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Relating Predator Community Ecology and Duck Nest Survival in Eastern South Dakota

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RELATING PREDATOR COMMUNITY ECOLOGY AND DUCK NEST SURVIVAL IN EASTERN SOUTH DAKOTA

BY

SAMANTHA R. FINO

A dissertation submitted in partial fulfillment of the requirements of the

Doctor of Philosophy

Major in Wildlife and Fisheries Science

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2023

DISSERTATION ACCEPTANCE PAGE
Samantha Fino

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

RELATING PREDATOR COMMUNITY ECOLOGY AND DUCK NEST SURVIVAL IN EASTERN SOUTH DAKOTA

SAMANTHA R. FINO

2023

As conversion of native grasslands and wetlands to croplands continues in the Prairie Pothole Region (PPR), managers are tasked with maintaining sustainable waterfowl populations. Mesopredator community dynamics is a hypothesized mechanism driving spatiotemporal variation of waterfowl nest survival in the PPR, yet studies often lack detailed information on mesopredator species occurrence and abundance. Therefore, understanding spatial and temporal variation in behaviors of mesopredators provides valuable insights for understanding predator-prey interactions between mesopredators and upland duck nests. Further, differences in a predator community resulting from lethal removal of dominant species may influence composition and space use patterns of subordinate and non-target mesopredators, potentially affecting prey through mesopredator release. Our study was conducted in two counties in eastern South Dakota, one with ongoing standardized annual coyote removal (i.e., Faulk; the treatment county) for the last 30 years, and the other receiving no standardized coyote removal (i.e., Hand; the control county). To quantify the nest predator community and potential interactions among mesopredators, I deployed 4 camera trapping surveys, each 3 weeks in length, conducted during the nesting seasons each year (i.e., May–July, 2018–2020). I evaluated species-specific detection and occupancy patterns, then explored co-occupancy relationships among mesopredator species (i.e., coyotes [Canis latrans], striped skunks [Mephitis mephitis], raccoons [Procyon lotor], and American badger [Taxidea taxus]). To evaluate spatiotemporal changes in resource selection and movements, I used integrated step-selection functions from radio-marked mesopredators. Lastly, I simultaneously searched for and monitored nests, and incorporated developed predator-derived covariates from occupancy models and integrated step-selection functions with associated landscape characteristics to compare with direct nest site metrics in logistic exposure nest survival models to understand predator-prey interactions.

We found that mesopredators increased movement rates and home range size during periods when common resources were in shorter supply. Across the study area, detection probabilities of mesopredators were 1.7-7.1 times greater in 2018, when duck nest densities were lowest, and 5.2-7.1 times higher during early-season surveys (May) when food resources (i.e., nests, small mammals, invertebrates, vegetation) were expected to be sparse compared to summer. These results suggest individuals increased movement frequencies or distances to locate sufficient food resources or to avoid negative interspecific interactions. Observed elevated detection rates at times of lower food resources (i.e., early spring and in 2018) coincided with greater average step lengths and daily movement rates of radio-marked raccoons and striped skunks during the pre-nesting period compared to other times of the year, as well as greater average home range size and daily movement rates of raccoons in 2018 compared with subsequent years. Similarly, 2018 was associated with greatest probabilities of mesopredator co-occurrence, suggesting that low food resource availability may aggregate sympatric species. Coexistence of mesopredators corresponded with spatiotemporal segregation of similar

selection and movement patterns by sympatric mesopredator species throughout the nesting periods and in both counties for landscape characteristics associated with waterfowl nest site selection and high nest density. Further, direct species overlap of space use was mostly observed during the post-nesting period, when food resource abundances were suspected to be highest. Mesopredators would behave similarly in relation to a landscape characteristic but in different counties or different nesting periods which allowed for niche partitioning, avoidance of negative interspecific species interactions via increased movements, or both, allowing for sympatric species to coexist when food resources are scarce and presents an elevated risk of nest failure earlier in the nesting season.

Because our study area comprised two counties with suspected differences in coyote densities due to the presence/absence of active coyote removal management (i.e., coyote occupancy in the treatment county was 44% lower compared to the control county), it allowed an opportunity to test predictions of the mesopredator release hypothesis. This hypothesis predicts that if densities of the dominant predator are reduced (e.g., annual lethal removal of coyotes), densities or movements of subordinate predators should increase since the need to alter behaviors to avoid negative interactions is comparatively reduced. Raccoon occupancy probability was 30% greater in the treatment compared to the control county. Average home range size and daily movements of raccoons and coyotes were greater in the treatment county than in the control county. Additionally, in the treatment county, detection probability of a member of the nest predator guild was not different when a coyote was present or absent nor if a coyote was detected or not, potentially implying the reduced density, distribution, and/or movements of coyotes did not influence those of other mesopredators. Further, spatiotemporal differences in selection and movement between coyotes and smaller mesopredators (e.g., raccoons and striped skunks) were largely not observed in the treatment county, indicating coyotes were not depressing or influencing the behaviors of other mesopredator species which would thereby suggest a presence of mesopredator release. Alternatively, in the control county, spatiotemporal differences in selection and movement between coyotes and smaller mesopredators were widely observed and indicate that subordinate species may have altered their space use to avoid or decrease encounters when coyotes were at greater densities. Such behavior would presumably minimize a predation risk effect as a result of higher coyote densities that were due to a lack of standardized coyote removal management. Importantly, our study provided support that standardized annual coyote removal (i.e., the treatment county) induced mesopredator release and indirectly reduced nest survival via increased occupancy, greater movements, more extensive space use by subordinate mesopredators due to decreased interspecific competition. To this end, daily duck nest survival rates were 0.965 (95% CI = 0.961, 0.969) in the treatment county compared to 0.974 (95% CI = 0.971, 0.978) in the control county.

Finally, our study revealed that, in the context of a productive landscape with ample and evenly distributed food resources and seasonal nest success rates that exceed sustainable management levels (i.e., all county and waterfowl species estimates were >25%), direct nest site metrics were sufficient in quantifying landscape and patch characteristics that influence nest survival. Although predator-derived covariates better explained variation in daily nest survival for distance to nearest surface water and patch area landscape characteristics compared to direct nest site metrics, predator-derived covariates were not present in the most supported nest survival model. However, our findings reflected those from other studies; the relationship between nest survival and fate of nearest neighboring nest at time of the nest searching effort, as well as observed and common prey searching behavior of mesopredators during the core nesting period and in relation to landscape characteristics associated with increased food resource availability and nest site selection by ducks (i.e., based on habitat characteristics and or on the local density of conspecifics), suggests that mesopredators may key in on specific prey once encountering it and congregate in areas of high nest density. Our results also support previous studies in that nest depredation events are diluted in patches with higher nest densities as well as camouflaged from mesopredators when patches have taller grass heights around the nest. By investigating and evaluating mechanisms that drive nest survival, I hope our research helps to inform future management endeavors to be efficient and effective. Further, while several studies have found that removing predators from the landscape resulted in increased duck nest survival, our study will help guide and inform management decisions on focal predator species, timing, and associated landscape characteristics of such strategies. And lastly, by overlaying simultaneous predator-prey geospatial data, our project can assist in the prioritization of patches for habitat management and restoration efforts that benefit upland game bird productivity.

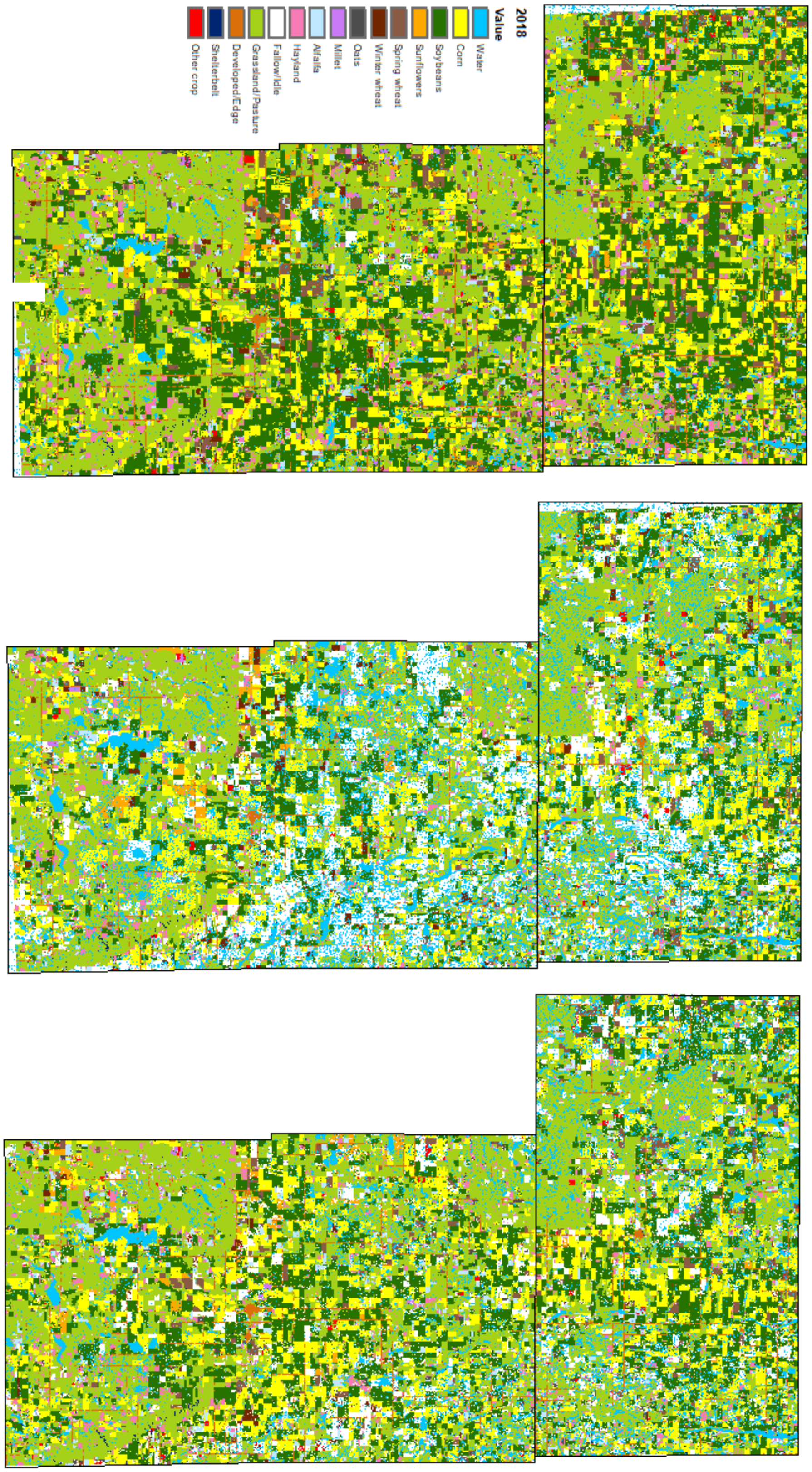
2018
Value
Water
Corn
Soybeans
Sunflowers
Spring wheat
Winter wheat
Oats
Millet
Alfalfa
Hayland
Fallow/Idle
Grassland/Pasture
Developed/Edge
Shelterbelt
Other crop

Figure A. Land cover of the treatment (North) and the control (South) counties, Eastern South Dakota, USA, in 2018 (left), 2019 (center), and 2020 (right).

Interaction among mesopredators in a fragmented prairie ecosystem

ABSTRACT

Mesopredator community composition and movement behaviors are hypothesized mechanisms driving spatiotemporal variation of waterfowl nest survival in the Prairie Pothole Region, yet studies often lack detailed information on mesopredator species occurrence and abundance. Further, differences in a predator community resulting from lethal removal of dominant species may influence composition and space use patterns of subordinate and non-target mesopredators, potentially affecting prey through mesopredator release. To better understand the spatiotemporal dynamics of mesopredators in relation to landscape and environmental variables, as well as interactions among mesopredators, I compared dynamic occupancy modeling results from 4 camera trapping surveys, each 3 weeks in length, conducted during the nesting season (i.e., May–July) at two locations in eastern South Dakota, United States from 2018–2020. One location has had ongoing annual coyote (*Canis latrans*) removal (i.e., the treatment county) for the last 30 years, whereas no annual coyote removal has occurred in the other (i.e., the control county). I evaluated species-specific detection and occupancy patterns and explored co-occupancy relationships among mesopredator species (i.e., coyotes, striped skunks [*Mephitis mephitis*], raccoons [*Procyon lotor*], and American badger [*Taxidea taxus*]). Coyote occupancy probability was 44% lower and raccoon occupancy probability 30% greater in the treatment compared to the control county, supporting predictions of the mesopredator release hypothesis. Additionally, higher detection rates of coyotes occurred in the absence of members of the nest predator guild, suggesting coyotes may not be a dominant community member in the treatment county. Across the study area, detection probabilities of mesopredators were 1.7-7.1 times greater in 2018, when duck nest densities were least, and 5.2-7.1 times higher during earlier surveys when food resources were expected to be reduced compared to summer (i.e., nests and small mammals), suggesting individuals increased movement frequencies or distances to locate sufficient food resources or to avoid negative interspecific interactions. Similarly, 2018 was associated with greatest probabilities of mesopredator co-occurrence, suggesting that low food resource availability may aggregate sympatric species. The coexistence of mesopredators I observed may be facilitated by niche separation, avoidance of negative interspecific species interactions via increased movements, or both mechanisms. In addition, our results suggest that active removal of coyotes, a dominant predator species, may have induced a mesopredator release that could have reduced nest survival of ground nesting game birds in the area.

KEY WORDS camera trapping, co-occurrence, competitive release, mesopredators, occupancy modeling, predator control, South Dakota

The Prairie Pothole Region (hereafter, PPR) of North America is a mosaic of wetlands and grasslands that supports high densities of breeding waterfowl (Anatidae) (Reynolds 2000). As grassland conversion to agriculture continues in the PPR, managers are tasked with maintaining waterfowl productivity in this increasingly fragmented landscape (Drever et al. 2007). Depredation is the primary cause of nest failure (54-85% of nest losses) for upland-nesting ducks, and nest survival is the most influential factor affecting vital rates and population dynamics (Ricklefs 1969, Johnson et al. 1987, Klett et al. 1988, Sargeant and Raveling 1992, Martin 1995). Many species of various taxa depredate waterfowl nests; however, mesopredators have the greatest impact on nest survival (Sovada et al. 2000, Phillips et al. 2003, 2004).

Increasing fragmentation in the PPR can lead to more frequent predator encounters with duck nests. For example, larger blocks of grassland have been associated with increased nest survival because it is hypothesized that predator foraging behavior becomes diluted with increasing patch size (Phillips et al. 2003, Horn et al. 2005). Similarly, nest survival was lower when nests were closer to habitat edges, potentially due to predators using edges to improve foraging efficiency (Ray 2000). Nest survival has also been positively associated with denser vegetation (and often native) cover, suggesting that it provided greater concealment of nests from predators (Schranck 1972, Clark and Shutler 1999). Additionally, neighboring nests were more likely to share the same fate than non-neighboring nests (Ringelman et al. 2012), implying that predators developed a search image based on what prey resources were seasonally available. Although these suggested mechanisms relating nest survival to predator behavior have some empirical support, few avian studies have examined predator-prey relationships simultaneously.

Investigating patterns of detection and occurrence for mesopredators can elucidate their associations to landscape variables, environmental conditions, and species interactions. In the PPR, coyotes (*Canis latrans*) are a dominant predator, potentially suppressing or affecting activity patterns of smaller carnivores. Suppression of mesopredators by dominant predators has been suggested to explain variation in nest survival (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003). However, some research has suggested that mesopredator species in the PPR are often positively associated with one another, suggesting that differences in their ecology or temporal activity facilitate coexistence (Crimmins et al. 2015, Schoener 1974, Lesmeister et al. 2015). Further, variation in prey resources may influence spatiotemporal variation in mesopredator community composition.

Intraguild predation (IGP) theory characterizes members of a predator community as dominant or subordinate predators that compete for shared resources. Traditional IGP describes direct interference competition where the dominant species kills the subordinate species for food (Palomares and Caro 1999, Kamler and Gipson 2004, Kimbrell et al. 2007), but because this is rare with mammalian predators, extensions of this theory include behavioral differences, changes in vigilance, and use of alternative prey resources that lead to coexistence (Heithaus 2001, Holt and Huxel 2007, Wilson et al. 2010). Avoidance, an example of an extended IGP theory, is one hypothesized mechanism of mesopredator release hypothesis (MRH). The MRH predicts that removal or reduction in density or distribution of a dominant predator will result in increased densities, greater movements, and more extensive space use by subordinate mesopredators (Estes 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). Further, the hypothesis predicts subordinate and generally smaller mesopredators will alter their behaviors to avoid interacting with dominant and often larger predators; this phenomenon is described as a variation of the “predation risk effect.” Coyotes have been documented as the dominant predator in a community consisting of other canids (Ralls and White 1995, Sovada et al. 1998, Kitchen et al. 1999, White et al. 2000) and raccoons (*Procyon lotor*; Andrews and Boggess 1978, Clark et al. 1989, Hasbrouck et al. 1992, O’Connell et al. 1992). However, some studies have suggested coyotes may influence the behavior of smaller mesopredators and other members of the ecosystem indirectly (Rogers and Caro 1998, Crooks and Soulé 1999, Henke and Bryant 1999).

Camera-traps are a noninvasive and efficient method for surveying predator communities to better understand relationships mesopredator species have with their environment and one another (Gompper et al. 2006, Kelly et al. 2012). Camera-trap surveys can provide data to be used in dynamic occupancy models (MacKenzie et al. 2003), uni-directional co-occurrence models (Richmond et al. 2010, Yackulic et al. 2014), and multi-species occupancy models (Rota et al. 2016) while accounting for imperfect detection and varying environmental conditions. From 2018 to 2020, I conducted a camera trap study in eastern South Dakota to explore mesopredator species occurrence and potential effects of landscape- and patch-level metrics that may elucidate mechanisms behind spatiotemporal variation in duck nest survival. Spatiotemporal variation in occupancy probabilities can be used to infer space use patterns of sympatric mesopredators (Lesmeister et al 2015, Lonsinger et al. 2017, Lombardi et al. 2020, Dart 2021). Additionally, variation in probability of detection, generally considered a nuisance parameter, may provide insight to relative differences in movement, home range size, and relative abundance (citations).

To better understand mesopredator space use, I investigated factors hypothesized to drive their individual distributions, compared the influence of coyote occurrence on a nest predator guild between one county with long term annual coyote removal and another with no history of systemic coyote removal, and compared the co-occurrence of mesopredator species in years with different nest densities. I tested a prediction of the mesopredator release hypothesis, wherein areas of annual coyote removal management would result in increased detection and occupancy probabilities of subordinate mesopredators. I also tested predictions of the IGP hypothesis by determining if low food resource availability (i.e., either earlier in the season or interannual differences) associated with increased detection and co-occurrence probabilities of mesopredators. Improving understanding of space use by different predator species and potential interspecific relationships, habitat management strategies can be developed to minimize depredation rates of nests in fragmented landscapes.

METHODS

Study area

I studied occupancy of mesopredators in four townships within Faulk and Hand Counties in eastern South Dakota, 2018–2020. I selected adjacent counties with similar amounts and composition of grasslands and wetlands, and townships with high predicted breeding duck pair densities (Reynolds et al. 2006). Faulk County has had ongoing standardized coyote removal since the 1990s, whereas no standardized coyote removal has occurred in Hand County (B. Curtis, South Dakota Department of Game, Fish and Parks [SDGFP], personal communication). Hereafter, Faulk County will be referred to as the treatment county because of the continued application of coyote removal management, and Hand County will be referred to as the control county. The proximity and contrasting coyote management of sites allowed for efficient investigation of nesting and predator ecology simultaneously and with respect to predator management strategies.

Our study area was located in the Drift Prairie or Glaciated Plains physiographic region of the PPR. Average elevation is ~481 m above MSL and the annual average temperature ranged from -6° C (December) to 21° C (June), during 2018–2020. The average annual precipitation during 2018-2020 was 55 cm of rainfall and 93 cm of snowfall (US Climate Data, 2020). Both counties have low population densities; the treatment county had a population of 2,299 people whereas the control county's population was 3,191 people and both counties averaged 0.5 housing units/km^2 and average human densities of 1.5 people/km^2 (US Census Bureau 2019). The landscape was a mosaic of row crop agriculture and grasslands that surrounded farmsteads; composition of the treatment county was approximately 16% corn (*Zea mays*), 22% soybean (*Glycine max*), and 29% pasture, whereas the control county was generally similar with approximately 14% corn, 19% soybean, and 36% pasture. Proportion of wetlands were approximately 6.6% in the treatment county and 4.9% in the control county.

Noninvasive mesopredator surveys

We conducted mammalian predator camera-trap surveys during 3 waterfowl nesting seasons: 5 May–28 July 2018, 4 May–27 July 2019, 2 May–25 July 2020. I equipped camera-trap stations with Moultrie M-40 IR motion-triggered trail cameras mounted 1 m above the ground with a clear view of a scent-lure and bait station placed approximately 5 m from cameras. Because there were various species of mammalian mesopredators on the landscape, I used Friskies® wet cat food as bait and Caven's Yodel Dog as lure. I smeared the lure on the bottom of the cat food can and secured it with a garden staple to the ground. I checked cameras, and refreshed or replaced lure and bait weekly.

We used a cluster sampling method to allocate camera sites to maximize spatial and temporal resolution of captured images. Townships were 93.2 km^2 and divided evenly into 36 sections (i.e., 2.6 km^2). Within 18 sections of a township, I placed a camera trap station in 3 of the 4 quadrants of selected sections. In areas where I were granted land access, I randomly selected sections and quadrants and ensured that the boundaries shared by adjacent sections and quadrants only had one camera-trap station. Because predators frequently use habitat edges (Andrén 1995, Dijak and Thompson III 2000, Lariviere and Messier 2011), I placed camera-trap stations systematically along the mid-point of habitat edges. Having camera-trap stations along habitat edges also promoted their functional longevity compared to rangeland and cropland, because movement of grass, crops, or cattle commonly triggers cameras. Camera-trap stations were placed ≥2 km from potential waterfowl grassland nesting habitat and from one another; 2 km was approximately the smallest home range size and minimum average movements among the mesopredator species in our study area (i.e., striped skunk [*Mephitis mephitis*]; Greenwood et al. 1997, Bixler and Gittleman 2000, Weissinger et al. 2009). I ensured that camera-trap station locations were on different quadrant lines when selected quadrants were adjacent, and I deployed cameras for ~21 days before being relocating them to another township for the next survey. I sampled townships at random and the order differed annually. At each camera-trap station and at the start of each deployment, using a Robel’s pole (Robel et al. 1970), I recorded percentage of visual obstruction and concealment in each cardinal direction at 5 m from the camera-trap station.

To identify species of interest for analyses, I recorded the camera ID, GPS location coordinates, number of days the camera was active, and total number of photos, photos of animals, and photos of mesopredators, and at each camera trap station. For each photo of a mesopredator, I recorded date, time, temperature, moon phase, species, number of individuals, if there was any unique individual-identifier present (ear tag or collar), presence of offspring, and a scaled confidence of the photo-processer's species identification (1 = confident of species identification, 2 = fairly sure of species identification, 3 = unsure of species identification). Data were organized from 21 survey days into three 7-day sampling occasions per camera-trap location per year, resulting in a robust nested sampling design (Pollock 1982, Mackenzie et al. 2003). Species not detected in all three years and those with <1% detections were not included in further analyses aside from inclusion in the nest predator guild.

Index of nest density

We systematically searched grassland fields for nests during the waterfowl nesting season (7 May 2018–6 July 2018, 6 May 2019–5 July 2019, 4 May 2020–3 July 2020) and searched fields using crews of 2 that dragged a 50-m cable-chain behind 2 all-terrain vehicles (Klett et al. 1986). Nest searching occurred between 0800 and 1400 to maximize the probability of hens being on nests (Klett et al. 1986, Gloutney et al. 1993, Sovada et al. 2000, Loos and Rower 2004, Walker 2011). Assuming each field was representative of others in the area at that given time, I only searched each field once to maximize spatial coverage of the study area. I maintained a daily rotation of nest searching in each township to capture temporal variation in the number of active nests. When crews located a nest, I recorded the host species, GPS location, clutch size, estimated incubation stage by candling (Weller 1956), and marked the nest with a flag placed 10 m north (Fisk 2010). I revisited each nest every 7–10 days until the nest was either destroyed, abandoned (hen absent and no advance in incubation), or successful (≥1 egg hatched; Klett et al. 1986). Assuming a laying rate of 1 egg/day, I estimated nest initiation dates by backdating based on clutch size and estimated incubation stage at each nest visit. Nests that were abandoned (i.e., cold eggs with no progression of development) were excluded from analyses. I assigned a survival status (successful, failed due to depredation, abandoned) to each nest once a fate was determined. Nest searching methods were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 17-103A).

Because I nest searched each field once per year, it would have been inappropriate to use distance to nearest active nest and/or failed nest, as well as nest density of the nearest grassland patch at the time of the camera-trap survey, as covariates in analyses. However, because I rotated the township in which I searched for nests daily, the number of active nests in each township would be a better representation of nest density as a prey resource compared to alternative metrics. To maximize temporal variation of relative nest density, I used a nest density index covariate in the detection structure of our models. The nest density index was not consistent throughout each camera-trap survey, but rather varied weekly and represented potential relative food availability throughout the nesting season, which in turn may have influenced movements. To get a greater variation of nest density indices over time, the nest density index covariate in the detection structure of our models was the total number of known active nests on the first day of the week corresponding to the respective week, year, and township of the camera-trap survey (Appendix S1.1).

Small mammal index of abundance

We conducted small mammal trapping surveys during the waterfowl nesting season (aforementioned dates in 2018-2020) to estimate indices of small mammal abundance. I surveyed the small mammal community using 8.9×7.6×22.9 cm Sherman traps (H.B. Sherman Inc., Tallahassee, TN, USA) and 49.0×15.2×15.2-cm live-capture #202 Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI, USA). I placed traps 10 m apart in 8 x 10 grids covering 80-m^2 areas of grass nesting cover and replicated this in each township once per month, which equated to 3 times per field season. I randomly selected grid locations within the townships, separated by ≥5 km (Mohr 1947). I baited traps with a frozen as a bait ball made of a peanut butter-oat mixture and rebaited as necessary. I checked traps at 0700 and 1900 daily for 5 consecutive days to assess local species richness (Manley et al. 2006). Traps were deployed Sunday evenings and retrieved at the end of the sampling period (800 trap nights per survey). Malfunctioning traps, where the door was closed without capture, bait was missing without capture, or a trap was missing or broken, were reset, rebaited, or replaced (Nelson and Clark 1973). I soaked traps in a mild beach solution (45 ml/3.8 L) for 10 minutes as necessary between trapping sessions (Mills et al. 1995) to minimize the influence of scent on future capture events.

We recorded trap outcomes, such as if a trap was open, sprung, or sprung with a capture. When a capture occurred, I recorded species, sex, age (juveniles or adults), breeding status (pregnant, lactating, enlarged testes or nonbreeding), and weight prior to marking and/or releasing the animal (Kunz et al. 1996). I marked newly captured individuals with numbered ear tags (Kent Scientific Corporation, Torrington, CT, USA) and noted recaptures prior to release. Handling methods followed the guidelines approved by the American Society of Mammalogists for wild animals in research (Sikes et al. 2016) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 17-103A).

The small mammal index of abundance was not consistent throughout each camera-trap survey, but rather varied weekly and represented potential variation in food abundance throughout the nesting season, which may have influenced movements. To maximize variation in small mammal abundance indices over time, the small mammal abundance index covariate was comprised of the total number of unique individuals captured (all species pooled) in a small mammal survey corresponding to the respective township, week, and year of the camera-trap survey (Appendix S1.2).

Detection and occupancy covariates

We identified seven survey-specific covariates that may directly or indirectly influence detection probability of mesopredators; these covariates varied in space and time. Weekly average daily low temperature and precipitation, and moon phase on the first day of the survey, were included as county-specific detection covariates. I also included temporal covariates accounting for year and sampling-period effects (i.e., the three 7-day sampling occasions in the same location), because temporal changes in resources may have influenced detection rates (e.g., changes in densities of food resources as spring transitions into summer may influence movement patterns). Finally, township-level detection covariates included an index of nest density (Appendix S1.1) and the index of small mammal abundance (Appendix S1.2) corresponding to the week of the camera-trap survey. I included these indices as time-varying only and as an index of food resources on the landscape, because our nest and small mammal monitoring occurred sporadically rather than systematically across the study area, and therefore were not consistent throughout each camera-trap survey (i.e., site-specific). These indices could not be used in the occupancy structure of the models because proper use of site-specific covariates in that respect would have required weekly nest searches and small mammal surveys in all patches nearest to each camera station during the same weeks of the camera-trap survey.

We quantified landscape- and patch-level metrics hypothesized to influence occupancy of mesopredator species; these covariates were site-specific and did not vary with time. I created a cover-type layer for each year in ArcMap 10.5.1 that combined year-specific rasters from the U.S. Geological Survey (hereafter, USGS) Dynamic Surface Water Extent using Landsat Collection 1 Level-3 (Jones 2015) and the U.S. Department of Agriculture (hereafter, USDA) National Agricultural Statistics Service CropScape Cropland data layer (USDA 2018, 2019, 2020). I identified eight covariates that may have directly or indirectly (i.e., via avoidance if occupied by another mesopredator species) influenced spatial dynamics of mesopredators at the site level. I evaluated all covariates for collinearity using Pearson correlation tests (Vatcheva et al. 2016); if $r > 0.70$ for two covariates, depending on the specific covariates, I either (1) used only one of the two covariates in subsequent analyses and based retention of a covariate on the lower AIC value when the covariates were run in individual models, or; (2) averaged the values to create a cohesive covariate. The first covariate was a binary variable representing county differences in coyote removal management. If systematic coyote removal in the treatment county decreased coyote density, I anticipated greater occupancy estimates in the treatment county of other mesopredators that typically minimize overlap with coyotes (Terborgh and Winter 1980, Estes 1996, Gehrt and Clark 2003).

Fragmentation and perennial cover may influence mesopredator space use (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007, Phillips et al. 2004, Amundson et al. 2012, Crimmins et al. 2015) and was characterized in 5 ways: (1) distance to active farmstead (km); (2) distance to abandoned farmstead (km); (3) proportion of grassland cover type within a 1.6 km radius (%); (4) the dominate crop (soybeans or corn) within a 1.6 km radius, and; (5) percentage of vegetative thickness on the first day of the first survey. The concealment and visual obstruction covariates were highly correlated ($r = 0.84$), and thus ultimately represent one covariate I labeled as vegetative thickness. Vegetative thickness was an average of all concealment and visual obstruction measurements at each camera site and described as a percentage (0-100%).

Water accessibility may also influence mesopredator space use (Phillips et al. 2003, Horn et al. 2005) and was characterized in two ways: (1) the proportion of water within a 1.6 km radius (%), and; (2) the distance to nearest surface water (km). Proportion of water within a 1.6 km radius and distance to nearest surface water were not strongly correlated ($r = -0.38$). I chose a radius of 1.6 km for these covariates because it reflects functional-management units for this study area, being fragmented 2.6 km^2 gridded sections within a township for agricultural and livestock purposes. I believed that the proportion of available nesting cover (i.e., quality grassland patches) and water on the landscape were likely a result of various land use practices (e.g., impacts from agricultural practices used on cultivated cropland or livestock), which thereby may have influenced how mesopredators used the landscape.

Multi-season and multi-species occupancy models for four species

We used Program MARK (White and Burnham 1999) to fit occupancy models. Dynamic occupancy models allowed for evaluation of the influence of within-season and site-specific covariates on patterns of detection (p) and occupancy (ψ) for each mesopredator species (coyote, striped skunk, raccoon, American badger [*Taxidea taxus*]) individually. Dynamic occupancy models assumed site independence and population closure for each year (MacKenzie et al. 2003). I used a sequential-by-sub-model approach for model selection using Akaike's Information Criterion (AIC) for competing models (ΔAIC ≤ 2), starting with modeling for p and then for ψ. Morin et al. (2020) found that a sequential-by-sub-model approach for model selection was sufficient for determining the top dynamic occupancy model when compared to secondary-candidate-set and build-up strategies. I fit all possible combinations of predictors for p while maintaining the global structure for ψ and the null structure for colonization (γ) and extinction (ε). If models failed to convergence, I fit all possible combinations of predictors for p while maintaining the null structure for ψ. I then calculated cumulative model weights; covariates absent from the best-supported model but present in competing models for p (ΔAIC ≤ 2.0) were carried over when running sub-models for ψ if variable weights were >0.5. Next, using the most-parsimonious structure for p, and null structures for γ and ε, I fit all-possible-combinations of predictors for ψ to identify the most-supported occupancy structure. Variable weights were again calculated to confirm consistency and presence of important covariates in the most-supported model. During both sub-model processes, models that had convergence issues or contained uninformative parameters were removed from the set of competitive models (Leroux et al. 2019). I did not include covariates for γ and ε due to data scarcity. Survey effect (i.e., within-year variation) was not included in striped skunk and American badger models due to data scarcity. Otherwise, the same environmental variables were used for each species because I fit all possible combinations of predictors for *p* and ψ, suggesting that each species' most-supported model would include important variables relating to their differing ecologies.

We conducted a second analysis to elucidate how co-occurrence between coyotes and other nest predators differed as a result of the lethal removal management of coyotes. Because the counties in our study area differed in coyote removal management, I used co-occurrence modeling to evaluate the influence coyote occurrence on a nest predator guild's probabilities of detection and occupancy. I suspected differences in coyote detection and occupancy between the two counties could drive differences in co-occurrence relationships with a nest predator guild. Co-occurrence models compare relationships between a dominant and subordinate entity and assumes occupancy of the dominant entity is independent of the occurrence of the subordinate entity. All covariates in the most supported dynamic occupancy model for each individual entity were incorporated into each of the 12 co-occurrence models which were structured differently to represent the various potential co-occurrence relationships between the dominant and subordinate entities (Richmond et al. 2010, Yackulic et al. 2014). Therefore, I conducted a single-species dynamic occupancy model (MacKenzie et al. 2003) for the nest predator guild (any nest predator species, expect for coyotes, known to commonly depredate waterfowl nests were included) and coyotes, respectively and separately for each county, using the sequential-by-sub-model approach using the global structure, fitting all-possible-combinations as described above (Appendix S1.3).

Using the most-supported coyote and nest predator guild dynamic models for each county, I built 12 co-occurrence models for each county respectively that evaluated the conditional p and ψ of the nest predator guild. Thus, because the effect of the covariate county cannot be evaluated in a co-occurrence analysis, to understand differences in relationships among mesopredator community members between counties, the analyses needed to be spatially separated. Additionally, because there was variation in coyote occupancy throughout the study area (i.e., coyote occupancy < 1), I were able to apply a co-occurrence analysis with coyotes as the dominant entity. Survey effect as well as colonization and extinction covariates were not included in these single-species dynamic models due to convergence issues when including them with co-occurrence models.

Finally, I analyzed multi-species occupancy models (Rota et al. 2016) for 2018 and 2020, in accordance with the assumption of annual closure, to better understand what covariates influence the co-occupancy of mesopredator species (coyote, striped skunk, and raccoon) when nest densities differed between years. This third analysis employs a bidirectional evaluation of interspecific interactions compared to uni-directional co-occurrence modeling (Richmond et al. 2010, Yackulic et al. 2014). Further, because dynamic occupancy modeling utilizes detection and occupancy estimates from the first closed survey to derive detection and occupancy estimates of subsequent closed surveys (MacKenzie et al. 2003), and because dynamic multi-species occupancy models are still evolving and require large datasets (MacKenzie et al. 2021), I evaluated co-occupancy in separate years. With the intention of comparing two years with different nest densities, I excluded 2019 because it had fewer camera-trap data compared to 2020. I used the dynamic, single-species occupancy models for 2018 and ran single-season, single-species occupancy models (MacKenzie et al. 2002) for each mesopredator species in 2020 (Appendix S1.4). The covariates present in the most-supported models for each species were used when fitting all-possible-combinations of predictors for co-occupancy including that species, respective to year. All models with multiple covariates for an interactive species parameter failed to converge, and therefore I were restricted to models with a single variable per interactive species parameter due to data limitations. For all models, I maintained null structures for the individual species portions of p and ψ because influence of survey- and site- specific covariates on patterns of each species' detection and occupancy was already evaluated in our dynamic single-species models. In all of our analyses, 95% confidence intervals of parameter estimates that did not include zero were considered meaningful, and those that included zero were considered to have no effect on detection or occupancy.

RESULTS

Field sampling and landscape characteristics

Sampling effort included 216 sites in 2018, 202 in 2019 and 215 in 2020 after accounting for occasional camera malfunctions and changes in site accessibility. Total trap nights were 3,542 in 2018, 3,141 in 2019, and 3,733 in 2020. A camera was active for an average of 17.0 ± 7.0 (SD) days in 2018, 15.5 ± 6.3 (SD) days in 2019, and 17.4 ± 4.5 (SD) days in 2020. I collected 4,290,710 photos, of which 5,405 were of a predator species and were classified as 1,165 independent detections: 24% were coyote, 59% were raccoon, 7% were striped skunk, 3% were American badger, 2% were domestic cat (*Felis catus*), 1% were opossum (*Didelphis virginiana*), <1% were red fox (*Vulpes vulpes*), and

<1% were long-tailed weasel (*Mustela frenata*; Table 1.1). Landscape characteristics were summarized to describe the study area (Table 1.2).

Index of nest density

We searched 57 km^2, 36 km^2, and 36 km^2, and monitored 109, 684, and 935 nests in 2018, 2019, and 2020 respectively. The most supported generalized linear Poisson model included township, year, and week. Because the number of marked nests varied by township and search period, using an index of nest density as a temporally varying covariate in the detection structure of models was supported. There were 4.9 times more marked nests in Alden, 1.9 times more marked nests in Saratoga, and 1.5 times more marked nests in Fairview compared to that in Bryant. There were 9.7 more marked nests in 2020 and 7.3 times more marked nests in 2019 compared to 2018. Nest density peaked during weeks 4-6 (Appendix S1.1).

Small mammal index of abundance

We captured 189 individuals during 2018, 143 individuals in 2019, and 187 individuals in 2020. Average capture success (i.e., catch/effort) was 7.5% ± 1.1% in 2018, 3.1% ± 0.7% in 2019, and 4.4% ± 1.3% in 2020. Our most-supported generalized linear Poisson model failed to detect differences in index of abundance between townships in any year. Index of abundance of small mammals was greater in 2018 and 2020 compared to 2019, and 1.8-2.6 times greater in surveys conducted in later months compared to earlier months (Appendix S1.2).

Patterns of occupancy and detection

The best-approximating model of coyote detection and occupancy probabilities was 0.587 AIC units from the next best model and captured 1.3% (n = 4,096) of the model weight. This model included variables accounting for moon illumination and surveys in the detection structure, and county and crop in the occupancy structure. Detection probability of coyotes was positively associated to moon illumination (β = 0.185, SE = 0.094, 95% CI = 0.001, 0.368), varied across surveys but not years (Fig. 1.1), and decreased with subsequent surveys (survey 1: 0.455 ± 0.092, survey 2: 0.254 ± 0.090, survey 3: 0.217 ± 0.078, survey 4: 0.175 ± 0.060). Occupancy probability of coyote was greater in the control county (0.702 ± 0.079) than the treatment county (0.396 ± 0.098; Fig. 1.2), and 2.3 times greater when soybeans dominated the landscape compared to corn (95% CI = 1.0-5.1; Appendix S1.5).

The best-approximating model of striped skunk detection and occupancy probabilities was 0.914 AIC units from the next best model and captured 2.2% (*n* = 1,970) of the model weight. This model included variables accounting for average daily low temperature and small mammal index of abundance in the detection structure, and county, proportion of grassland, and distance to nearest surface water in the occupancy structure. Detection probability of striped skunks increased as index of small mammal abundance increased (β = 0.040, SE = 0.014, 95% CI = 0.013, 0.066) and was 0.7 times (95% CI: 0.6-0.7) greater with each 1 ºC increase in daily minimum temperature. Occupancy probability of striped skunks increased 9.6 times greater (95% CI: 9.3-9.9) for each 10% increase in grassland and increased 30.5 times per every kilometer closer to nearest surface water (95% CI = 1.0-974.6; Appendix S1.5).

The best-approximating model of raccoon detection and occupancy probabilities was 0.185 AIC units from the next best model and captured 3.7% (*n* = 4,096) of the model weight. This model included variables accounting for year and survey in the detection structure, and county, distance to active farmstead, vegetative thickness, proportion of grassland, crop, and proportion of surface water in the occupancy structure. Detection probability of raccoons varied across surveys and years (Fig. 1.1), and overall decreased through time with subsequent surveys (survey 1: 0.422 ± 0.078, survey 2: 0.373 ± 0.094, survey 3: 0.197 ± 0.064, survey 4: 0.332 ± 0.063) and years (2018: 0.412 ± 0.056, 2019: 0.204 ± 0.081, 2020: 0.377 ± 0.087). Occupancy probability of raccoons was greater in the treatment county (0.908 ± 0.076) than the control county (0.695 ± 0.106; Fig. 1.2) and was 6.8 times greater when the dominant crop was soybeans (95% CI = 1.8- 25.6). Occupancy probability of raccoons decreased 4.8 times for every 10 km farther away from nearest active farmstead (95% CI = 2.4-9.5), 9.4 times for each 10% increase in percent of proportion of grassland (95% CI = 9.0-9.9), and 6.9 times for each 10% increase in percent of proportion of surface water (95% CI = 5.3-9.0; Appendix S1.5).

The best-approximating model of American badger detection and occupancy probabilities was 0.303 AIC units from the next best model and captured 11.7% (*n* = 19) of the model weight. This model included variables accounting for average daily low temperature and small mammal index of abundance in the detection structure, and county in the occupancy structure. Detection probability of American badger increased 0.6 times for each 1 degree increase of temperature (95% CI = 0.6-0.7; Appendix S1.5).

Coyote and nest predator guild co-occurrence

In the treatment county, detection probabilities decreased with subsequent years (2018: 0.35 ± 0.08, 2019: 0.19 ± 0.08, 2020: 0.05 ± 0.03) for coyotes. Alternatively, detection probabilities were greater in 2020 (0.56 ± 0.08) compared to 2018 (0.38 ± 0.05) and 2019 (0.32 ± 0.10) for the nest predator guild. Occupancy probability of the nest predator guild was 8.4 times greater for each 10% decrease in percent proportion of surface water (95% CI = 7.0-9.3; Appendix S1.3). Occupancy probability of coyotes (0.237 ± 0.060) was lower than that of the nest predator guild (0.614 ± 0.096). In the treatment county, the most-supported dynamic co-occurrence model described equal detection and occupancy probabilities of a member of the nest predator guild regardless of coyote presence or absence (Appendix S1.5). However, the probability of detection for coyotes in the treatment county was higher when a member of the nest predator guild was absent in the 2018 ($p^A = 0.383 \pm 0.167$, $r^A = 0.360 \pm 0.097$), but not in subsequent years (2019: $p^A = 0.047 \pm 0.040$, $r^A = 0.266 \pm 0.120$; 2020: $p^A = 0.011 \pm 0.011$, $r^A = 0.060 \pm 0.039$).

In the control county, detection probability of coyotes or the nest predator guild did not vary by year. Instead, both the index of nest density and index of small mammal abundance were positively associated with detection and similar for both coyotes (β = 0.074, SE = 0.015, 95% CI = 0.045, 0.104) and the nest predator guild (β = 0.072, SE = 0.020, 95% CI = 0.032, 0.111). Index of nest density was positively associated with detection probability of coyotes (β = 0.006, SE = 0.002, 95% CI = 0.002, 0.011). Detection probability was 0.6 times less for coyotes (95% CI = 0.5-0.6) and the nest predator guild (95% CI = 0.5-0.6) with each increase in degree C of temperature in the control county. Occupancy probability of coyotes was 0.3 times greater for every meter closer to the nearest surface water (95% CI = <0.1-79.3). Occupancy probability of the nest predator guild was 14.8 times greater with each 10% decrease in percent proportion of surface water (95% CI = 10.5-20.8), and 1.0 times greater with every increase in percent vegetative thickness (95% CI = 1.0-1.1; Appendix S1.3). Occupancy probability of coyotes (0.780 ± 0.094) was similar to that of the nest predator guild (0.684 ± 0.074). In the control county, the most-supported dynamic co-occurrence model described equal occupancy probabilities of a member of the nest predator guild regardless of coyote presence or absence, as well as equal detection probabilities of coyotes regardless of the presence or absence of a member of the nest predator guild and for a member of the nest predator guild regardless of if a coyote was detected or not (Appendix S1.5). However, the probability of detection for a member of the nest predator guild in the control county was higher when a coyote was also present ($p^B = 0.086 \pm 0.050$, $r^{BA} = 0.479 \pm 0.061$; $p^B = 0.052 \pm 0.043$, $r^{BA} = 0.509 \pm 0.079$; $p^B = 0.056 \pm 0.038$, $r^{BA} = 0.499 \pm 0.075$).

Multi-species occupancy

The most-supported 2018 multi-species occupancy model included county for co-occurrence of coyote and striped skunk, proportion of surface water for co-occurrence of coyote and raccoon, and crop for the co-occurrence of striped skunk and raccoon. The co-occurrence of coyote and striped skunk was 0.2 times greater in the control county than in the treatment county (95% CI = 0.1-0.3), and the co-occurrence of striped skunk and raccoon was 4.3 times greater when soybeans were the dominant crop (95% CI = 1.8-10.4; Appendix S1.5). The average probability that a site was unoccupied (i.e., all three species were absent) was 0.321 (SE = 0.052, 95% CI = 0.228, 0.430). The average probability that a site was occupied by all three species was 0.257 (SE = 0.044, 95% CI = 0.180, 0.352; Fig. 1.3). In 2018, the probability of all three species being present at a site was 13.0 times greater than in 2020. Additionally, the probability a site was unoccupied by all three species was only 1.2 times greater than if a site was occupied by all three species.

The most-supported multi-species occupancy model for 2020 included the nearest distance to abandoned farmstead for co-occurrence of coyote and striped skunk, and the null structure for co-occurrence of coyote and raccoon and for striped skunk and raccoon (perhaps due to data scarcity). The co-occurrence of coyote and striped skunk was 2.6 times greater for every km away from the nearest distance to abandoned farmstead (95% CI = 1.0-6.5; Appendix S1.5). The average probability that a site was unoccupied (i.e., all three species were absent) was 0.615 (SE = 0.047, 95% CI = 0.520, 0.702; Fig. 1.3). The average probability that a site was occupied by all three species was 0.020 (SE = 0.017, 95% CI = 0.004, 0.103; Fig. 1.3). The probability a site was unoccupied by all three species was 31.1 times greater than if a site was occupied by all three species, whereas the probability a site was occupied by any combination of 1-2 mesopredator species was 0.6-6.8 times greater than if a site was occupied by all three species.

DISCUSSION

Mesopredator space use is influenced by the configuration and size of habitat patches on the landscape, and evaluating these relationships is critical to understanding predator-prey interactions (Palmer 1988, Stenseth and Lidicker 1992, Phillips et al. 2004). However, predator space use may also be influenced by other factors, including prey distribution and intraguild interactions (Estes 1996, Crooks and Soule 1999, Gehrt and Clark 2003). I infer from our results that differences in seasonal and annual food availability and variation in lethal coyote management between two counties that were similar in landscape configuration yielded different predator community compositions and space use dynamics that may have indirectly influenced nest survival of ground-nesting ducks. Further, our results demonstrated that camera trapping methods were effective in evaluating predator community composition of generalist species. Although radio-marking is a superior method to evaluate fine-scale spatiotemporal space use and movements due to its innately higher resolution, the number of interspecific interactions between marked individuals would likely be low. If detection rates are high and enough data is collected to fit co-occurrence and multi-species occupancy models, this approach may be applied to other species and systems to understand interspecific interactions.

Mesopredators in our study moved more within their home ranges when food resources were low, both within years and among years. Variation in detection probability has been used to interpret changes in abundance (MacKenzie and Kendall 2002, Crosby and Elmore 2019) or movement (Royle and Nichols 2003, Popescu et al. 2014, Stewart et al. 2018), changes in the abundance or movement of other species (Lonsinger et al. 2017, Steenweg et al. 2019), and changes in resource availability (Carbone and Gittleman 2002, Mackenzie 2006, Rich et al. 2017). Higher detection probabilities of raccoons and striped skunks coincided with greater average step lengths, home range sizes, and daily movement rates of radio-marked individuals (Chapter 2), suggesting that variation in detection probabilities partially resulted from variation in movements. Moreover, detection rates were greatest at times of lower food resources (e.g., early spring and in 2018), suggesting that mesopredators modified movements (increased movement rates and home range size) to find adequate resources when they were in shorter supply (Greenwood 1981, Sovada et al. 1995, Greenwood et al. 1999, Sovada et al. 2000, Phillips et al. 2003, 2004, Azevedo et al. 2006, Haffele et al. 2013).

Our support for this relationship is primarily indirect, with variation in detection rates related more to intra- and inter-annual variation in food resources rather than directly by indices of nest density or small mammal abundance. The lack of direct support may suggest that additional food sources other than eggs and small mammals (e.g., insects, vegetation, crops), or perhaps the cumulative amount of available and accessible food resources, resulted in varying movement rates and resulting detection probabilities (Rivest and Bergernon 1981, Kaufmann 1982, Greenwood et al. 1999, Conover 1998, Humberg et al. 2007).

Our results indicated that mesopredators aggregated in response to reduced resource densities, potentially leading to negative interactions and associations among species (Holt and Polis 1997, Verdy and Amarasekare 2010). Differences in rates of coexistence between 2018 and 2020 (low vs. high relative resource abundance) support the prediction of foraging theory (Stephens and Krebs 1986) that niche separation allows for coexistence of similar species during times of resource scarcity (Schoener 1974, Lesmeister et al. 2015, Davis et al. 2018, Santos et al. 2019). For example, co-occurrence of coyotes and striped skunks was maintained in the treatment county, where occurrence of coyotes was lower, perhaps by the sharing of resources between fewer individuals and at farther distances from abandoned farmsteads, a common refuge and denning site for mesopredators that may result in competition. Indeed, many generalist mesopredator species use anthropogenic resources (Lesmeister et al. 2015, Chitwood et al. 2020, Amspacher et al. 2021), as demonstrated in the most-supported dynamic single-species model for raccoons which may have allowed for segregation and decreased potential conflicts with other mesopredators. Although niche segregation may only partially explain coexistence (Garrott et al. 1993, Litvaitis and Villafuerta 1995, Prange and Gehrt 2004, Cove et al. 2012), I believe sympatric members of the mesopredator community expressed different activity or space use patterns (Chapter 2) when resources were limited and/or unevenly distributed across the landscape (Schoener 1974, Heithaus 2001, Azevedo et al. 2006, Gehrt and Prange 2007, Holt and Huxel 2007, Lesmeister et al. 2015, Davis et al. 2018).

Differences in community composition between counties with and without lethal coyote management supported predictions of the mesopredator release hypothesis (Rogers and Caro 1998, Crooks and Soulé 1999, Henke and Bryant 1999, Kamler and Gipson 2004). This hypothesis predicts that if densities of the dominant predator are reduced (e.g., annual lethal removal of coyotes), densities or movements of subordinate predators should increase since the need to alter behaviors to avoid negative interactions is comparatively minimized (Estes 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). I found that the probability of coyote occupancy decreased 4 times, while probability of raccoon occupancy increased 4 times and occupancy probability of nest predators collectively (other than coyotes) increased 9 times compared to that of the control county. These findings suggest that coyote removal was likely successful at reducing coyote densities in the area and increased densities of other medopredators, as predicted by the mesopredator release hypothesis.

Reduced densities of the dominant predator also are predicted to result in more extensive movements of subordinate predators. In addition to variation in detection probability linking with movement rates (Royle and Nichols 2003, Popescu et al. 2014, Stewart et al. 2018), movement rates and home range sizes are often positively associated

(Johnson et al. 1980, Borger et al. 2008, Van Moorter et al. 2015). Activity patterns and behaviors that I documented in our study lend further support to the mesopredator release hypothesis. First, average home range size of raccoons was 3.0 times larger in the treatment county compared to the control county (Chapter 2). Our co-occurrence models for the treatment county revealed that detection probabilities of coyotes decreased with subsequent years while the trend in detection probabilities of the nest predator guild was overall increasing, which may indicate that members of that guild, predominantly raccoons, became more active as coyote movements declined (Arjo and Pletscher 1999, Heithaus 2001, Janssen et al. 2007, Choh et al. 2010). A temporal covariate was not present in the most-supported detection models for coyotes or a nest predator guild in the control county, indicating that detection probabilities did not change appreciably over time. Additionally, in our co-occurrence model for the treatment county, detection probability of a member of the nest predator guild was not different when a coyote was present or absent nor if a coyote was detected or not, potentially implying the density, distribution, and/or movements of coyotes did not influence those of other mesopredators (Prugh et al. 2009, Brashares et al. 2010, Elmhagen et al. 2010). Although occupancy probability of a member of the nest predator guild for either county was not different when a coyote was present or absent, I speculate that the coyote removal management in the treatment county influenced the behaviors of raccoons and other sympatric nest predator guild members (Gehrt and Clark 2003, Gehrt and Prange 2007, Prange and Gehrt 2007, Chitwood et al. 2020).

Although I believe the simultaneous predator-prey data collection and analyses revealed trends and relationships that have implications for managing duck nest survival, I recognize that complex models require large datasets (MacKenzie et al. 2020). For example, our three seasons of data prevented us from exploring variation in rates of extinction and colonization as well as potential time-lagged increases in the mesopredator occupancy or detection probabilities with respect to variation in environmental conditions (Ringelman et al. 2018). Few detections of striped skunk and American badger resulted in our inability to consider within- or among-year effects, and it is only in these scenarios when temporal covariates caused model convergence issues where biological detection covariates (i.e., index of nest density and small mammal abundance) were present in most-supported models. The most-supported dynamic single-species model for all species never included temporal (i.e., year and survey) and biological detection covariates simultaneously, and I speculate that an interaction existed among predictor variables of food resources and temporal covariates. Perhaps temporal covariates are more indicative of other biological processes, such as mating and reproduction than food resource availability. Temporal covariates may also reflect resources I did not measure or suggest that the indices of food resources I used did not well represent food availability. Due to low detections of striped skunk and American badgers, I recognize that the nest predator guild data is dominated by detections of raccoons, but reflects accurate proportionality and abundances of members of the mesopredator community. I believe it is reasonable to speculate on striped skunk behavior despite low detections rates because other studies have documented similar trends; thus, it seems reasonable these patterns may be similar to those of raccoons given that both species are synanthropic (Gehrt and Prange 2007, Lesmeister et al. 2015, Amspacher et al. 2021). However, such logic cannot be applied to American badgers when detection rates are low, because this species is unique in the mesopredator community. Thus, research specifically investigating badger relationships with other potential competitors is warranted. With more data on members of the nest predator guild, the potential for competitive exclusion by coyotes should be investigated independently based on the different life-histories of these species.

Interactions among the mesopredator community and their relationships with the environment help to explain why environmental conditions and landscape characteristics covary with duck nest survival. Some of the hypothesized explanations of factors influencing duck nest survival were supported by the trends I observed. For example, striped skunks and raccoons were negatively associated with proportion of grassland in a 1,600-m radius, suggesting they occurred more commonly in small patches of habitat and closer to edges. These two factors have been associated with lower survival of nests placed experimentally in these types of locations (Ray 2000, Phillips et al. 2003, Horn et al. 2005). Our results may also inform the relationship between density or thickness of vegetation and duck nest survival. For example, although heavier cover may better conceal duck nests (Schranck 1972, Clark and Shutler 1999), occupancy probability of the nest predator guild in our study was positively associated with vegetative thickness. Therefore, both predator and prey appear to select locations with similar characteristics. I found that nests may be a greater risk of depredation earlier in the nesting season when available food resources (i.e., nest density and small mammal abundance indices) were low and mesopredator activity was elevated; this result contradicts the observed temporal relationships reported by Ringelman et al. (2018) in regards to prey search-image development over time. Further, the coyote removal management that occurred in our treatment county may have negatively influenced rates of game bird nest survival by supporting differences in nest predator composition and space use (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003). By evaluating detection and occupancy probabilities of mesopredators in relation to variation in nest density and landscape characteristics, as well as in comparison to those of other members of the mesopredator community, waterfowl nest survival and productivity models may describe predator-prey relationships in the PPR more thoroughly.

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DATA ACCESSIBILITY STATEMENT

Data will be archived and deposited in Dryad’s publicly accessible repository.

CONFLICT OF INTEREST

The authors have declared that no competing interested exist.

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TABLES

Table 1.1. Number of carnivore photos identified as and naïve occupancy (ψ) for coyote (*Canis latrans*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and American badger (*Taxidea taxus*) across 216 sites in 2018, 202 sites in 2019, and 215 sites in 2020, in eastern South Dakota, USA.

Year	**Number of carnivore photos**				**Naïve ψ**			
	Coyote	Raccoon	Striped skunk	Badger	Coyote	Raccoon	Striped skunk	Badger
2018	177	454	39	27	0.33	0.47	0.13	0.11
2019	56	48	15	5	0.18	0.13	0.04	0.02
2020	51	180	28	8	0.15	0.19	0.06	0.02
Total	284	682	82	40				

Table 1.2. Summary of occupancy covariates.

Covariate	**Range**	**Mean**	**SD**
Distance to nearest active farmstead (km)	<0.1–3.5	1.3	0.8
Distance to nearest abandoned farmstead (km)	0–5.4	1.8	1.1
Distance to nearest surface water (m)	0–634	152.6	138.2
Vegetative thickness (%)	0–100	18. 8	17.3
Proportion of grassland within a 1600-m radius (%)	5–76	57.0	2.0
Proportion of water within a 1600-m radius (%)	0–32	6.9	3.0

FIGURES

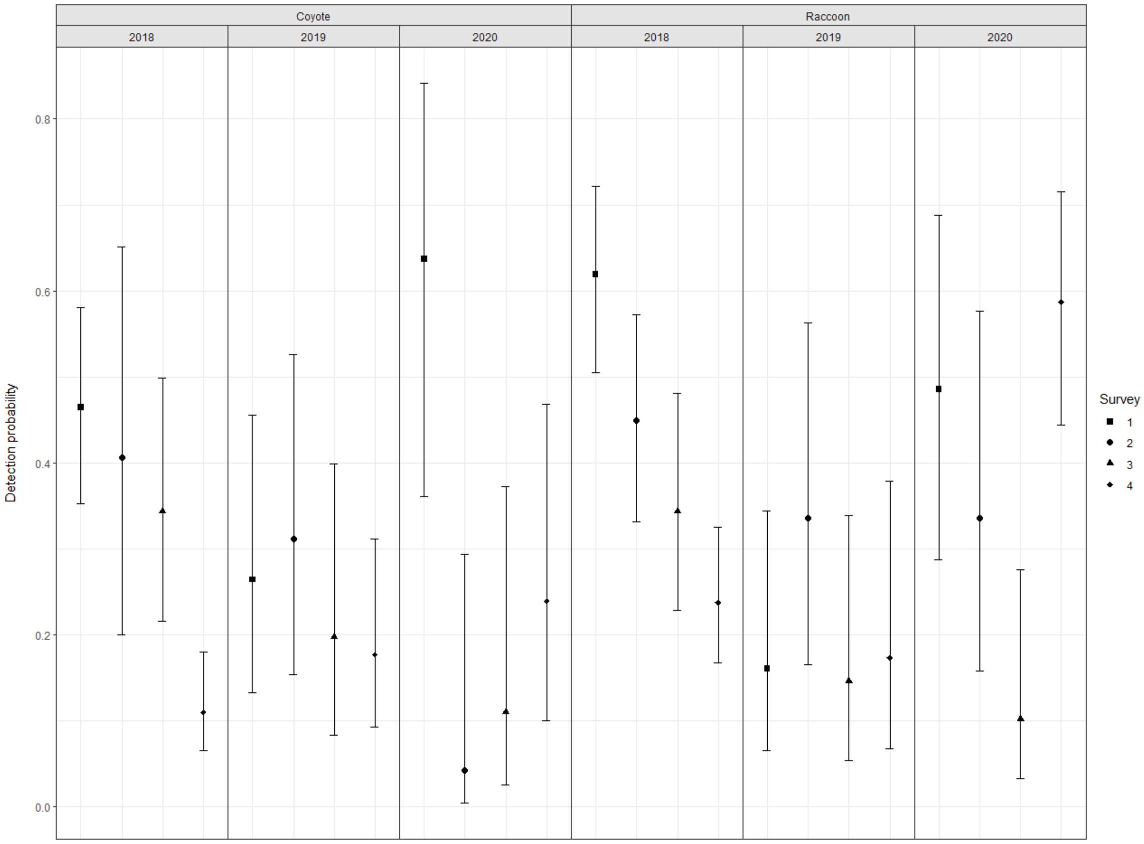

Figure 1.1. Detection probabilities of coyotes (*Canis latrans*) and raccoons (*Procyon lotor*) as a function of year and survey in eastern South Dakota, USA, 2018-2020. Detection probability, with 95% confidence intervals, is plotted based on the best model structure for each species using the mean values for other numeric covariates. Survey 1 = May weeks 1-3, survey 2 = May week 4 and June weeks 1-2, survey 3 = June weeks 3-4 and July week 1, survey 4 = July weeks 2-4.

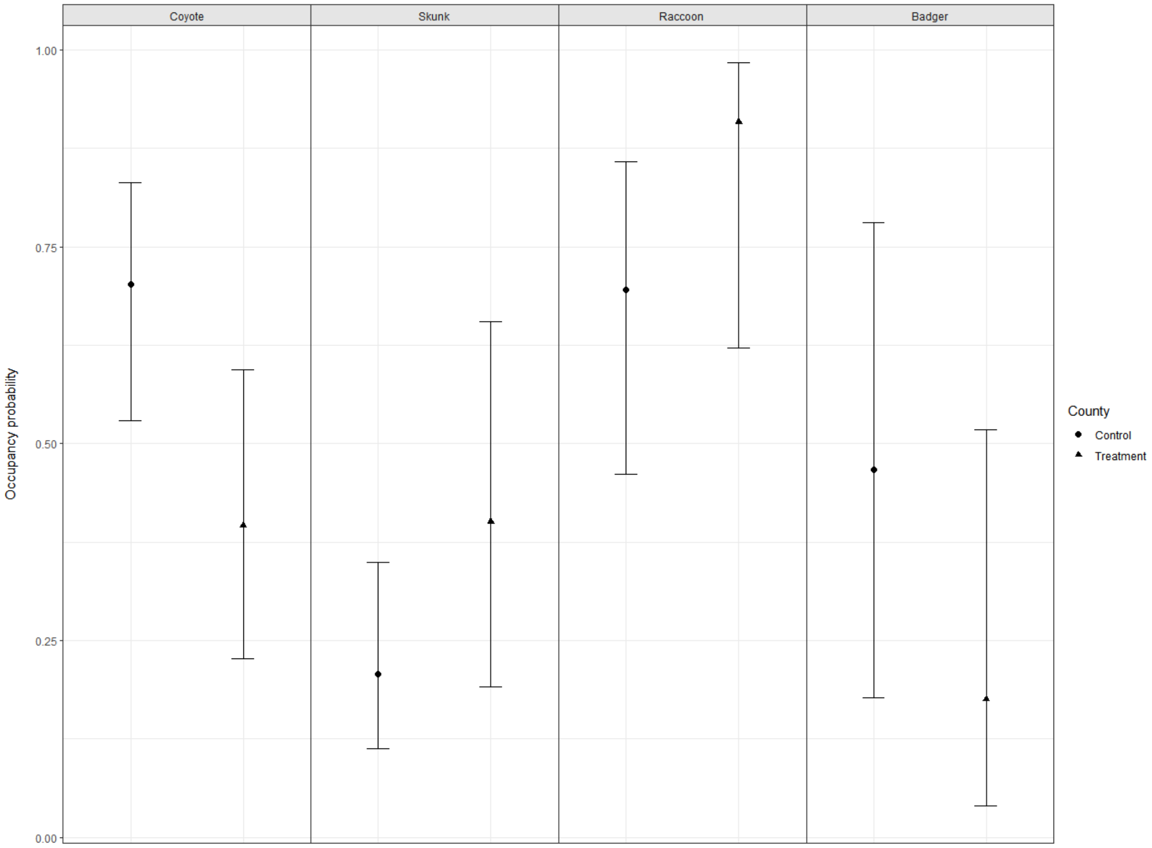

Figure 1.2. Occupancy probabilities of coyotes (*Canis latrans*), striped skunk (*Mephitis mephitis*), raccoons (*Procyon lotor*), and American badger (*Taxidea taxus*) as a function of county in eastern South Dakota, USA, 2018-2020. Occupancy probability, with 95% confidence intervals, is plotted based on the best model structure for each species using the mean values for other numeric covariates.

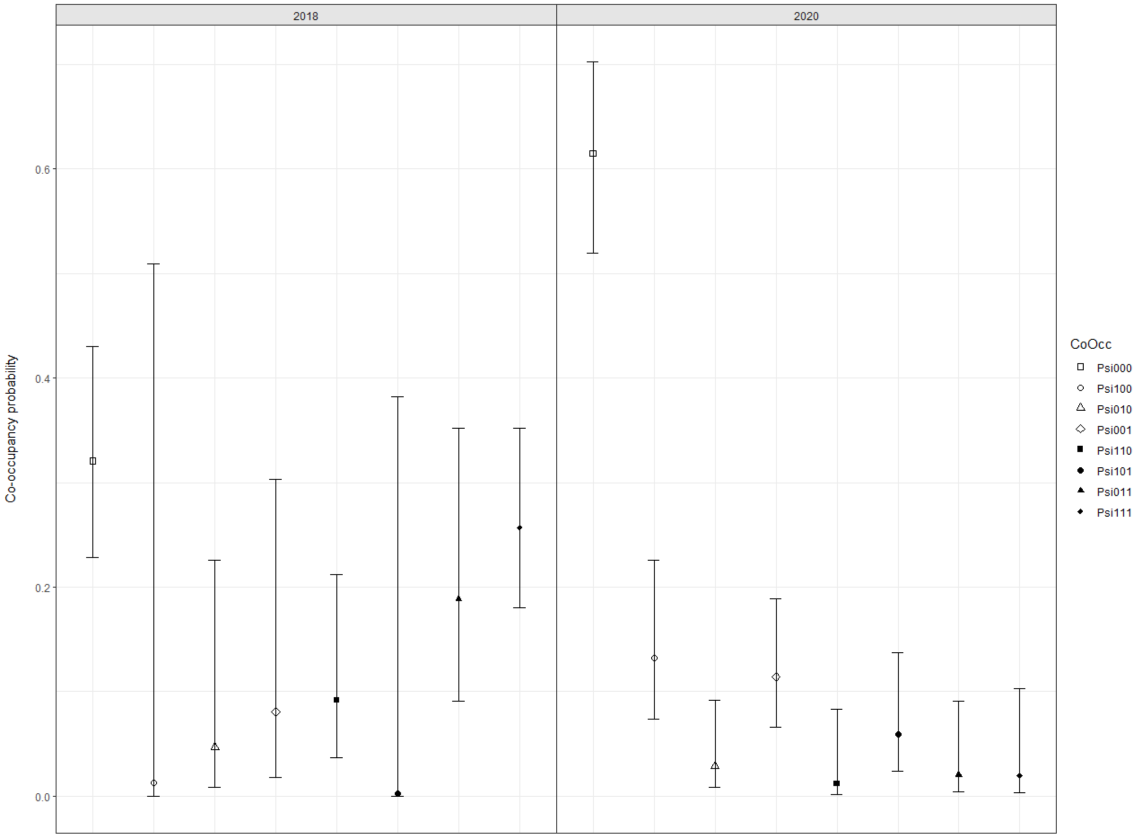

Figure 1.3. Co-occurrence occupancy probabilities of coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*) in eastern South Dakota, USA, 2018 and 2020. Co-occurrence occupancy probabilities, with 95% confidence intervals, are plotted based on the best model structure for each species using the mean values for other numeric covariates. Psi000 = when all species are absent, Psi100= when only coyotes are present, Psi010 = when only striped skunks are present, Psi001 = when only raccoons are present, Psi110 = when coyotes and striped skunks are both present but raccoons are absent, Psi101 = when coyotes and raccoons are both present but striped skunks are absent, Psi011 = when striped skunks and raccoons are both present but coyotes are absent, Psi111 = when all species are present.

Appendix S1.1: Summarized and model selection results for the covariate relative nest density index in eastern South Dakota, USA, 2018-2020.

Table S1.1.1. Summary of nests found by species. Green-wing teal (*Anas carolinensis*) and redhead (*Aythya americana*) nests were <10 for any year and thereby not included below.

Year	**Number of nests found**				
	Blue-wing teal (*Anas discors*)	Gadwall (*Mareca strepera*)	Mallard (*Anas platyrhynchos*)	Northern pintail (*Anas acuta*)	Northern shoveler (*Spatula clypeata*)
2018	25	22	22	36	4
2019	329	39	19	170	118
2020	494	87	52	196	99
Total	848	148	93	402	221

Table S1.1.2. The nest density index covariate in the detection structure of occupancy models by township.

Week	Alden	Bryant	Fairview	Saratoga
	2018			
1	15	7	15	16
2	23	13	17	16
3	27	14	18	18
4	24	15	14	22
5	21	16	10	22
6	12	8	6	20
7	3	2	3	10
8	2	1	1	3
9	2	1	1	0
10	0	0	0	0
11	0	0	0	0
12	0	0	0	0
	2019			
1	34	20	52	48
2	62	32	79	61
3	91	37	105	75
4	127	50	129	75
5	137	65	142	81
6	148	64	139	88
7	148	55	114	85
8	122	36	79	71
9	93	23	49	66
10	51	7	27	52
11	10	1	7	24
12	2	0	3	14
	2020			
1	152	51	61	89
2	211	74	79	121
3	238	96	87	156
4	239	102	84	176
5	220	112	64	182
6	159	100	42	185
7	98	83	34	172
8	65	62	24	152

9	32	33	19	98
10	13	19	14	64
11	4	4	5	18
12	1	1	1	7

Table S1.1.3. Model selection results of relative support for generalized linear Poisson models with number of active identified nests as the response variable in eastern South Dakota, 2018-2020.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**LL**
~ Township+Year+Week	17	1856.660	0.000	1.000	-908.900
~Year+Week	14	2524.620	667.960	0.000	-1246.680
~ Township+Year	6	4944.980	3088.320	0.000	-2466.190
~Township+Week	15	5488.400	3631.740	0.000	-2727.330
~Year	3	5614.100	3757.440	0.000	-2803.970
~Week	12	6156.600	4299.940	0.000	-3065.110
~Township	4	8577.510	6720.850	0.000	-4284.610
~1	2	9198.850	7342.190	0.000	-4597.380

Table S1.1.4. Model parameter estimates for the best supported generalized linear Poisson models with number of active identified nests as the response variable across 129 km^2 dragged fields in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Z value**	**P value**
Intercept	2.359	0.065	36.048	<0.001
Bryant	-0.766	0.035	-21.966	<0.001
Fairview	-0.535	0.032	-16.549	<0.001
Saratoga	-0.124	0.029	-4.337	<0.001
2019	1.987	0.052	38.236	<0.001
2020	2.277	0.051	44.485	<0.001
Week 2	0.342	0.055	6.180	<0.001
Week3	0.541	0.053	10.180	<0.001
Week4	0.634	0.052	12.134	<0.001
Week 5	0.652	0.052	12.514	<0.001
Week 6	0.548	0.053	10.330	<0.001
Week 7	0.365	0.055	6.644	<0.001
Week 8	0.097	0.058	1.661	0.099
Week 9	-0.295	0.065	-4.558	<0.001
Week 10	-0.843	0.077	-10.944	<0.001
Week 11	-2.037	0.124	-16.374	<0.001
Week 12	-2.961	0.190	-15.546	<0.001

Table S1.1.5. Parametric bootstrapped estimates of index of nest density from a generalized linear Poisson model in eastern South Dakota, 2018-2020. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk (alpha=0.05). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

Category 1	**Category 2**	**Index of abundance confidence intervals of bootstrap estimates**
Township		
Alden	Bryant	(4.86,6.71)*>
Alden	Fairview	(3.71,5.24)*>
Alden	Saratoga	(0.67,1.84)*>
Bryant	Fairview	(-1.75,-0.86)*<
Bryant	Saratoga	(-5.25,-3.74)*<
Fairview	Saratoga	(-3.81,-2.59)*<
Year		
2018	2019	(-30.84,-21.34)*<
2018	2020	(-100.98,-83.77)*<
2019	2020	(-73.53,-60.22)*<
Week		
1	2	(-5.78,-2.84)*<
1	3	(-9.35,-5.99)*<
1	4	(-11.36,-7.73)*<

1	5	(-11.58,-8.14)*<
1	6	(-9.52,-6.02)*<
1	7	(-6.08,-3.24)*<
1	8	(-2.38,0.27)
1	9	(1.51,4.04)*>
1	10	(4.83,7.37)*>
1	11	(7.95,10.69)*>
1	12	(8.76,11.55)*>
2	3	(-4.95,-1.85)*<
2	4	(-6.87,-3.37)*<
2	5	(-7.32,-3.90)*<
2	6	(-5.26,-1.88)*<
2	7	(-1.86,1.00)
2	8	(1.75,4.75) *>
2	9	(5.45,8.54) *>
2	10	(8.82,12.04) *>
2	11	(11.77,15.41) *>
2	12	(12.57,16.39) *>
3	4	(-3.56,-0.07)*<
3	5	(-3.82,-0.51)*<
3	6	(-1.85,1.45)
3	7	(1.27,4.54)*>

3	8	(4.97,8.12)*>
3	9	(8.65,12.07)*>
3	10	(11.85,12.57)*>
3	11	(14.85,19.06)*>
3	12	(15.62,19.94)*>
4	5	(-2.06,1.35)*<
4	6	(-0.03,3.31)
4	7	(3.08,6.52)*>
4	8	(6.64,10.16)*>
4	9	(10.30,14.12)*>
4	10	(13.38,17.66)*>
4	11	(16.41,21.09)*>
4	12	(17.16,22.01)*>
5	6	(0.26,3.66)*>
5	7	(3.41,6.68)*>
5	8	(7.09,10.38)*>
5	9	(10.66,14.31)*>
5	10	(13.89,17.89)*>
5	11	(16.78,21.38)*>
5	12	(17.48,22.32)*>
6	7	(1.51,4.75)*>
6	8	(5.07,8.45)*>
6	9	(8.65,12.27)*>

6	10	(11.86,15.91)*>
6	11	(14.81,19.20)*>
6	12	(15.61,20.15)*>
7	8	(2.27,5.14)*>
7	9	(6.02,8.83)*>
7	10	(9.24,12.34)*>
7	11	(12.26,15.79)*>
7	12	(13.00,16.64)*>
8	9	(2.49,5.18)*>
8	10	(5.82,8.46)*>
8	11	(8.87,11.83)*>
8	12	(9.63,12.74)*>
9	10	(2.29,4.40)*>
9	11	(5.47,7.58)*>
9	12	(6.31,8.42)*>
10	11	(2.47,3.96)*>
10	12	(3.27,4.76)*>
11	12	(0.46,1.24)*>

Appendix S1.2: Summarized data and model selection results for the covariate small mammal index of abundance in eastern South Dakota, USA, 2018-2020.

Table S1.2.1. Summary of small mammals found by species. House mouse (*Mus musculus*), meadow jumping mouse (*Zapus hudsonicus*), least weasel (*Mustela nivalis*), brown rats (*Rattus norgevicus*), harvest mice (*Reithrodontomys* spp.), least shrews (*Cyptotis parva*), and northern short-tailed shrews (*Blarina brevicauda*) were <10 for any year and thereby not included below.

Year	**Number of individuals found**			
	Deer mouse (*Permoyscus* spp.)	Thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*)	Vole (*Microtus* spp.)	Northern grasshopper mouse (*Anas acuta*)
2018	134	28	14	0
2019	92	18	12	13
2020	71	6	126	0
Total	297	52	152	13

Table S1.2.2. The small mammal index abundance covariate in the detection structure of occupancy models by township.

Small Mammal Survey	**1**	**2**	**3**
Camera-trap Week	1-4	5-8	9-12
	2018		
Alden	26	13	16
Bryant	8	25	20
Fairview	13	21	29
Saratoga	10	8	8
	2019		
Alden	4	14	5
Bryant	4	3	11
Fairview	2	18	20
Saratoga	11	4	13
	2020		
Alden	3	7	29
Bryant	3	40	22
Fairview	6	4	18
Saratoga	2	7	46

Table S1.2.3. Model selection results of relative support for generalized linear Poisson models with number of unique individuals as the response variable in eastern South Dakota, 2018-2020.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	w_i	**LL**
~Year+Survey	5	340.630	0.000	0.940	0.940
~Township+Year+Survey	8	346.170	5.540	0.060	1.000
~Survey	3	365.640	25.010	0.000	1.000
~Township+Survey	6	370.000	29.370	0.000	1.000
~Year	3	401.540	60.910	0.000	1.000
~Township+Year	6	405.890	65.260	0.000	1.000
~1	1	427.160	86.530	0.000	1.000
~Township	4	430.550	89.920	0.000	1.000

Table S1.2.4. Model parameter estimates for the best supported generalized linear Poisson models with number of unique individuals as the response variable across 36 80m^2 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Z value**	**P value**
Intercept	2.218	0.118	18.803	<0.001
2019	-0.592	0.119	-4.958	<0.001
2020	-0.052	0.102	-0.510	0.610
Survey 2	0.578	0.130	4.438	<0.001
Survey 3	0.946	0.123	7.703	<0.001

Table S1.2.5. Parametric bootstrapped estimates of index of abundance of small mammals from a generalized linear Poisson model in eastern South Dakota, 2018-2020. Statistical significance with a 95% confidence interval estimated by bootstrapping is noted by an asterisk (alpha=0.05). The symbol > indicates the item in the column on the left is significantly greater than the item in the column on the right. The symbol < indicates the item in the column on the right is significantly greater than the item in the column on the left.

Category 1	**Category 2**	**Index of abundance confidence intervals of bootstrap estimates**
Township		
Alden	Bryant	(-3.80,0.95)
Alden	Fairview	(-3.51,1.21)
Alden	Saratoga	(-1.61,2.82)
Bryant	Fairview	(-1.98,2.79)
Bryant	Saratoga	(-0.26,4.44)
Fairview	Saratoga	(-0.65,4.00)
Year		
2018	2019	(2.31,5.82)*>
2018	2020	(-1.19,2.27)
2019	2020	(-5.28,-1.86)*<
Survey		
1	2	(-10.33,-3.76)*<
1	3	(-18.33,-9.72)*<
2	3	(-11.06,-3.31)*<

Appendix S1.3: Results of dynamic, single-species models for ψ and *p* for coyotes and a nest predator guild, separated by two counties, in eastern South Dakota, USA, 2020.

Table S1.3.1. Explanatory variables used in candidate occupancy models to evaluate variation in estimated detection and occupancy of mesopredators in eastern South Dakota, during May–July, 2018–2020.

Variable Type	**Variable**	**Description**
Detection	moon	Moon illumination at the start of the survey (scale 0-4, 0 = new moon)
	temp	Average low temperature (°C), by county
	precip	Sum of precipitation (cm), by county
	sm	Small mammal index of abundance/80m^2, by township
	nest	Index of nest density, by township
	yr	Year effect (1,2)
	sess	Session effect (y1s1, y1s2, y1S1.3, y2s1…etc)
Occupancy	county	Faulk or Hand
	year1	Camera deployed in 2018, binary
	year2	Camera deployed in 2019, binary
	d_act	Distance to nearest active farm (km)
	d_abn	Distance to nearest active farm (km)
	vt	Vegetative thickness (%)
	p_g	Proportion of grassland, 1600m radius
	crop	Dominant crop, 1600m radius (soybean or corn)
	p_w	Proportion of surface water, 1600m radius
	d_w	Distance to nearest surface water (m)

Table S1.3.2. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for coyote detection (*p*) and occupancy (ψ) structures in Faulk County, South Dakota. Total number of models in the set *n* = 512.

Model	**K**	**AIC*c***	**ΔAIC*c***	***w*i**	**LL**
p(yr) ψ(.)	6	406.305	0.000	0.040	394.034
p(yr+moon) ψ(.)	7	406.417	0.112	0.038	392.054
p(yr) ψ(vt)	7	407.569	1.264	0.021	393.206
p(yr+moon) ψ(vt)	8	407.655	1.350	0.020	391.187
p(yr) ψ(p_w)	7	407.697	1.392	0.020	393.334
p(yr+moon) ψ(d_act)	8	407.751	1.446	0.019	391.284
p(yr) ψ(d_act)	7	407.777	1.472	0.019	393.415
p(yr) ψ(d_w)	7	407.937	1.633	0.018	393.575
p(yr+moon) ψ(p_w)	8	407.954	1.649	0.018	391.486
p(yr+moon) ψ(d_w)	8	408.131	1.826	0.016	391.664
p(yr) ψ(crop)	7	408.232	1.927	0.015	393.869
p(yr+moon) ψ(crop)	8	408.290	1.985	0.015	391.822

Table S1.3.3. Model parameter estimates for the best supported dynamic model for coyote detection (*p*) and occupancy (ψ) structures across 116 sites in Faulk County, South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	-2.994	0.633	-4.234	-1.753
yr1 effect	2.379	0.737	0.935	3.824
yr2 effect	1.523	0.521	0.502	2.545
ψ intercept	-1.167	0.329	-1.812	-0.522
ε intercept	0.044	1.065	-2.043	2.131
γ intercept	-0.552	0.678	-1.880	0.776

Table S1.3.4. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for coyote detection (*p*) and occupancy (ψ) structures in Hand County, South Dakota. Total number of models in the set *n* = 8192.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(sm+temp+nest) ψ(p_w+d_w)	9	704.847	0.000	0.004	686.249
p(sm+precip+temp+nest) ψ(p_w+d_w)	10	705.927	1.088	0.003	685.203
p(sm+temp+nest+moon) ψ(p_w+d_w)	10	706.099	1.260	0.002	685.375
p(sm+temp+nest) ψ(p_w+d_w+d_act)	10	706.476	1.637	0.002	685.753
p(sm+temp+nest) ψ(p_w+d_w+p_g)	10	706.795	1.956	0.001	686.072

Table S1.3.5. Model parameter estimates for the best supported dynamic model for coyote detection (*p*) and occupancy (ψ) structures across 112 sites in Hand County, South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	-0.222	0.768	-1.726	1.283
sm	0.074	0.015	0.045	0.104
nest	0.006	0.002	0.002	0.011
temp	-0.040	0.012	-0.063	-0.018
ψ intercept	-1.581	1.037	-3.615	0.452
p_w	0.472	0.258	-0.034	0.977
d_w	5.562	2.918	0.158	11.281
ε intercept	-1.012	0.475	-1.942	-0.082
γ intercept	-2.978	2.548	-7.971	2.016

Table S1.3.6. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for a nest predator guild detection (*p*) and occupancy (ψ) structures in Faulk County, South Dakota. Total number of models in the set *n* = 8192.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	***w*$_i$**	**LL**
p(precip+temp+yr) ψ(p_g+crop+p_w)	11	768.559	0.000	0.041	745.693
p(nest+precip+temp+yr) ψ(p_g+crop+p_w)	12	768.591	0.032	0.041	743.565
p(nest+temp+yr) ψ(p_g+crop+p_w)	11	769.151	0.592	0.037	746.285
p(temp+yr) ψ(p_g+crop+p_w)	10	769.415	0.857	0.037	748.696
p(precip) ψ(p_g+crop+p_w)	8	769.613	1.054	0.033	753.145
p(precip+yr) ψ(p_g+crop+p_w)	10	769.881	1.323	0.031	749.162
p(yr) ψ(p_g+crop+p_w)	9	770.030	1.471	0.031	751.443
p(nest+precip+temp+yr) ψ(p_g+p_w)	11	770.286	1.727	0.030	747.420
p(sm+nest+precip+temp+yr) ψ(p_g+crop+p_w)	13	770.419	1.860	0.030	743.218
p(.)ψ(p_g+crop+p_w)	7	770.420	1.861	0.029	756.057
p(nest+precip) ψ(p_g+crop+p_w)	9	770.540	1.981	0.026	751.953

Table S1.3.7. Model parameter estimates for the best supported dynamic model for a nest predator guild detection (*p*) and occupancy (ψ) structures across 116 sites in Faulk County, South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	4.038	2.140	-0.155	8.232
precip	-0.279	0.164	-0.599	0.042
temp	-0.057	0.031	-0.117	0.004
yr1 effect	-0.423	0.346	-1.102	0.256
yr2 effect	-1.299	0.492	-2.264	-0.335
ψ intercept	2.194	1.319	-0.391	4.778
p_g	-0.040	0.021	-0.082	0.195
crop	1.168	0.602	-0.011	2.347
p_w	-0.176	0.089	-0.350	-0.072
ε intercept	1.082	0.403	0.293	1.871
γ intercept	-0.639	0.276	-1.181	-0.098

Table S1.3.8. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for a nest predator guild detection (*p*) and occupancy (ψ) structures in Hand County, South Dakota. Total number of models in the set *n* = 4096.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(sm+temp+nest) ψ(vt+p_g+crop+p_w)	11	654.686	0.000	0.028	631.814
p(sm+temp) ψ(vt+p_g+crop+p_w)	10	655.303	0.617	0.021	634.579
p(sm+temp+nest) ψ(d_act+vt+p_g+crop+p_w)	12	655.807	1.121	0.016	630.774
p(sm+temp+moon) ψ(vt+p_g+crop+p_w)	11	655.840	1.155	0.016	632.969
p(sm+temp+nest+moon) ψ(vt+p_g+crop+p_w)	12	655.935	1.250	0.015	630.902
p(sm+temp) ψ(d_act+vt+p_g+crop+p_w)	11	656.456	1.771	0.012	633.585
p(sm+temp+nest) ψ(vt+p_g+p_w)	10	656.554	1.868	0.011	635.830

Table S1.3.9. Model parameter estimates for the best supported dynamic model for a nest predator guild detection (*p*) and occupancy (ψ) structures across 112 sites in Hand County, South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	1.422	0.983	-0.505	3.350
sm	0.072	0.020	0.032	0.111
nest	0.005	0.003	-0.001	0.011
temp	-0.052	0.015	-0.081	-0.023
ψ intercept	2.522	1.473	-0.364	5.408
vt	0.045	0.016	0.014	0.076
p_g	-0.043	0.023	-0.089	0.195
crop	1.181	0.632	-0.056	2.419
p_w	-0.393	0.174	-0.733	-0.053
ε intercept	0.915	0.432	0.069	1.762
γ intercept	-1.485	0.346	-2.164	-0.806

Appendix S1.4: Results of single-season, single-species models for ψ and p for three mesocarnivore species in eastern South Dakota, USA, 2020.

Table S1.4.1. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for coyote (*Canis latrans*) detection (*p*) and occupancy (ψ) structures. Total number of models in the set *n* = 4093.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(sm+temp+moon) ψ(d_abn+d_w)	7	249.617	0.000	0.025	235.076
p(temp+moon) ψ(d_abn+d_w)	6	249.972	0.355	0.021	237.568
p(temp+moon) ψ(d_abn+d_w+p_w)	7	250.833	1.216	0.013	236.292
p(sm+temp+moon) ψ(d_abn+d_w+p_w)	8	250.925	1.308	0.013	234.226
p(sm+temp+moon) ψ(d_abn+d_w+vt)	8	250.928	1.311	0.013	234.229
p(sm+temp+moon) ψ(d_abn+d_w+crop)	8	250.955	1.338	0.013	234.256
p(temp+moon) ψ(d_abn+d_w+crop)	7	251.085	1.468	0.012	236.544
p(sm+temp+moon) ψ(d_abn+p_g+d_w)	8	251.148	1.531	0.012	234.449
p(sm+temp+moon) ψ(global)	14	251.211	1.594	0.011	221.111
p(temp+moon) ψ(d_abn+d_w+vt)	7	251.346	1.728	0.010	236.804
p(temp+moon) ψ(d_abn+p_g+d_w)	7	251.419	1.802	0.010	236.878

Table S1.4.2. Model parameter estimates for the best supported dynamic model for coyote (*Canis latrans*) detection (*p*) and occupancy (ψ) structures across 215 sites in eastern South Dakota, United States, 2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	8.946	3.018	3.031	14.862
sm	0.032	0.020	-0.008	0.071
temp	-0.177	0.047	-0.269	-0.085
moon	-0.883	0.398	-1.664	-0.102
ψ intercept	-6.542	3.335	-13.078	-0.006
d_abn	2.419	1.389	-0.303	5.142
d_w	47.010	26.229	4.399	98.419

Table S1.4.3. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for striped skunk (*Mephitis mephitis*) detection (*p*) and occupancy (ψ) structures. Total number of models in the set $n = 8193$.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(temp+sm+precip) ψ(p_g)	6	132.077	0.000	0.049	119.673
p(moon+temp+sm) ψ(p_g)	6	132.366	0.289	0.042	119.962
p(temp+sm+precip) ψ(county+p_g+d_abn)	8	132.529	0.452	0.039	115.830
p(moon+temp+sm+precip) ψ(p_g)	7	132.616	0.539	0.037	118.075
p(temp+sm+precip) ψ(p_g+crop)	7	132.828	0.751	0.033	118.287
p(moon+temp+sm) ψ(p_g+county)	7	132.896	0.819	0.032	118.355
p(temp+sm+precip) ψ(p_g+d_w)	7	132.931	0.854	0.032	118.390
p(moon+temp+sm) ψ(p_g+crop)	7	133.164	1.087	0.028	118.623
p(temp+sm+precip) ψ(county+crop)	7	133.174	1.097	0.028	118.633
p(temp+sm+precip) ψ(p_g+county+crop+d_abn)	9	133.183	1.106	0.028	114.305
p(moon+temp+sm) ψ(p_g+county+d_abn)	8	133.239	1.162	0.027	116.540
p(moon+temp+sm) ψ(p_g+county+d_w)	8	133.241	1.164	0.027	116.542
p(moon+temp+sm) ψ(p_g+d_w)	7	133.264	1.187	0.027	118.723
p(moon+temp+sm+precip) ψ(p_g+crop)	8	133.292	1.215	0.026	116.593
p(temp+sm+precip) ψ(p_g+vt)	7	133.346	1.269	0.026	118.805
p(temp+sm+precip)	8	133.383	1.306	0.025	116.684

ψ(county+p_g+d_act)					
p(moon+temp+sm+precip) ψ(county+p_w+d_abn+d_w)	10	133.441	1.364	0.025	112.363
p(moon+temp+sm) ψ(p_g+d_abn)	7	133.457	1.380	0.024	118.916
p(moon+temp+sm+precip) ψ(p_g+d_w)	8	133.471	1.394	0.024	116.772
p(moon+temp+sm+precip) ψ(p_g+county+d_abn)	9	133.548	1.471	0.023	114.670
p(moon+temp+sm+precip) ψ(p_g+county+crop)	9	133.568	1.491	0.023	114.690
p(temp+sm+precip) ψ(p_g+d_act)	7	133.595	1.518	0.023	119.054
p(temp+sm+precip) ψ(p_g+county+d_abn+d_w+p_g)	10	133.612	1.535	0.023	112.533
p(moon+temp+sm+precip) ψ(county+d_abn+crop+p_w+d_w)	11	133.648	1.577	0.022	110.348
p(moon+temp+sm) ψ(p_g+county+crop)	8	133.690	1.613	0.022	116.991
p(temp+sm+precip) ψ(county)	6	133.704	1.627	0.022	121.300
p(temp+sm+precip) ψ(p_g+county+d_abn+p_w+crop+d_w)	11	133.790	1.713	0.021	110.490
p(moon+temp+sm) ψ(p_g+vt)	7	133.935	1.858	0.019	119.394
p(temp+sm+precip) ψ(p_g+county+vt)	8	133.992	1.915	0.019	117.293
p(moon+temp+sm+precip) ψ(p_g+vt)	8	134.039	1.962	0.018	117.340

Table S1.4.4. Model parameter estimates for the best supported dynamic model for striped skunk (*Mephitis mephitis*) detection (*p*) and occupancy (ψ) structures across 215 sites in eastern South Dakota, United States, 2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	13.77	5.84	2.31	25.22
sm	0.10	0.04	0.02	0.17
precip	-2.00	0.94	-3.83	-0.17
temp	-0.26	0.10	-0.46	-0.06
ψ intercept	-0.49	0.81	-2.08	1.10
p_g	-0.047	0.022	-0.091	-0.003

Table S1.4.5. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for raccoon (*Procyon lotor*) detection (p) and occupancy (ψ) structures. Total number of models in the set n = 2049.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(.) ψ(county)	3	370.167	0.00	0.015	364.053
p(temp+nest) ψ(county)	5	370.309	0.142	0.014	360.022
p(.) ψ(county+vt)	4	371.343	1.176	0.008	363.153
p(.) ψ(county+crop)	4	371.373	1.206	0.008	363.182
p(.) ψ(county+p_g)	4	371.456	1.289	0.008	363.265
p(temp+nest) ψ(county+vt)	6	371.473	1.306	0.008	359.070
p(temp+nest) ψ(county+crop)	6	371.511	1.344	0.008	359.107
p(temp) ψ(county)	4	371.539	1.372	0.008	363.349
p(temp+nest) ψ(county+p_g)	6	371.654	1.487	0.007	359.250
p(nest) ψ(county)	4	371.799	1.632	0.007	363.609
p(.) ψ(county+d_abn)	4	372.085	1.918	0.006	363.895
p(.) ψ(county+d_w)	4	372.124	1.957	0.006	363.934

Table S1.4.6. Model parameter estimates for the best supported dynamic model for raccoon (*Procyon lotor*) detection (*p*) and occupancy (ψ) structures across 215 sites in eastern South Dakota, United States, 2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	-0.01	0.22	-0.45	0.42
ψ intercept	-1.73	0.30	-2.32	-1.15
county	0.82	0.38	0.09	1.56

Appendix S1.5: Model selection results of competing (<2 ΔAICc) dynamic single-species occupancy models for coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and American badger (*Taxidea taxus*), co-occurrence occupancy models for coyotes and a nest predator guild, and competing (<2 ΔAICc) multi-species occupancy models including coyote, striped skunk, and raccoon, in eastern South Dakota, USA, 2018-2020, used to identify the most supported model parameterization and evaluate the important of environmental covariates on the probabilities of detection (*p*) and occupancy (ψ), using program MARK (White and Burnham 1999).

Table S1.5.1. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for coyote (*Canis latrans*) detection (*p*) and occupancy (ψ) structures. Total number of models in the set *n* = 4096.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	***w*$_i$**	**LL**
p(moon+sess) ψ(county+crop)	16	1108.271	0.000	0.013	1075.386
p(moon+sess) ψ(county+crop+p_w)	17	1108.857	0.587	0.010	1073.861
p(moon+sess) ψ(county+crop+d_act)	17	1109.275	1.004	0.008	1074.278
p(moon+temp+sess) ψ(county+crop)	17	1109.668	1.397	0.006	1074.671
p(moon+sess) ψ(county+crop+d_act+p_w)	18	1109.669	1.398	0.006	1072.553
p(temp+sess) ψ(county+crop)	16	1109.814	1.544	0.006	1076.930
p(moon+sess) ψ(county+crop+p_w+d_w)	18	1109.937	1.666	0.006	1072.821
p(sess) ψ(county+crop)	15	1110.111	1.840	0.005	1079.331
p(moon+sess) ψ(county)	15	1110.224	1.953	0.005	1079.445

Table S1.5.2. Model parameter estimates for the best supported dynamic model for coyote (*Canis latrans*) detection (*p*) and occupancy (ψ) structures across 228 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	-2.417	0.338	-3.079	-1.755
moon	0.185	0.094	0.001	0.368
y1s1	1.961	0.359	1.258	2.663
y1s2	1.550	0.532	0.508	2.593
y1s3	1.225	0.435	0.373	2.077
y2s1	0.564	0.429	-0.277	1.405
y2s2	0.969	0.457	0.074	1.864
y2s3	0.188	0.494	-0.781	1.157
y3s1	1.612	0.380	0.866	2.357
y3s2	-2.080	1.058	-4.154	-0.006
y3s3	-0.932	0.669	-2.243	0.379
ψ intercept	0.028	0.419	-0.792	0.849
county	-1.281	0.499	-2.259	-0.302
crop	0.830	0.410	0.025	1.634
ε intercept	-0.366	0.492	-1.331	0.598
γ intercept	-0.873	0.423	-1.702	-0.045

Table S1.5.3. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for striped skunk (*Mephitis mephitis*) detection (*p*) and occupancy (ψ) structures. Total number of models in the set *n* = 1970.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(temp+sm) ψ(county+p_g+d_w)	9	502.416	0.000	0.022	484.126
p(temp+sm) ψ(p_g+d_w)	8	503.330	0.914	0.014	487.099
p(temp+sm+precip) ψ(county+p_g+d_w)	10	503.751	1.336	0.011	483.397
p(temp+sm) ψ(county+p_g+d_w+crop)	10	503.799	1.383	0.011	483.445
p(temp+sm) ψ(county+p_g+d_w+d_abn)	10	503.802	1.387	0.011	483.448
p(temp+sm) ψ(county+p_g+d_w+vt)	10	504.341	1.925	0.008	483.986
p(temp+sm+precip) ψ(p_g+d_w)	9	504.341	1.926	0.008	486.052

Table S1.5.4. Model parameter estimates for the best supported dynamic model for striped skunk (*Mephitis mephitis*) detection (*p*) and occupancy (ψ) structures across 228 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	3.241	1.247	0.797	5.685
sm	0.040	0.014	0.013	0.066
temp	-0.091	0.022	-0.133	-0.048
ψ intercept	-0.321	0.853	-1.993	1.351
county	0.942	0.576	-0.187	2.071
p_g	-0.039	0.016	-0.070	-0.007
d_w	3.418	1.767	0.046	6.882
ε intercept	0.171	0.528	-0.863	1.205
γ intercept	-3.395	0.956	-5.268	-1.523

Table S1.5.5. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for raccoon (*Procyon lotor*) detection (p) and occupancy (ψ) structures. Total number of models in the set $n = 4096$.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(yr+sess) ψ(county+d_act+vt+p_g+crop+p_w)	21	1294.133	0.000	0.037	1250.619
p(yr+sess+temp) ψ(county+d_act+vt+p_g+crop+p_w)	22	1294.319	0.185	0.034	1248.657
p(yr+sess+nest) ψ(county+d_act+vt+p_g+crop+p_w)	22	1294.997	0.864	0.024	1249.336
p(yr+sess) ψ(county+d_act+vt+p_g+crop+p_w+d_abn)	22	1295.499	1.366	0.019	1249.837
p(yr+sess+temp+precip) ψ(county+d_act+vt+p_g+crop+p_w)	22	1295.506	1.373	0.019	1247.690
p(yr+sess+temp) ψ(county+d_act+vt+p_g+crop+p_w+d_abn)	23	1295.679	1.545	0.017	1247.863

Table S1.5.6. Model parameter estimates for the best supported dynamic model for raccoon (*Procyon lotor*) detection (p) and occupancy (ψ) structures across 228 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	0.350	0.293	-0.224	0.923
yr1 effect	-1.517	0.368	-2.238	-0.795
y1s1	1.654	0.323	1.021	2.287
y1s2	0.963	0.313	0.349	1.576
y1s3	0.521	0.346	-0.157	1.199
yr2 effect	-1.912	0.612	-3.112	-0.712
y2s1	-0.091	0.699	-1.462	1.279
y2s2	0.879	0.660	-0.415	2.172
y2s3	-0.204	0.720	-1.615	1.207
y3s1	-0.408	0.518	-1.423	0.606
y3s2	-1.033	0.576	-2.163	0.096
y3s3	-2.526	0.676	-3.851	-1.201
ψ intercept	3.552	1.544	0.526	6.579
county	1.470	0.735	0.029	2.911
d_act	-0.729	0.348	-1.411	-0.047
vt	0.028	0.010	0.007	0.048
p_g	-0.060	0.023	-0.105	-0.015
crop	1.910	0.679	0.580	3.241
p_w	-0.370	0.134	-0.633	-0.107

ε intercept	0.761	0.383	0.010	1.513
γ intercept	-1.075	0.260	-1.584	-0.565

Table S1.5.7. Model selection results of relative support of competing (<2 ΔAICc) dynamic models for American badger (*Taxidea taxus*) detection (p) and occupancy (ψ) structures. Total number of models in the set n = 19.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
p(temp+sm) ψ(county)	7	329.634	0.000	0.117	315.455
p(temp+sm) ψ(d_act)	7	329.937	0.303	0.100	315.758
p(temp+sm) ψ(.)	6	330.119	0.485	0.092	317.985
p(temp+sm) ψ(county+d_act)	8	330.524	0.889	0.075	314.292
p(temp+sm) ψ(county+p_w)	8	330.558	0.924	0.074	314.327
p(temp+sm) ψ(p_w)	7	330.786	1.152	0.066	316.607
p(temp+sm) ψ(crop+d_act)	8	331.070	1.436	0.057	314.839
p(temp+sm) ψ(county+vt)	8	331.119	1.485	0.056	314.888

Table S1.5.8. Model parameter estimates for the best supported dynamic model for American badger (*Taxidea taxus*) detection (*p*) and occupancy (ψ) structures across 228 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p intercept	0.624	1.355	-2.031	3.278
sm	0.028	0.022	-0.015	0.072
temp	-0.055	0.023	-0.099	-0.010
ψ intercept	-0.132	0.715	-1.533	1.268
county	-1.417	0.838	-3.061	0.226
ε intercept	2.108	1.204	-0.252	4.468
γ intercept	-2.535	0.645	-3.799	-1.271

Table S1.5.9. Model selection results of relative support of dynamic co-occurrence models involving coyote (*Canis latrans*) and a nest predator guild in Faulk County, South Dakota, USA. The structures for detection (*p*) and occupancy (ψ) were held constant at its most respective parsimonious structure.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
$p^A, r^A, p^B=r^{BA}=r^{Ba}, \psi^A, \psi^{BA}=\psi^{Ba}$	20	1164.607	0.000	0.915	1121.769
$p^A=r^A, p^B=r^{BA}=r^{Ba}, \psi^A, \psi^{BA}=\psi^{Ba}$	17	1169.359	4.752	0.085	1133.312

p^A = detection probability of coyotes given a member of the nest predator guild was absent, p^B = detection probability of a member of the nest predator guild given coyotes were absent, r^A = detection probability of coyotes given a member of the nest predator guild was also present, r^{BA} = detection probability of a member of the nest predator guild given coyotes were present and coyotes were detected, r^{Ba} = detection probability of a member of the nest predator guild given coyotes were present and coyotes were not detected, ψ^A = occupancy probability of coyotes, ψ^{BA} = occupancy probability of a member of the nest predator guild given coyotes were present, ψ^{Ba} = occupancy probability of a member of the nest predator guild given coyotes were absent.

Table S1.5.10. Model parameter estimates for the best supported dynamic co-occurrence model involving coyote (*Canis latrans*) and a nest predator guild detection (p) and occupancy (ψ) structures across 116 sites in Faulk County, South Dakota, United States, 2018-2020. ^{A} refers to the dominate species coyote and ^{B} refers to the subordinate nest predator guild.

Parameter	**β**	**SE**	**Lower**	**Upper**
p^A intercept	-4.469	1.004	-6.437	-2.500
p^A yr1 effect	3.992	1.225	1.591	6.393
p^A yr2 effect	1.463	1.133	-0.758	3.685
$p^B/r^{BA}/r^{Ba}$ intercept	3.885	2.136	-0.301	8.072
$p^B/r^{BA}/r^{Ba}$ precip	-0.264	0.165	-0.587	0.058
$p^B/r^{BA}/r^{Ba}$ temp	-0.054	0.031	-0.115	0.006
$p^B/r^{BA}/r^{Ba}$ yr1 effect	-0.424	0.353	-1.116	0.269
$p^B/r^{BA}/r^{Ba}$ yr2 effect	-1.241	0.494	-2.211	-0.272
r^A intercept	-2.744	0.687	-4.090	-1.397
r^A yr1 effect	2.170	0.807	0.589	3.752
r^A yr2 effect	1.731	0.687	0.383	3.078
ψ^A intercept	-1.275	0.326	-1.914	-0.635
ψ^{BA}/ψ^{Ba} intercept	2.179	1.361	-0.488	4.847
ψ^{BA}/ψ^{Ba} p_g	-0.040	0.022	-0.082	0.003
ψ^{BA}/ψ^{Ba} crop	1.158	0.607	-0.033	2.348
ψ^{BA}/ψ^{Ba} p_w	-0.176	0.092	-0.356	0.005
γ^A intercept	0.895	1.853	-2.737	4.527

γ^B intercept	-0.671	0.267	-1.194	-0.148
ε^A intercept	-0.876	1.678	-4.166	2.413
ε^B intercept	1.117	0.386	0.361	1.872

Table S1.5.11. Model selection results of relative support of dynamic co-occurrence models involving coyote (*Canis latrans*) and a nest predator guild in Hand County, South Dakota, USA. The structures for detection (*p*) and occupancy (ψ) were held constant at its most respective parsimonious structure.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**	**LL**
$p^A=r^A, p^B, r^{BA}=r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	24	1346.642	0.000	0.398	1294.504
$p^A=r^A, p^B, r^{BA}, r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	28	1348.097	1.455	0.192	1286.419
$p^A, r^A, p^B=r^{BA}=r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	24	1348.428	1.786	0.163	1296.290
$p^A, r^A, p^B, r^{BA}=r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	28	1348.638	1.996	0.147	1286.960
$p^A, r^A, p^B, r^{BA}, r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	32	1349.399	2.757	0.100	1277.910
$p^A=r^A, p^B=r^{BA}=r^{Ba}, \psi^\text{A}, \psi^\text{BA}=\psi^\text{Ba}$	20	1360.920	14.278	<0.001	1318.063

p^A = detection probability of coyotes given a member of the nest predator guild was absent, p^B = detection probability of a member of the nest predator guild given coyotes were absent, r^A = detection probability of coyotes given a member of the nest predator guild was also present, r^BA = detection probability of a member of the nest predator guild given coyotes were present and coyotes were detected, r^Ba = detection probability of a member of the nest predator guild given coyotes were present and coyotes were not detected, ψ^A = occupancy probability of coyotes, ψ^BA = occupancy probability of a member of the nest predator guild given coyotes were present, ψ^Ba = occupancy probability of a member of the nest predator guild given coyotes were absent.

Table S1.5.12. Model parameter estimates for the best supported dynamic co-occurrence model involving coyote (*Canis latrans*) and a nest predator guild detection (p) and occupancy (ψ) structures across 112 sites in Hand County, South Dakota, United States, 2018-2020. ^{A} refers to the dominate species coyote and ^{B} refers to the subordinate nest predator guild.

Parameter	**β**	**SE**	**Lower**	**Upper**
p^{A}/r^{A} intercept	0.208	0.812	-1.383	1.798
p^{A}/r^{A} sm	0.066	0.017	0.033	0.099
p^{A}/r^{A} nest	0.005	0.002	0.001	0.010
p^{A}/r^{A} temp	-0.041	0.012	-0.066	-0.017
p^{B} intercept	1.314	2.674	-3.928	6.556
p^{B} sm	0.163	0.058	0.049	0.277
p^{B} nest	0.003	0.009	-0.014	0.019
p^{B} temp	-0.115	0.048	-0.210	-0.021
r^{BA}/r^{Ba} intercept	1.309	1.168	-0.980	3.598
r^{BA}/r^{Ba} sm	0.069	0.023	0.024	0.114
r^{BA}/r^{Ba} nest	0.005	0.003	-0.001	0.012
r^{BA}/r^{Ba} temp	-0.044	0.018	-0.079	-0.010
ψ^{A} intercept	-0.378	0.833	-2.011	1.254
ψ^{A} p_w	0.180	0.167	-0.148	0.508
ψ^{A} d_w	2.353	1.992	-1.551	6.257
ψ^{BA}/ψ^{Ba} intercept	5.103	2.095	0.996	9.209
ψ^{BA}/ψ^{Ba} vt	0.050	0.021	0.010	0.091

ψ^{BA}/ψ^{Ba} p_g	-0.076	0.032	-0.138	-0.013
ψ^{BA}/ψ^{Ba} crop	1.717	0.805	0.140	3.294
ψ^{BA}/ψ^{Ba} p_w	-0.641	0.230	-1.092	-0.190
γ^{A} intercept	-0.904	0.461	-1.807	<0.001
γ^{B} intercept	-0.783	0.577	-1.914	0.349
ε^{A} intercept	0.070	0.499	-0.908	1.048
ε^{B} intercept	-0.124	0.583	-1.267	1.018

Table S1.5.13. Model selection results of relative support of competing (<2 ΔAICc) top multi-species occupancy (ψ) models for 2018. Total number of models in the set $n = 280$. ^{A} refers to parameters for coyote (*Canis latrans*),^{B} refers parameters for striped skunk (*Mephitis mephitis*), and ^{C} refers parameters for raccoon (*Procyon lotor*).

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	***w*i**	**LL**
$p^A(.)p^B(.)p^C(.)$ $\psi^A(.)\psi^B(.)\psi^C(.)\psi^{AB}(\text{county})\psi^{AC}(\text{p\_w})\psi^{BC}(\text{crop})$	12	1468.283	0.000	0.350	1442.746
$p^A(.)p^B(.)p^C(.)$ $\psi^A(.)\psi^B(.)\psi^C(.)\psi^{AB}(\text{county})\psi^{AC}(\text{p\_g})\psi^{BC}(\text{crop})$	12	1468.445	0.162	0.322	1442.908

Table S1.5.14. Model parameter estimates for the best supported multi-species occupancy (ψ) model for 2018 across 216 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p^{A} intercept	-0.266	0.167	-0.593	0.062
p^{B} intercept	-2.328	0.224	-2.767	-1.889
p^{C} intercept	-0.077	0.142	-0.355	0.202
ψ^{A} intercept	-3.242	2.203	-7.561	1.076
ψ^{B} intercept	-1.924	0.970	-3.826	-0.023
ψ^{C} intercept	-1.381	0.758	-2.867	0.105
ψ^{AB} intercept	4.873	2.598	-0.219	9.965
ψ^{AB} county	-1.919	0.421	-2.745	-1.093
ψ^{AC} intercept	-0.363	1.033	-2.388	1.662
ψ^{AC} p_w	0.002	0.002	-0.002	0.006
ψ^{BC} intercept	1.794	1.480	-1.106	4.694
ψ^{BC} crop	1.460	0.447	0.584	2.337

Table S1.5.15. Model selection results of relative support of competing (<2 ΔAICc) top multi-species occupancy (ψ) models for 2020. Total number of models in the set $n = 48$. ^{A} refers to parameters for coyote (*Canis latrans*),^{B} refers parameters for striped skunk (*Mephitis mephitis*), and ^{C} refers parameters for raccoon (*Procyon lotor*).

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**	**LL**
$p^{A}(.)p^{B}(.)p^{C}(.)$ $\psi^{A}(.)\psi^{B}(.)\psi^{C}(.)\psi^{AB}(d\_abn)\psi^{AC}(.)\psi^{BC}(.)$	10	803.713	0.000	0.171	782.635
$p^{A}(.)p^{B}(.)p^{C}(.)$ $\psi^{A}(.)\psi^{B}(.)\psi^{C}(.)\psi^{AB}(d\_abn)\psi^{AC}(d\_abn)\psi^{BC}(.)$	11	805.300	1.586	0.140	781.999
$p^{A}(.)p^{B}(.)p^{C}(.)$ $\psi^{A}(.)\psi^{B}(.)\psi^{C}(.)\psi^{AB}(d\_abn)\psi^{AC}(county)\psi^{BC}(.)$	11	805.654	1.941	0.140	782.354

Table S1.5.16. Model parameter estimates for the best supported multi-species occupancy (ψ) model for 2020 across 215 sites in eastern South Dakota, United States, 2018-2020.

Parameter	**β**	**SE**	**Lower**	**Upper**
p^A intercept	-0.961	0.317	-1.583	-0.340
p^B intercept	-1.053	0.538	-2.106	0.001
p^C intercept	-0.023	0.226	-0.466	0.419
ψ^A intercept	-1.538	0.343	-2.210	-0.867
ψ^B intercept	-3.065	0.626	-4.293	-1.838
ψ^C intercept	-1.686	0.288	-2.250	-1.122
ψ^{AB} intercept	0.642	1.178	-1.667	2.951
ψ^{AB} d_abn	0.947	0.474	0.017	1.876
ψ^{AC} intercept	0.876	0.581	-0.263	2.014
ψ^{BC} intercept	1.335	0.795	-0.223	2.893

Comparing spatiotemporal influence of factors on mesopredator space use and movements

ABSTRACT

Mesopredator space use and movements have been hypothesized as a primary mechanism to explain variation in duck nest survival. Therefore, understanding spatial and temporal variation in mesopredators habitat selection and movement behaviors can provide valuable insight for understanding interactions between mesopredators and upland duck nests. I used integrated step-selection functions to quantify spatiotemporal variation in resource selection and movements of 4 mesopredator species in relation to habitat features in Faulk and Hand Counties, eastern South Dakota, United States from 2018–2020. One location has had ongoing annual coyote (*Canis latrans*) removal (i.e., the treatment county) for the last 30 years, whereas no annual coyote removal has occurred in the other (i.e., the control county). I found evidence of behavior changes of increased time spent in an area and more thorough searching by striped skunks, suggesting potential prey-switching and indicating elevated risk to nests. Additionally, spatiotemporal segregation of similar space use patterns by sympatric mesopredator species of landscape characteristics associated with waterfowl nest site selection suggested differences in ecological niches that allowed for coexistence. Such direct species overlap of space use was mostly observed during the post-nesting period (i.e., July 16-Nov. 15), when food would have been most abundant. Lastly, raccoons and striped skunks in the treatment county demonstrated more expansive space use compared to their conspecifics in the control county. The variation in coyote densities across the study area created differences in community composition that resulted in a disparity of smaller mesopredator space use varying from potential avoidance of negative interactions with coyotes and minimize a predation risk effect, or lack thereof (i.e., mesopredator release). I did not observe changes in movement behavior in American badgers with respect to coyote suppression activities, which, based on their space use of patch centers and specialist ecology, could impact nest survival more than previously documented. As one of the first studies to quantify home range, resource selection, and movement of mesopredators in relation to landscape characteristics that are most impactful to duck nest survival in the PPR, I have demonstrated a contemporary way to understand spatiotemporal variation of space use within the predator community.

KEY WORDS Integrated step-selection functions, mesopredators, movement, resource selection, South Dakota

The Prairie Pothole Region (PPR) of North America was historically a mosaic of wetlands and grasslands that supported high densities of breeding waterfowl (Anatidae; Reynolds 2000). Past and ongoing conversion of native grassland to cultivated cropland and drainage of wetlands in the PPR have created a fragmented landscape, yet the area remains critical to breeding ducks, which require both landscape components to successfully reproduce (Reynolds and Shaffer 2007, Wong et al. 2012, Bartzen et al. 2017, Lark 2020). Nest survival is the most influential factor affecting duck population dynamics (Ricklefs 1969, Martin 1995, Hoekman 2002) and depredation is the major cause of waterfowl nest failure (54-85%; Klett et al. 1988, Sargeant and Raveling 1992). Many species of various taxa consume waterfowl eggs, but medium-sized mammalian predators (hereafter, mesopredators) have the greatest impact on nest survival (Sovada et al. 2000, Phillips et al. 2003, 2004).

Understanding spatiotemporal variation in nest survival and the relative impact of duck nest depredation requires information on mesopredator space use and movements, which are influenced by spatial configuration of habitat patches (Palmer 1988, Stenseth and Lidicker 1992, Phillips et al. 2004). The few studies in the PPR that have quantified mesopredator space use (Kamler and Gipson 2003, Phillips et al. 2003, Crimmins et al. 2015) indirectly linked prairie fragmentation with declines in duck production (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007, Amundson et al. 2012). For example, duck nest survival was greater in areas with 45-55% grassland than areas with 15-20% grassland (Horn et al. 2005), potentially because of closer proximities to patch edges (including wetland edges) where mesopredators preferentially search for prey (Crabtree et al. 1989, Kantrud 1993, Clark and Shutler 1999, Ray 2000, Sovada et al. 2000). Additionally, other studies revealed that nest survival was positively correlated with the proportion of perennial grassland on the landscape (Reynolds 2001, Stephens et al. 2005), suggesting that predator foraging efficiency became diluted as patch size increased (Phillips et al. 2003, Horn et al. 2005). Many mesocarnivore species are generalists and have relatively large home ranges (Sargeant and Warner 1972, Greenwood et al. 1997, Kamler and Gipson 2003, Chronert 2007), which allows them to evaluate variation in prey density and develop seasonal and density-dependent foraging dynamics (Schmidt and Whelan 1999). For example, mesopredators may change their space use behaviors in response to prey density and search for specific prey once they have been encountered (Crabtree et al. 1989, Ackerman 2002, Larivière and Messier 2000, 2001, Nams 1997, Phillips et al. 2003, 2004). Ringelman (2018) observed that nests in close proximity to neighbors and with earlier initiation dates had higher survival rates than those initiated later. These results suggested that clustered nests may have benefited from the effect of dilution during the early nesting period but are more vulnerable later in the nesting season as mesopredators hone their search images (Andrén 1995). Despite these hypotheses, simultaneous investigation of mesopredators and duck nest survival has been rare.

Movement and space use of mesopredators also may be influenced by predator community structure and interspecific interactions. In the PPR, coyotes (*Canis latrans*) are a dominant predator, affecting habitat use and movements of smaller carnivores (Sargeant et al. 1987, Johnson et al. 1996). Mesopredator avoidance of coyotes is one hypothesized mechanism of mesopredator release hypothesis (MRH). The MRH predicts that removal or reduction in density or distribution of a dominant predator will result in increased densities, greater frequency and or distance of movements, or more extensive space use by subordinate mesopredators with reduced need to alter behaviors to avoid negative interactions (Estes 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). Coyote-induced suppression of other mesopredator individuals and populations may lead to increased duck nest survival in areas with greater coyote densities (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003). Previous research indicated that mesopredator species in the PPR positively associated with one another, with differences in ecological niche or temporal activity allowing for co-occurrence (Schoener 1974, Heithaus 2001, Holt and Huxel 2007, Crimmins et al. 2015, Davis et al. 2018). Efforts to quantify movements and behaviors of multiple species simultaneously could provide greater insights about these complex interactions.

Habitat-selection and movement analyses allow for determining associations between space use and local environment conditions (i.e., current landscape characteristics). Advances in remote sensing (Kays et al. 2015) allow for collection of fine-scale spatiotemporal data, promoting improved comparisons of environmental covariates from animal locations with locations assumed available to the animal (Boyce and McDonald 1999, Thurfjell et al. 2014, Fieberg et al. 2021). I investigated seasonal (hereafter, referred to as periods) and annual landscape and patch characteristics related to nest survival that potentially influenced changes in mesopredator space use by analyzing resource selection and movements patterns of 4 GPS-collared mesopredator species (raccoon, striped skunk, coyote, and American badger [*Taxidea taxus*]) using integrated step-selection functions (iSSF; Fieberg et al. 2021). Our objectives were to: (1) evaluate temporal variation in resource selection and movements of mesopredators in relation to the primary nesting period of ducks; (2) evaluate spatial variation in resource selection and movements in relation to variation in coyote densities caused by on-going coyote removal management activities; and (3) identify relative risks of nest depredation based on space use and behaviors of mesopredators. Overall, our aim was to provide insight on the theorized primary mechanism of predator mediated behavior influencing nest survival rates in the PPR.

METHODS

Study Area

We studied space use of mesopredators in four townships within Faulk and Hand Counties in eastern South Dakota from 2018-2020. I selected these adjacent counties because they had similar amounts and compositions of grasslands and wetlands, and townships with high predicted breeding duck pair densities (Reynolds et al. 2006). Additionally, Faulk County has had annual, systematic coyote removal since the 1990s, whereas no annual systematic coyote removal has occurred in Hand County (B. Curtis, South Dakota Department of Game, Fish and Parks [SDGFP], personal communication). Hereafter, Faulk County will be referred to as the treatment county because of the influence the coyote removal management had on the relative abundance of coyotes in that county (i.e., significantly lower occupancy probability, Fino Chapter 1) and Hand County will be referred to as the control county. The proximity of sites and long-standing contrast in coyote removal management allowed for an efficient investigation of nesting and predator ecology simultaneously and specifically with respect to potential differences due to predator management and community composition.

Both counties are on the western edge of the Drift Prairie or Glaciated Plains physiographic region of the PPR. Average elevation is ~481 m above MSL in both counties and the annual average temperature ranged from -6° C (December) to 21° C (June), during 2018-2020. The average annual precipitation during 2018-2020 was 55 cm of rainfall and 93 cm of snowfall (US Climate Data, 2020). Both counties were rural; the treatment county had a population of 2,299 people whereas the control county's population was 3,191 people and both counties averaged 0.5 housing units/km^2 and average human densities of 1.5 people/km^2 (US Census Bureau 2019). The landscape was a mosaic of croplands, pastures, and grasslands/haylands that surrounded farmsteads. Agricultural composition of the treatment county was approximately 16% corn (*Zea mays*), 22% soybean (*Glycine max*), and 29% pasture, whereas the control county was generally similar with approximately 14% corn, 19% soybean, and 36% pasture.

Radio-marking animals

We captured and radio-marked mesopredators in early springs 2018-2020, prior to waterfowl nesting, starting in March when nightly minimum temperatures were ≥-4° C and continued until all transmitters were deployed. I set traps where I detected signs of mesopredator presence (e.g., scat, tracks) and checked traps daily starting at 08:00 in an effort to not adversely affect predator behaviors. Traps met Best Management Practice specifications established by the International Association of Fish and Wildlife Agencies (AFWA 2006). Coyotes and American badgers were captured using MB-550 OLIL coil-spring foothold traps (Minnesota Trapline Products, Inc., Pennock, MN) (Turnbull et al. 2011), restrained with a catch pole, and immobilized with tiletamine-zolazepam and ketamine using a jab stick (Kreeger and Arnemo 2007). Striped skunks and raccoons were captured using Tomahawk live traps (Tomahawk, Hazelhurst, WI) and immobilized with tiletamine-zolazepam and ketamine by hand with the help of a cage divider (Kreeger and Arnemo 2007). After the animal was processed, I administered yohimbine as the immobilization reversal.

Morphometrics were recorded, such as neck, chest, and crown-to-rump length (cm), as well as age estimated from tooth wear (juvenile or adult), weight (kg), and sex. I fit coyotes and American badgers with a G5-2A Iridium/GPS unit (325g), and raccoons and striped skunks with a W500 Wildlink GPS logger unit (65g; Advanced Telemetry Systems). American badgers were not radio-marked in 2018 because their contribution to the mesopredator community was thought to be minimal but emerged as potentially important. For raccoons and striped skunks, I set collars to record a location every half hour from 2 hours before sunset to 2 hours after sunrise, the period when mammalian predators are most active (Rovero et al. 2013, Trolliet et al. 2014, Burton et al. 2015, Caravaggi et al. 2017). Transmitters were set to record one location per hour. Trapping and handling methods followed the guidelines approved by the American Society of Mammalogists for wild animals in research (Sikes et al. 2016) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 17-103A). Radio-marked animals were monitored weekly, and I attempted to download data opportunistically. Red foxes, although a historically important waterfowl nest predator in the PPR (Sovada 2000, Phillips et al. 2003, 2004), were not included in this study due to local low densities.

Spatiotemporal and environmental covariates

To quantified landscape and patch-level metrics believed to influence space use of study subjects, I created a cover-type layer for each study year in ArcMap 10.5.1. This layer combined year-specific rasters from the USGS Dynamic Surface Water Extent using Landsat Collection 1 Level-3 and the USDA National Agricultural Statistics Service CropScape Cropland data layer. I believe this approach provided the best time-specific and detailed depiction of land cover for each year during the study, and these land cover rasters were used to delineate covariate rasters. I initially identified 20 environmental covariates that may have influenced mesopredator movements and resource selection. I evaluated all covariates for collinearity using Pearson correlation and considered 2 covariates highly correlated if $r \geq 0.65$ (Vatcheva et al. 2016). In these instances, single-parameter models for each predictor variable were compared and the predictor variable present in the model with the greatest AIC value was eliminated from further analyses. Fragmentation, cover, and water accessibility may influence mesopredator space use in relation to duck nest survival (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007, Phillips et al. 2003, 2004, Horn et al. 2005, Amundson et al. 2012, Crimmins et al. 2015) and covariates were characterized by land cover type, distance to a land cover feature, and proportion of a certain land cover type. Land cover was originally classified into 8 distinct cover types: surface water, corn, soybeans, other crops, fallow/idle, pasture, developed, and shelterbelts. Because ducks nest primarily in grassland cover types (Hohman et al. 2014, Gallman 2020) and not all marked individuals were located in all cover types (leading to convergence issues), I combined fallow/idle and pasture into one dummy coded land cover covariate (i.e., non-cropped vegetation, generally perennial grassland) for use in subsequent analyses in lieu of the individual cover type estimates. There were 2 distance-to-nearest (m) land cover type covariates: distance to nearest surface water and edge (including roads). Distances to nearest developed and nearest shelterbelt were not included in iSSFs because these landscape features were uncommon in mesopredator geospatial datasets, and distance to nearest grassland was not prioritized given the previously-decided perennial grassland land cover type covariate. Patch area (km^2) was used as a covariate to characterize fragmented patches and is more often referenced in the literature, so perimeter:area ratio from analysis. Four covariates were species-specific: proportion of grassland within the average 95% kernel density estimation (hereafter KDE) home range and within the average core 50% KDE home range, and proportion of surface water within the average 95% KDE home range and within the average core 50% KDE home range. Finally, 1 covariate was intended to represent functional-management units of our study area (i.e., fragmented sections within a township for agricultural and livestock purposes), specifically the proportion of grassland within a 1-square mile area around a GPS location based on the size of township sections. I believed that the proportion of available nesting cover (i.e., quality grassland patches) and surface water on the landscape were at least partly due to land use practices of landowners (i.e., impacts from agricultural practices used on cultivated cropland or livestock). Proportion of grassland within the average 95% KDE home range and the average core 50% KDE home range were highly correlated (*r* = 0.69), as were the proportion of surface water within the average 95% KDE home range and the average core 50% KDE home range (*r* = 0.72). When these highly correlated covariates were used in different models with other covariates of interest, the AIC values were the same. Thus, I discarded the 2 covariates incorporating the average core 50% KDE home range due to the generalist and opportunistic nature of these radio-marked species (Lesmeister et al. 2015, Chitwood et al. 2020, Amspacher et al. 2021). I also discarded the covariate proportion of grassland within a 1-square mile area of locations because it was highly correlated with proportion of grassland within the average 95% KDE home range (*r* = 0.70) and the latter covariate would more accurately captured species-specific behavior. In total, our final analyses included 6 environmental covariates intended to explain variation in mesopredator movements and resource selection. I centered to the mean and scaled all covariates so they were standardized prior to analysis.

Integrated step selection functions

Location data from radio-marked individuals were grouped by species, county, and period. I established three periods based on temporal changes in the number of observed active nests. Location of marked individuals were categorized into period based on date as follows: February 15 to April 30 was considered the pre-nesting period, May 1-July 15 the core nesting period (these dates contained 90% of all monitored active nests), and July 16 to November 15 was considered the post-nesting period. I excluded GPS locations collected from November 16 to February 14 (all years) from analysis because average low temperatures were below -4° C and some mesopredator species were less active due to torpor and denning. If I had ≤200 GPS points and ≤10 days of data for any given marked individual in any of aforementioned periods, those data were excluded from further analyses; this amount of data was approximately when home range size plateaued, which I estimated using 95% KDEs (package adehabitatHR; Calenge 2006). I calculated average home range size (ha) for each species by county, sex, year, and each unique county-period subgroup. Subgroups with <5 unique individuals were not included in comparisons involving population-level inference (i.e., pre-period American badgers).

We fit iSSF for each unique subgroup using the package amt within Program R (Signer et al. 2019). I regularized timesteps of location data to a sampling rate of 60 minutes and tolerance of 5 minutes, and summarized average step length and daily movement (sum of step lengths in a 24 hours period) for each species by county, sex, year, and unique subgroup. I analyzed these data using general linear models and specified a Gamma distribution and log-link function to estimate variation in and predict average home range size by county, sex, year, and each unique county-period subgroup for each species (Appendix S2.1). I fit a gamma distribution to the step lengths and a von Mises distribution to the turn angles using maximum likelihood from the created movement bursts (Avgar 2016, Signer et al. 2019) and used these distributions to generate and pair 10 random steps with each observed step. Additionally, I calculated the log-transformed distance of step length and the cosine of turning angle for each step

(Benhamou 2006). I extracted covariates for the end point of each step in the iSSFs (observed and random) and removed locations that fell outside of the raster layers' boundaries from analysis (<0.001%). I fit a global model to the resulting data which included each covariate alone (for resource selection inference), the interaction of the covariate with the log-transformed step length (for movement rate inference), and the interaction of the covariate with the cosine turning angle (for deviation from a straight-forward motion inference). I calculated nonparametric bootstrapped 95% confidence intervals based on 10,000 samples from unique subgroup sample inverse variance-weighted mean values (Lele and Keim 2006, Johnson et al. 2008) with the package boot (Canty and Ripley 2017) using the adjusted bootstrap percentile method. I used overlap of 95% confidence intervals to compare relationships of selection and movement with various environmental covariates among species, counties, and periods.

RESULTS

Field sampling and landscape characteristics

We radio-marked 64 individuals in 2018, 59 in 2019, and 73 in 2020. These marked animals yielded 104,886 GPS locations in 2018, 97,892 GPS locations in 2019, and 88,028 GPS points in 2020 (Table 2.1). I collected 145,249 locations of marked animals in the treatment county and 145,557 locations in the control county. After data cleaning, I analyzed data from 285,618 GPS locations (raccoon: 89,707, striped skunk: 56,144, coyote: 123,358, American badger: 16,409) belonging to 129 individuals and 258 unique subgroups. Because I compared used and available GPS points within each individual home range, and in order to increase sample size of each subgroup, I pooled data from individuals of the same species regardless of sex or year, resulting in 22 population-level subgroups. Landscape characteristics were summarized to describe the study area (Table 2.2).

Average home range sizes and movements

Raccoons — Average home range size was 50% times larger in the treatment county compared to the control county. On average, males had 2.8 times larger home ranges, 73 m longer step lengths, and 1.8 km longer daily movements than females (Table 2.3). Average step length was 87-127 m longer during the pre-nesting period in the treatment county compared to the core nesting period in both counties. Average daily movement was 1.0-1.5 km shorter during the pre- and core nesting periods in the control county compared to the pre-nesting period in the treatment county (Table 2.4).

Striped skunks — Average home range size, step length, and daily movement did not differ among counties, sexes, and years (Table 2.3). Average step length was 95-170 m longer during the pre-nesting period compared to other nesting periods in both counties. Average daily movement distance was 1.1-1.7 km greater during the pre-nesting period in the treatment county compared to the core and post-nesting periods in the control county. Average daily movement distance was 1.6 km larger during the pre-nesting period compared to the post-nesting period in the control county (Table 2.4).

Coyotes — Average home range size was 2.8 times larger in the treatment county compared to control county, 2.9 times larger for females compared to males, and 8.2 times larger in 2020 compared to 2018. Average daily movement distances were 2.2 km longer in the treatment county compared to the control county, and 4.2-5.6 km longer in 2019 and 2020 compared to 2018 (Table 2.3). Average home range size was 8.4-10.5 times greater during the core and post-nesting periods in the treatment county compared to the pre-nesting period in the control county. Average daily movement distance during the post-nesting period in the treatment county was 4.1 km larger than that of the pre-nesting period in the control county (Table 2.4).

American badgers — Average home range size was 2.2 times greater for males than for females (Table 2.3). Average home range size, step lengths, and daily movement distances did not differ among county-period subgroups (Table 2.4).

Selection of landscape characteristics

Perennial grassland cover type — Raccoons preferentially selected for locations in grasslands during the pre-nesting period in the control county and during the core nesting period in both counties. Striped skunks used locations in grasslands less than they were available in the control county during the pre- and post-nesting periods, but more than they were available during the core nesting. Coyotes used grasslands less than their availability during the post-nesting period in both counties.

Distance to nearest surface water — Relative probability of use increased as locations became closer to surface water for raccoons in the control county and for striped skunks in the treatment county during the pre-nesting period. During the core nesting period in both counties, relative probability of use for coyotes increased at locations closer to surface water.

Distance to patch edge — In the control county, raccoons used locations closer to patch edges more than they were available during the core nesting period while coyotes did do less than that of their availability during the core and post-nesting periods. American badgers preferentially selected for farther distances to patch edges in both counties during the core nesting period and for nearer distances to patch edges during the post-nesting period in the control county.

Patch size — During the pre-nesting period in the treatment county, relative probability of use for striped skunks increased with smaller patches.

Proportion of perennial grasslands — In the control county, raccoons and striped skunks preferentially selected for greater proportions of grassland during the post-nesting period. During the core nesting period in the treatment county, American badgers used locations in lower proportions of grasslands more than their availability.

Proportion of surface water — During the post-nesting period, relative probability of use of raccoons increased with greater proportion of surface water in the control county and with lower proportions of surface water in the treatment county, but the opposite relationships were observed for striped skunks. In the control county, coyotes selected for greater proportions of surface water during the pre-nesting period (Fig. 2.1, Appendix S2.2).

Relationships between movement rate and landscape characteristics

Perennial grassland cover type — In the control county, step lengths decreased during the core nesting period for raccoons and striped skunks but increased during the pre- and post-nesting periods for striped skunks. Coyote step lengths increased during the pre-nesting period in the treatment county, the core nesting period in the control county, and the post-nesting period in both counties.

Distance to nearest surface water — For striped skunks, step lengths increased as distance from surface water increased during the pre-nesting period in the treatment county. During the core nesting period in the control county, step lengths increased for coyotes and decreased for American badgers with farther distances from surface water.

Distance to patch edge — Step lengths increased as raccoon locations were closer to patch edges during all nesting periods in both counties. Coyote step lengths increased when closer to patch edges during all nesting periods in the control county, as well as during the core nesting period in the treatment county. For American badgers, step lengths increased closer to patch edges during the core nesting period in both counties.

Patch size — In the treatment county, step lengths increased as patch size increased during the pre-nesting period for striped skunks and as patch size decreased during the core nesting period for American badgers.

Proportion of perennial grasslands — In the control county, step lengths of raccoons and striped skunks increased as proportions of grassland decreased during the post-nesting period. In the treatment county, striped skunk step lengths increased as proportions of grasslands decreased during the core nesting period, while those of coyotes during the pre-nesting period and those of American badgers during the core nesting period, increased as proportions of grasslands increased.

Proportion of surface water — Step lengths increased as proportions of surface water decreased during the core nesting period in both counties and during the post-nesting period in the control county for raccoons, during the post-nesting period in the treatment county for striped skunks, and during the pre-nesting period in the control county for coyotes (Fig. 2.2, Appendix S2.2).

Relationships between movement direction and landscape characteristics

Perennial grassland cover type — Turning angles of raccoons deviated from a straight-forward direction in both counties during the core nesting period while turning angles of striped skunks were of a similar direction during the post-nesting period in the control county. Coyote demonstrated a straight forward direction during the core nesting period in the treatment county and during the post-nesting period in both counties.

Distance to nearest surface water — During the pre-nesting period, turning angles deviated from a straight-forward direction with closer distances to surface water for raccoons in the treatment county and for striped skunks in the control county. American badgers maintained a forward directions when farther from surface water during the core nesting period in the control county and during the post-nesting period in the treatment county.

Distance to patch edge — Turning angles deviated from a forward trajectory when closer to patch edges during the pre-nesting period in the control county and during the core nesting period in the treatment for raccoons, during the pre-nesting period in the treatment county for striped skunks, and during the core nesting period in the control county for coyotes and American badgers.

Patch size — Turning angles of coyotes maintained a more forward direction when in larger sized patches during the post-nesting period in the treatment county.

Proportion of perennial grasslands — During the core nesting period in the control county, turning angles of striped skunks deviated from a forward trajectory with decreasing proportions of grassland. American badgers maintained a more forward trajectory with increasing proportions of grassland during the post-nesting period in the treatment county.

Proportion of surface water — Turning angles deviated from a forward trajectory with decreasing proportions of surface water during the post-nesting period in the treatment county for striped skunks and during the pre-nesting period in the control county for coyotes (Fig. 2.3, Appendix S2.2).

DISCUSSION

Overall, I found sparse evidence of temporal variation in mesopredator resource selection and movements with respect to time periods defined by the nesting phenology of ducks (i.e., pre-, core-, and post-nesting periods), suggesting that annual variation in nest density and nesting activity did not elicit strong changes to mesopredator movement behaviors. Striped skunks in the control county appeared to be an exception to this pattern; they selected grassland cover and their step lengths decreased (i.e., spending more time in that particular area) in this cover type during the core nesting period. However, striped skunks avoided grasslands and step lengths increased in this cover type during the pre- and post- nesting periods. This phenomenon may be indicative of prey switching associated with nest phenology, and supports the idea that striped skunks may search for specific prey types once they encounter them and consequently congregate in areas of high nest density (Crabtree et al. 1989, Ackerman 2002, Larivière and Messier 2000, 2001, Nams 1997, Phillips et al. 2003, 2004).

Space use of other mesopredator species, however, was similar regardless of nesting period, likely due to consistency in overall food availability (i.e., nest density peaked in early June, small mammal indices of abundance peaked in July [Fino, Chapter 1], continual growth of vegetation and row crops as summer progressed) that resulted in a productive landscape with compensatory resources distributed over time. While mesopredators may have still been prey switching (i.e., they focus on the seasonally most abundant prey), I may not have observed such changes in behavior because different prey items are associated with similar landscape characteristics (Miller and Getz 1977, Gollan et al. 2009, Mulligan et al. 2013) or hunting for various prey items may require similar behaviors. Duck nests were one part of the overall diet of mesopredators and greater landscape, and considering all the foods and abundant forage that these generalist species consume, significant behavior changes in response to selective food resource availability were not detected.

Our results also revealed support for the mesopredator release hypothesis. I found spatiotemporal differences in space use in relation to different coyote removal management strategies in each county. Coyote occupancy probability was 44% lower and raccoon occupancy probability 30% greater in the treatment than the control county (Fino, Chapter 1), providing evidence of different predator community compositions between counties. For example, in response to fewer coyotes in the treatment county, raccoons had larger home ranges and longer daily movements compared to the control county, a prediction of mesopredator release (Estes 1996, Crooks and Soule 1999, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). Behavioral differences between different sized species in the control county indicated that smaller mesopredators altered their space use, potentially to avoid or decrease encounters with coyotes and minimize predation risk (Heithaus 2001, Holt and Huxel 2007, Wilson et al. 2010). Such examples of spatiotemporal differences between coyotes and raccoons or striped skunks include opposite space use patterns of a particular landscape characteristic during a specific nesting period or similar space use patterns of a certain landscape characteristic during different nesting periods. Interestingly, I did not observe spatiotemporal variation in selection and movements for American badgers, indicating that such a dominant-subordinate relationship with coyotes was not present.

Resource selection and movement behaviors documented during the core nesting period favored landscape characteristics that have been shown to associate with higher nest densities or nest site selection and mesopredator use (Kantrud 1984, 1993, Larivière and Messier 2000, Ray 2000, Sovada et al. 2000, Phillips et al. 2003, 2004, Lesmeister et al. 2015). These behaviors may lead to increased frequency of incidental nest depredations, because such movement patterns may allow individuals to cover greater areas or hunt more efficiently (Johnson et al. 1989, Sovada et al. 2000, Coates et al. 2008). Moreover, our results were consistent with mechanisms hypothesized by other studies (i.e., cover density and patch size [Crabtree et al. 1989, Gosselink et al. 2003, Doyle et al. 2019], distance to edge [Clark and Shutler 1999, Barding and Nelson 2002], high nest density [Lesmeister et al. 2015, Lariviere and Messier 2000]). It is important to note that I did not detect avoidance of a particular landscape characteristic during the pre- and post-nesting periods in contrast to selection of that same landscape characteristic during the core nesting period. However, habitat selection by multiple mesopredator species related to landscape characteristics (e.g., nearer distances to surface water, greater proportions of grasslands) indicative of increased food abundance (Bowman and Harris 1980, Sietman et al. 1994, Nocera and Dawe 2008, Haffele et al. 2013), nest site selection by ducks (i.e., based on habitat characteristics [Ringelman 2014], and the local density of conspecifics [Ringelman et al. 2016]), suggested an increased risk to duck nest survival during the core nesting period.

Although some mesopredator species exhibited similar selection and movement patterns to each other, space use was often segregated spatially, temporally, or both. Spatial variation was expressed as similar selection occurring in different counties or opposite trends of selection occurring in the same county. Temporal variation resulted from similar selection occurring during different periods. Some examples of spatiotemporal segregation included: (1) raccoons and striped skunks both selected for nearer distances to surface water during the pre-nesting season but in different counties; (2) raccoons selected for lower proportions, but striped skunks selected for greater proportions, of surface water during the post-nesting period in the treatment county; however, the opposite phenomena occurred in the control county, and; (3) American badgers selected for nearer distances to patch edges during the post-nesting period, whereas raccoons did so during the core nesting period in the control county. The competitive exclusion principle supports the idea of spatiotemporal differences in activities by sympatric species due to niche separation (Schoener 1974, Heithaus 2001, Holt and Huxel 2007, Crimmins et al. 2015, Davis et al. 2018), which in turn allows for co-occurrence, independent of prey response (Holt 1977, Voorthees and Cassel 1980, Norrdahl and Korpimaki 2000, Devries and Armstrong 2011, Haffele et al. 2013). Further, our results demonstrated that direct species overlap was possible during the post-nesting period when additive food resources have accumulated, thus providing increased food resource availability (Bowman and Harris 1980, Sietman et al. 1994, Nocera and Dawe 2008, Haffele et al. 2013).

As one of the first studies to provide quantitative results on home range, resource selection, and movement patterns of mesopredators in relation to landscape characteristics that influence duck nest survival, I aimed to provide better insight into predator-prey interactions. Our study elucidated that members of the mesopredator community selected similar habitat characteristics as those often selected by nesting ducks (Larivière and Messier 2000, 2001, Phillips et al. 2003, 2004, Crimmins et al. 2015). This overlap likely led to increased risk of nest depredation due to increased interactions with multiple predator species and a continuous risk of depredation throughout the nesting period because sympatric species had similar use and movements patterns, but at different times of the year (i.e., temporal variation in similar space use between species). These landscape characteristics are important to document, but some may be better than others at explaining mechanisms that affect nest survival. Patch size has been hypothesized to indirectly influence nest survival (Crabtree et al. 1989, Sovada et al. 2000, Horn et al. 2005, Fisk 2010), but I generally did not observe selection and movement patterns that strongly related to patch size. Further, coyote removal management in the treatment county may have indirectly and negatively influenced duck nest survival (Sovada et al. 1995, Estes 1996, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003). An environment with decreased densities of coyotes would reduce the risk of negative interactions with subordinate mesopredator species, thereby encouraging more impactful nest predators to use preferred habitat characteristics throughout the entire the nesting season. However, I were unable to account for nest density or nest proximity in analyses because I were not searching, marking, and monitoring nests within the same patches on a regular and frequent basis over time, and, therefore, lacked prey-specific covariates. Hence, it is possible that the distributions and densities of the prey resources themselves, rather than landscape and patch characteristics, influenced mesopredator behavior. Future studies that have the resources may wish to integrate prey-related covariates into their mesopredator selection and space use analyses.

MANAGEMENT IMPLICATIONS

Effective management of breeding waterfowl requires an understanding of mesopredator community dynamics. With similar, and often shared, space use patterns by mesopredators and nesting ducks, evaluating how the landscape changes over time (i.e., habitat loss and fragmentation of high quality patches) may reveal areas with increased predator-prey interactions (i.e., greater risk of nest depredation). Additionally, it is important to consider how management implemented on the landscape (e.g., predator removal management) might influence behaviors of other mesopredators. For example, targeted removal of raccoons and striped skunks may be a cost-effective method to increase duck nest survival (Schranck 1972, Greenwood 1986, Garrettson and Rohwer 2001, Shively 2003, Chodachek and Chamberlain 2006, Pearse and Lester 2007, Pieron and Rohwer 2010, Amundson et al. 2012, Pieron et al. 2012), yet such efforts may need to be executed regularly to continually suppress mesopredator densities. In areas where coyote are the sole target of reduction, reducing or eliminating this management practice could increase coyote densities and help to restrict spatiotemporal movements of other mesopredators that more often target duck nests. Alternatively, American badgers, recognized as a primary nest predator in the PPR (S. Felege, University of North Dakota, personal communication), may be a more suitable target for removal management to mitigate declining duck nest survival because they use core nesting habitats and appear to be minimally influenced by coyotes.

We acknowledge that although considering mesopredator space use independently may provide insight on the community's impact on nest survival, doing so may not mean that overall nest survival rates especially poor or below sustainability levels. Selection of, and movements in, habitats with similar characteristics by multiple mesopredator species, as well as by a variety of prey species, may indicate the presence of high-quality habitat patches with abundant resources (Bowman and Harris 1980, Sietman et al. 1994, Nocera and Dawe 2008, Haffele et al. 2013). In addition to the potential for increased food resources for mesopredators in these patches, higher densities of duck nests may dilute depredation events (Phillips et al. 2003, Horn et al. 2005). In this scenario, increased use by mesopredators may not have an influential impact on short-term overall duck recruitment. I acknowledge that these high-quality patches likely have far broader ecological value and contribute disproportionately to environmental diversity. Examination of nest survival rates simultaneously with mesopredator behavior is necessary to effectively evaluate these predator-prey relationships and to develop realistic and appropriate habitat and game bird management that is impactful.

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DATA ACCESSIBILITY STATEMENT

Data will be archived and deposited in Dryad's publicly accessible repository.

CONFLICT OF INTEREST

The authors have declared that no competing interested exist.

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Table 2.1. Summary of sample sizes from captured individuals and GPS data in eastern South Dakota, 2018–2020.

Species	**Raccoon**	**Striped Skunk**	**Coyote**	**American badger**	**Total**
Captured individuals	121	102	44	30	297
Radio-marked individuals	70	67	41	18	196
Individuals with obtained datasets	53	39	29	17	138
Total GPS points	91,377	58,102	123,658	17,669	290,806
Average GPS points per individual	1,724	1,490	4,264	1,039	2,107
Standard Deviation	1,477	1,045	2,143	456	1,840

Table 2.2. Summary of landscape covariates, including the range and standard deviation (SD) around averaged values.

Covariate	**Range**	**Mean**	**SD**
Distance to nearest developed cover type (m)	0.0–2,716	397.6	374.8
Distance to nearest shelterbelt (m)	0.0–8,444	1,093.70	883.3
Distance to nearest surface water (m)	0.0–1209	118.2	117
Distance to nearest grassland cover type (m)	0.0–1,421	84.4	142.4
Distance to nearest cover type edge (m)	0.0–612	37.2	53.4
Patch area (km^2)	<0.1–293	10.1	43.7
Patch perimeter:area ratio	<0.1–0.1	<0.1	<0.1
Proportion of grassland cover type within a 95% Kernel Density Estimator home range size	<0.1–0.8	0.2	<0.1
Proportion of surface water cover type within a 95% Kernel Density Estimator home range size	<0.1–0.1	<0.1	<0.1

Table 2.3. County, sex[1], and annual average 95% Kernel Density Estimator home range size (ha), step length (m), and daily movement (km) with respective 90% confidence intervals of mesopredator species in eastern South Dakota, during Feb–Nov, 2018–2020.

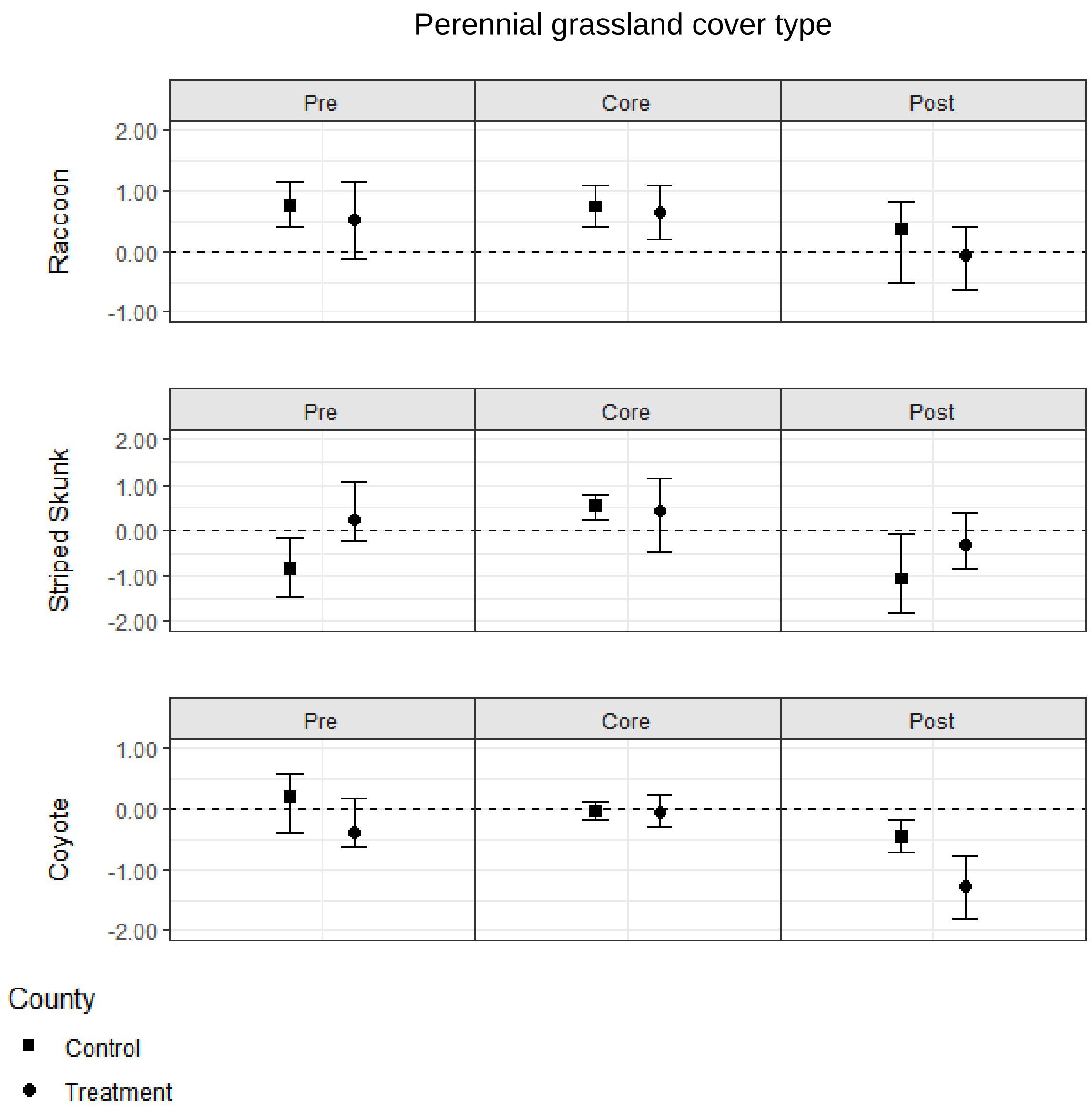
	Home range size		**Step lengths**		**Daily movements**		**N**
	Mean	90% CI	Mean	90% CI	Mean	90% CI	
Raccoon							48
Treatment Co.	448.2	363.6 – 552.9	198	174 - 226	3.9	3.5 - 4.3	23
Control Co.	294.5	232.3 – 354.3	174	151 - 200	3.1	2.7 - 3.5	25
Female	216	170.4 – 274.6	153	134 - 172	2.7	2.4 – 3.0	21
Male	611	482.1 – 784.6	226	198 - 257	4.5	4.1 - 5.1	27
2018	413.7	324.1 – 525.9	171	151 - 194	3.7	3.4 - 4.2	18
2019	332	249.9 – 439.3	185	159 - 215	3.3	2.9 - 3.8	14
2020	352.5	250.9 – 495.3	204	171 - 242	3.4	2.9 - 3.9	16
Striped skunk							35
Treatment Co.	505.3	389.6 – 655.4	215	192 - 240	3.4	3.0 - 3.7	17
Control Co.	547.4	426.3 – 702.9	202	181 - 226	2.9	2.6 - 3.3	18
Female	413.7	328.7 – 525.9	209	189 - 230	3.2	2.9 - 3.5	21
Male	668.6	490.4 – 911.6	209	183 - 237	3.1	2.7 - 3.5	14
2018	587.1	422.1 – 816.6	204	179 - 235	3.3	2.9 - 3.8	11
2019	623.4	471.1 – 824.8	217	192 - 245	3.1	2.7 - 3.5	11
2020	397.5	282.9 – 558.5	204	176 - 235	3	2.6 - 3.5	13
Coyote							29
Treatment Co.	12,396.50	7,444.0 – 20,438.4	392	344 - 450	10.4	9.3 - 11.8	12
Control Co.	4,381.60	2,711.3 – 7,152.2	361	321 - 412	8.2	7.3 - 9.3	17
Female	12,521.10	7,747.8 – 20,438.4	351	314 - 392	8.2	7.4 - 9.3	18
Male	4,338.00	2,528.0 – 7,370.0	407	361 - 459	10.4	9.1 - 11.8	11
2018	2,684.30	1,194.1 – 5,974.0	388	321 - 464	12.8	10.6 - 15.6	8
2019	6,871.70	3,771.3 – 12,521.1	420	365 - 478	8.6	7.4 - 9.9	10
2020	21,920.30	12,030.1 – 39,941.5	334	290 - 380	7.2	6.3 - 8.4	11
American Badger							17
Treatment Co.	558.5	397.5 – 776.8	305	255 - 369	2	1.5 - 2.5	6
Control Co.	702.9	547.4 – 893.5	293	255 - 334	2.4	2.0 - 2.8	11
Female	426.3	309.6 – 581.2	279	235 - 330	2.1	1.6 - 2.6	6
Male	920.7	689.0 – 1,218.2	321	273 - 372	2.2	1.8 - 2.7	11
2019	623.4	426.3 – 902.5	347	281 - 424	2.1	1.6 - 2.8	6
2020	629.7	500.3 – 792.5	257	228 - 293	2.2	1.8 - 2.6	11

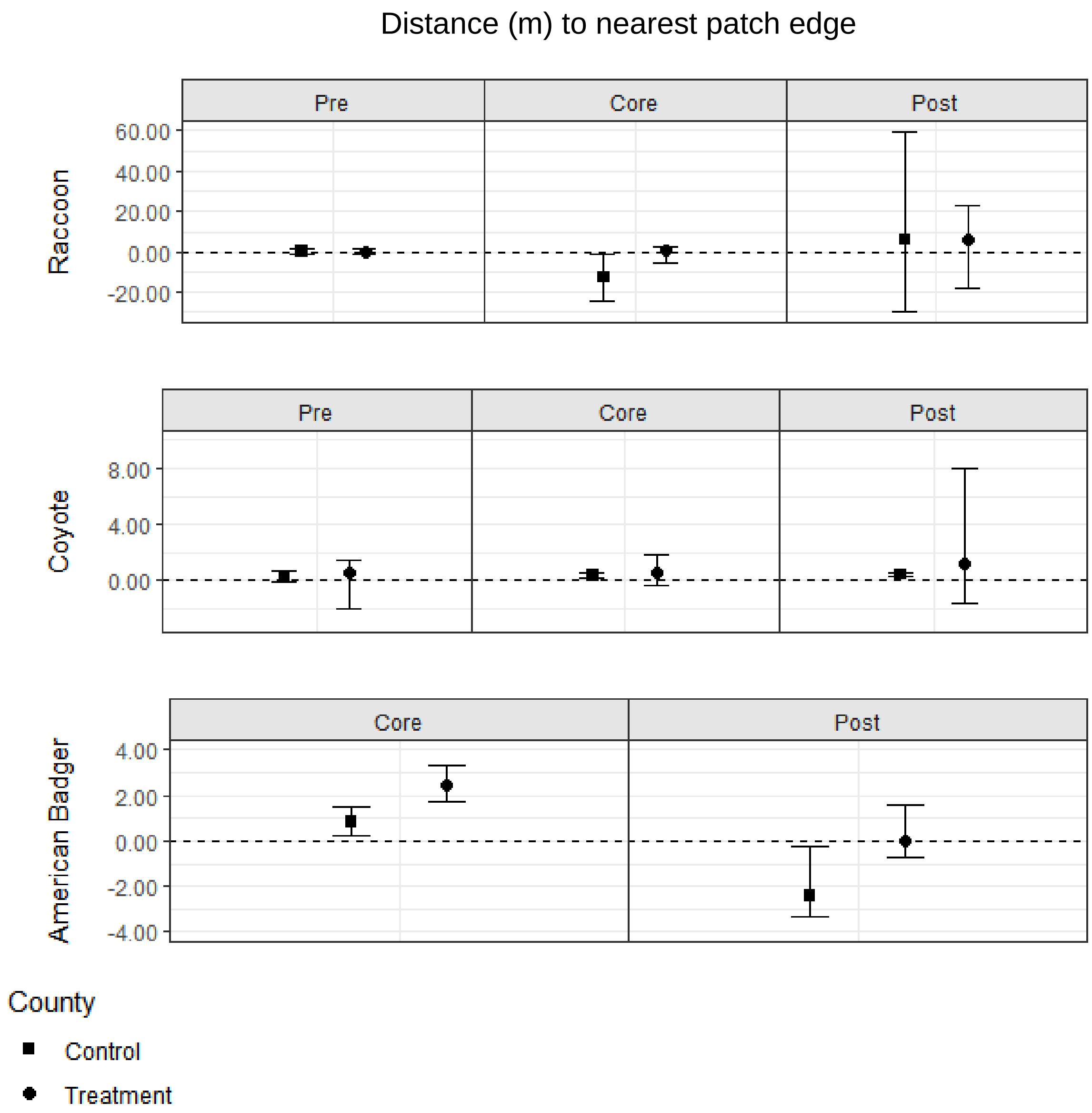
[1] Sex ratios for coyotes were 5M:7F in the Treatment County and 6M:11F in the Control County.

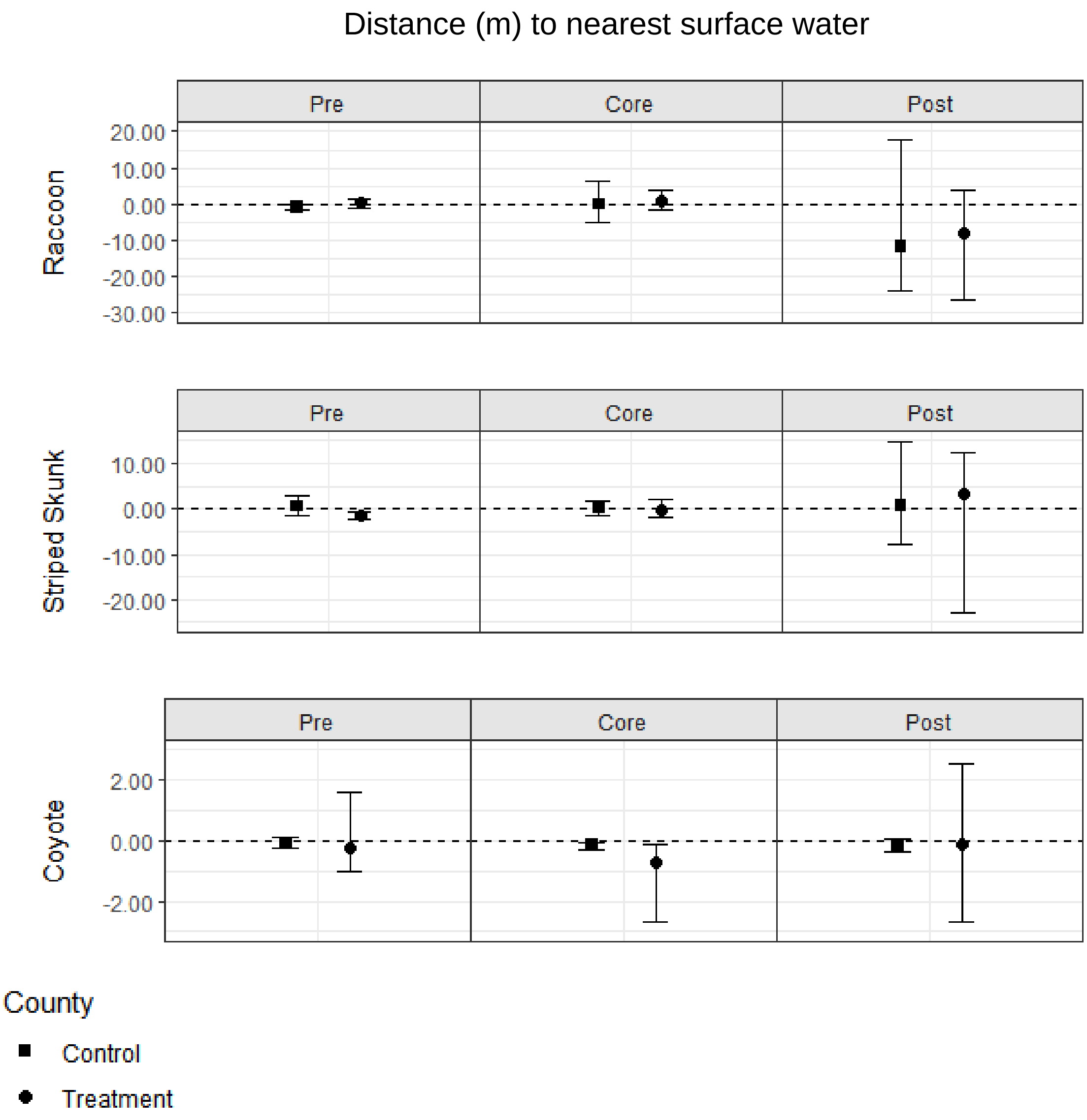
Table 2.4. Model-predicted 95% KDE home range size (ha), step length (m), and daily movement (km) with 90% confidence intervals of mesopredator species in different counties during different within-year periods in eastern South Dakota, during Feb–Nov, 2018–2020.

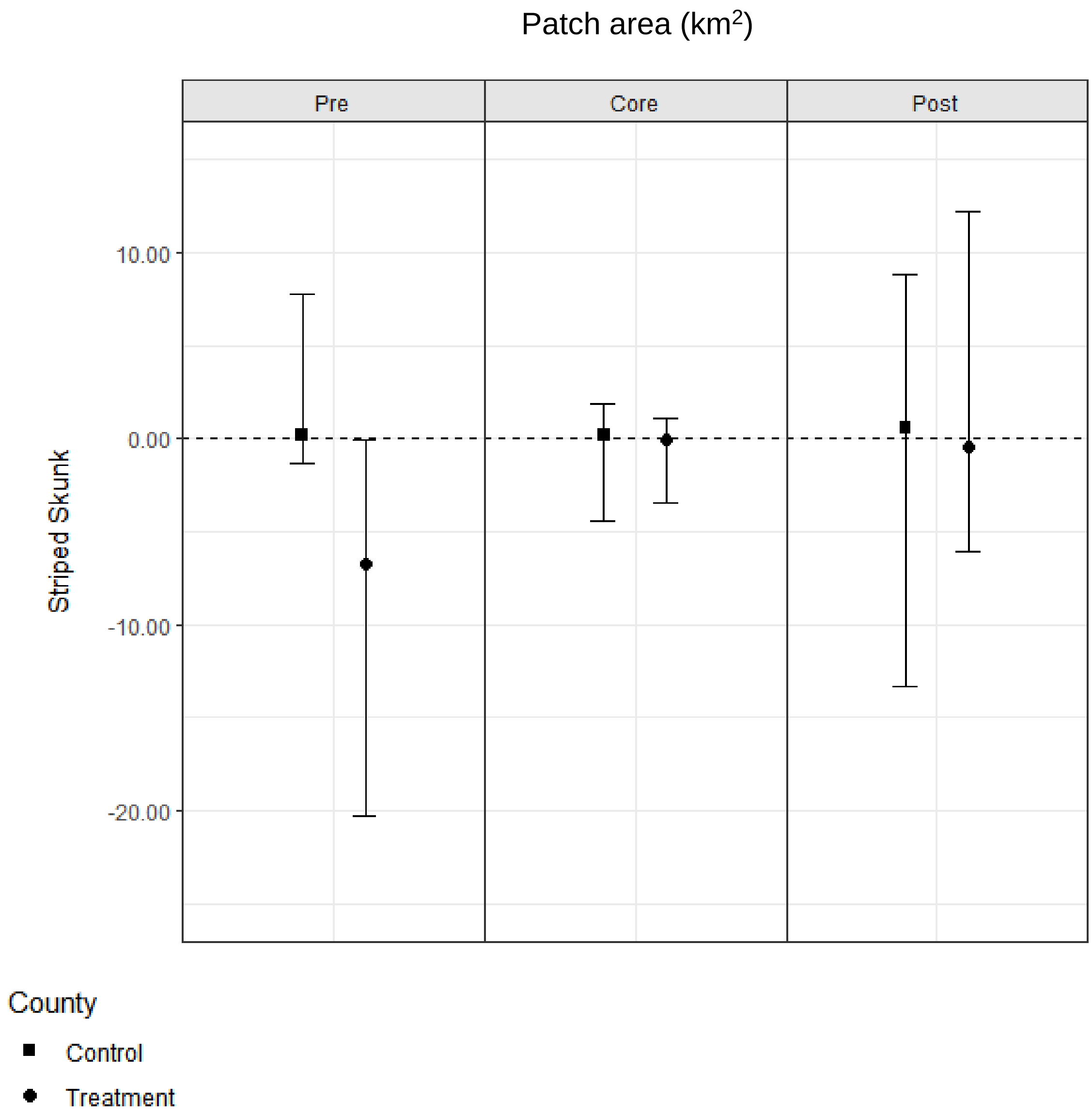
	Home range size		**Step lengths**		**Daily movement**		**N**
	Mean	90% CI	Mean	90% CI	Mean	90% CI	
Raccoon							
Treatment Co.							
Pre	404.7	291.2 – 564.1	265	221 - 314	4.3	3.7 – 5.0	19
Core	444.6	325.4 – 605.0	178	150 - 209	4	3.5 - 4.6	21
Post	504.3	291.0 – 875.8	167	125 - 224	3.5	2.7 - 4.4	7
Control Co.							
Pre	344.9	255.7 – 466.5	194	166 - 228	3.3	2.9 - 3.7	23
Core	256.8	176.8 – 374.3	138	113 - 167	2.8	2.4 - 3.3	15
Post	289.8	150.8 – 558.5	198	140 - 279	3.2	2.4 - 4.3	5
Striped skunk							
Treatment Co.							
Pre	471.1	318.4 – 702.9	287	242 - 340	4	3.4 - 4.8	12
Core	605	430.2 – 858.5	192	166 - 221	3.2	2.7 - 3.7	16
Post	448.2	264.1 – 769.1	181	144 - 226	2.9	2.3 - 3.7	7
Control Co.							
Pre	769.1	538.2 – 1113.4	317	273 - 372	3.9	3.3 - 4.5	14
Core	623.4	439.7 – 875.8	178	154 - 206	2.9	2.5 - 3.4	15
Post	342.1	195.8 – 598.9	147	116 - 185	2.3	1.8 - 2.9	6
Coyote							
Treatment Co.							
Pre	8,064.00	2,219.8 – 29,294.9	412	305 - 550	11	8.1 - 15.0	5
Core	17,071.60	7,518.9 – 38,761.0	327	273 - 395	9.2	7.5 - 11.1	12
Post	13,700.30	5,797.4 – 32,375.9	446	369 - 545	11.1	9.1 - 13.7	11
Control Co.							
Pre	1,628.10	531.2 – 5,040.0	388	299 - 503	7	5.3 - 9.1	8
Core	8,393.10	4,126.4 – 17,071.6	327	279 - 384	8.7	7.3 - 10.3	17
Post	6,217.80	3,026.5 – 12,774.0	376	321 - 446	9.4	7.8 - 11.1	16
American Badger							
Treatment Co.							
Core	552.9	345.6 – 884.6	284	219 - 365	1.8	1.3 - 2.6	5
Post	564.1	374.3 – 849.9	330	265 - 416	2.1	1.6 - 2.9	6
Control Co.							
Core	623.4	434.9 – 884.6	252	209 - 305	2	1.5 - 2.6	8
Post	792.5	575.5 – 1,091.3	337	284 - 403	2.8	2.2 - 3.5	10

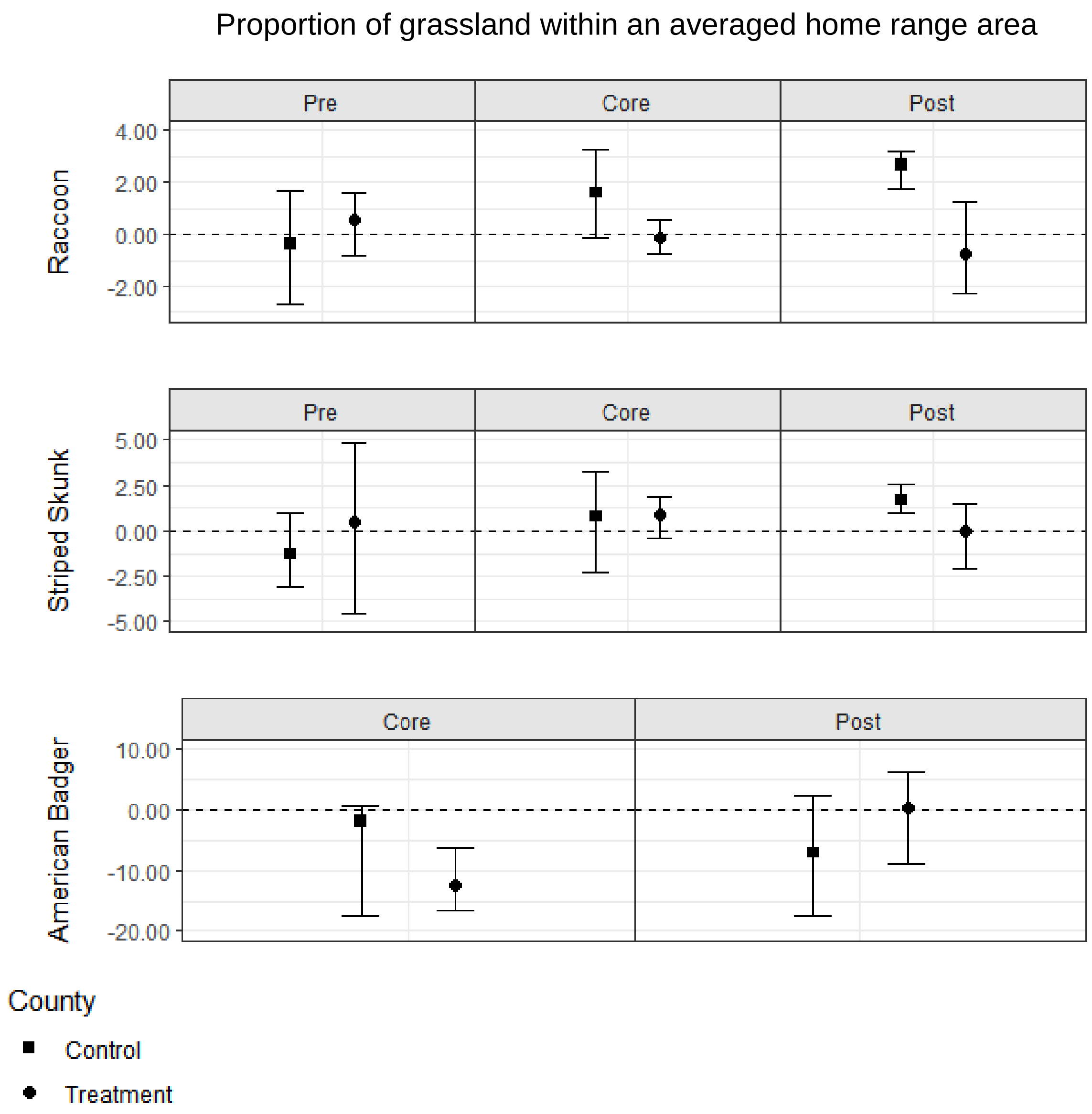
Figure 2.1. Bootstrapped population means and 95% confidence intervals from integrated step selection function models of GPS-collared raccoons, striped skunks, coyotes, and American badgers from 2018 to 2020 describing the influence of landscape characteristics on resource selection. If space use was not significant across counties and period for a mesopredator species, it was not included.


Perennial grassland cover type
Pre
Core
Post
Raccoon
2.00
1.00
0.00
-1.00
Striped Skunk
2.00
1.00
0.00
-1.00
-2.00
Coyote
1.00
0.00
-1.00
-2.00
County
■ Control
● Treatment


Distance (m) to nearest patch edge
Raccoon
Pre
Core
Post
60.00
40.00
20.00
0.00
-20.00
Coyote
Pre
Core
Post
8.00
4.00
0.00
American Badger
Core
Post
4.00
2.00
0.00
-2.00
-4.00
County
■ Control
● Treatment


Distance (m) to nearest surface water
Pre
Core
Post
Raccoon
20.00
10.00
0.00
-10.00
-20.00
-30.00
Striped Skunk
10.00
0.00
-10.00
-20.00
Coyote
2.00
0.00
-2.00
County
■ Control
● Treatment


Patch area (km²)
Pre
Core
Post
10.00
0.00
-10.00
-20.00
Striped Skunk
County
■ Control
● Treatment


Proportion of grassland within an averaged home range area
Pre
Core
Post
Raccoon
4.00
2.00
0.00
-2.00
Pre
Core
Post
Striped Skunk
5.00
2.50
0.00
-2.50
-5.00
Core
Post
American Badger
10.00
0.00
-10.00
-20.00
County
■ Control
● Treatment

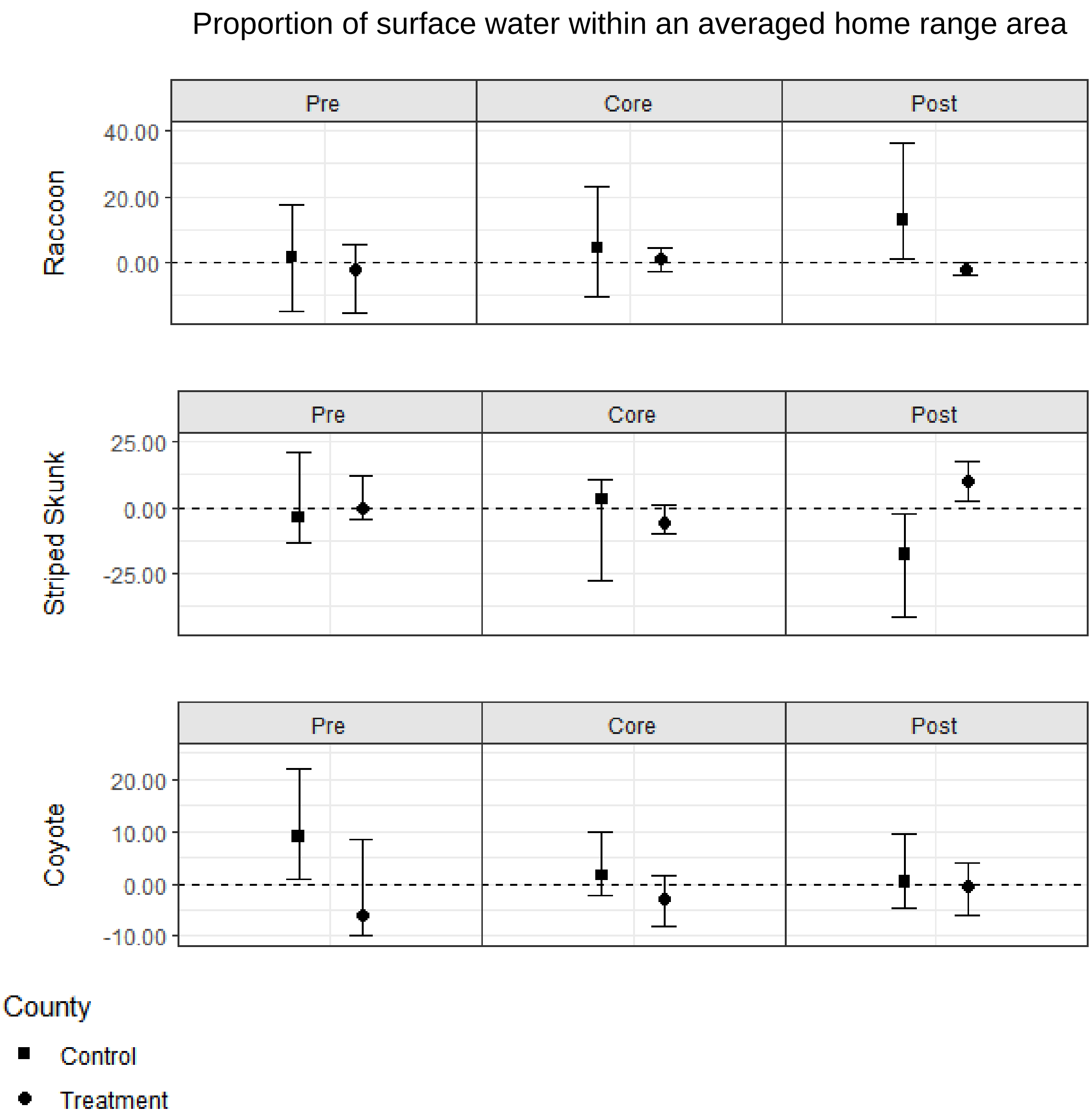
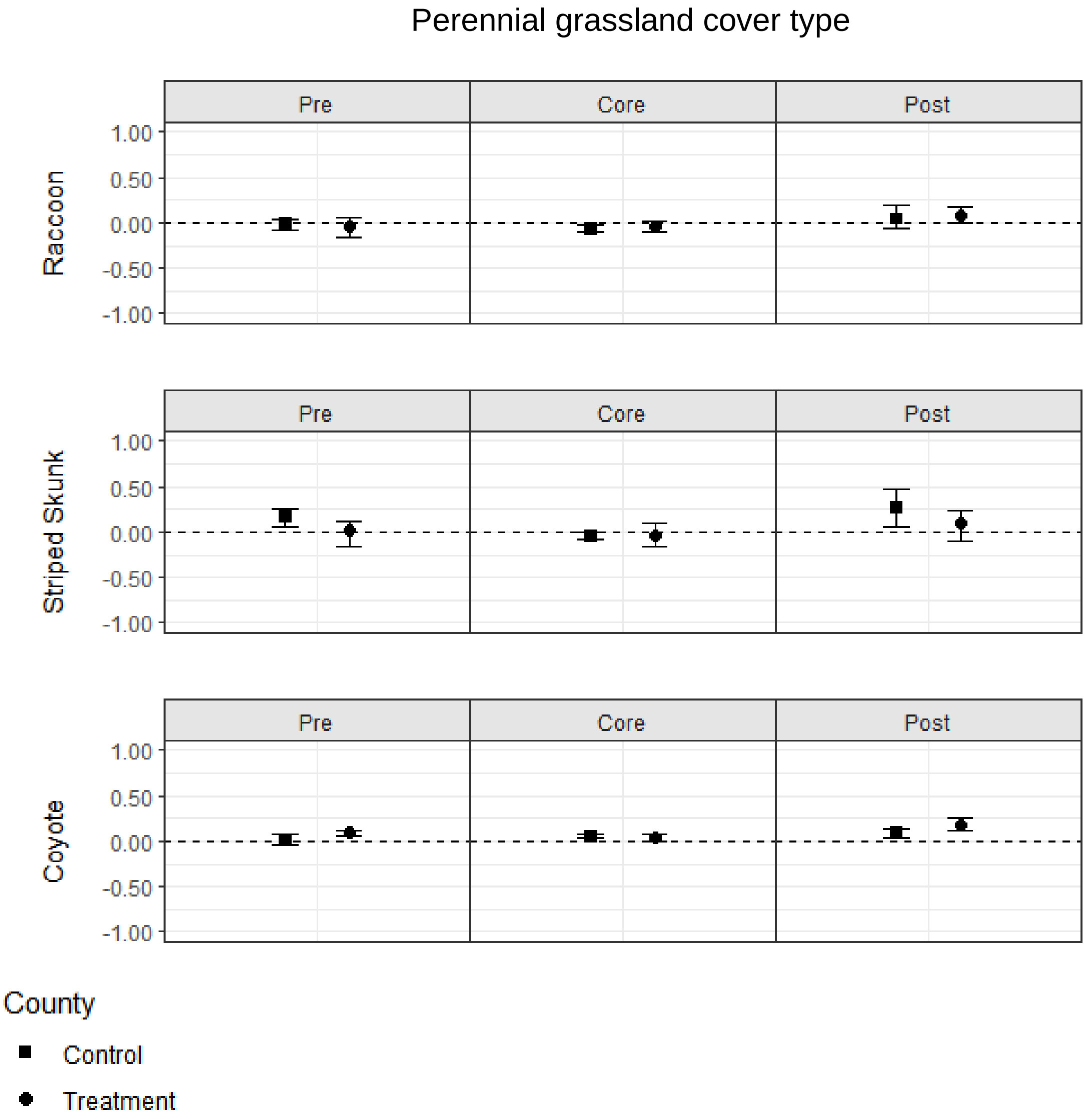
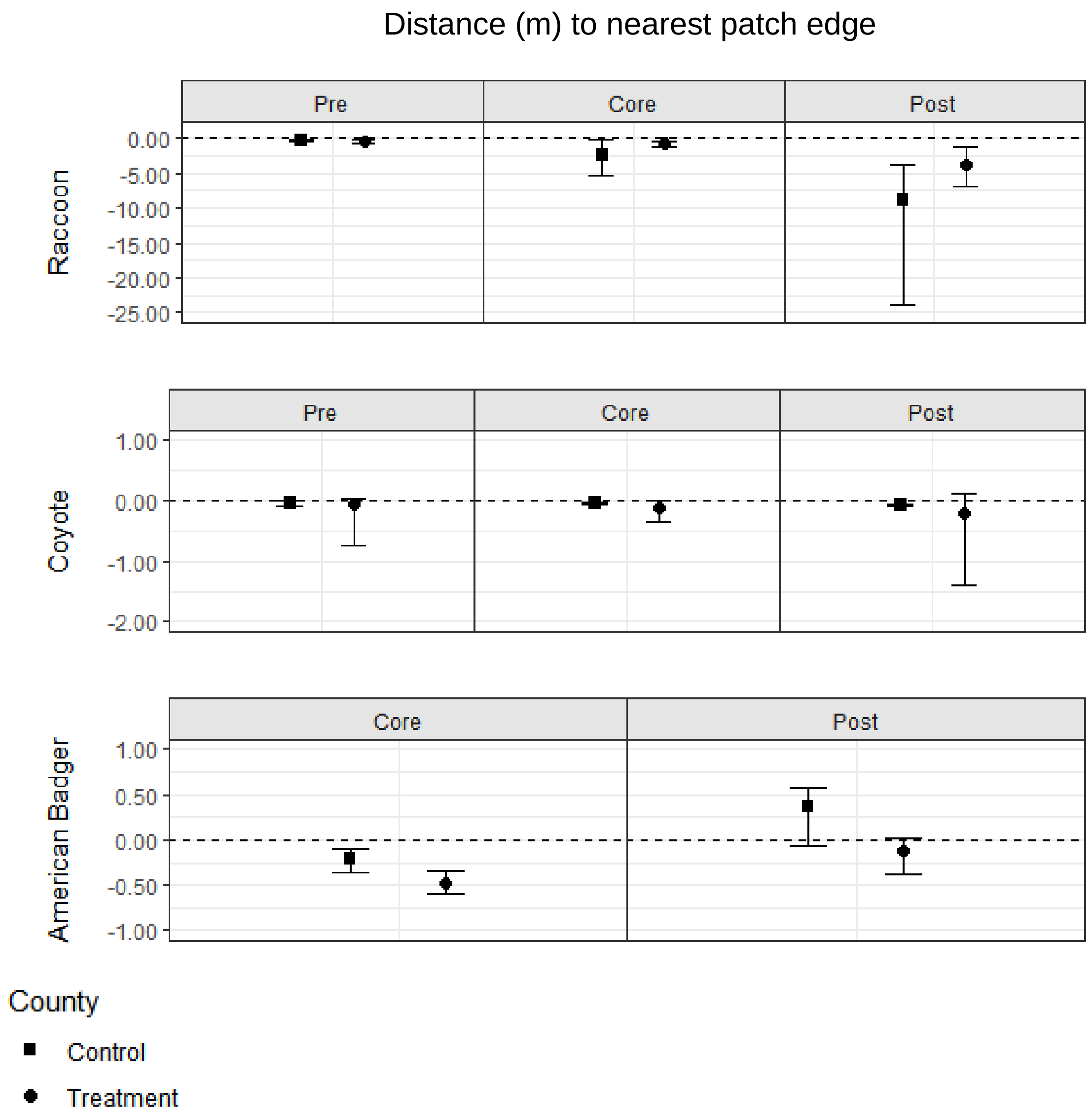
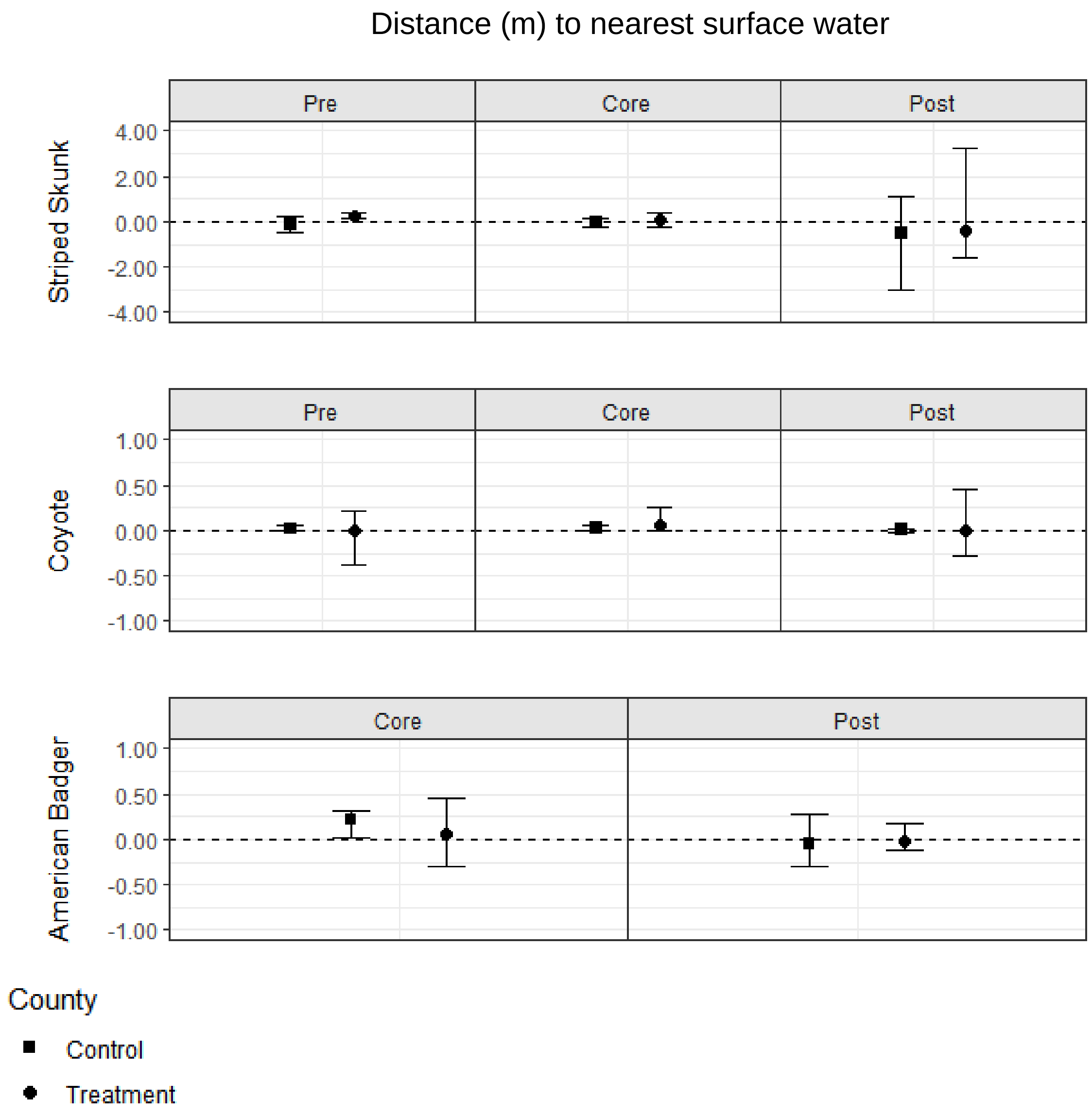
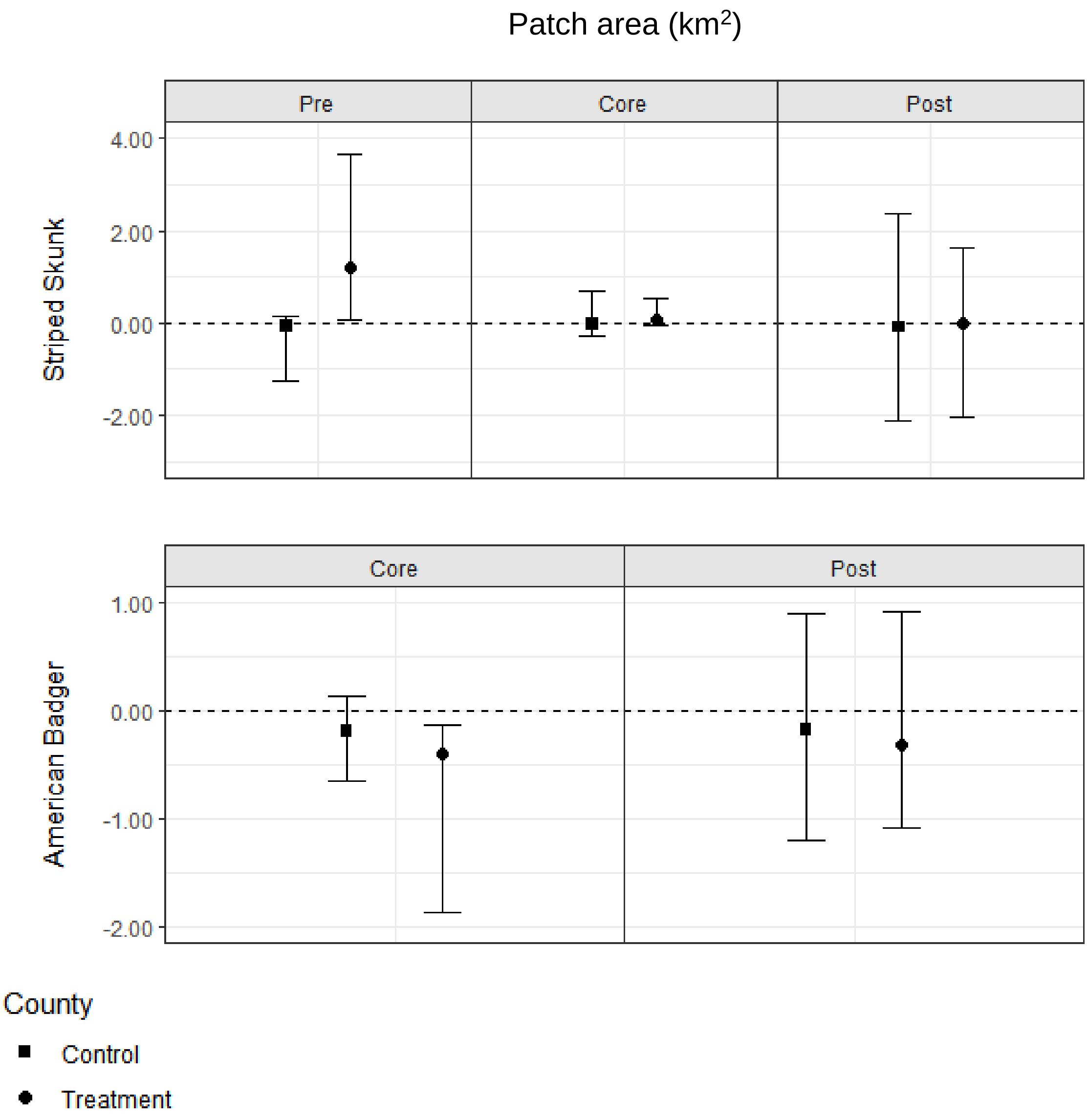

Proportion of surface water within an averaged home range area
Pre
Core
Post
Raccoon
40.00
20.00
0.00
Pre
Core
Post
Striped Skunk
25.00
0.00
-25.00
Pre
Core
Post
Coyote
20.00
10.00
0.00
-10.00
County
■ Control
● Treatment

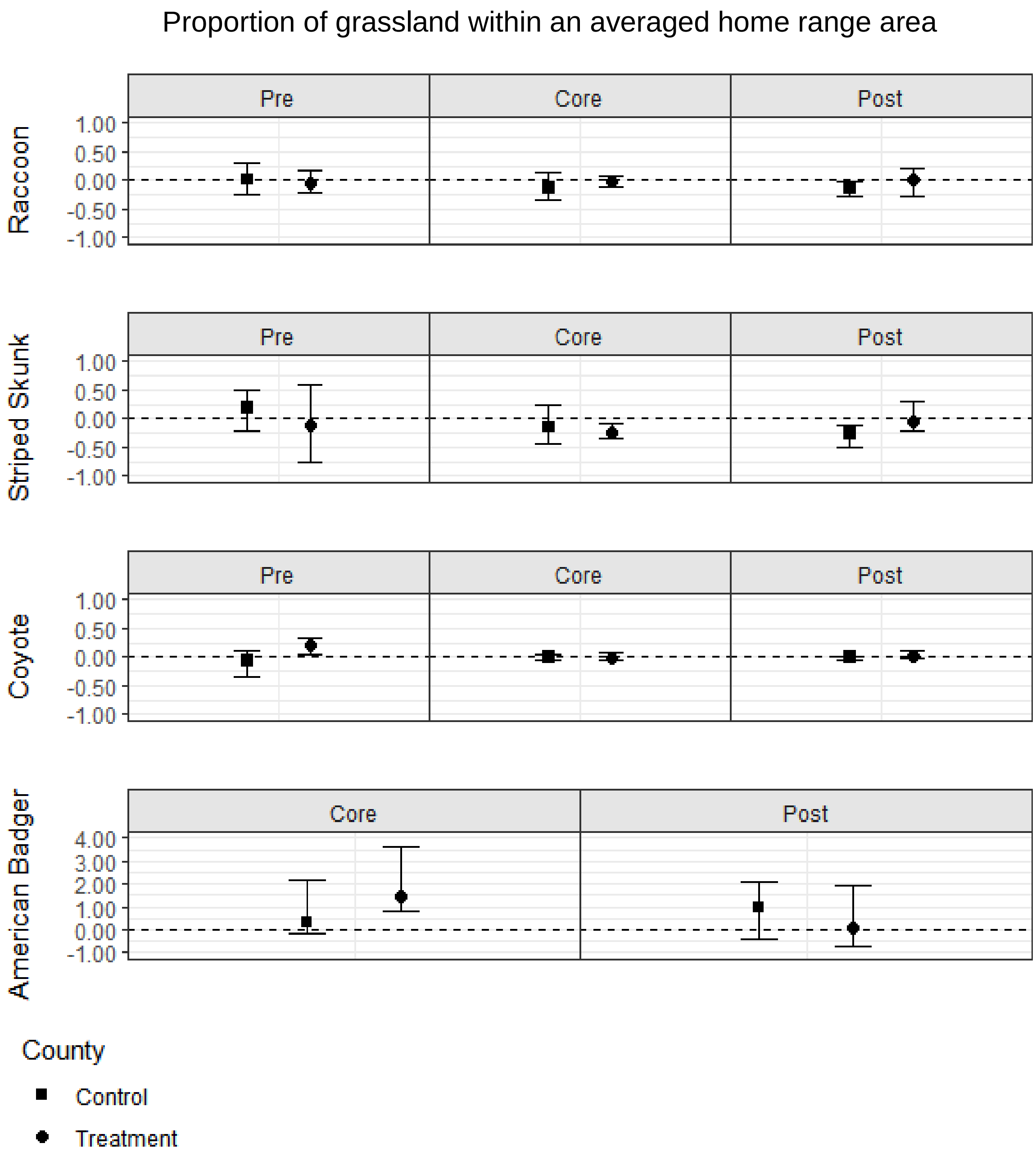
Figure 2.2. Bootstrapped population means and 95% confidence intervals from integrated step selection function models of GPS-collared raccoons, striped skunks, coyotes, and American badgers from 2018 to 2020 describing the influence of landscape characteristics on movement rate (interaction between the covariate and logtransformed step length). If space use was not significant across counties and period for a mesopredator species, it was not included.


Perennial grassland cover type
Pre
Core
Post
Raccoon
Striped Skunk
Coyote
1.00
0.50
0.00
-0.50
-1.00
County
■ Control
● Treatment


Distance (m) to nearest patch edge
Raccoon
Pre
Core
Post
0.00
-5.00
-10.00
-15.00
-20.00
-25.00
Coyote
Pre
Core
Post
1.00
0.00
-1.00
-2.00
American Badger
Core
Post
1.00
0.50
0.00
-0.50
-1.00
County
■ Control
● Treatment


Distance (m) to nearest surface water
Striped Skunk
Coyote
American Badger
Pre
Core
Post
4.00
2.00
0.00
-2.00
-4.00
1.00
0.50
0.00
-0.50
-1.00
County
■ Control
● Treatment


Patch area (km²)
Pre
Core
Post
Striped Skunk
4.00
2.00
0.00
-2.00
Core
Post
American Badger
1.00
0.00
-1.00
-2.00
County
■ Control
● Treatment


Proportion of grassland within an averaged home range area
Pre
Core
Post
Raccoon
Striped Skunk
Coyote
American Badger
1.00
0.50
0.00
-0.50
-1.00
4.00
3.00
2.00
1.00
0.00
-1.00
County
■ Control
● Treatment

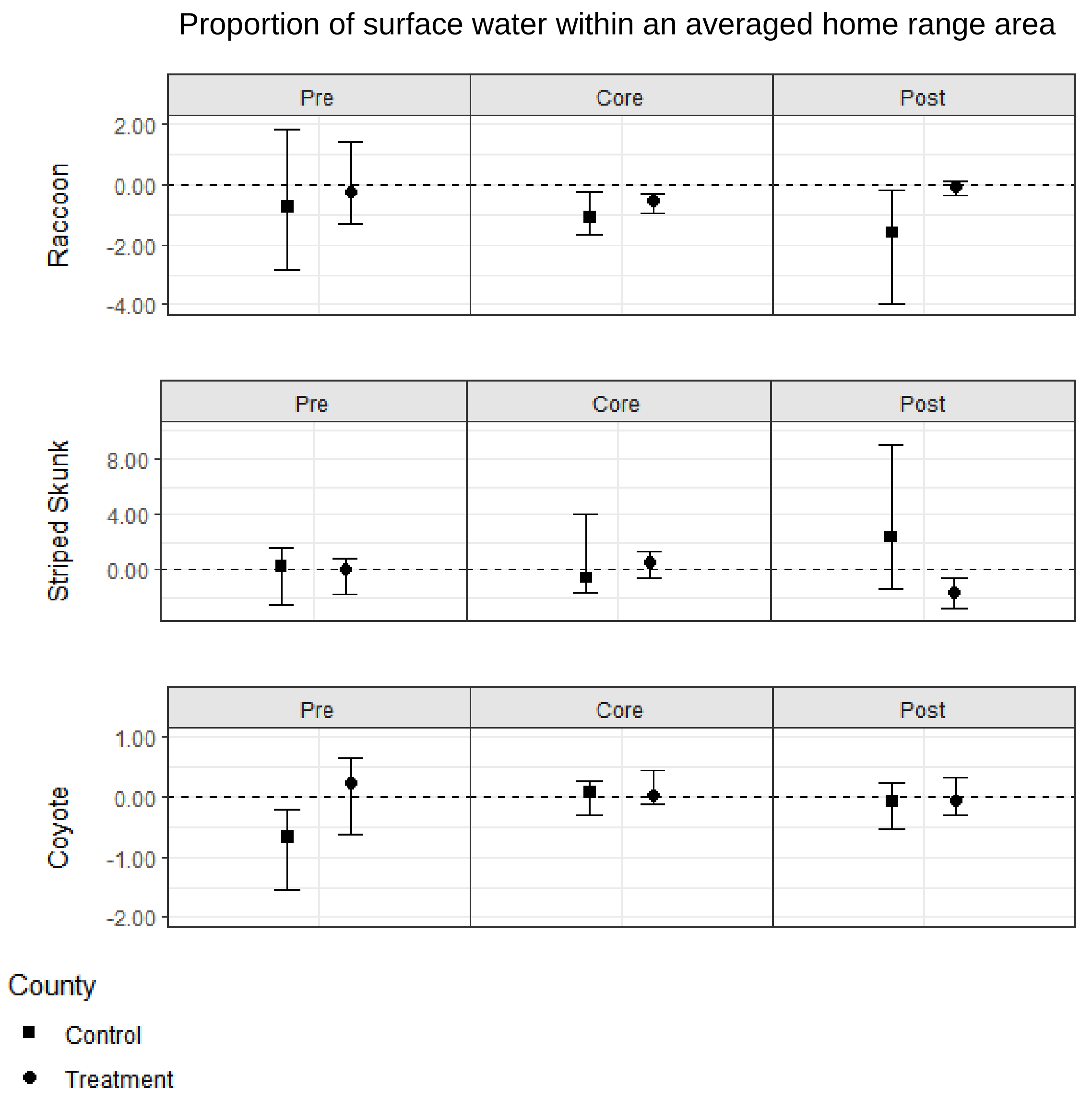
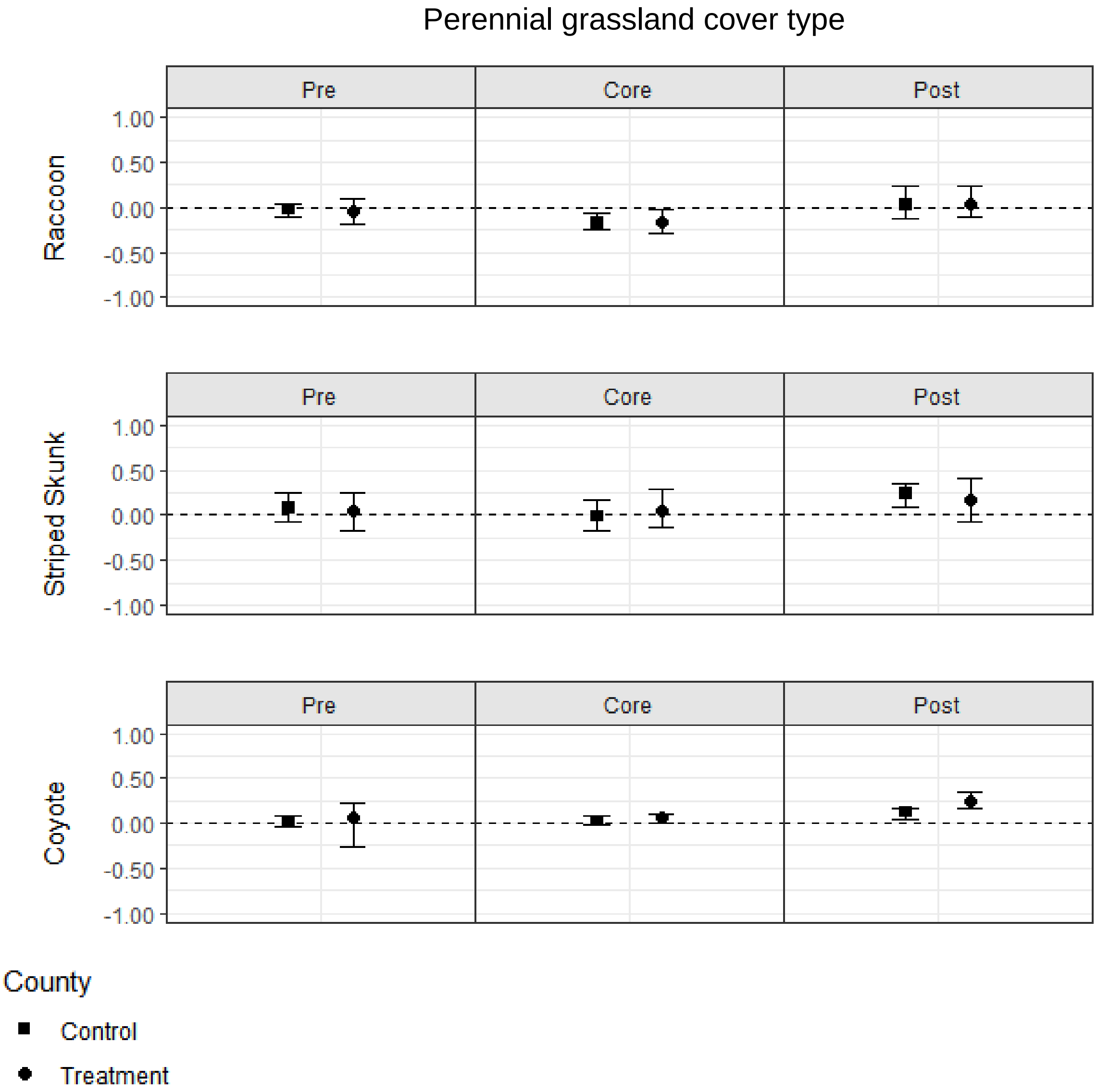
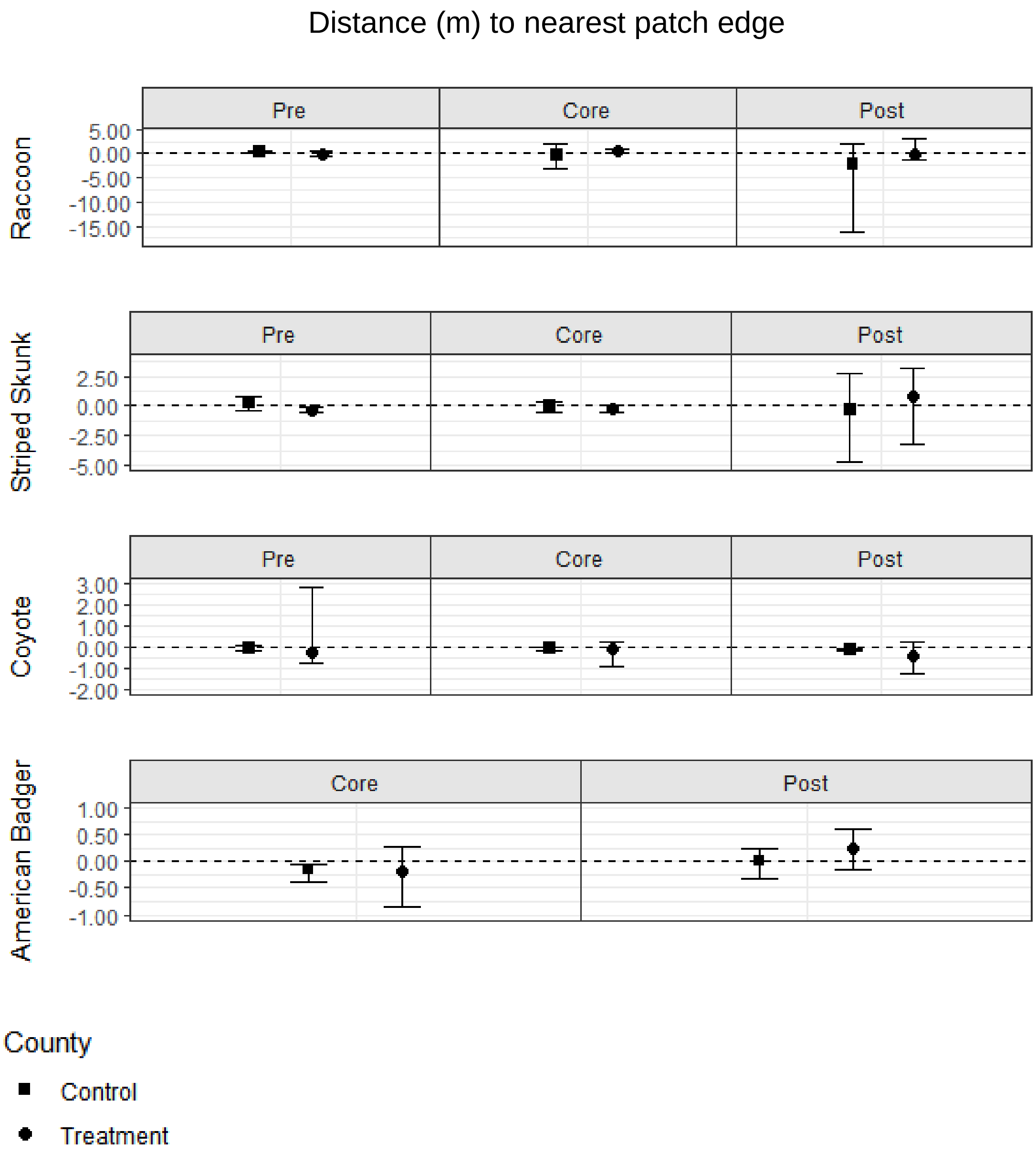
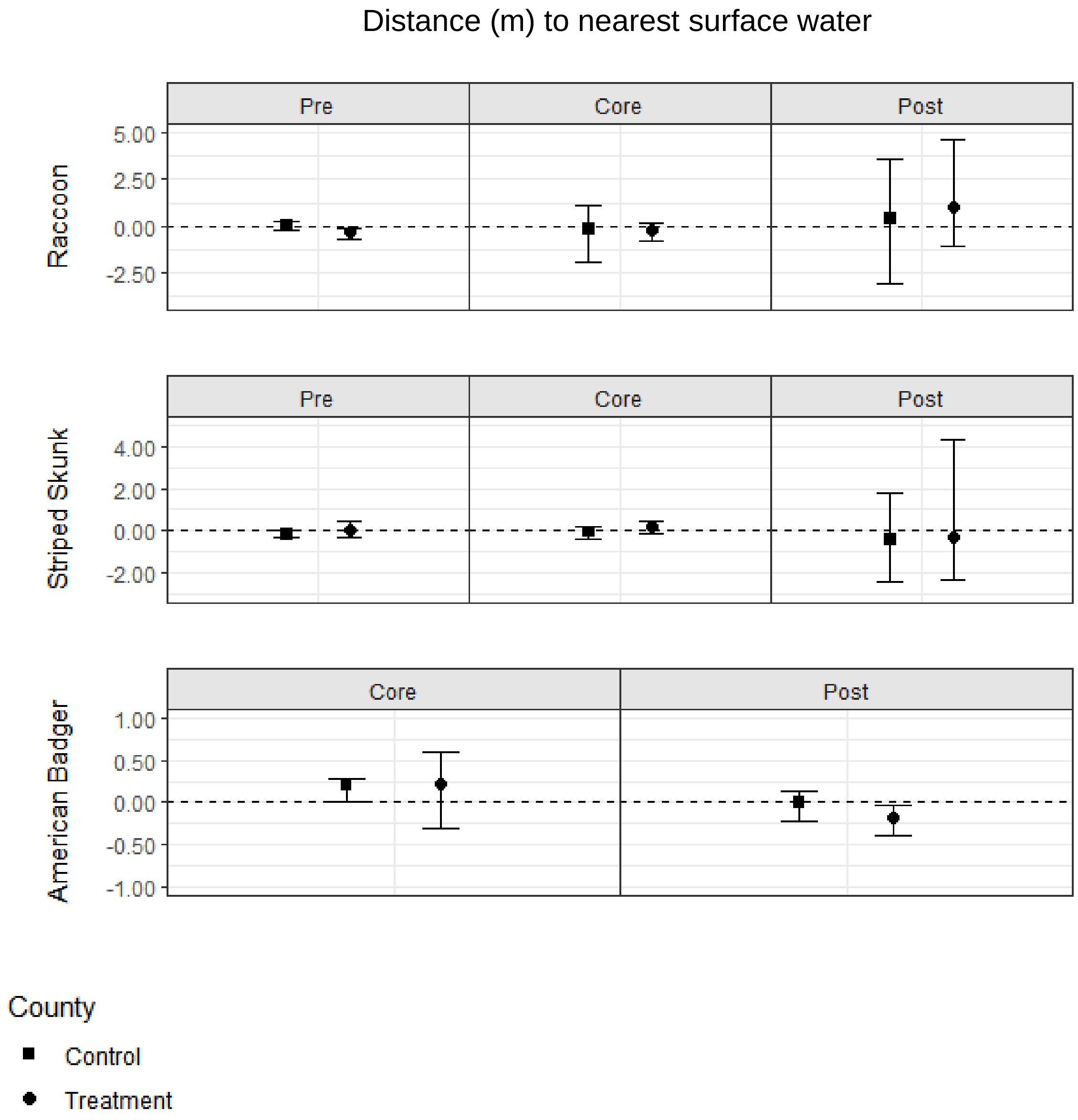
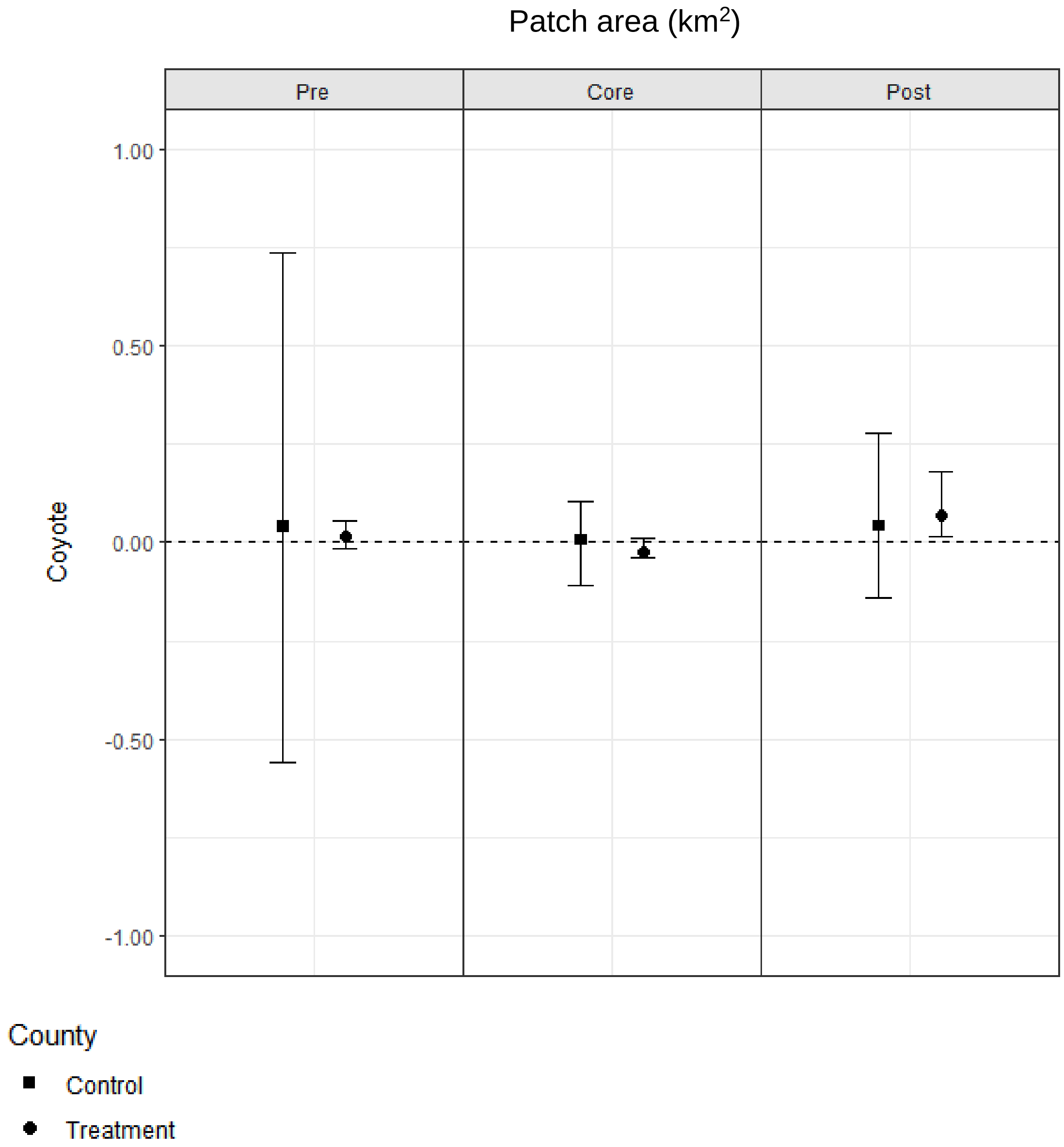

Proportion of surface water within an averaged home range area
Pre
Core
Post
Raccoon
2.00
0.00
-2.00
-4.00
Striped Skunk
8.00
4.00
0.00
Coyote
1.00
0.00
-1.00
-2.00
County
■ Control
● Treatment

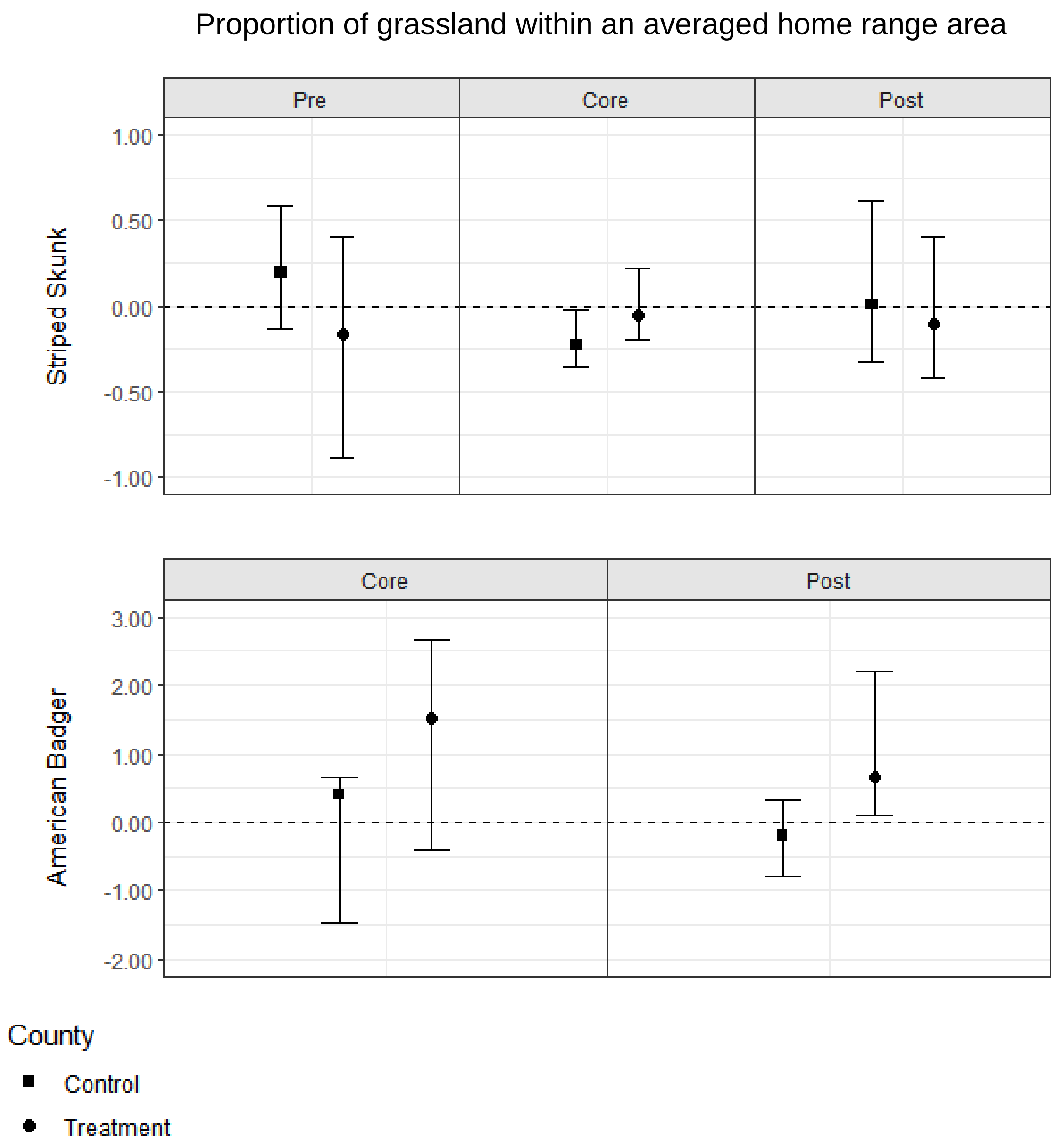
Figure 2.3. Bootstrapped population means and 95% confidence intervals from integrated step selection function models of GPS-collared raccoons, striped skunks, coyotes, and American badgers from 2018 to 2020 describing the influence of landscape characteristics on deviation from a straight direction of movement (interaction between the covariate and cosine turn angle). If space use was not significant across counties and period for a mesopredator species, it was not included.

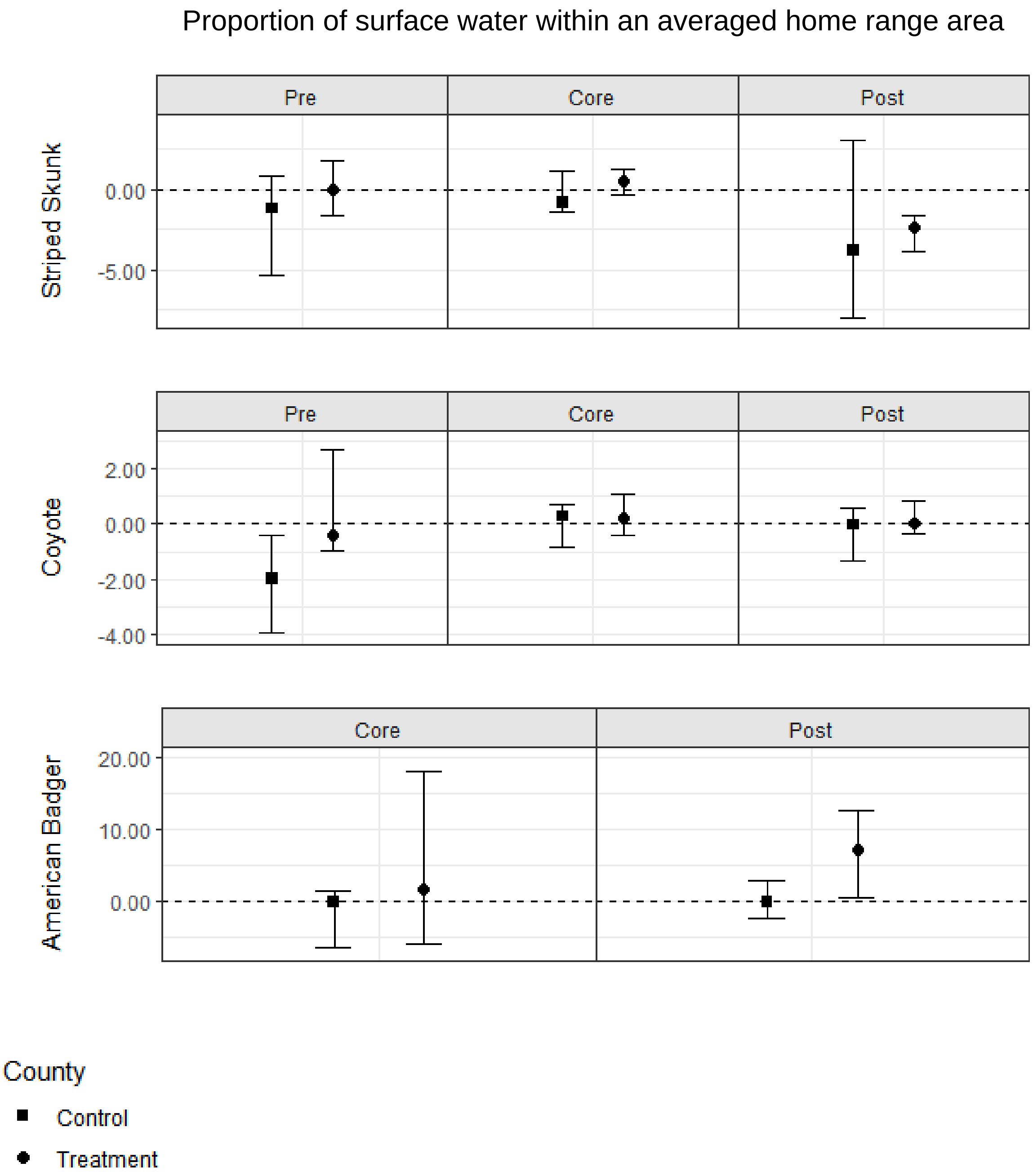

Perennial grassland cover type
Pre
Core
Post
Raccoon
Striped Skunk
Coyote
1.00
0.50
0.00
-0.50
-1.00
County
■ Control
● Treatment


Distance (m) to nearest patch edge
Raccoon
Pre
Core
Post
5.00
0.00
-5.00
-10.00
-15.00
Striped Skunk
2.50
0.00
-2.50
-5.00
Coyote
3.00
2.00
1.00
0.00
-1.00
-2.00
American Badger
1.00
0.50
0.00
-0.50
-1.00
County
Control
Treatment


Distance (m) to nearest surface water
Raccoon
Pre
Core
Post
5.00
2.50
0.00
-2.50
Striped Skunk
Pre
Core
Post
4.00
2.00
0.00
-2.00
American Badger
Core
Post
1.00
0.50
0.00
-0.50
-1.00
County
■ Control
● Treatment


Patch area (km²)
Pre
Core
Post
1.00
0.50
0.00
-0.50
-1.00
Coyote
County
■ Control
● Treatment


Proportion of grassland within an averaged home range area
Pre
Core
Post
Striped Skunk
1.00
0.50
0.00
-0.50
-1.00
Core
Post
American Badger
3.00
2.00
1.00
0.00
-1.00
-2.00
County
■ Control
● Treatment


Proportion of surface water within an averaged home range area
Striped Skunk
Pre
Core
Post
0.00
-5.00
Coyote
Pre
Core
Post
2.00
0.00
-2.00
-4.00
American Badger
Core
Post
20.00
10.00
0.00
County
■ Control
● Treatment

Appendix S2.1: Summary tables of general linear models using a Gamma distribution and log-link function to estimate variation in average 95% KDE home range, step length, and daily movement (response variables) by county, sex, year, and each unique county-period subgroup for each species.

Table S2.1.1. Model parameter estimates for general linear models of predicted average 95% KDE home range, step length, and daily movement by county, sex, year, and each unique county-period subgroup for each species.

Covariate	**Estimate**	**SE**	**p-value**
	Raccoon Home Range		
Intercept	1.094	0.247	<0.001
Control county	-0.549	0.292	0.064
Post-nesting period	0.126	0.376	0.739
Pre-nesting period	-0.094	0.270	0.728
Male	1.045	0.183	<0.001
2019	-0.216	0.217	0.322
2020	-0.157	0.234	0.506
Control county:post-nesting period	-0.004	0.578	0.994
Control county:pre-nesting period	0.389	0.394	0.326
	Raccoon Step Length		
Intercept	4.900	0.130	<0.001
Control county	-0.249	0.154	0.109
Post-nesting period	-0.058	0.198	0.770
Pre-nesting period	0.398	0.142	0.006
Male	0.393	0.096	0.000
2019	0.072	0.114	0.527
2020	0.171	0.123	0.169
Control county:post-nesting period	0.415	0.304	0.176
Control county:pre-nesting period	-0.058	0.208	0.780

Raccoon Daily Movement			
Intercept	1.202	0.112	<0.001
Control county	-0.356	0.133	0.009
Post-nesting period	-0.149	0.171	0.384
Pre-nesting period	0.060	0.122	0.624
Male	0.534	0.083	0.000
2019	-0.123	0.098	0.216
2020	-0.110	0.106	0.305
Control county:post-nesting period	0.278	0.262	0.293
Control county:pre-nesting period	0.091	0.179	0.612
Striped skunk Home Range			
Intercept	1.674	0.232	<0.001
Control county	0.025	0.294	0.933
Post-nesting period	-0.298	0.366	0.418
Pre-nesting period	-0.249	0.306	0.419
Male	0.476	0.246	0.058
2019	0.061	0.239	0.799
2020	-0.387	0.296	0.195
Control county:post-nesting period	-0.298	0.529	0.575
Control county:pre-nesting period	0.466	0.425	0.277
Striped skunk Step Length			
Intercept	5.240	0.098	<0.001
Control county	-0.071	0.124	0.572
Post-nesting period	-0.058	0.155	0.711
Pre-nesting period	0.405	0.130	0.003

Male	-0.004	0.104	0.972
2019	0.058	0.101	0.569
2020	-0.008	0.125	0.948
Control county:post-nesting period	-0.141	0.224	0.531
Control county:pre-nesting period	0.172	0.180	0.343
Striped skunk Daily Movement			
Intercept	1.222	0.099	<0.001
Control county	-0.087	0.125	0.489
Post-nesting period	-0.084	0.156	0.592
Pre-nesting period	0.233	0.130	0.079
Male	-0.033	0.105	0.752
2019	-0.063	0.102	0.538
2020	-0.085	0.126	0.503
Control county:post-nesting period	-0.162	0.225	0.476
Control county:pre-nesting period	0.048	0.181	0.790
Coyote Home Range			
Intercept	4.661	0.583	<0.001
Control county	-0.713	0.664	0.287
Post-nesting period	-0.222	0.689	0.748
Pre-nesting period	-0.751	0.928	0.422
Male	-1.068	0.410	0.012
2019	0.943	0.582	0.110
2020	2.101	0.628	0.001

Control county:post-nesting period	-0.080	0.896	0.929
Control county:pre-nesting period	-0.882	1.188	0.461
Coyote Step Length			
Intercept	5.741	0.134	<0.001
Control county	-0.004	0.152	0.979
Post-nesting period	0.309	0.158	0.055
Pre-nesting period	0.222	0.213	0.301
Male	0.153	0.094	0.110
2019	0.081	0.134	0.545
2020	-0.148	0.144	0.307
Control county:post-nesting period	-0.167	0.206	0.421
Control county:pre-nesting period	-0.053	0.273	0.846
Coyote Daily Movement			
Intercept	2.429	0.140	<0.001
Control county	-0.058	0.160	0.718
Post-nesting period	0.199	0.166	0.235
Pre-nesting period	0.187	0.223	0.404
Male	0.227	0.099	0.025
2019	-0.407	0.140	0.005
2020	-0.573	0.151	0.000
Control county:post-nesting period	-0.121	0.215	0.576
Control county:pre-nesting period	-0.410	0.286	0.157
American badger Home Range			

Intercept	1.316	0.350	0.001
Control county	0.118	0.322	0.719
Post-nesting period	0.017	0.332	0.960
Male	0.771	0.244	0.004
2020	0.013	0.267	0.961
Control county:post-nesting period	0.230	0.421	0.591
American badger Step Length			
Intercept	5.723	0.190	<0.001
Control county	-0.120	0.175	0.500
Post-nesting period	0.159	0.180	0.388
Male	0.136	0.132	0.313
2020	-0.290	0.145	0.057
Control county:post-nesting period	0.140	0.229	0.545
American badger Daily Movement			
Intercept	0.557	0.262	0.041
Control county	0.097	0.241	0.690
Post-nesting period	0.171	0.248	0.499
Male	0.065	0.182	0.724
2020	0.004	0.200	0.982
Control county:post-nesting period	0.161	0.315	0.613

Appendix S2.2: Results of integrated step-selection functions for four mesopredator species during three periods in two counties located in eastern South Dakota, USA, 2018-2020.

Table S2.2.1. Explanatory variables used in resource selection functions to compare behaviors of mesopredator species in different counties and periods in eastern South Dakota, during Feb–Nov, 2018–2020.

Covariate	Description
grasslandY	Cover type: grassland (includes fallow patches)
dist_edge	Distance to nearest edge of any cover type (m)
dist_water	Distance to nearest water cover type (m)
patch_area	Patch area (km^2)
prop95grass	Proportion of grassland cover type within the area of the respective species' average 95% KDE home range
prop95water	Proportion of water cover type within the area of the respective species' average 95% KDE home range
log_sl_	Log of the step length
cos_ta_	Cosine of the turn angle

Table S2.2.2. Ordinary nonparametric bootstrapped iSSF mean estimates and 95% confidence intervals of each covariate for each county-period pairing for each species. Statistically significant covariates have confidence intervals that do not overlap zero (α = 0.05). "Pre" refers to the combined pre- and early nesting periods (i.e., Feb. 15 – April 30), "Core" refers to the primary nesting period (i.e., May 1 – July 15), and "Post" refers to the combined late and post-nesting periods (i.e., July 16 – Nov. 15).

Covariate	**Mean**	**LCI**	**UCI**
Raccoon Pre Treatment			
grasslandY	0.539	-0.128	1.160
grasslandY:log_sl	-0.048	-0.166	0.064
grasslandY:cos_ta	-0.046	-0.191	0.096
distedge	0.139	-1.198	1.667
distedge:log_sl	-0.355	-0.640	-0.130
distedge:cos_ta	-0.054	-0.457	0.538
distwater	0.275	-1.147	1.196
distwater:log_sl	-0.066	-0.263	0.178
distwater:cos_ta	-0.345	-0.708	-0.102
patcharea	-0.039	-0.450	0.229
patcharea:log_sl	-0.024	-0.084	0.034
patcharea:cos_ta	0.035	-0.103	0.237
prop95grass	0.554	-0.785	1.572
prop95grass:log_sl	-0.049	-0.204	0.165
prop95grass:cos_ta	-0.043	-0.234	0.162
prop95water	-2.492	-15.628	5.067
prop95water:los_sl	-0.210	-1.275	1.408
prop95water:cos_ta	0.338	-1.042	2.092
log_sl	0.132	-0.781	1.186

cos_ta	0.024	-1.253	1.170
Raccoon Core Treatment			
grasslandY	0.654	0.199	1.105
grasslandY:log_sl	-0.038	-0.100	0.029
grasslandY:cos_ta	-0.170	-0.287	-0.024
distedge	0.637	-5.101	2.688
distedge:log_sl	-0.654	-1.101	-0.403
distedge:cos_ta	0.425	0.008	0.976
distwater	0.943	-1.697	3.792
distwater:log_sl	-0.387	-1.034	0.001
distwater:cos_ta	-0.191	-0.795	0.135
patcharea	-0.019	-1.138	0.762
patcharea:log_sl	-0.024	-0.158	0.082
patcharea:cos_ta	-0.052	-0.167	0.130
prop95grass	-0.144	-0.778	0.576
prop95grass:log_sl	-0.010	-0.113	0.065
prop95grass:cos_ta	0.011	-0.147	0.091
prop95water	1.059	-2.972	3.986
prop95water:los_sl	-0.508	-0.950	-0.264
prop95water:cos_ta	-0.874	-1.390	0.064
log_sl	-0.795	-2.161	0.312
cos_ta	0.388	-0.685	1.854
Raccoon Post Treatment			
grasslandY	-0.079	-0.619	0.401
grasslandY:log_sl	0.079	-0.010	0.173
grasslandY:cos_ta	0.031	-0.099	0.243
distedge	6.456	-18.425	22.863
distedge:log_sl	-3.827	-6.815	-1.116

distedge:cos_ta	-0.236	-1.315	3.165
distwater	-8.090	-26.351	3.760
distwater:log_sl	0.813	-0.960	3.597
distwater:cos_ta	0.975	-1.092	4.640
patcharea	0.383	-3.130	1.176
patcharea:log_sl	-0.079	-0.214	0.430
patcharea:cos_ta	-0.057	-0.247	0.007
prop95grass	-0.746	-2.271	1.267
prop95grass:log_sl	0.007	-0.278	0.220
prop95grass:cos_ta	0.062	-0.250	0.353
prop95water	-2.286	-4.019	-0.176
prop95water:los_sl	-0.036	-0.365	0.152
prop95water:cos_ta	-0.579	-1.403	0.446
log_sl	-1.128	-1.685	-0.362
cos_ta	0.249	-0.912	2.687
Raccoon Pre Control			
grasslandY	0.758	0.396	1.138
grasslandY:log_sl	-0.016	-0.081	0.043
grasslandY:cos_ta	-0.027	-0.105	0.039
distedge	0.451	-0.952	1.784
distedge:log_sl	-0.293	-0.535	-0.077
distedge:cos_ta	0.292	0.051	0.552
distwater	-0.859	-1.705	-0.048
distwater:log_sl	0.097	-0.054	0.244
distwater:cos_ta	0.003	-0.216	0.213
patcharea	0.739	-9.046	3.849
patcharea:log_sl	-0.092	-0.570	1.586
patcharea:cos_ta	-0.092	-0.702	1.212

prop95grass	-0.390	-2.683	1.644
prop95grass:log_sl	0.010	-0.233	0.320
prop95grass:cos_ta	0.053	-0.306	0.313
prop95water	1.530	-15.333	17.410
prop95water:los_sl	-0.738	-2.865	1.830
prop95water:cos_ta	-1.503	-3.428	0.868
log_sl	-0.226	-2.861	2.627
cos_ta	-0.096	-2.457	2.702
Raccoon Core Control			
grasslandY	0.732	0.409	1.081
grasslandY:log_sl	-0.064	-0.090	-0.022
grasslandY:cos_ta	-0.176	-0.253	-0.073
distedge	-12.734	-24.597	-0.902
distedge:log_sl	-2.280	-5.336	-0.078
distedge:cos_ta	-0.363	-3.019	1.885
distwater	-0.104	-4.911	6.333
distwater:log_sl	-0.501	-1.627	0.183
distwater:cos_ta	-0.167	-1.954	1.133
patcharea	0.241	-2.076	1.171
patcharea:log_sl	-0.039	-0.133	0.289
patcharea:cos_ta	-0.101	-0.392	1.503
prop95grass	1.599	-0.103	3.269
prop95grass:log_sl	-0.132	-0.344	0.130
prop95grass:cos_ta	0.010	-0.242	0.340
prop95water	4.319	-10.722	23.103
prop95water:los_sl	-1.083	-1.647	-0.226
prop95water:cos_ta	0.036	-1.298	1.400
log_sl	-3.236	-4.624	-1.356

cos_ta	0.031	-3.233	3.988
Raccoon Post Control			
grasslandY	0.367	-0.516	0.836
grasslandY:log_sl	0.037	-0.066	0.188
grasslandY:cos_ta	0.023	-0.123	0.238
distedge	6.208	-29.546	59.424
distedge:log_sl	-8.825	-23.941	-3.774
distedge:cos_ta	-2.311	-16.296	1.977
distwater	-11.562	-23.993	17.749
distwater:log_sl	1.317	-3.753	3.598
distwater:cos_ta	0.374	-3.033	3.546
patcharea	0.928	-0.948	6.247
patcharea:log_sl	-0.138	-1.895	0.251
patcharea:cos_ta	-0.946	-3.563	0.365
prop95grass	2.659	1.757	3.220
prop95grass:log_sl	-0.139	-0.267	-0.027
prop95grass:cos_ta	0.008	-0.191	0.273
prop95water	12.798	0.945	36.093
prop95water:los_sl	-1.592	-3.956	-0.197
prop95water:cos_ta	0.351	-2.079	3.317
log_sl	-6.588	-17.393	-2.015
cos_ta	-2.184	-11.822	2.413
Striped skunk Pre Treatment			
grasslandY	0.244	-0.239	1.083
grasslandY:log_sl	0.011	-0.153	0.110
grasslandY:cos_ta	0.059	-0.179	0.242
distedge	-0.097	-1.187	2.328
distedge:log_sl	-0.164	-0.712	0.117

distedge:cos_ta	-0.399	-0.549	-0.124
distwater	-1.310	-2.151	-0.677
distwater:log_sl	0.248	0.166	0.378
distwater:cos_ta	0.040	-0.289	0.429
patcharea	-6.722	-20.301	-0.121
patcharea:log_sl	1.187	0.053	3.681
patcharea:cos_ta	0.057	-0.821	2.901
prop95grass	0.498	-4.578	4.807
prop95grass:log_sl	-0.105	-0.757	0.611
prop95grass:cos_ta	-0.163	-0.889	0.400
prop95water	-0.594	-4.765	12.154
prop95water:los_sl	0.066	-1.781	0.829
prop95water:cos_ta	-0.022	-1.673	1.727
log_sl	1.043	-1.764	2.650
cos_ta	-0.069	-1.634	1.384
Striped skunk Core Treatment			
grasslandY	0.417	-0.463	1.149
grasslandY:log_sl	-0.039	-0.158	0.108
grasslandY:cos_ta	0.044	-0.129	0.283
distedge	0.261	-2.233	1.694
distedge:log_sl	-0.251	-0.504	0.076
distedge:cos_ta	-0.208	-0.455	0.091
distwater	-0.213	-1.975	1.978
distwater:log_sl	0.110	-0.201	0.378
distwater:cos_ta	0.197	-0.102	0.482
patcharea	-0.064	-3.417	1.092
patcharea:log_sl	0.078	-0.066	0.549
patcharea:cos_ta	-0.080	-0.490	0.253

prop95grass	0.847	-0.394	1.867
prop95grass:log_sl	-0.255	-0.335	-0.095
prop95grass:cos_ta	-0.050	-0.199	0.225
prop95water	-5.811	-9.984	1.075
prop95water:los_sl	0.531	-0.626	1.263
prop95water:cos_ta	0.532	-0.317	1.242
log_sl	0.374	-0.322	1.287
cos_ta	0.880	0.360	1.552
Striped skunk Post Treatment			
grasslandY	-0.334	-0.850	0.413
grasslandY:log_sl	0.094	-0.098	0.246
grasslandY:cos_ta	0.166	-0.067	0.404
distedge	2.745	-3.880	27.687
distedge:log_sl	-1.465	-5.678	0.041
distedge:cos_ta	0.844	-3.212	3.227
distwater	3.220	-22.662	12.403
distwater:log_sl	-0.359	-1.591	3.205
distwater:cos_ta	-0.302	-2.377	4.307
patcharea	-0.491	-6.040	12.219
patcharea:log_sl	-0.021	-2.033	1.617
patcharea:cos_ta	-0.133	-1.430	2.309
prop95grass	-0.007	-2.096	1.432
prop95grass:log_sl	-0.035	-0.210	0.292
prop95grass:cos_ta	-0.107	-0.424	0.407
prop95water	9.743	2.227	17.585
prop95water:los_sl	-1.651	-2.847	-0.613
prop95water:cos_ta	-2.421	-3.818	-1.583
log_sl	-0.689	-2.762	0.666

cos_ta	0.295	-2.160	3.303
Striped skunk Pre Control			
grasslandY	-0.857	-1.475	-0.145
grasslandY:log_sl	0.165	0.055	0.263
grasslandY:cos_ta	0.075	-0.081	0.247
distedge	-1.301	-3.114	0.778
distedge:log_sl	0.025	-0.325	0.300
distedge:cos_ta	0.203	-0.370	0.820
distwater	0.509	-1.612	2.786
distwater:log_sl	-0.123	-0.512	0.245
distwater:cos_ta	-0.168	-0.346	-0.011
patcharea	0.146	-1.300	7.782
patcharea:log_sl	-0.066	-1.271	0.165
patcharea:cos_ta	0.172	-0.929	0.460
prop95grass	-1.274	-3.111	1.009
prop95grass:log_sl	0.187	-0.199	0.487
prop95grass:cos_ta	0.193	-0.136	0.586
prop95water	-3.860	-13.425	21.179
prop95water:los_sl	0.204	-2.528	1.578
prop95water:cos_ta	-1.201	-5.358	0.818
log_sl	-1.168	-1.965	-0.503
cos_ta	-0.667	-2.916	0.560
Striped skunk Core Control			
grasslandY	0.521	0.223	0.806
grasslandY:log_sl	-0.046	-0.086	-0.005
grasslandY:cos_ta	-0.011	-0.170	0.166
distedge	-0.542	-3.611	1.472
distedge:log_sl	-0.005	-0.324	0.470

distedge:cos_ta	-0.042	-0.475	0.333
distwater	0.068	-1.452	1.688
distwater:log_sl	-0.036	-0.246	0.163
distwater:cos_ta	-0.059	-0.393	0.218
patcharea	0.140	-4.467	1.863
patcharea:log_sl	-0.026	-0.267	0.678
patcharea:cos_ta	0.053	-0.479	1.049
prop95grass	0.785	-2.245	3.233
prop95grass:log_sl	-0.150	-0.448	0.234
prop95grass:cos_ta	-0.225	-0.356	-0.026
prop95water	3.024	-27.930	10.967
prop95water:los_sl	-0.599	-1.591	4.029
prop95water:cos_ta	-0.843	-1.401	1.144
log_sl	0.550	-0.446	3.323
cos_ta	0.283	-0.645	1.695
Striped skunk Post Control			
grasslandY	-1.068	-1.829	-0.091
grasslandY:log_sl	0.267	0.051	0.468
grasslandY:cos_ta	0.243	0.087	0.347
distedge	-1.418	-28.944	25.146
distedge:log_sl	-1.023	-6.279	3.375
distedge:cos_ta	-0.266	-4.667	2.746
distwater	0.679	-7.597	14.969
distwater:log_sl	-0.504	-3.040	1.074
distwater:cos_ta	-0.420	-2.444	1.837
patcharea	0.529	-13.291	8.819
patcharea:log_sl	-0.093	-2.107	2.392
patcharea:cos_ta	-0.025	-0.728	2.755

prop95grass	1.669	0.980	2.543
prop95grass:log_sl	-0.251	-0.486	-0.103
prop95grass:cos_ta	0.009	-0.327	0.619
prop95water	-18.118	-42.031	-2.119
prop95water:los_sl	2.332	-1.362	9.082
prop95water:cos_ta	-3.834	-7.981	3.097
log_sl	0.637	-3.967	4.659
cos_ta	-1.459	-3.399	1.964
Coyote Pre Treatment			
grasslandY	-0.387	-0.608	0.196
grasslandY:log_sl	0.095	0.053	0.120
grasslandY:cos_ta	0.067	-0.253	0.219
distedge	0.581	-2.046	1.401
distedge:log_sl	-0.056	-0.743	0.042
distedge:cos_ta	-0.261	-0.709	2.819
distwater	-0.255	-0.991	1.630
distwater:log_sl	0.000	-0.370	0.220
distwater:cos_ta	0.226	-0.918	0.461
patcharea	-0.126	-0.268	0.025
patcharea:log_sl	0.002	-0.008	0.017
patcharea:cos_ta	0.016	-0.017	0.054
prop95grass	-1.921	-3.330	0.010
prop95grass:log_sl	0.201	0.060	0.324
prop95grass:cos_ta	0.017	-0.288	0.666
prop95water	-5.889	-9.881	8.374
prop95water:los_sl	0.231	-0.629	0.654
prop95water:cos_ta	-0.431	-0.948	2.681
log_sl	0.226	-0.465	0.450

cos_ta	-0.334	-2.158	2.562
Coyote Core Treatment			
grasslandY	-0.041	-0.307	0.238
grasslandY:log_sl	0.042	0.001	0.086
grasslandY:cos_ta	0.058	0.010	0.101
distedge	0.543	-0.332	1.776
distedge:log_sl	-0.104	-0.361	-0.002
distedge:cos_ta	-0.102	-0.884	0.240
distwater	-0.727	-2.651	-0.105
distwater:log_sl	0.058	-0.010	0.252
distwater:cos_ta	0.141	-0.081	0.521
patcharea	-0.012	-0.115	0.079
patcharea:log_sl	-0.005	-0.017	0.006
patcharea:cos_ta	-0.023	-0.037	0.009
prop95grass	-0.321	-1.306	0.537
prop95grass:log_sl	-0.004	-0.046	0.071
prop95grass:cos_ta	0.096	-0.073	0.297
prop95water	-2.803	-8.008	1.434
prop95water:los_sl	0.033	-0.122	0.438
prop95water:cos_ta	0.202	-0.401	1.060
log_sl	0.024	-0.122	0.373
cos_ta	0.027	-0.401	0.935
Coyote Post Treatment			
grasslandY	-1.284	-1.813	-0.775
grasslandY:log_sl	0.185	0.111	0.260
grasslandY:cos_ta	0.243	0.174	0.341
distedge	1.168	-1.632	8.060
distedge:log_sl	-0.198	-1.396	0.130

distedge:cos_ta	-0.369	-1.265	0.285
distwater	-0.129	-2.703	2.540
distwater:log_sl	0.000	-0.270	0.454
distwater:cos_ta	0.050	-0.564	0.620
patcharea	-0.037	-0.530	0.246
patcharea:log_sl	-0.009	-0.039	0.033
patcharea:cos_ta	0.071	0.015	0.182
prop95grass	-0.666	-1.784	0.092
prop95grass:log_sl	0.011	-0.028	0.101
prop95grass:cos_ta	-0.011	-0.116	0.075
prop95water	-0.450	-6.109	4.128
prop95water:los_sl	-0.042	-0.300	0.327
prop95water:cos_ta	0.039	-0.357	0.848
log_sl	-0.107	-0.654	0.185
cos_ta	-0.124	-1.020	0.364
Coyote Pre Control			
grasslandY	0.202	-0.382	0.586
grasslandY:log_sl	0.014	-0.037	0.073
grasslandY:cos_ta	0.024	-0.029	0.081
distedge	0.265	-0.091	0.653
distedge:log_sl	-0.048	-0.091	-0.003
distedge:cos_ta	-0.006	-0.164	0.132
distwater	-0.071	-0.261	0.099
distwater:log_sl	0.021	-0.009	0.054
distwater:cos_ta	0.038	-0.070	0.191
patcharea	-0.920	-5.780	0.418
patcharea:log_sl	0.083	-0.115	0.450
patcharea:cos_ta	0.041	-0.561	0.736

prop95grass	1.986	-0.647	5.020
prop95grass:log_sl	-0.062	-0.347	0.110
prop95grass:cos_ta	-0.174	-0.997	0.307
prop95water	8.964	0.929	22.152
prop95water:los_sl	-0.666	-1.554	-0.195
prop95water:cos_ta	-2.003	-3.971	-0.417
log_sl	-0.332	-0.916	-0.091
cos_ta	-1.244	-2.029	-0.765
Coyote Core Control			
grasslandY	-0.038	-0.188	0.128
grasslandY:log_sl	0.055	0.036	0.073
grasslandY:cos_ta	0.026	-0.020	0.076
distedge	0.352	0.176	0.539
distedge:log_sl	-0.048	-0.069	-0.026
distedge:cos_ta	-0.056	-0.122	0.024
distwater	-0.166	-0.308	-0.061
distwater:log_sl	0.027	0.006	0.049
distwater:cos_ta	0.035	-0.019	0.097
patcharea	0.035	-0.743	0.191
patcharea:log_sl	-0.009	-0.077	0.031
patcharea:cos_ta	0.006	-0.107	0.106
prop95grass	0.454	-0.463	2.197
prop95grass:log_sl	-0.001	-0.052	0.037
prop95grass:cos_ta	0.026	-0.175	0.156
prop95water	1.655	-2.332	9.977
prop95water:los_sl	0.080	-0.303	0.270
prop95water:cos_ta	0.263	-0.860	0.706
log_sl	0.007	-0.304	0.158

cos_ta	0.065	-0.781	0.360
Coyote Post Control			
grasslandY	-0.449	-0.716	-0.189
grasslandY:log_sl	0.091	0.040	0.139
grasslandY:cos_ta	0.121	0.051	0.174
distedge	0.394	0.231	0.545
distedge:log_sl	-0.075	-0.099	-0.053
distedge:cos_ta	-0.094	-0.149	-0.041
distwater	-0.183	-0.372	0.032
distwater:log_sl	0.007	-0.018	0.028
distwater:cos_ta	0.058	-0.010	0.148
patcharea	-0.164	-0.718	0.340
patcharea:log_sl	0.022	-0.102	0.062
patcharea:cos_ta	0.042	-0.141	0.277
prop95grass	0.325	-0.630	0.920
prop95grass:log_sl	0.001	-0.039	0.029
prop95grass:cos_ta	-0.002	-0.100	0.057
prop95water	0.495	-4.486	9.701
prop95water:los_sl	-0.071	-0.516	0.235
prop95water:cos_ta	-0.026	-1.342	0.564
log_sl	-0.086	-0.497	-0.001
cos_ta	-0.021	-1.321	0.255
American badger Core Treatment			
grasslandY	1.052	-1.086	3.288
grasslandY:log_sl	-0.059	-0.490	0.293
grasslandY:cos_ta	-0.048	-0.687	0.360
distedge	2.445	1.744	3.333
distedge:log_sl	-0.484	-0.598	-0.339

distedge:cos_ta	-0.200	-0.854	0.272
distwater	0.273	-1.972	2.076
distwater:log_sl	0.063	-0.304	0.464
distwater:cos_ta	0.211	-0.307	0.598
patcharea	2.109	-0.587	9.273
patcharea:log_sl	-0.394	-1.880	-0.137
patcharea:cos_ta	0.021	-0.438	3.615
prop95grass	-12.386	-16.562	-6.271
prop95grass:log_sl	1.495	0.772	3.669
prop95grass:cos_ta	1.514	-0.418	2.652
prop95water	-9.856	-46.490	44.955
prop95water:los_sl	-0.819	-8.339	2.408
prop95water:cos_ta	1.548	-6.168	18.197
log_sl	-0.743	-3.017	1.128
cos_ta	0.492	-4.674	12.909
American badger Post Treatment			
grasslandY	0.803	-1.073	2.535
grasslandY:log_sl	-0.130	-0.376	0.168
grasslandY:cos_ta	-0.111	-0.315	0.125
distedge	-0.031	-0.738	1.619
distedge:log_sl	-0.115	-0.384	0.018
distedge:cos_ta	0.240	-0.139	0.620
distwater	0.471	-0.838	1.329
distwater:log_sl	-0.014	-0.125	0.179
distwater:cos_ta	-0.177	-0.381	-0.024
patcharea	2.017	-5.471	4.269
patcharea:log_sl	-0.313	-1.087	0.922
patcharea:cos_ta	0.229	-0.099	1.301

prop95grass	0.293	-8.788	6.134
prop95grass:log_sl	0.123	-0.736	1.929
prop95grass:cos_ta	0.654	0.111	2.218
prop95water	-22.164	-60.287	49.934
prop95water:los_sl	2.132	-9.252	7.719
prop95water:cos_ta	7.040	0.408	12.579
log_sl	1.436	-4.616	4.556
cos_ta	4.460	0.341	8.745
American badger Core Control			
grasslandY	0.796	-0.373	2.174
grasslandY:log_sl	-0.093	-0.319	0.139
grasslandY:cos_ta	0.053	-0.064	0.248
distedge	0.843	0.237	1.494
distedge:log_sl	-0.209	-0.364	-0.107
distedge:cos_ta	-0.152	-0.375	-0.050
distwater	-0.861	-1.323	0.170
distwater:log_sl	0.217	0.027	0.312
distwater:cos_ta	0.198	0.020	0.282
patcharea	1.321	-1.311	4.996
patcharea:log_sl	-0.196	-0.658	0.142
patcharea:cos_ta	-0.223	-4.306	2.848
prop95grass	-1.926	-17.560	0.614
prop95grass:log_sl	0.337	-0.117	2.183
prop95grass:cos_ta	0.403	-1.462	0.647
prop95water	4.358	-9.983	21.016
prop95water:los_sl	0.675	-1.860	1.625
prop95water:cos_ta	-0.196	-6.618	1.268
log_sl	0.490	-1.347	1.916

cos_ta	-0.128	-5.061	1.233
American badger Post Control			
grasslandY	-0.009	-0.818	0.526
grasslandY:log_sl	0.061	-0.032	0.185
grasslandY:cos_ta	0.061	-0.125	0.286
distedge	-2.425	-3.329	-0.261
distedge:log_sl	0.365	-0.067	0.581
distedge:cos_ta	0.011	-0.331	0.253
distwater	0.640	-1.248	2.088
distwater:log_sl	-0.047	-0.306	0.281
distwater:cos_ta	0.006	-0.218	0.130
patcharea	0.823	-4.424	8.342
patcharea:log_sl	-0.172	-1.205	0.908
patcharea:cos_ta	-0.283	-0.656	0.080
prop95grass	-7.113	-17.596	2.434
prop95grass:log_sl	0.969	-0.366	2.098
prop95grass:cos_ta	-0.197	-0.798	0.326
prop95water	11.616	-69.724	36.295
prop95water:los_sl	-1.430	-4.663	9.856
prop95water:cos_ta	-0.225	-2.518	2.721
log_sl	-0.826	-4.105	9.687
cos_ta	0.136	-2.879	2.801

Incorporating mesopredator space use into nest survival models for upland-nesting ducks

ABSTRACT

As cropland conversion of native grasslands and wetlands continues in the Prairie Pothole Region, managers are tasked with maintaining sustainable waterfowl productivity. When landscape characteristics have been identified as influential to duck nest survival, past researchers hypothesized that mesopredator densities and space use were primary mechanisms driving these relationships. I simultaneously quantified space use of mesopredators and monitored duck nests to better understand predator-prey interactions in eastern South Dakota, where two different ongoing strategies of coyote removal management occurred during 2018-2020. I developed predator-derived covariates using occupancy models and integrated step-selection functions of four mesopredator species to explain spatiotemporal variation in nest survival. Using logistic exposure models and fates of 1,728 nests, I found that predator-derived covariates for distance to nearest surface water and patch area landscape characteristics best explained variation in daily nest survival compared to associated traditional nest site metrics. However, direct nest site metrics were more often sufficient in quantifying variables that influenced nest survival. Our results suggested a strong association between increased seasonal space use and movement rates of mesopredators during the pre-nesting period and decreased daily nest survival rates of early-nest initiating waterfowl species (i.e., mallards [0.961, 95% CI = 0.950, 0.971] and northern pintails [0.966, 95% CI = 0.960, 0.971]) compared to later-nest initiating waterfowl species (i.e., gadwall [0.978, 95% CI = 0.972, 0.983] and blue-winged teal [0.974, 95% CI = 0.971, 0.978]) that may indicate increased depredation risk at times of lower food resources (e.g., early spring). Importantly, our study provided support for the mesopredator release hypothesis and revealed that ongoing standardized annual coyote removal (i.e., the treatment county) indirectly reduced nest survival via increased occupancy, greater movements, more extensive space use by subordinate mesopredators due to decreased interspecific competition; daily nest survival rates were 0.974 (95% CI = 0.971, 0.978) in the control county compared to 0.965 (95% CI = 0.961, 0.969) in the treatment county. While understanding spatiotemporal predator-prey dynamics is important for appropriate and efficient habitat and wildlife management to mitigate declines in waterfowl productivity on a fragmented landscape, creating and incorporating predator-derived covariates may be unnecessary.

KEY WORDS dabbling ducks, mesopredators, nest survival, Prairie Pothole Region, South Dakota

The Prairie Pothole Region (PPR) of North America historically was a mosaic of wetlands and grasslands that supports high densities of breeding waterfowl (Anatidae; Reynolds 2000). Past and continuing conversion of native grassland to cultivated cropland and drainage of wetlands in the PPR have created a fragmented landscape, specifically for breeding ducks, which require both habitats to successfully reproduce (Reynolds and Shaffer 2007, Wong et al. 2012, Bartzen et al. 2017, Lark 2020). Nest survival is one of the most influential factors affecting population dynamics of birds (Ricklefs 1969, Martin 1995, Hoekman 2002), and depredation is the major cause of waterfowl nest failure (54-85%; Klett et al. 1988, Sargeant and Raveling 1992). Many species of various taxa consume waterfowl eggs, but medium-sized mammalian predators, hereafter mesopredators, generally have the greatest impact on nest survival (Sovada et al. 2000, Phillips et al. 2003, 2004).

Fragmentation of the PPR has coincided indirectly with declines in duck production because of mesopreadtor behaviors and resultant increased predator-prey interactions (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007, Amundson et al. 2012). Factors reported to influence duck nest fates include patch size (Crabtree et al. 1989), the amount of grassland habitat and wetland density in the nesting area (Stephens et al. 2005), and cover density (Schranck 1972, Lokemoen et al. 1984). Predation rates of nests have been hypothesized to relate to landscape and patch metrics because many mesopredator species tend to increase in relative abundance with increasing edge habitat due to more foraging opportunities and reduced nest cover that increases foraging efficiency (Clark and Shutler 1999, Ray 2000). In this scenario, nest depredation rates become diluted with increasing patch size (Phillips et al. 2003, Horn et al. 2005) and nests in heavier cover are more protected via camouflage (Schranck 1972, Lokemoen et al. 1984). Proximity of neighboring active nests and date of nest initiation have also been found to explain variation in duck nest survival (Andrén 1995, Ringelman 2014, Ringelman et al. 2018), suggesting that mesopredators exhibit seasonal and density-dependent predation (Crabtree et al. 1989, Schmidt and Whelan 1999, Ackerman 2002, Larivière and Messier 2000, 2001, Nams 1997, Phillips et al. 2003, 2004). Lastly, some evidence supports the idea that predator community composition may also influence duck nest survival (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003).

Local anthropogenic reduction in predator density (hereafter, predator management) has been conducted in attempts to increase duck nest survival and, subsequently, local recruitment. Several studies have indeed found that removing nest predators from the landscape increased duck nest survival (Schranck 1972, Greenwood 1986, Garrettson and Rohwer 2001, Shively 2003, Pearse and Ratti 2004, Pieron and Rohwer 2010, Pieron et al. 2012). However, removal of a dominant community member may result in a mesopredator release. The mesopredator release hypothesis (hereafter, MRH) predicts that removal or reduction in density or distribution of a dominant predator will result in increased densities, greater movements, more extensive space use by subordinate mesopredators due to decreased interspecific competition (Estes 1996, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). As a result, some studies have suggested that a lack of suppression of mesorpedators by dominant predators may lead to decreased nest survival (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003). Therefore, predator management of dominant species in the PPR (i.e., coyotes) may indirectly decrease duck nest survival.

Despite investigations suggesting mesorpedator space use and resource selection may drive variation in duck nest survival, simultaneous investigations of mesopredators and duck nest survival has been rare. Therefore, I used camera-traps to better understand relationships between mesopredators, their environment, and one another (Gompper et al. 2006, Kelly et al. 2012). Additionally, I used radio-telemetry data (Kays et al. 2015), a more-invasive but fine-scale method, to quantify associations between space use and current landscape characteristics as a means to understand nest predator space use, movements, and their relationships with duck nest survival. Simultaneous data collection and incorporation of estimates into nest survival models can be directly integrated into nest survival analyses to test hypotheses about mechanisms behind factors influencing nest survival and provide insights on the influence of landscape characteristics and predator-prey interactions on nest survival.

By gaining a better understanding of space use by different mesopredator species in relation to duck nest survival, habitat management efforts can be developed more precisely to minimize nest depredation. Our results may also influence predator management decisions based on how nest survival could vary among differing mesopredator community compositions and space use patterns. Additionally, our results may guide future studies in identifying what data are necessary to accurately describe predator-prey interactions in the PPR. By utilizing spatiotemporal data from four mesopredator species (Fino Chapters 1 and 2), I developed and integrated predator-derived covariates into nest survival models. Our objectives were to: (1) estimate waterfowl nest survival in two counties with different coyote densities due to coyote removal management; (2) identify whether landscape-level covariates or corresponding predator-derived covariates better described variation in nest survival, and; (3) within the best hypothesized mechanism (landscape- vs. predator-derived covariates), determine which specific factors best explained variation in nest survival in eastern South Dakota. Overall, our aim was to identify which mesopredator movement patterns in relation to landscape characteristics supported hypothesized mechanisms of duck nest survival in the PPR so that waterfowl productivity could be more efficiently and effectively managed.

METHODS

Study Area

We studied nest survival of dabbling ducks in four townships in the neighboring Faulk and Hand Counties in eastern South Dakota from 2018-2020. I selected adjacent counties with similar amounts and composition of grasslands and wetlands, and townships with high predicted breeding duck pair densities based on the USFWS thunderstorm map (Reynolds et al. 2006). Importantly, the treatment county (Faulk) has had ongoing standardized annual coyote removal (i.e., via aerial gunning) since the 1990s, thus influencing coyote relative abundance in that county (Fino Chapter 1), whereas no standardized coyote removal has occurred in the control county (Hand; B. Curtis, South Dakota Department of Game, Fish and Parks [SDGFP], personal communication). The proximity of sites and long-standing contrast in coyote removal management allowed for an efficient investigation of nesting and predator ecology simultaneously and specifically with respect to potential differences due to predator management.

Both counties are on the western edge of the Prairie Coteau ecoregion of the PPR. Average elevation is ~481 m above MSL in both counties and the annual average temperature ranged from -6° C (December) to 21° C (June), during 2018–2020. The average annual precipitation during 2018-2020 was 55 cm of rainfall and 93 cm of snowfall (US Climate Data, 2020). Both counties were rural; the treatment county had a population of 2,299 people whereas the control county's population was 3,191 people and both counties averaged 0.5 housing units/km^2 and average human densities of 1.5 people/km^2 (US Census Bureau 2019). The landscape was a mosaic of croplands, pastures, and grasslands/haylands that surrounded farmsteads. Agricultural composition of the treatment county was approximately 16% corn (*Zea mays*), 22% soybean (*Glycine max*), and 29% pasture, whereas the control county was generally similar with approximately 14% corn, 19% soybean, and 36% pasture.

Nest searching and monitoring

We systematically searched grasslands for upland nesting ducks during May through July 2018-2020 with crews of 2 persons that dragged a 50 m cable-chain behind ATVs (Klett et al. 1986) between 0800 and 1400, to maximize the probability of hens being on nests (Gloutney et al. 1993, Sovada et al. 2000, Loos and Rohwer 2004, Walker 2011). The area I were able to search each year was based on landowner permission, access, and flooding. When crews located a nest, they recorded UTM coordinates and marked them with a flag placed 10 m north of the nest (Fisk 2010). Crews recorded clutch size, estimated incubation stage by candling (Weller 1956), and revisited each nest every 7-10 days until the nest was either destroyed, abandoned (hen absent and no advance in incubation), or successful (≥1 egg hatched; Klett et al. 1986). Assuming a laying rate of 1 egg/day, I estimated nest initiation dates by backdating based on clutch size and estimated incubation stage. I removed from analyses that I were unable to relocate or believed were abandoned due to investigator disturbance.

Small mammal index of abundance

We conducted small mammal trapping surveys during the waterfowl nesting season (aforementioned dates in 2018-2020) to estimate indices of small mammal abundance. I surveyed the small mammal community using 8.9×7.6×22.9 cm Sherman traps (H.B. Sherman Inc., Tallahassee, TN, USA) and 49.0×15.2×15.2-cm live-capture #202 Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, WI, USA). I placed traps 10 m apart in 8×10 grids covering 80m^2 of grass nesting cover and replicated this in each township once per month, 3 times per year. I randomly selected grid locations within the townships, separated by ≥5 km (Mohr 1947). Traps were deployed Sunday evenings and retrieved at the end of the sampling period. I baited traps with a peanut butter-oats mixture frozen as a bait ball and rebaited as necessary. I checked traps at 0700 and 1900 daily for 4 consecutive days to assess local species richness (Manley et al. 2006). Non-functioning traps, where the door was closed without capture, bait was missing without capture, or a trap was missing or broken, were reset, rebaited, or replaced (Nelson and Clark 1973). I soaked traps in a mild beach solution (CDC recommends 45 ml/3.8 liters) for 10 minutes between trapping weeks as necessary (Mills et al. 1995). Trapping and handling methods followed the guidelines approved by the American Society of Mammalogists for wild animals in research (Sikes et al. 2016) and were reviewed and approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 17-103A).

We recorded trap outcomes, such as if a trap was open, sprung, or sprung with a capture, and when a capture occurred I recorded species, sex, age (juveniles or adults), breeding status (pregnant, lactating, enlarged testes or nonbreeding), and weight prior to release (Kunz et al. 1996). I marked new captures with numbered ear tags (Kent Scientific Corporation, Torrington, CT, USA) and noted previously captured individuals prior to release. Due to low recapture rates, I used count data, a Poisson distribution, and a generalized linear model to estimate index of abundance of small mammals among counties, townships, years and surveys (1-3), using the total number of unique individuals (all species included) captured in a survey as the dependent variable. I conducted parametric bootstrapped pairwise comparisons with a 95% confidence interval to test for differences in estimated indices of abundance among counties, townships, years, and surveys.

Raptor index of abundance

We conducted opportunistic roadside surveys during the waterfowl nesting season (5 May 2018-28 July 2018, 4 May 2019-27 July 2019, 2 May 2020-25 July 2020) to index the abundance of raptor and corvid species in the study areas (Andersen et al. 1985, Fuller and Mosher 1987, Andersen 2007). When a raptor or corvid was spotted, I recorded the date, time, location, species, number of individuals, and activity of the individual(s). I used a 0.5 km radius around each raptor record, based on minimum observed home range size of a breeding pair of commonly occurring raptor species (Preston and Beane 1993, Bennett and Bloom 2005), and removed any duplicate observations. I indexed abundance using count data of observed number of individual raptors in each township (± 5 individuals to account for observer error) and acknowledge that this was a descriptive variable.

Environmental covariates

We measured vegetation within grassland fields that were searched for nesting waterfowl. After nest fate has been determined, I visually estimated percent cover of grasses, forbs, bare ground, and litter in 1 m^2 quadrats 5 m away in each cardinal direction from the nest site as well as at the nest (Daubenmwere 1959, Madden et al. 2000). At each nest visit, I used a modified Robel pole (Benkobi et al. 2000) to estimate vertical height and density of vegetation at nest sites as well as at a 5 m distance from the nest in each cardinal direction (Robel 1970). Effective leaf height was considered as the average height of tallest grass leaves within 5 m of the Robel pole (Quamen 2007). I measured litter depth with a ruler (Fisk 2010) and considered dead vegetation from previous years as litter where it has formed a mat-like layer, roughly continuous to the ground (Madden et al. 2000). These environmental covariates (percentage of grass, forbs, bare ground, litter,

litter depth, and low and high vegetation height measurements), collected at the nest and averaged from each cardinal direction, represented potential local influences on duck nest survival (i.e., cover). Other local metrics believed to influence duck nest survival either directly or indirectly and included in analysis were relative nest density, distance to nearest neighboring active nest and the fate of that nest, initiation date, and estimated hatch date. Lastly, county- and township-level covariates included the indices of raptor density and small mammal abundance, respectively, as raptors may kill hens which leads to nest failure (Andersen et al. 1985, Ramakka and Woyewodzic 1993, Devries et al. 2003, Taylor 2003, Andersen 2007) and small mammals may contribute to nest depredation events (Sargeant et al. 1998, Garrettson and Rohwer 2001) and serve as prey to mesopredators.

We also quantified patch-level metrics believed to influence duck nest survival by creating a cover type layer for each year in ArcMap 10.5.1. This layer combined year-specific rasters from the USGS Dynamic Surface Water Extent using Landsat Collection 1 Level-3 and the USDA National Agricultural Statistics Service CropScape Cropland data layer. I believe this provided the best time-specific and detailed depiction of land cover for each year during the study, and these year-specific land cover rasters were used delineate year-specific covariate rasters. I identified 9 patch-level environmental covariates for each nest that may influence duck nest survival: distance (m) to nearest surface water and edge (including roads) land cover types, patch area (km^2), and percentages of surface water, row crop, and perennial cover each at two spatial scales (10.4 km^2 and 41.4 km^2; Reynolds et al. 2001, Stephens et al. 2005).

Because landscape-level covariates influence duck nest survival indirectly via mesopredator space use (Sargeant et al. 1993, Beauchamp et al. 1996, Drever et al. 2007, Phillips et al. 2003, 2004, Horn et al. 2005, Amundson et al. 2012, Crimmins et al. 2015), I compiled modified environmental covariates derived from simultaneous collected mesopredator data and results (Fino Chapters 1 and 2). I derived 3 species-specific space use metrics that were the product of the nest's corresponding value for each landscape covariate and associated estimated slope parameter (β) for resource selection, step-length, and turn-angle from the integrated step-selection functions (Fieberg et al. 2021) during the core nesting period. Species-specific betas were available for distance to surface water, distance to edge, patch area, percentage of surface water and percentage of perennial cover within the species-specific average KDE home range area, and respectively corresponded with the patch-level environmental covariates for each nest. For each landscape covariate and each of the three predator space use betas, I also included an additive predator covariate that was a composite of all four species, each weighted by the respective occupancy covariate, for a community-level perspective (104 total derived predator covariates). This additive predator-derived covariate incorporated species-specific space use relative to the landscape characteristic (Fino Chapter 2) as well as a metric representative of variation of occupancy across the landscape to best describe a cumulative risk of nest depredation. The species-specific occupancy probability (Ψ) used in this process was the averaged site-specific occupancy probability estimates from the associated most supported model within an average home range area of the nest (Fino Chapter 1). The predator-modified covariates allowed for different predator species to have individualized relationships with patch and landscape variables (Fino Chapter 2) and inclusion of species-specific occupancy probabilities based on nest predator community compositions that varied across the study area allowed for an index of intensity of space use.

We centered and scaled landscape covariates so they were standardized to the mean and standard deviation prior to analysis. I tested all covariates for collinearity (r); if $r > 0.65$ for two covariates, I remedied this by eliminating one of the two predictors so both covariates were not included in the same model (Vatcheva et al. 2016). For some pairs or sets of related covariates with high collinearity (e.g., percentages of surface water at 10.4 km^2 and 41.4 km^2, or percentage of grass at the nest and averaged percentage of grass surrounding the nest), ad hoc single-variable models were competed against one another to identify the covariate that explained the most variability in nest survival; related highly-collinear covariates that explained less variability in nest survival than their counterparts were removed from further analyses. Because I found high collinearity between predator-derived covariates across all species for each landscape characteristic (i.e., similar space use patterns between species, Fino Chapter 2), the aforementioned additive community-level covariates were used in nest survival models to capture holistic depredation risk to active nests. Additionally, there was generally high collinearity between the patch-level environmental covariate at the nest and the 3 corresponding space use predation-level covariates. I used this information to develop ad hoc singular competing models to identify which derived covariate of each landscape characteristic best explained variation in nest survival. I used Akaike's Information Criterion (AIC) for competing models ($\Delta AIC \leq 2$), and if the direct patch-level environmental covariate at the nest was competitive with any corresponding predator-derived covariate, the direct nest metric version of the covariate remained in the analysis over the predator-derived covariates. However, if multiple predator-derived covariates explained more variation in nest survival compared to the corresponding patch-level environmental covariate at the nest, those predator-derived covariates remained in analysis but were not used in the same global model for estimating nest survival.

We used logistic exposure (Shaffer 2004) to estimate the daily survival rate of nests as a function of year, county, species, nest site habitat covariates, landscape-level habitat covariates, and predator-derived space use covariates (White and Burnham 1999). For each landscape characteristic, I used either the direct landscape-level habitat metric associated with nest locations or the additive predator-derived covariate. If the frequency of presence of each covariate in competing models (ΔAIC ≤ 2.0) was >50%, the covariate was determined to be an informative variable and was used in developing the model from which to predict daily nest survival rates (hereafter, DSR) and probability of nest success. Direction and magnitude of parameter estimates and associated variance estimates were used to evaluate meaningfulness of associations.

RESULTS

Field sampling and landscape characteristics

During field seasons, I searched for nests in the annual average areas (± SD) of the following townships: 12.7 km^2 (± 2.1) in Alden, 8.5 km^2 (± 4.0) in Bryant, 10.0 km^2 (± 2.0) in Fairview, and 11.3 km^2 (± 4.0) in Saratoga. I marked 1,728 waterfowl nests (Table 3.1), comprised of 848 blue-winged teal (*Anas discors*), 148 gadwall (*Mareca strepera*), 10 green-winged teal (*Anas carolinensis*), 93 mallard (*Anas platyrhynchos*), 402 northern pintail (*Anas acuta*), 221 northern shoveler (*Spatula clypeata*), and 6 redhead (*Aythya* *americana*). I did not include green-winged teal and redhead nests in nest survival analyses due to small sample sizes. Landscape and habitat characteristics associated with nests were summarized to describe the study area (Table 3.2).

Small mammal and raptor indices of abundance

We captured 189 individual small mammals during 2018, 143 individuals in 2019, and 187 individuals in 2020. Average capture success (i.e., catch/effort) was 7.5% ± 1.1% in 2018, 3.1% ± 0.7% in 2019, and 4.4% ± 1.3% in 2020. Our most-supported generalized linear Poisson model failed to detect differences in index of abundance between townships in any year. The index of small mammal abundance was greater in 2018 and 2020 than in 2019, and was 1.8-2.6 times greater in surveys conducted in later months compared to earlier months (Appendix S1.2).

We counted 328 raptors (Appendix S3.1) during the study. **I** estimated approximately 42 raptors per township in the control county and 31 raptors per township in the treatment county in 2018, 43 and 31, respectively, in 2019, and 42 and 30, respectively, in 2020.

Nest survival

The direct patch-level metric at the nest for distance to nearest patch edge and percentages of grassland and surface water within a 41.4 km^2 radius better explained nest survival variation compared to the predator-derived versions of the covariates for these landscape characteristics. The predator-derived space use covariate for distance to nearest surface water and patch area better explained nest survival variation compared to the direct nest site versions of the covariates for these landscape characteristics. After removing correlated covariates and running all possible combinations of remaining covariates, 71 models were within <2 ΔAIC (Appendix S3.2). Our final model I used for inference included: county, waterfowl species, small mammal index of abundance, percentages of bare ground within a 1 m^2 area around the nest, fate of the nearest neighboring nest on the day the nest was initially found, nest density of the patch when searched, average height of grass at each cardinal point 10 m from the nest, and percentage of surface water within a 41.4 km^2 radius about the nest site (Table 3.3).

DSR and probability of nest success was 0.974 (95% CI = 0.971, 0.978) and 43% (95% CI = 38-47%) respectively in the control county, and 0.965 (95% CI = 0.961, 0.969) and 31% (95% CI = 26-35%) respectively in the treatment county. DSR and probability of nest success of gadwall (0.978, 95% CI = 0.972, 0.983 and 47%, 95% CI = 38-56% respectively) and blue-wing teal (0.974, 95% CI = 0.971, 0.978 and 43%, 95% CI = 38-47% respectively) was greater than that of mallards (0.961, 95% CI = 0.950, 0.971 and 27%, 95% CI = 18-36% respectively) and Northern pintails (0.966, 95% CI = 0.960, 0.971 and 31%, 95% CI = 26-37% respectively; Figs. 3.1 and 3.2). DSR and probability of nest success increased 1-3% for each additional small mammal, each 1% increase in bare ground within a 1 m^2 area around the nest, each individual (1 nest/patch) increase in nest density of the patch on date of nest searching effort, and each 1 cm increase in vegetation height (Figs. 3.3 and 3.4). DSR and probability of nest success was 0.981 (95% CI = 0.978, 0.983) and 52% (95% CI = 47%, 57%) respectively if the nearest neighboring nest at time of nest searching effort was successful, and 0.967 (95% CI = 0.962, 0.971) and 33% (95% CI = 28%, 38%), respectively, if it failed.

DISCUSSION

Mesopredator space use and behaviors are often considered mechanisms of spatiotemporal variation in duck nest survival (Palmer 1988, Stenseth and Lidicker 1992, Sargeant et al. 1993, Beauchamp et al. 1996, Phillips et al. 2004, Drever et al. 2007, Amundson et al. 2012). By simultaneously assessing predator community composition and resource selection of multiple mesopredator species (Fino Chapters 1 and 2) in conjunction with duck nest monitoring, our findings contribute to a more comprehensive understanding of predator-prey relationships in the PPR. Our study is one of the first to incorporate direct mesopredator occupancy, habitat selection, and movement patterns into nest survival models to evaluate predator-derived landscape covariates in explaining variation in duck nest survival that may provide potential improvements to traditional methods. Additionally, our analyses revealed the comparative influence of predator-derived covariates with the associated landscape characteristics in explaining nest survival, thereby informing future projects on efficient study design and sufficient variables of interest to quantify. Lastly, our results provided insight on how differing coyote removal management strategies may indirectly affect nest survival (Terborgh and Winter 1980, Soule et al. 1988, Estes 1996, Gehrt and Clark 2003).

In the context of our study area, no predator-derived covariates were informative variables in most supported nest survival models (i.e., the frequency of presence in competing models [ΔAIC ≤ 2.0] was <50%). However, when compared individually to other within-landscape characteristics, predator-derived covariates sometimes performed better. Mesopredator resource selection and movement rates have been identified as mechanisms of nest survival in relation to distance to nearest surface water (Phillips et al. 2003, Stephens et al. 2005) and patch size (Crabtree et al. 1989, Sargeant et al. 1993, Beauchamp et al. 1996, Clark and Shutler 1999, Ray 2000, Stephens et al. 2003, Horn et al. 2005, Drever et al. 2007, Amundson et al. 2012). Sometimes, though, direct nest site metrics sufficed, perhaps because mesopredators are generalists and, as such, predator-derived covariates were not appreciably better in describing variation in nest survival.

Depredations of nests by mesopredators could be largely incidental when hunting for prey. The relationship between nest survival and fate of nearest neighboring nest at time of the nest searching effort coincided with observed and common prey searching behavior of mesopredators during the core nesting period (Fino Chapter 2). Mesopredators selected for landscape characteristics associated with increased food resource availability (Bowman and Harris 1980, Sietman et al. 1994, Nocera and Dawe 2008, Haffele et al. 2013), suggesting they may key in on specific prey once encountering it and congregate in areas of high nest density (Crabtree et al. 1989, Ackerman 2002, Larivière and Messier 2000, 2001, Nams 1997, Phillips et al. 2003, 2004). Our results also support those of previous studies, in that nest depredation events can be diluted in patches with higher nest densities (Andren 1991, Larivière and Messier 2000, 2001, Phillips et al. 2003, 2004, Ringelman 2012, 2014) and nests may be better camouflaged from mesopredators when patches have taller cover (Schranck 1972, Lokemoen et al. 1984, 1990, Clark and Shutler 1999, Phillips et al. 2004). Not only does vegetation, as protection for nests and a food resource for mesorpedators, grow as the nesting season progressed, but I also observed a positive association between nest survival and the small mammal index of abundance, as well as the increasing trend of small mammal index of abundance over time (i.e., summer). With increased food resource availability and accessibility evenly distributed across the landscape, animal become satiated providing safety for the remaining prey.

Although season date was not present in the most supported nest survival model, I detected a strong association between nest survival of early-initiating species and seasonal movement rates of mesopredators that may indicate increased depredation risk earlier in the nesting season. Mallards and Northern pintail initiate nests earlier than other waterfowl species in the PPR, and our study revealed lower nest survival rates for these species compared to species like Gadwall and blue-wing teal that nest later in the season. Additionally, increased estimated detection rates for raccoons at times of lower food resources (e.g., early spring; Fino Chapter 1) coincided with greater average step lengths and daily movement rates of radio-marked raccoons and striped skunks during the pre-nesting period compared to other times of the year (Fino Chapter 2). These results suggest that mesopredators modified movement patterns (increased movement rates and home range size) to find adequate common resources when food was in shorter supply (Greenwood 1981, Sovada et al. 1995, Greenwood et al. 1999, Sovada et al. 2000, Phillips et al. 2003, 2004, Azevedo et al. 2006, Haffele et al. 2013). Contradicting temporal density-dependent theories of decreased nest survival as the nesting season progresses due to search-image development by mesopredators (Ringelman et al. 2018), increased space use earlier in the nesting season, when food resources are relatively low, may elevate the risk of depredation of nests initiated earlier in the year. Our results indicate that risk of nest failure may decline as alternative food resources become available and accessible on the landscape as the nesting season progresses.

Our results suggest that duck nest survival was indirectly influenced by variation in coyote densities caused by on-going coyote removal management activities, a prediction of the MRH. The reduction in density and distribution of coyotes in the treatment county resulted in increased densities, greater movements, more extensive space use by subordinate mesopredators due to decreased interspecific competition (Estes 1996, Terborgh et al. 1999, Prugh et al. 2009, Brashares et al. 2010). Coyote occupancy probability was 44% lower and raccoon occupancy probability 30% greater in the treatment than the control county (Fino, Chapter 1), providing evidence of different predator community compositions between counties. Further, raccoons had larger home ranges and longer daily movements in the treatment compared to the control county, and I observed behavioral differences between species in the control county that indicated smaller mesopredators altered their space use (Fino, Chapter 2), potentially to avoid or decrease encounters with coyotes and minimize predation risk (Heithaus 2001, Holt and Huxel 2007, Wilson et al. 2010). Consequently, the lack of coyote-induced suppression of mesopredators resulted in lower nest survival (Sovada et al. 1995, Crooks and Soule 1999, Henke and Bryant 1999, Gompper 2002, Gehrt and Clark 2003).

On a productive landscape that can support levels of seasonal nest success adequate to promote duck population sustainability (>15-20%; Cowardin et al. 1985, Greenwood 1986, Klett et al. 1986, Greenwood et al. 1990), expensive efforts to understand fine-scale spatiotemporal mesopredator space use may not be necessary to quantify or incorporate, and traditional nest site metrics may suffice in understanding factors influencing duck nest survival. Our study revealed that predator-based covariates may better describe variation in nest survival for certain landscape characteristics, thus supporting some hypotheses from previous studies. However, knowledge of mesopredator habitat selection and movement rates to inform more effective management strategies may only be impactful in the context of harsh environmental conditions when additive and confounding pressures to nest survival are present. Importantly, our project revealed potential top-down implications of coyote removal management efforts (Sovada et al. 1995, Estes 1996, Crooks and Soule 1999, Henke and Bryant 1999, Terborgh et al. 1999, Gompper 2002, Gehrt and Clark 2003, Prugh et al. 2009, Brashares et al. 2010) and may be used to develop alternative considerations, such as seasonal timing or focal species, when considering predator management strategies to encourage waterfowl productivity.

MANAGEMENT IMPLICATIONS

It is evident that coyote reduction in the treatment county, as a result of coyote removal management, had an indirect influence of upland nesting gamebirds. More specifically, the community-level effects of coyote-specific removal management should be holistically evaluated. Historically, removing smaller mesopredators from the landscape resulted in increased duck nest survival (Garrettson and Rohwer 2001, Chodachek and Chamberlain 2006, Pearse and Lester 2007, Pieron and Rohwer 2010, Pieron et al. 2012), however the top-down impacts from coyote removal management in relation to duck nest survival were previously unknown. I suspect landowners may perceive coyotes as causing a greater negative effect because of their perception of coyote predation of livestock and other game species (e.g., white-tailed deer [*Odocoileus virginianus*]) as a result of a common social construct surrounding coyotes (Kellert 1985, Treves and Karanth 2003, Graham et al. 2005), however they are unfamiliar with the impacts that lethal coyote management may indirectly have on upland game bird productivity. Focusing on the removal of coyotes associated with livestock-damage and human-wildlife conflict versus a blanketed county-wide effort may be a more appropriate way to balance the needs of the public with those of the ecosystem. Lastly, studies across the nation have found general support for lethal predator control (Messmer et al. 1999, Slagle et al. 2017), and I believe this is likely due to the discrepancy of perspectives between the proximate (i.e., depredations) and ultimate (i.e., habitat loss and fragmentation) causes of nest failure (Fino et al. *in press*). As a result, outreach and educational programs by state and federal agencies that describe reducing nest depredation rates in different, sustainable, value-added ways (e.g., Conservation Reserve Program) may increase regional awareness of how protection or restoration of contiguous grasslands in row crop dominated systems can provide valuable resources to increase game bird abundances. Further, an emphasis on maximizing primary nesting habitats is integral when developing effective management options for increasing upland game bird productivity, and improving ecosystem health as a whole.

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DATA ACCESSIBILITY STATEMENT

Data will be archived and deposited in Dryad's publicly accessible repository.

CONFLICT OF INTEREST

The authors have declared that no competing interested exist.

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Table 3.1. Summary of sample sizes from duck nest searching efforts in eastern South Dakota, 2018-2020.

Year	2018	2019	2020	Total
Area searched (km^2)	56	36	36	128
Dates of search	23 April to 11 July	6 May to 12 July	3 May to 12 July	
Nests marked	109	684	935	1,728
Successful nests	40	343	479	862
Depredated nests	58	312	379	749
Inviable or abandoned nests	11	29	77	117

Table 3.2. Summary of landscape and nest site covariates for duck nests found in eastern South Dakota, USA, 2018-2020.

Covariate	**Range**	**Mean**	**SD**	**Median**
Distance to nearest surface water (m)	0.0–624.3	97.2	75.5	84.9
Distance to nearest cover type edge (m)	0.0–365.0	48.9	52.7	30.0
Patch area (km^2)	<1.0–292.5	15.1	49.8	2.7
Percentage of surface water cover type within a 10.4 km^2 radius	4.4–74.1	33.8	12.6	31.7
Percentage of row crop cover type within a 10.4 km^2 radius	0.6–30.3	16.8	6.8	16.8
Percentage of perennial cover type within a 10.4 km^2 radius	14.8–77.2	47.4	11.4	49.2
Percentage of surface water cover type within a 41.4 km^2 radius	15.3–64.1	37.5	9.5	38.4
Percentage of row crop cover type within a 41.4 km^2 radius	1.4–30.5	15.9	6.3	15.6
Percentage of perennial cover type within a 41.4 km^2 radius	28.3–64.0	44.6	7.3	43.8
Percent grass at nest site	0.0–100.0	63.6	25.8	70.0
Percent forbs at nest site	0.0–100.0	11.2	19.0	0.0
Percent bare ground at nest site	0.0–80.0	4.0	9.2	0.0
Percent litter at nest site	0.0–75.0	15.0	15.7	10.0
Average percent grass around nest site	0.0–100.0	57.4	22.1	60.0
Average percent forbs around nest site	0.0–100.0	10.7	14.2	5.0
Average percent bare around nest site	0.0–65.0	5.5	10.7	0.0
Average percent litter around nest site	0.0–77.5	20.2	17.4	17.5
Average tallest height of grass at nest	0.0–248.8	48.4	21.0	46.3
Average shortest height of grass at nest	0.0–100.0	31.5	14.0	30.0
Relative distance of nearest neighboring nest (m)	<1.0–2,598.8	123.2	193.4	74.5
Nest density at time of field search	1.0–122.0	41.2	30.2	36.0
Age of nest when found	1.0–35.0	14.0	7.6	13.0
Estimated initiation date (Julian)	99.0–192.0	142.0	17.1	140.0
Estimated hatch date (Julian)	135.0–224.0	175.0	16.2	173.0

Table 3.3. Model parameter estimates for the best approximating generalized linear model formulated to explain variation in nest survival (*n* = 1,728 nests) in eastern South Dakota, USA, 2018-2020.

Parameter	**Estimate**	**SE**	**95% CI**
Intercept	2.433	0.147	2.145 – 2.721
County	-0.324	0.070	-0.461 – -0.187
Spp: GADW	0.136	0.137	-0.133 – 0.405
Spp: MALL	-0.446	0.139	-0.718 – -0.174
Spp: NOPI	-0.308	0.083	-0.471 – 0.145
Spp: NSHO	-0.159	0.104	-0.363 – 0.045
SM	0.020	0.007	0.006 – 0.034
NestBareground	0.008	0.004	0.001 – 0.016
NNestFate	0.553	0.070	0.416 – 0.690
Nestdens	0.007	0.001	0.005 – 0.009
ARH	0.007	0.002	0.003 – 0.011
Water_414	0.126	0.072	-0.015 – 0.267

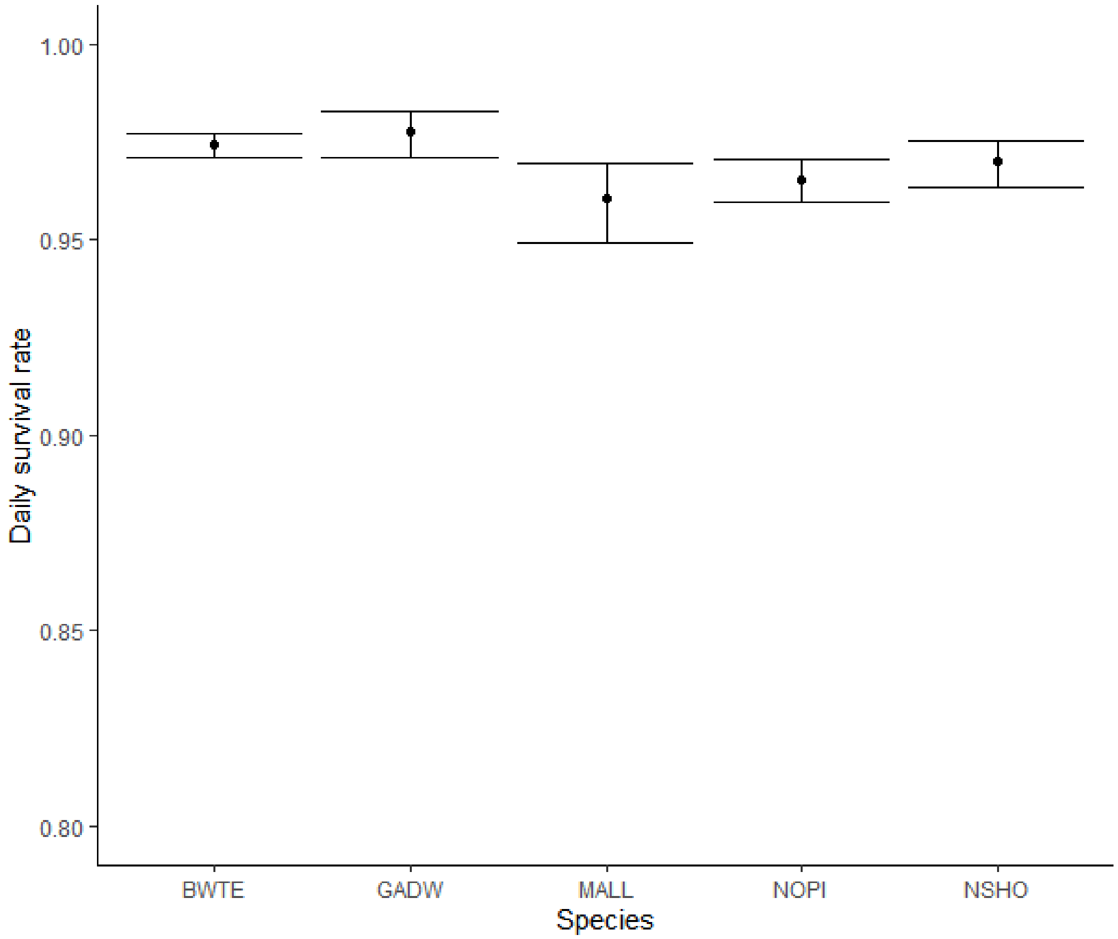

Figure 3.1. Daily nest survival rate and 95% confidence intervals by waterfowl species in eastern South Dakota, USA, from 2018 to 2020.

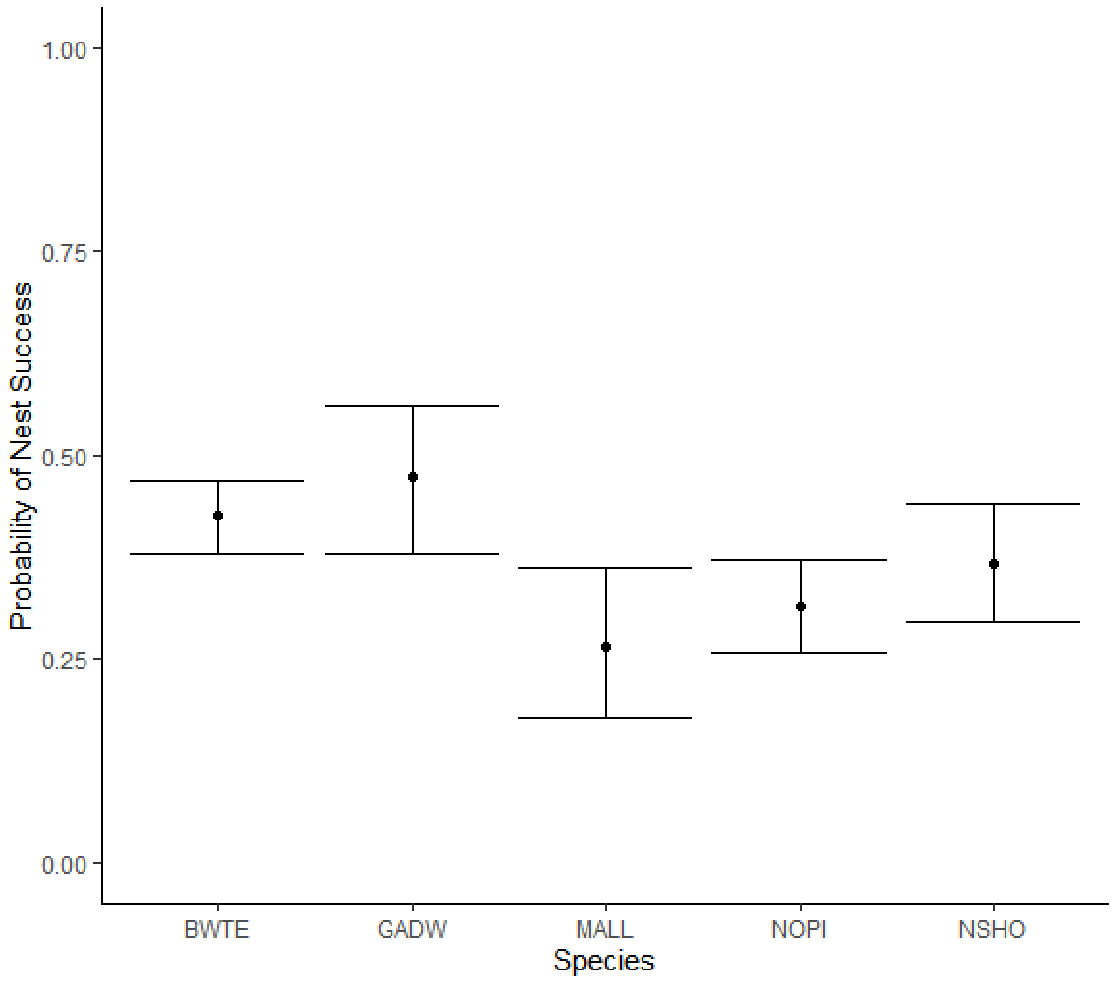

Figure 3.2. Seasonal nest success and 95% confidence intervals by waterfowl species in eastern South Dakota, USA, from 2018 to 2020.

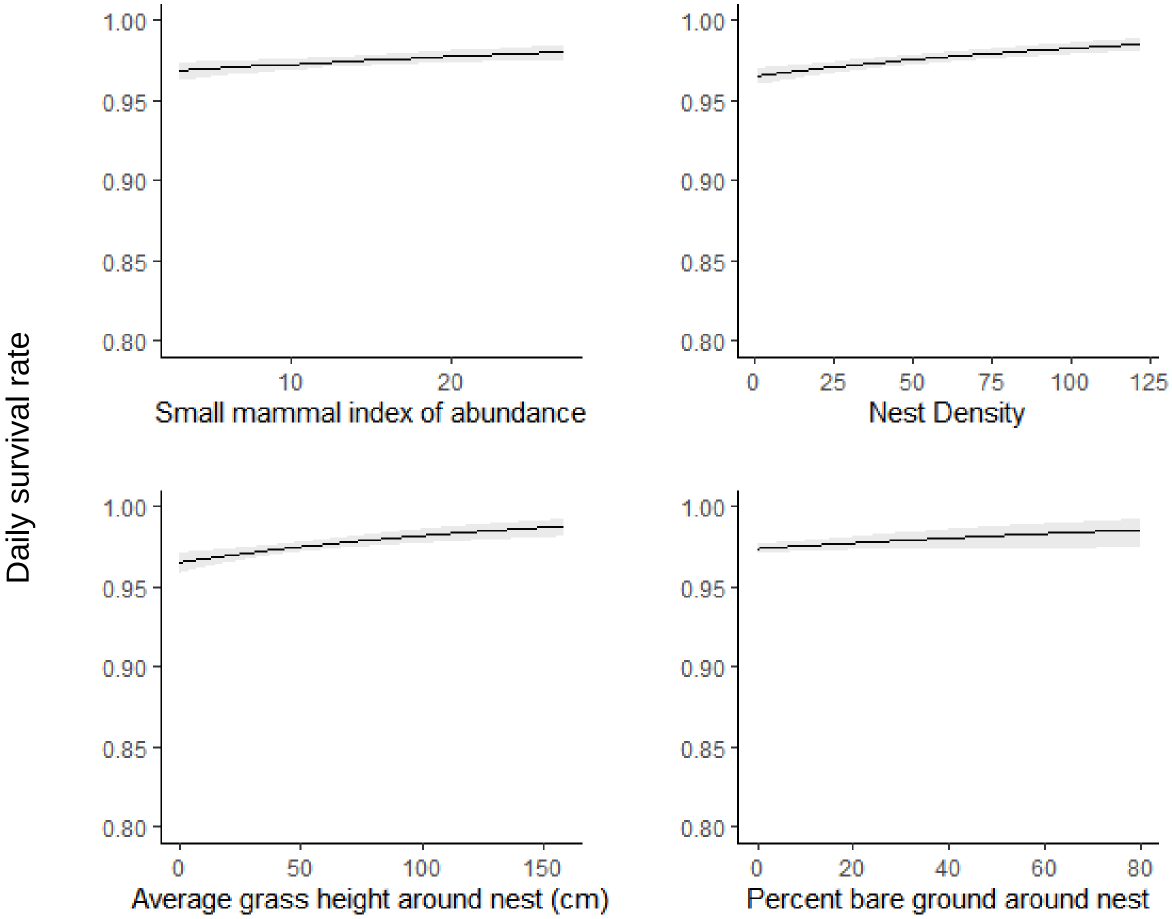

Figure 3.3. Daily nest survival rate and 95% confidence intervals as a function of influential landscape characteristics from the best supported model in eastern South Dakota, USA, from 2018 to 2020.

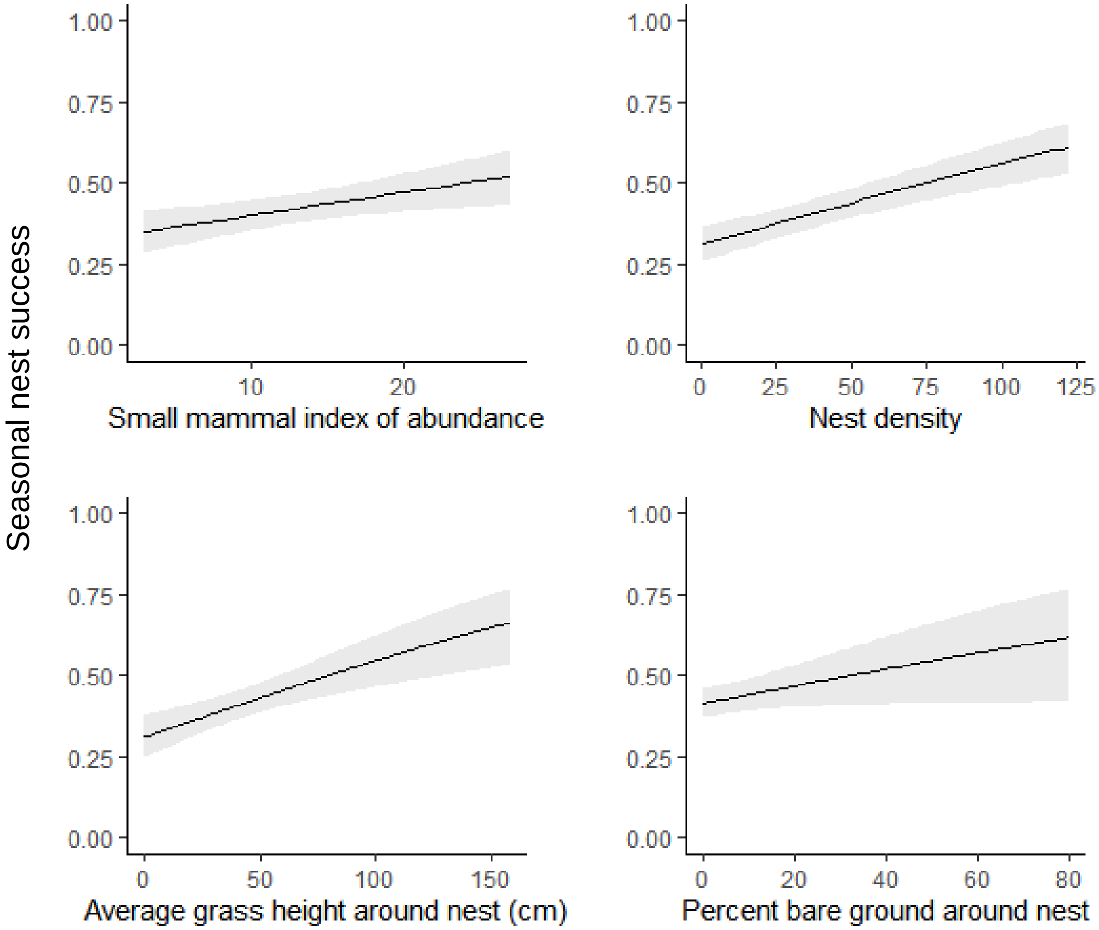

Figure 3.4. Seasonal nest success and 95% confidence intervals as a function of influential landscape characteristics from the best supported model in eastern South Dakota, USA, from 2018 to 2020.

Appendix S3.1: Summarized data for raptor index of abundance in eastern South Dakota, USA, 2018-2020.

Table S3.1.1. Summary of raptors detected by species. Burrowing owl (*Athene cunicularia*), bald eagle (*Haliaeetus leucocephalus*), golden eagle (*Aquila chrysaetos*), and rough-legged hawk (*Buteo lagopus*) were <5 for any year and thereby not included below.

Year	Red-tailed hawk (*Buteo jamaicensis*)	Northern harrier (*Circus hudsonius*)	Swainson's hawk (*Buteo swainsoni*)	Great horned owl (*Bubo virginianus*)
2018	108	25	23	14
2019	103	30	1	4
2020	98	33	4	6
Total	176	88	28	24

Appendix S3.2: Summarized model selection results of relative support for generalized linear binomial models incorporating logistic exposure (Shaffer 2004) with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics for 5 landscape covariates in eastern South Dakota, USA, 2018-2020.

Table S3.2.1. Explanatory variables used in candidate generalized linear binomial models to evaluate variation in nest survival in eastern South Dakota, during May–July, 2018–2020.

Variable	Description
NestMetric	Direct covariate of the landscape characteristic from the active nest location
Pred_Select	Predator-derived covariate relating to the selection of the landscape characteristic
Pred_Step	Predator-derived covariate involving the movement rate in relation to the landscape characteristic
Pred_Turn	Predator-derived covariate involving the movement direction in relation to the landscape characteristic
Year	2018-2020
County	Treatment or Control
Species	MALL, NOPI, NSHO, BWTE, GADW, etc.
Day	Nesting season date
Raptor	Index of abundance of raptors
SM	Index of abundance of small mammals
NestForbs	Proportion of forbs within 1m^2 around nest
NestBareground	Proportion of bare ground within 1m^2 around nest
AvgGrass	An average of proportion of grass within 1m^2 area 10m from nest in each cardinal direction
AvgLitter	An average of proportion of litter within 1m^2 area 10m from

	nest in each cardinal direction
NNestFate	Fate of nearest neighboring nest at time of nest searching effort
NNestDist	Distance to nearest neighboring nest at time of nest searching effort (m)
Nestdens	Nest density of patch at time of nest searching effort
ARH	Average highest height of grass at each cardinal point of nest (cm)
Distedge	Distance from active nest to nearest patch edge
Peren_414	Proportion of perennial cover within a 41.4km^2 radius around active nest
Water_414	Proportion of surface water within a 41.4km^2 radius around active nest
Pred _distwater	The additive predator-derived covariate involving movement in relation to distance to nearest surface water (m)
Pred_patcharea	The additive predator-derived covariate involving movement in relation to patch area (km^2)

Table S3.2.2. Summarized model selection results of relative support for generalized linear binomial models with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics in relation to distance to nearest surface water.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
~Pred_Turn	2	4220.67	0.00	0.44	-2108.33
~Pred_Step	2	4221.56	0.89	0.28	-2108.78
~Pred_Select	2	4222.06	1.40	0.22	-2109.03
~NestMetric	2	4224.77	4.10	0.06	-2110.39

Table S3.2.3. Summarized model selection results of relative support for generalized linear binomial models with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics in relation to distance to nearest patch edge.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
~Pred_Turn	2	4224.13	0.00	0.33	-2110.06
~Pred_Select	2	4224.33	0.20	0.30	-2110.16
~NestMetric	2	4224.49	0.37	0.28	-2110.25
~Pred_Step	2	4226.60	2.48	0.10	-2111.30

Table S3.2.4. Summarized model selection results of relative support for generalized linear binomial models with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics in relation to patch area.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
~Pred_Step	2	4221.61	0.00	0.58	-2108.80
~Pred_Turn	2	4223.03	1.43	0.29	-2109.52
~Pred_Select	2	4225.40	3.79	0.09	-2110.70
~NestMetric	2	4226.68	5.08	0.05	-2111.34

Table S3.2.5. Summarized model selection results of relative support for generalized linear binomial models with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics in relation to proportion of grassland within a 10.4 km^2 and 41.4 km^2 radius.

Model	K	AIC_c	ΔAIC_c	w_i	LL
~NestMetric	2	4225.87	0.00	0.16	-2110.93
~Pred_Turn_41.4	2	4225.88	0.01	0.16	-2110.94
~Pred_Step_41.4	2	4226.03	0.17	0.15	-2111.02
~Pred_Select_41.4	2	4226.07	0.20	0.15	-2111.03
~Pred_Select_10.4	2	4226.35	0.49	0.13	-2111.18
~Pred_Turn_10.4	2	4226.37	0.51	0.13	-2111.19
~Pred_Step_10.4	2	4226.40	0.53	0.12	-2111.20

Table S3.2.6. Summarized model selection results of relative support for generalized linear binomial models with nest survival as the response variable comparing the direct nest metric with 3 additive predator-derived metrics in relation to proportion of surface water within a 10.4 km^2 and 41.4 km^2 radius.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
~NestMetric	2	4208.31	0.00	1.00	-2102.16
~Pred_Select_41.4	2	4223.95	15.64	0.00	-2109.98
~Pred_Step_10.4	2	4224.11	15.80	0.00	-2110.06
~Pred_Select_10.4	2	4224.41	16.09	0.00	-2110.20
~Pred_Turn_41.4	2	4224.85	16.54	0.00	-2110.43
~Pred_Turn_10.4	2	4225.31	17.00	0.00	-2110.66
~Pred_Step_41.4	2	4225.39	17.08	0.00	-2110.69

Table S3.2.7. Summarized model selection results of relative support for generalized linear binomial models for nest survival, comparing global models that contain different combinations of covariates present in previously competing ad hoc single models. The global portion of the models include: Year + County + Species + Day + Raptor + SM + NestForbs + NestBareground + AveGrass + AvgLitter + NNestFate + NNestDist + Nestdens + ARH + Distedge + Peren_414 + Water_414.

Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
~Global+TurnDistWater+TurnPatchArea	25	4062.45	0.00	0.18	-2006.19
~Global+SelectDistWater+TurnPatchArea	25	4062.52	0.07	0.17	-2006.23
~Global+StepDistWater+TurnPatchArea	25	4062.55	0.10	0.17	-2006.24
~Global+TurnDistWater+StepPatchArea	25	4062.60	0.15	0.17	-2006.27
~Global+SelectDistWater+StepPatchArea	25	4062.68	0.23	0.16	-2006.31
~Global+StepDistWater+StepPatchArea	25	4062.70	0.23	0.16	-2006.32

Table S3.2.8. Frequency of covariate presence in summarized model selection results of relative support for competitive (<2 ΔAIC) generalized linear binomial models for nest survival. Using covariates from the global model, 524,288 combinations were considered.

Covariate	Frequency (%)	Number of models with covariate present (*n* = 71)
Year	24.54	16
County	100.00	71
Species	100.00	71
Day	46.48	33
Raptor	8.45	6
SM	100.00	71
NestForbs	15.49	11
NestBareground	84.51	60
AvgGrass	16.90	12
AvgLitter	49.30	35
NNestFate	100.00	71
NNestDist	1.41	1
Nestdens	100.00	100
ARH	100.00	71
Distedge	36.62	26
Peren_414	5.63	4
Water_414	63.38	45
Pred _distwater	4.23	3

Pred_patcharea	11.27	8