold, T. W., and K. F. Higgins. 1986. Effects of shrub coverages on birds in North Dakota mixed-grass prairies. Canadian Field-Naturalist 100:10–14.

Atkins, A., P. Fitzpatrick, A. Ornithology, D. C. Excellence, and C. Town. 2017. Experimentally manipulating the landscape of fear to manage problem animals. The Journal of Wildlife Management 81:610–616.

Azpiroz, A. B., J. P. Isacch, R. A. Dias, A. S. Di Giacomo, C. S. Fontana, and C. M. Palarea. 2012. Ecology and conservation of grassland birds in southeastern South America: A review. Journal of Field Ornithology 83:217–246.

Bakker, K. K. 2003. The effect of woody vegetation on grassland nesting birds: An annotated bibliography. The Proceedings of the South Dakota Academy of Science 82:119–141.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4 67.

Benvenuti, B., A. D. Smith, C. S. Elphick, N. Ernst, A. I. Kovach, K. M. O'brien, and N. Pau. 2025. Automated telemetry reveals migratory movements and stopover timing of an endangered saltmarsh passerine. Avian Conservation and Ecology 20.

Bergin, T. M., L. B. Best, K. E. Freemark, and K. J. Koehler. 2000. Effects of landscape structure on nest predation in roadsides of a midwestern agroecosystem: A multiscale analysis. Landscape Ecology 15:131–143.

Berlanga, H., J. A. Kennedy, T. D. Rich, M. C. Arizmendi, C. J. Beardmore, P. J. Blancher, G. S. Butcher, A. R. Couturier, A. A. Dayer, D. W. Demarest, W. E. Easton, M. Gustafson, E. Iñigo-Elias, E. A. Krebs, P. A. Panjabi, V. Rodriguez Contreras, K. V. Rosenberg, J. M. Ruth, E. Santana Castellón, R. M. Vidal, and T. Will. 2010. Saving our shared birds: Partners in Flight-tri national vision for landbird conservation.

BirdLife International. 2003. Saving Asia's threatened birds : a guide for government and civil society. Cambridge: BirdLife International.

Blaum, N., E. Rossmanith, A. Popp, and F. Jeltsch. 2007. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. Acta Oecologica 31:86–92.

Boggie, M. A., C. R. Strong, D. Lusk, S. A. Carleton, W. R. Gould, R. L. Howard, C. Nichols, M. Falkowski, and C. Hagen. 2017. Rangeland Ecology & Management Impacts of Mesquite Distribution on Seasonal Space Use of Lesser Prairie-Chickens ☆. RAMA 70:68–77.

Bond, W. J., and G. F. Midgley. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philosophical Transactions of the Royal Society B: Biological Sciences 367:601–612.

Both, C., and M. E. Visser. 2000. Breeding territory size affects fitness: An experimental study on competition at the individual level. Journal of Animal Ecology 69:1021–1030.

Bowler, D. E., H. Heldbjerg, A. D. Fox, M. de Jong, and K. Böhning-Gaese. 2019. Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology 33:1120–1130.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. Ben Gustafson, P. Ziegler, and M. L. Casazza. 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology and Management 70:25–38.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526–538.

Davis, H. T., A. M. Long, J. A. Baumgardt, T. A. Campbell, and M. L. Morrison. 2019. Factors affecting nest success and predator assemblage of breeding birds in semiarid grasslands. Rangeland Ecology and Management 72:385–395.

Delaney, M. F., C. M. Moore, and J. M. Hamblen. 1992. Florida grasshopper sparrow management needs. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.

Dijak, W. D., and F. R. Thompson. 2016. Landscape and Edge Effects on the Distribution of Mammalian Predators in Missouri. The Journal of Wildlife Management 64:209–216.

Donald, P. F., F. J. Sanderson, I. J. Burfield, and F. P. J. van Bommel. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. Agriculture, Ecosystems and Environment 116:189–196.

Douglas, D. J. T., J. Waldinger, Z. Buckmire, K. Gibb, J. P. Medina, L. Sutcliffe, C. Beckmann, N. J. Collar, R. Jansen, J. Kamp, I. Little, R. Sheldon, A. Yanosky, and N. Koper. 2023. A global review identifies agriculture as the main threat to declining grassland birds. Ibis 165:1107–1128.

Flemming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188.

Flemming, C. M., and J. M. Calabrese. 2023. ctmm: continuous-time movement modeling.

Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman, and D. P. M. Zaks. 2011. Solutions for a cultivated planet. Nature 478:337–342.

Forrest, A. W. 2022. Habitat selection of the declining Cassin's sparrow in an imperiled grassland biome. Colorado State University - Pueblo.

Frey, C. M., W. E. Jensen, and K. A. With. 2008. Topographic patterns of nest placement and habitat quality for grassland birds in tallgrass prairie. American Midland Naturalist 160:220–234.

Gallagher, A. J., S. Creel, R. P. Wilson, and S. J. Cooke. 2017. Energy landscapes and the landscape of fear. Trends in Ecology and Evolution 32:88–96.

Graves, B. M., A. D. Rodewald, and S. D. Hull. 2010. Influence of woody vegetation on grassland birds within reclaimed surface mines. Wilson Journal of Ornithology 122:646–654.

Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico,

USA: an analysis of desertification processes in the American Southwest. Climate Change 17:305–330.

Hagan, C. A., and K. M. Giesen. 2020. Lesser prairie-chicken (*Tympanuchus pallidicintus*), verson 1.0. Birds of the Wolrd (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

Hannah, K. C., J. E. Put, and D. D. Hope. 2024. Seeing isn't always believing: visual observations underestimate space use in the eastern Grasshopper sparrow (*Ammodramus savannarum pratensis*). Avian Conservation and Ecology 19.

Heldbjerg, H., P. Sunde, and A. D. Fox. 2018. Continuous population declines for specialist farmland birds 1987-2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. Bird Conservation International 28:278–292.

Helzer, C. J. 1996. The Effects of Wet Meadow Fragmentation on Grassland Birds. University of Nebraska - Lincoln.

Herse, M. R., M. E. Estey, P. J. Moore, B. K. Sandercock, and W. A. Boyle. 2017. Landscape context drives breeding habitat selection by an enigmatic grassland songbird. Landscape Ecology 32:2351–2364.

Hill, J. M., and C. S. Elphick. 2011. Are grassland passerines especially susceptible to negative transmitter impacts? Wildlife Society Bulletin 35:362–367.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Honkavaara, J., M. Koivula, E. Korpimäki, H. Siitari, and J. Viitala. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. Oikos 98:505–511.

Huth, H. H., and D. Burkhardt. 1972. Der spektrale Sehbereich eines Violettohr-Kolibris. Naturwissenschaften 59.

Johnson, R. G., and S. A. Temple. 1990. Nest Predation and Brood Parasitism of Tallgrass Prairie Birds. The Journal of Wildlife Management 54:106–111.

Johnson, R. G., and S. A. Temple. 2016. Nest Predation and Brood Parasitism of Tallgrass Prairie Birds Author (s): Richard G . Johnson and Stanley A . Temple Published by : Wiley on behalf of the Wildlife Society Stable URL : http://www.jstor.org/stable/3808909. Journal of Wildlife Management 54:106–111.

Klug, P. E., S. L. Jackrel, and K. A. With. 2010. Linking snake habitat use to nest predation risk in grassland birds: The dangers of shrub cover. Oecologia 162:803–813.

Knopf, F. L. 1994. Avian Assemblages on Altered Grasslands. Studies in Avian Biology 15:247–257.

Krull, C. R., L. F. McMillan, R. M. Fewster, R. Van Der Ree, R. Pech, T. Dennis, and M. C. Stanley. 2018. Testing the feasibility of wireless sensor networks and the use of radio signal strength indicator to track the movements of wild animals. Wildlife Research 45:659–667.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401–1409.

Lautenbach, J. M., R. T. Plumb, S. G. Robinson, C. A. Hagen, D. A. Haukos, and J. C. Pitman. 2017. Lesser prairie-chicken avoidance of trees in a grassland landscape. Rangeland Ecology and Management 70:78–86.

Lee, J. H., and R. M. Buehrer. 2019. Fundamentals of received signal strength-based position location. Pages 369–404 *in* S. A. Zekavat and R. M. Buehrer, editors. Handbook of Position Location: Theory, Practice, and Advances. 2nd Editio. John Wiley and Sons, Inc., Hoboken, New Jersey.

Leonard, T. D., P. D. Taylor, and I. G. Warkentin. 2008. Landscape structure and spatial scale affect space use by songbirds in naturally patchy and harvested boreal forests. The Condor 110:467–481.

Leppla, R. R., and D. H. Gordon. 1978. Predation by Loggerhead shrike. Bulletin of the Oklahoma Ornithological Society 11:33.

Lohr, B., S. M. Wakamiya, and S. Ashby. 2013. The function of song types and song components in Grasshopper Sparrows (*Ammodramus savannarum*). Behaviour 150:1085–1106.

Luepold, S. B., F. Korner-nievergelt, Z. Züst, and G. Pasinelli. 2024. It's about her: male within-season movements are related to mate searching in a songbird 203 (5): 562-575.

Mazerolle, D. F., and K. A. Hobson. 2005. Territory size and overlap in male Ovenbirds: contrasting a fragmented and contiguous boreal forest 1781:1774–1781.

Mclaughlin, M. E., W. M. Janousek, J. P. Mccarty, and L. L. Wolfenbarger. 2014. Effects of urbanization on site occupancy and density of grassland birds in tallgrass prairie fragments. Journal of Field Ornithology 85:258–273.

Mineau, P., and M. Whiteside. 2013. Pesticide acute toxicity is a better correlate of U.S. grassland bird declines than agricultural intensification. PLoS ONE 8.

Møller, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. Oikos 56:240–246.

Morford, S. L., B. W. Allred, D. Twidwell, M. O. Jones, J. D. Maestas, C. P. Roberts, and D. E. Naugle. 2022. Herbaceous production lost to tree encroachment in United States rangelands. Journal of Applied Ecology 59:2971–2982.

Murphy, B. P., C. E. R. Lehmann, J. Russell-smith, and M. J. Lawes. 2014. Fire regimes and woody biomass dynamics in Australian savannas. Journal of Biogeography 41:133–144.

Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-fauria, U. Sass-klaassen, L. Esther, S. Boudreau, P. Rapars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6.

Naguib, M., M. Titulaer, J. R. Waas, K. van Oers, P. Sprau, and L. Snijders. 2022. Prior territorial responses and home range size predict territory defense in radio-tagged great tits. Behavioral Ecology and Sociobiology 76.

O'Leary, C. H., and D. W. Nyberg. 2000. Treelines between fields reduce the density of grassland birds. Natural Areas Journal 20:243–249.

Owensby, C. E., K. R. Blan, and O. G. Russ. 1973. Evaluation of Eastern redcedar (*Juniperus virginiana*) infestation in the northern Kansas Flint Hills. Journal of Range Management 26:256–260.

Paxton, K. L., K. M. Baker, Z. B. Crytser, R. M. P. Guinto, K. W. Brinck, H. S. Rogers, and E. H. Paxton. 2022. Optimizing trilateration estimates for tracking fine-scale movement of wildlife using automated radio telemetry networks. Ecology and Evolution 12:1–12.

Plumb, R. T., J. M. Lautenbach, S. G. Robinson, D. A. Haukos, V. L. Winder, C. A. Hagen, D. S. Sullins, J. C. Pitman, and D. K. Dahlgren. 2019. Lesser prairie-chicken space use in relation to anthropogenic structures. Journal of Wildlife Management 83:216–230.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. Auk 123:183–197.

Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41–52.

Preston, C. R., and R. D. Bean. 2024. Red-tailed hawk (*Buteo jamaicensis*). Cornell Lab of Ornithology.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA, USA.

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62:335–337.

Ratajczak, Z., J. M. Briggs, D. G. Goodin, L. Luo, R. L. Mohler, J. B. Nippert, and B. Obermeyer. 2016. The potential for transitions from tallgrass prairie to woodlands: are we operating beyond critical fire thresholds. Rangeland Ecology and Management 69:280–287.

Ratajczak, Z., J. B. Nippert, J. M. Briggs, and J. M. Blair. 2014. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the central great plains of North America. Journal of Ecology 102:1374–1385.

Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. The Journal of Wildlife Management 52:484–491.

Refnew, R. B. 2002. The influence of patch and landscape characteristics on grassland passerine density, nest success, and predators in southwestern Wisconsin pastures. Dissertation:274.

Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. Auk 122:618–636.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Ruth, J. M. 2015. Status assessment and conservation plan for the Grasshopper sparrow (*Ammodramus savannarum*). Version 1.0:109.

Samson, F., F. Knopf, and F. Knopf. 1994. Roundtable prairie conservation in North America. Bioscience 44 (6):418–421.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, C. Gary, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range stimates. Journal of Wildlife Management 63 (2): 739-747.

Seibold, S., M. M. Gossner, N. K. Simons, N. Blüthgen, J. Müller, D. Ambarlı, C. Ammer, J. Bauhus, M. Fischer, J. C. Habel, K. E. Linsenmair, T. Nauss, C. Penone, D. Prati, P. Schall, E. D. Schulze, J. Vogt, S. Wöllauer, and W. W. Weisser. 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574:671–674.

Silber, K. M., T. J. Hefley, H. N. Castro-Miller, Z. Ratajczak, and W. A. Boyle. 2024. The long shadow of woody encroachment: An integrated approach to modeling grassland songbird habitat. Ecological Applications 34:1–16.

Silverman, B. W. 1986. Density estimation for statistic and data analysis. Chapan & H. Boca Raton, Fl,USA.

Sirami, C., C. Seymour, G. Midgley, and P. Barnard. 2009. The impact of shrub encroachment on savanna bird diversity from local to regional scale. Diversity and Distributions 15:948–957.

Smith, R. L. 1963. Some ecological notes on the Grasshopper sparrow. The Wilson Bulletin 75:159–165.

Söderström, B., T. Pärt, and J. Rydén. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: An experiment and a review. Oecologia

117:108–118.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems and Environment 254:244–254.

Stevens, N., C. E. R. Lehmann, B. P. Murphy, and G. Durigan. 2017. Savanna woody encroachment is widespread across three continents. Global Change Biology 23:235–244.

Stewart, M. E. 1990. Impaled grasshopper sparrow in Jefferson county, Oklahoma. Bulletin of the Oklahoma Ornithological Society 23:16.

Sullins, D. S., D. A. Haukos, J. M. Lautenbach, J. D. Lautenbach, S. G. Robinson, M. B. Rice, B. K. Sandercock, J. D. Kraft, R. T. Plumb, J. H. Reitz, J. M. S. Hutchinson, and C. A. Hagen. 2019. Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence. Biological Conservation 238:108213.

Vickery, P. D. 2020. Grasshopper Sparrow (*Ammodramus savannarum*), version 1.0. Birds of the Wolrd (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.

van Vliet, H. E. J., and B. J. M. Stutchbury. 2018. Radiotagged fledgling Savannah Sparrows *Passerculus sandwichensis* at risk of entanglement in vegetation. Ibis 160:919–922.

Wallace, G., M. Elden, R. Boucher, and S. Phelps. 2022. An automated radiotelemetry system (ARTS) for monitoring small mammals. Methods in Ecology and Evolution 13:976–986.

Weiner, C. N., M. Werner, K. E. Linsenmair, and N. Blüthgen. 2011. Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks. Basic and Applied Ecology 12:292–299.

Wesche, K., B. Krause, H. Culmsee, and C. Leuschner. 2012. Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. Biological Conservation 150:76–85.

White, J. D. M., N. Stevens, J. T. Fisher, and C. Reynolds. 2024. Woody plant encroachment drives population declines in 20% of common open ecosystem bird species. Global Change Biology 30:1–14.

Wiens, J. A. 1969. An approach to the stdy of ecological relationships among grassland birds. Ornithological monographs 8:1–93.

Wiens, J. A. 1973. Interterritorial habitat variation in grasshopper and savannah sparrows. Ecology 54:877–884.

Williams, E. J., and W. A. Boyle. 2018. Patterns and correlates of within-season breeding dispersal: A common strategy in a declining grassland songbird. Auk 135:1–14.

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Wretenberg, J., Å. Lindström, S. Svensson, T. Thierfelder, and T. Pärt. 2006. Population trends of farmland birds in Sweden and England: Similar trends but different patterns of agricultural intensification. Journal of Applied Ecology 43:1110–1120.

xeno-canto. 2024. Loggerhead shrike - *Lanius ludovicianus*. https://xeno-canto.org/species/lanius-ludovicianus.

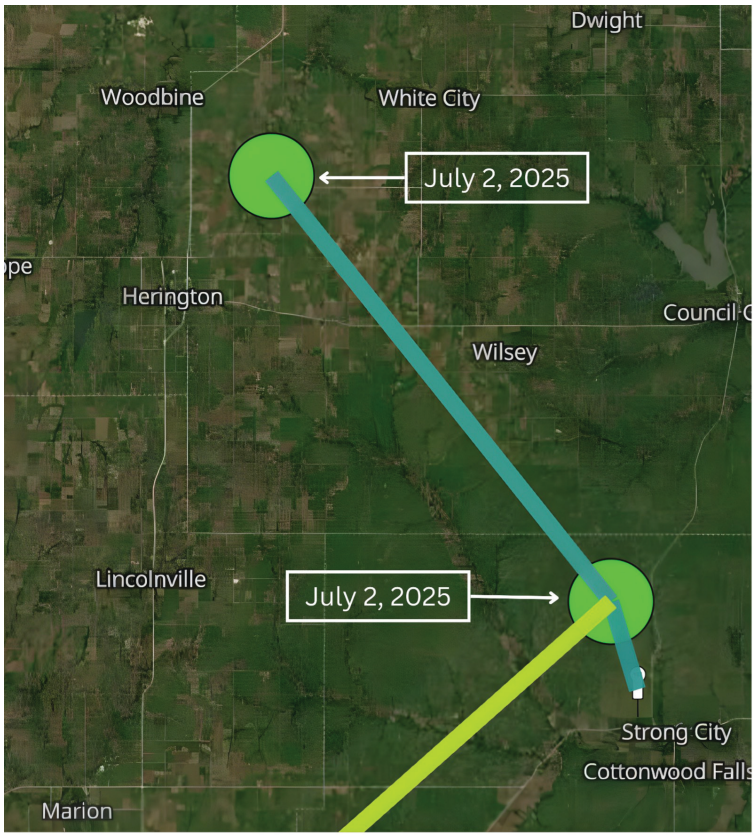
Yosef, R. 2020. Loggerhead shrike (*Lanius ludovicianus*). Cornell Lab of Ornithology.

Yosef, R., and T. C. Grubb. 1992. Territory size influences nutritional condition in nonbreeding Loggerhead shrikes (*Lanius ludovicianus*): a ptilochronology approach. Conservation Biology 6:447–449.

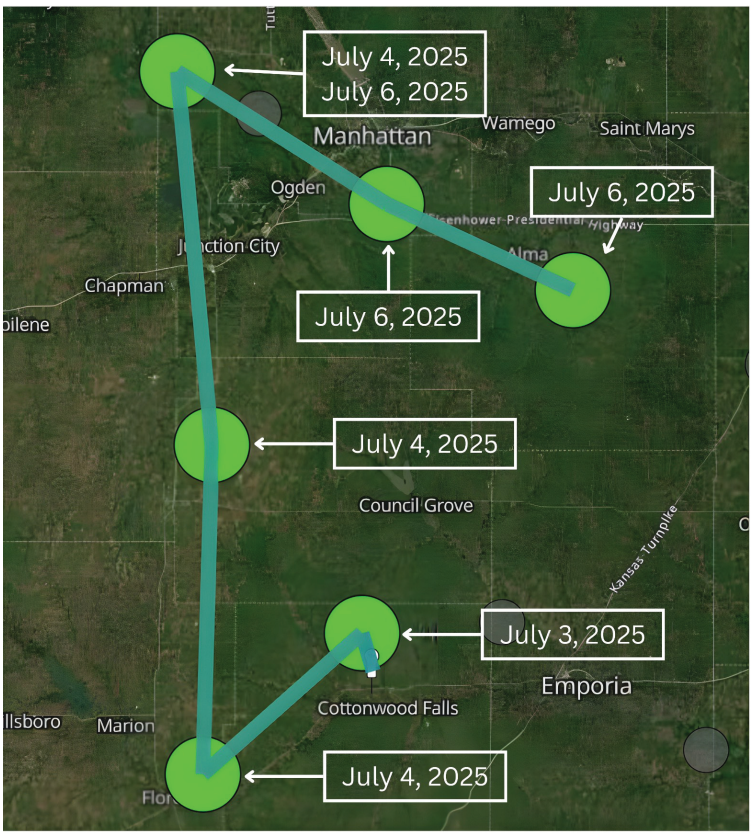
Zanette, L. Y., and M. Clinchy. 2019. Ecology of fear. Current Biology 29:309–313.

Appendix A - Motus Dispersal Maps

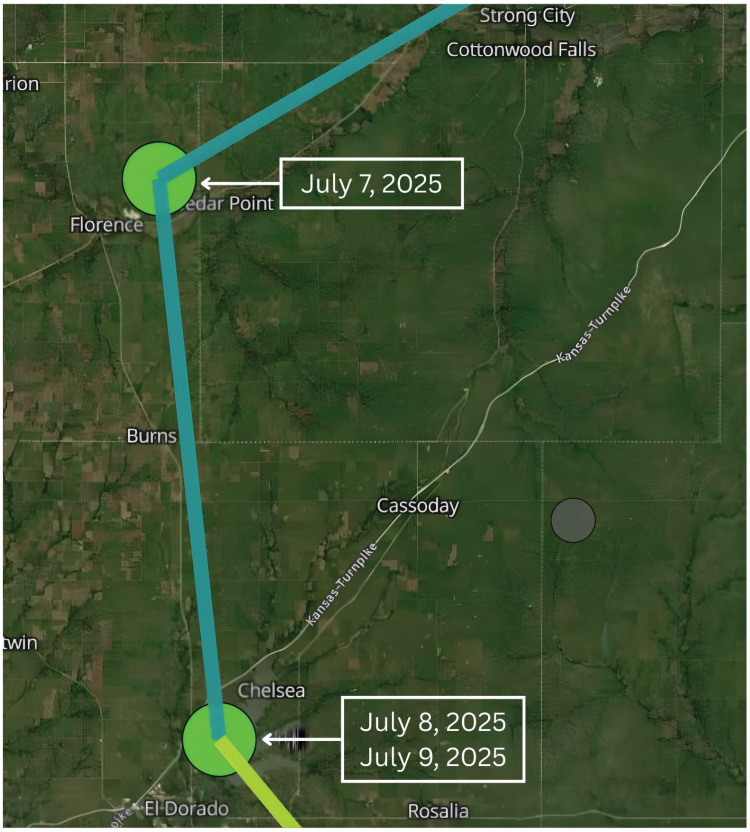
Appendix Figure A.1. Map showing long-distance breeding dispersal movements of sparrow 2D661E4C from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



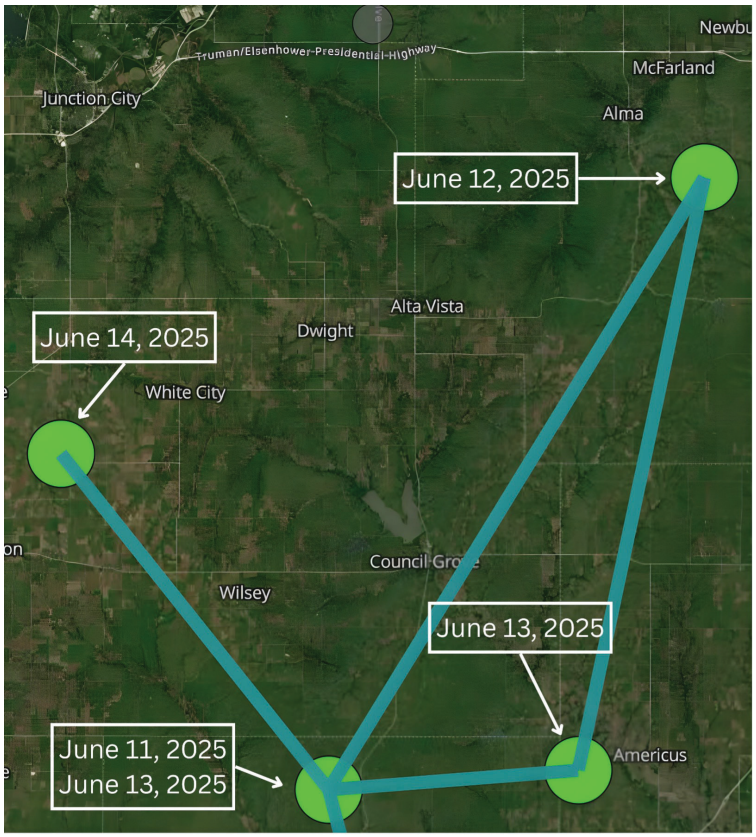
Appendix Figure A.2. Map showing long-distance breeding dispersal movements of sparrow 19192D78 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



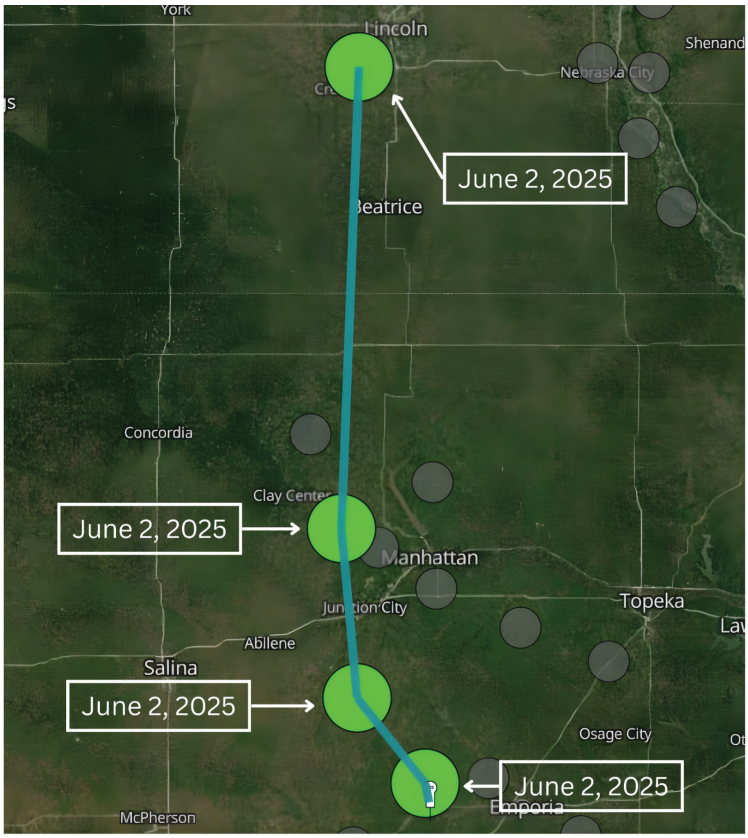
Appendix Figure A.3. Map showing long-distance breeding dispersal movements of sparrow 522D5566 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



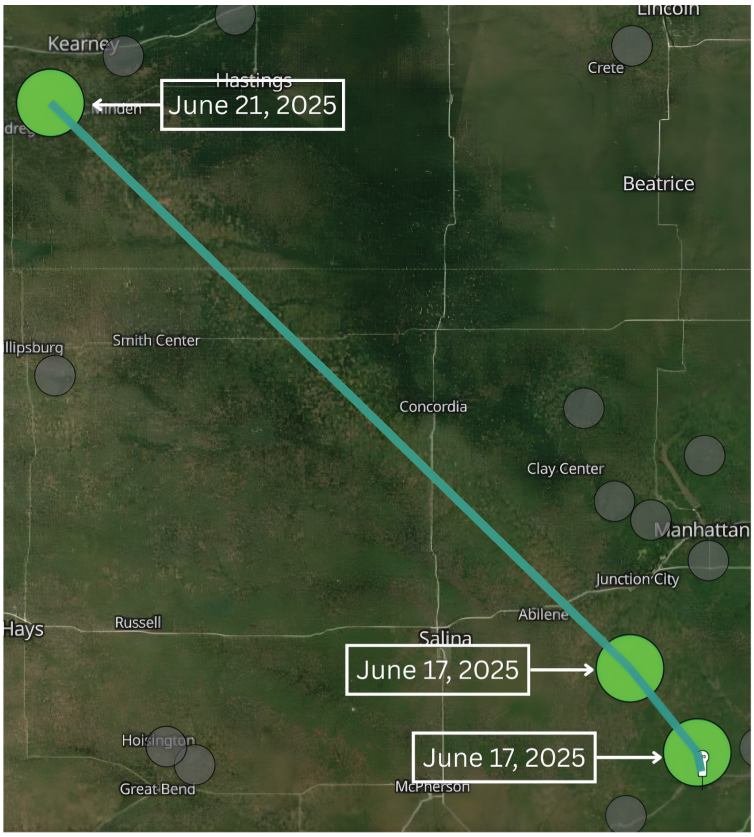
Appendix Figure A.4. Map showing long-distance breeding dispersal movements of sparrow 61333334 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



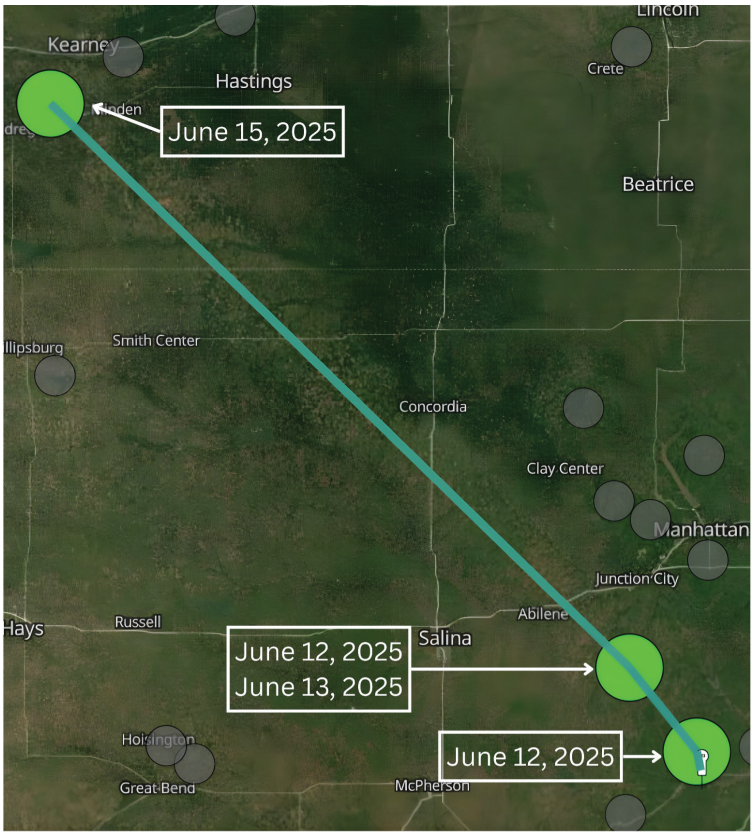
Appendix Figure A.5. Map showing long-distance breeding dispersal movements of sparrow 664B1961 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



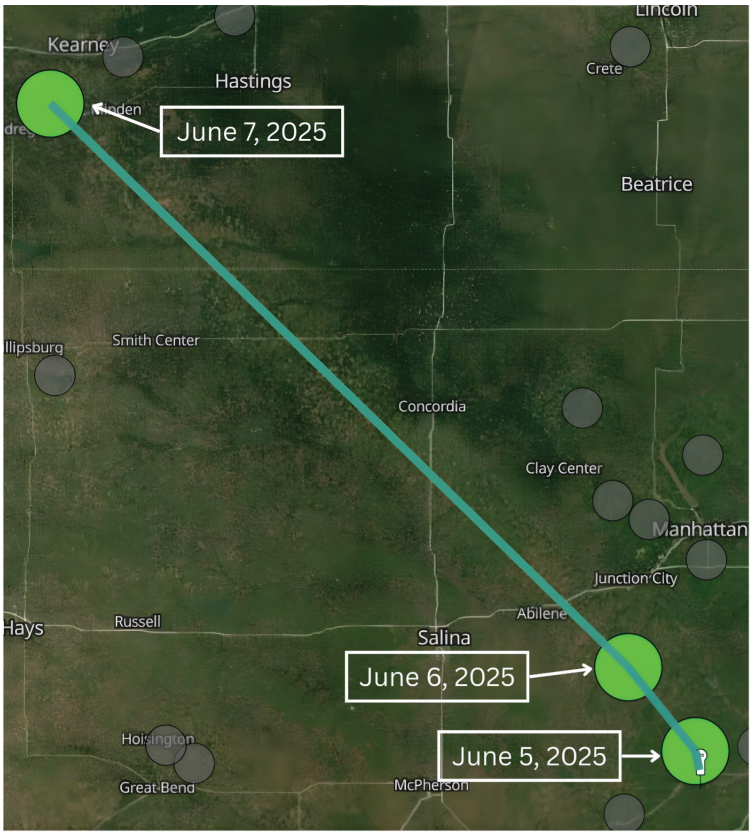
Appendix Figure A.6. Map showing long-distance breeding dispersal movements of sparrow 52666119 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



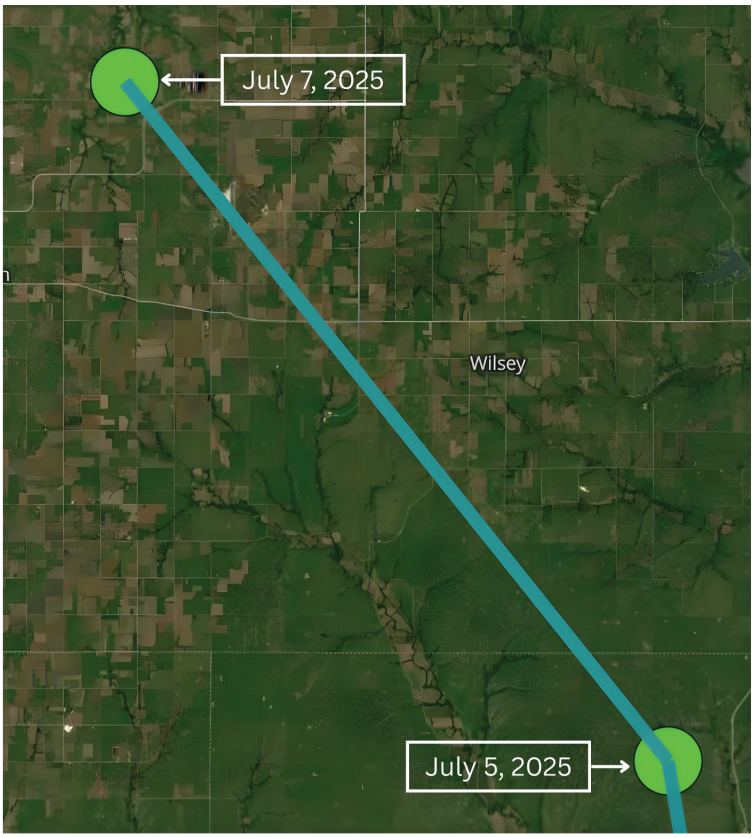
Appendix Figure A.7. Map showing long-distance breeding dispersal movements of sparrow 1E2A2A1E from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



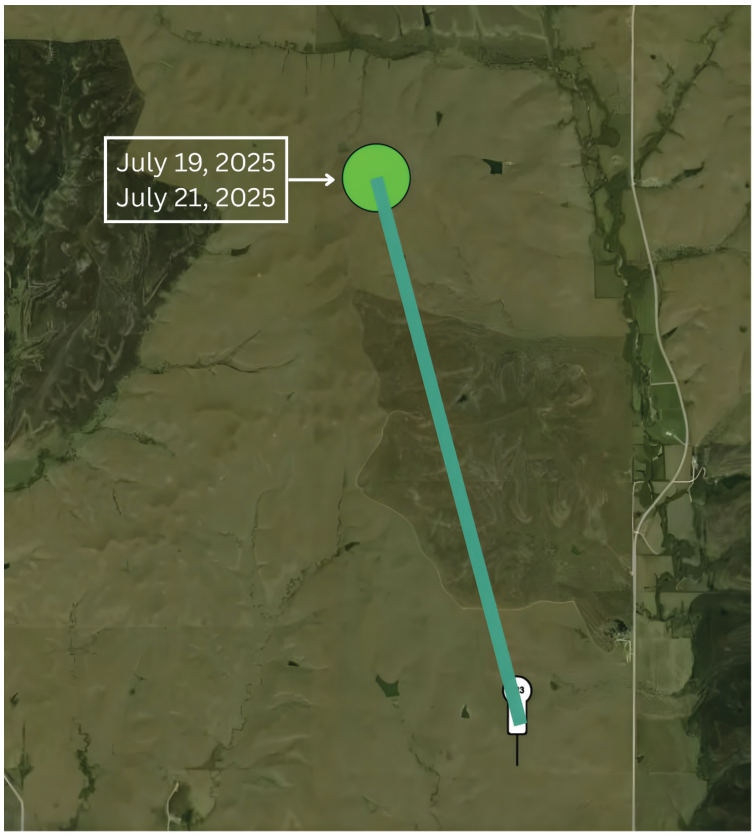
Appendix Figure A.8. Map showing long-distance breeding dispersal movements of sparrow 522D2D07 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.



Appendix Figure A.9. Map showing long-distance breeding dispersal movements of sparrow 2D2A4C61 from the Motus website (Motus.org). The large green dots represent Motus towers that have detected the bird. Dates represent the day the tag was detected by each Motus tower.

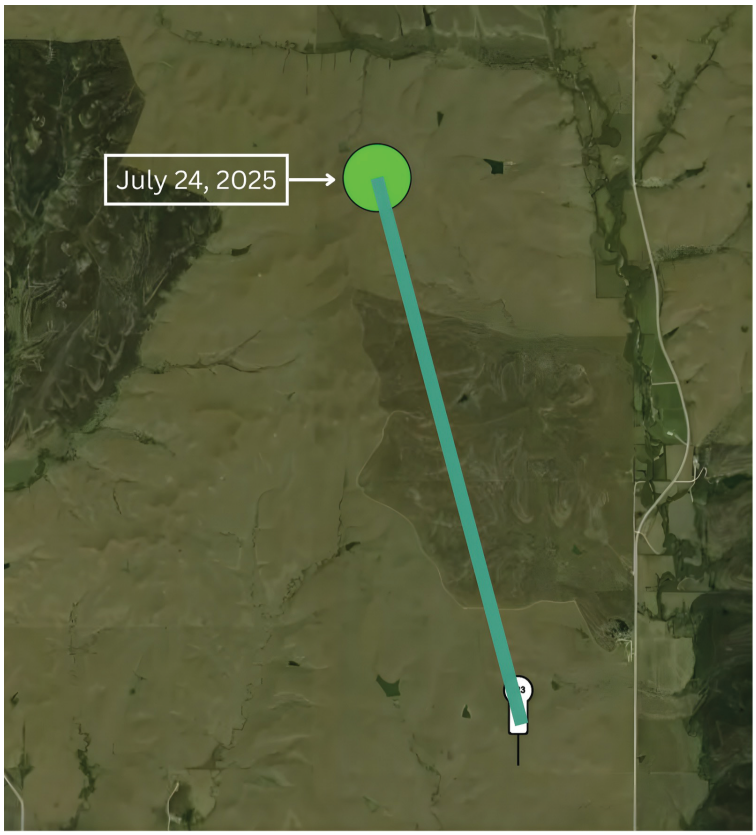


Appendix Figure A.10. Map showing long-distance breeding dispersal movements of sparrow 19664C1E from the Motus website (Motus.org). The large green dot represents a Motus towers that has detected the bird. Dates represent the day the tag was detected by each Motus tower. The white pin represents the tagging location.



Appendix Figure A.11. Map showing long-distance breeding dispersal movements of sparrow 34665266 from the Motus website (Motus.org). The large green dot represents a Motus towers that has detected the bird. Dates represent the day the tag was detected by each Motus tower. The white pin represents the tagging location.

Appendix Figure A.12. Map showing long-distance breeding dispersal movements of sparrow 074B4B4B from the Motus website (Motus.org). The large green dot represents a Motus towers that has detected the bird. Dates represent the day the tag was detected by each Motus tower. The white pin represents the tagging location.


July 24, 2025