Assessing occupancy and functional connectivity of eastern massasaugas (*Sistrurus catenatus*) across an agricultural-prairie landscape in northern Ohio

Thesis

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By

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Abstract

The federally threatened eastern massasauga rattlesnake (*Sistrurus catenatus*) occurs across the Great Lakes region of the midwestern United States in increasingly small and fragmented populations. While massasaugas are relatively well-studied among snakes, much is still unknown about their baseline habitat requirements, as well as how they move across heterogeneous landscapes. One of the most stable remaining populations outside the species strongholds of Michigan and Ontario is found at a wildlife area in northern Ohio.

My research objectives were to: 1) identify land use practices and habitat features that best predict massasauga occurrence at the wildlife area; and 2) determine how the wildlife area is functionally connected for massasaugas given the amount of active agricultural production still taking place on the landscape and the species' tendency not to travel great distances.

During the 2022 field season, I used adapted-Hunt drift fence technique (AHDriFT) camera arrays and timed constrained visual encounter surveys to assess massasauga occupancy and created single-species integrated occupancy models to establish which covariates best predicted occupancy. Massasaugas were more likely to occupy sites with a higher proportion of open herbaceous habitat, sites with a higher proportion of marginal habitat features like infrequently mowed ditches and field margins, and sites that had been out of agricultural production for a longer time.

I created a series of cumulative kernel density surfaces using three different dispersal kernels to analyze functional connectivity for massasaugas at the wildlife area. I also examined the potential impact of agriculture on connectivity by using three alternative resistance values for agriculture in the resistance surface. The probability of detecting dispersing massasaugas was highest in and around the heavily occupied center of the wildlife area. Using the mean rank for each of the 45 agricultural fields across the nine different density surfaces, I determined which fields dispersing massasaugas would most quickly encounter and potentially colonize if those fields were removed from agricultural production and restored.

The results of these analyses will help facilitate effective and adaptive management for the northern Ohio wildlife area massasauga population and will offer valuable insight into how massasaugas traverse heterogeneous landscapes across their range.

Dedication

To *Sistrurus catenatus*, whose right to exist I had to justify to way too many people over the course of this project.

Acknowledgments

To my best friend and our cats, my parents and brother, and my in-laws, thank you for always making me feel like there was nothing I couldn’t do. I usually didn’t believe it, but the reassurance was always comforting, and your support and confidence made this all possible. You kept me fed and housed, you kept the figurative wheels from falling off, and I wouldn’t have done it without you.

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Publications

Amber ED, Lipps Jr GJ, **Myers JM**, Smeenk NA, Peterman WE. 2021. Use of AHDriFT to efficiently survey for *Sistrurus catenatus*. Herpetological Conservation and Biology 16(1): 104-116.

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Gade, M. R., Gould, P. R., Wilk, A. J., Donlon, K. C., Brown, M. L., Behan, M. L., Roseman, M. A., Tutterow, A. M., Amber, E. D., Wagner, R. B., Hoffman, A. S., **Myers, J. M.**, & Peterman, W. E. (2023). Demography and space-use of Eastern Red-backed Salamanders (*Plethodon cinereus*) between mature and successional forests. Ecology and Evolution, 13(1), e9764. https://doi.org/10.1002/ece3.9764

Field of Study

Major Field: Environment and Natural Resources

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Chapter 1. Assessing the influence of historic land use and current habitat features on site occupancy of eastern massasaugas (*Sistrurus catenatus*) in northern Ohio

Abstract

Human activity is driving a global, but unevenly distributed decline in biodiversity. Reptiles, especially snakes, are understudied but are likely experiencing disproportionately severe declines. A lack of thorough biological and population-level information continues to delay species status assessments and hamper conservation efforts. The federally threatened eastern massasauga rattlesnake (*Sistrurus catenatus*) occurs across the Great Lakes region of the midwestern United States, and much is still unknown about their baseline habitat requirements. Surveying massasauga populations can be logistically challenging and time-consuming, and in many cases, the results are not widely applicable due to variation between populations range wide.

My goal was to identify which land use practices and habitat features best predict massasauga occurrence at a location in northern Ohio. During the 2022 field season, I used adapted-Hunt drift fence technique (AHDriFT) camera arrays and time-constrained visual encounter surveys to determine which fields were occupied by massasaugas and created single-species integrated occupancy models to establish which covariates best predicted occupancy. Massasaugas were more likely to occupy sites with a higher proportion of herbaceous field habitat within 100 m of the sampling location, sites with a higher proportion of marginal habitat features like infrequently mowed ditches and field margins within 100 m of the sampling

location, and sites that had been out of agricultural production for a longer time. My results will help guide future management of this important massasauga population and can be used elsewhere to evaluate the suitability of potential sites for restoration for massasaugas and the many other species that rely on grassland and prairie habitat.

Introduction

There has been a widespread awareness that human activity is driving global biodiversity declines and ecosystem collapse since at least the early 1990's (Cardinale 2012). A worldwide assessment of tetrapod risk based off the 2020 IUCN Red List determined that 40.7% of all amphibians, 25.4% of mammals, and 13.6% of all bird species are in danger of extinction (Cox et al. 2022). The first official assessment of reptiles on a global scale, which was not published until 2022, determined that 21.1% of all reptile species are threatened with extinction (Cox et al. 2022). Habitat loss and fragmentation resulting from land being transitioned to agriculture are frequently cited as the greatest threats to reptiles in the United States and around the world (Gibbons et al. 2000, Tollefson 2019, Cox et al. 2022).

Snakes account for nearly half of all reptile species diversity but remain understudied (Chen 2019). Nearly one in four snake species has an unknown conservation status due to a lack of population-level information (Zipkin 2020); even basic natural history information is unknown for many snakes (Santos 2007). Effective conservation and management can only occur when current and thorough information about species and populations is available (Bradke 2018). Even with the acknowledged lack of available data, there is overwhelming agreement among researchers that snake diversity is declining worldwide (Reading 2010).

The eastern massasauga rattlesnake (*Sistrurus catenatus*) is relatively well-studied, but a lack of natural history and population level data still hampers efforts to conserve the species. Eastern massasaugas inhabit primarily early successional vegetative communities, including wet meadows, fens, marshes, prairies, grasslands and abandoned or fallow agricultural fields (Lipps 2017). Massasaugas are declining across their range in the Great Lakes region of the United States and southern Ontario, Canada, and most remaining populations are small and highly fragmented (Szymanski 2016). A Species Status Assessment completed by the United States Fish and Wildlife Service (USFWS) in 2016 estimated that out of 558 historical massasauga populations that existed across the range, only 347 were presumed to still be extant. This number included both populations known to be extant and populations with unknown statuses, meaning the actual number of extant populations was likely lower (Szymanski 2016). In 2016, eastern massasaugas were listed as threatened in the United States under the Endangered Species Act of 1973, and they are state listed as endangered or of special concern in all 10 states in which they still occur. Habitat loss, either outright or through vegetative succession, is the most critical threat to massasaugas range-wide (Szymanski 2016).

Typically, massasauga research is conducted through the use of VHF radio telemetry, visual encounter surveys, systematic use of cover objects, or with drift fences and funnel or pitfall traps (Amber et al. 2017, Bartman 2016). Many of these methods are expensive and time consuming, and results can vary dramatically based on observer skill level and training (Amber et al. 2017). Massasauga research has previously focused on detailing and estimating individual movements and habitat use (e.g. Bailey et al. 2012, Weatherhead and Prior 1992), but few studies have attempted to quantify habitat requirements at the population- or landscape-level

(Thacker et al. 2023). Data related to landscape level habitat associations can be difficult to collect, given how few remaining landscapes are large enough that a single, large population can occupy different areas of that landscape (Szymanski 2016).

Massasaugas once occurred in at least 28 counties throughout western and northern Ohio and were listed as state endangered in 1996 (Lipps 2017). Today, only 10 populations remain in Ohio (Lipps 2017), most of which are small and isolated. The most stable remaining massasauga population in the state is located within the former Sandusky Plains region of northern central Ohio; the study site will not be explicitly identified in order to protect rare snakes and sensitive locations. I conducted time-constrained visual encounter surveys and used a novel variation of a camera trap array system called the adapted-Hunt drift fence technique (AHDriFT) to assess massasauga occupancy of fields within this study site. The objective of my research was to identify the specific land use practices and habitat features that best predicted occupancy for this population of massasaugas.

Methods

Study Site

My study site was a state-owned wildlife area in northern central Ohio. It contains some of the last remnants of the once expansive Sandusky Plains and is home to one of the more robust remaining populations of massasaugas in the state. Its 3,735 ha are broken up into approximately 154 management units of varying sizes and uses (**Figure 1**). Approximately two thirds of these units are either in agricultural production or grassland (Ohio Division of Wildlife brochure, unknown year), with the agricultural fields producing primarily corn in 2022, the year my field work was completed. The wildlife area was never widely or systematically surveyed to determine which fields were occupied by massasaugas prior to this study.

Management efforts at the wildlife area are focused on restoring degraded or fallow fields to prairie and controlling the spread of invasive plants, such as reed canary grass (*Phalaris arundinacea*) and cutleaf teasel (*Dipsacus laciniatus*). A variety of management techniques are regularly employed on site, including mowing and brush-hogging, prescribed fire, and herbicide application. Since the eastern massasauga received federal threatened status in 2016, the Ohio Division of Wildlife does not permit fields that have been out of agricultural production for one year or more to be tilled or disced for agricultural use thereafter (wildlife area technician from study site, personal communication, May 2022).

The remaining units not in cropland or grassland are a mixture of mature forest, early successional forest, shrubland, and open water or wetland complexes. In addition to being managed in part for the conservation of massasaugas and grassland-nesting birds, the wildlife area is also managed as a waterfowl and upland game hunting destination. Paved, relatively high traffic roads border the property to the north, east and west; a lower traffic paved road borders the property to the south and several gravel roads and management access roads are situated inside the wildlife area itself.

Data Collection

I assessed massasauga occupancy and field level habitat characteristics using two methods: 30 minute, time-constrained visual encounter surveys and a modification of the adapted-Hunt drift fence technique (AHDriFT) using 15 m linear drift fences in place of the Y-shaped arrays deployed by Amber et al. (2017). After establishing which of the 154 management units did not contain massasauga habitat, were still in active agriculture, or had planned management occurring during the 2022 field season, I identified a total of 70 candidate fields as potential sampling locations. From this list of 70 fields, I randomly selected the final survey fields to capture variability in field area and management history. I sampled 44 fields using visual encounter surveys and 43 fields using AHDriFT arrays; 23 fields were surveyed using both methods.

Visual Encounter Surveys

I conducted 107 visual surveys of 44 fields between April 12, 2022 and June 7, 2022. This sampling window initiated as massasaugas were leaving their hibernacula and dispersing across the landscape to begin their active season and ended when summer vegetation growth became too dense to effectively detect snakes. Visual encounter surveys consisted of 30 minute time-constrained, linear transect surveys with 2–13 surveyors.

At the beginning of each survey, I collected information about the environmental conditions in the field at the time (**Table 1**). Surveyors then walked parallel linear transects slowly in one direction for 15 minutes, switched directions and shifted over to avoid initial transect lines, and then walked 15 minutes back in the direction of the survey origin. Surveyors were spaced at a minimum of three meters apart, with more space between transects in larger fields. Each time a massasauga was located, the survey timer was stopped, a GPS point was taken, and basic behavior and landscape information were recorded.

Visual surveys were completed between dawn and approximately noon on days with a minimum daily high air temperature of 10 degrees Celsius and no significant rain at the time of the survey. Surveys ceased for the day when the ground temperature surpassed 30 degrees

Celsius, as very few snakes were observed basking once temperatures exceeded this threshold. Each surveyed field was sampled between two and five times to allow for detection probabilities to be estimated.

AHDriFT Surveys

I deployed a total of 43 AHDriFT arrays in 43 different fields between March 1, 2022 and May 24, 2022. Within-field array locations were selected by placing a random point in each of 43 pre-selected fields using the "sf" package in R studio (Pebesma 2018). Arrays were only moved from the randomly selected location if there was too much standing water present or if there were trees, shrubs or roots too large to be removed with a mattock or handheld trimmers. Arrays were always installed perpendicular to the long edge of the field to maximize opportunities for dispersing massasaugas to encounter the fence.

I constructed the AHDriFT arrays for this project using a modified version of the arrays from Amber et al. (2021); notable changes are shown in **Figure 2**. Each array system was constructed around a single linear drift fence made of 15 m long, 0.5 m tall aluminum flashing, which was placed in an approximately 10 cm-deep trench. The trench was hand-dug into the ground using mattocks and soil was back filled along the fence once it was placed in the trench to prevent animals from moving underneath. At the ends of each fence were inverted five-gallon buckets with Reconyx HP2X HyperFire 2 Professional Covert IR Cameras mounted on pieces of acrylic, which were then attached to the tops of the buckets facing down. The focal length of each camera was adjusted to 25.4 cm by the manufacturer. AHDriFT camera housing units had openings cut in each side to allow animals to enter and exit the buckets freely, and wooden guideboards were placed on the side of the bucket attached to the fence to direct animals into the unit. I programmed the cameras to take bursts of 3 images whenever the IR sensor detected an animal, and I set detection sensors to medium-high. Each camera used twelve rechargeable batteries and I changed camera batteries and SD cards monthly from May through November. I manually sorted images from the SD cards using the workflow for R studio package “camtrapR” (Niedballa et al. 2016) and then stored them on an external hard drive for future analysis.

Analysis

I completed all analyses for this study in R (v4.1.2, R Core Team 2021). Upon conclusion of the field season and removal of the AHDriFT arrays, I generated a summary of individual camera functionality using the “camtrapR” R package (Niedballa et al. 2016), as well as a species detection history for massasaugas. For the purposes of this project, a survey occasion constituted fifteen days, instead of the camtrapR default of seven days, to manage the number of zeroes generated by the relatively infrequent number of detections. I considered both cameras from a single array to be one sampling unit.

With the data collected from the visual encounter surveys and cameras, I generated a series of occupancy models using the “spOccupancy” R package to determine which covariates related to field history and current field habitat best predicted massasauga occupancy in surveyed fields. “spOccupancy” fits all models in a Bayesian framework and uses the Pólya-Gamma data augmentation approach (Doser et al. 2022). I used non-spatial single species integrated occupancy models which allow for two types of survey data to be included in the same model. To prepare covariates for analysis, I determined the center point for each AHDriFT array and for all visual encounter survey tracks and measured the amount of each predictor variable contained within a circular area around that point using the “landscapemetrics” R package (Hesselbarth et al. 2022). I evaluated 100 m, 250 m and 300 m buffers and found the 100 m buffers were most effective at predicting massasauga occupancy based on significance of parameters; only one covariate was statistically significant in both the 250 m and 300 m models. As such, all predictor variables in the occupancy portion of the models, with the exception of crop year, consist of the total area (in hectares) of the covariate within a 100 m circular buffer of the AHDriFT array centroid or the visual survey track center point. I scaled all continuous predictor variables prior to using them in models.

I considered occupancy to be the response variable in all models and examined a variety of occupancy predictor variables likely to be correlated with massasauga occupancy based on previous research and my own observations (**Table 2**). I included four incidence functions with ascending degrees of complexity as a way to examine whether or not connectivity predicted occupancy at the wildlife area. All connectivity incidence functions were given an α of 1000. For this set of incidence functions, the alpha term was used to scale massasauga dispersal to 1000 m based on some results from a 2022 genetic analysis at the northern Ohio wildlife area by Martin et al. and their classification of 1.1 km as a dispersal movement. Connectivity 1, the least complex incidence function, calculated connectivity based on distance to all fields. Connectivity 2 calculated connectivity based on distance to all fields occupied by massasaugas. Connectivity 3 calculated connectivity based on distance to massasauga occupied fields and area of contributing source fields, or fields *from which* massasaugas would be dispersing. Connectivity 4, the most complex function, calculated connectivity based on distance to massasauga occupied fields, area of contributing source fields, and area of receiving fields, or fields *to which* massasaugas would be dispersing.

I included clay and topographic wetness as predictor variables as a high water table is one of the habitat features most commonly associated with massasauga presence. During visual encounter surveys, I observed that massasaugas frequently inhabited fields with high densities of crayfish burrows and crayfish depend on moist soil and a high water table, as well. The clay covariate was an aggregation of all clay soil types present on the Web Soil Survey soil map of the study site. Clay soil drains poorly and holds water for longer than many other soil types, making it seem most likely to be compatible with massasauga and crayfish moisture needs. I created the topographic wetness index covariate in ArcMap using 2019 digital elevation models (DEMs) for the two counties the wildlife area occupies to assess how different areas on the landscape accumulated water as an alternative way to measure soil moisture.

I examined field, agriculture, forest, water, anthropogenic, other, road-rail, road-paved, road-gravel and road-busy as occupancy predictor variables as these were the primary land cover types at the wildlife area. Field consisted of herbaceous dominated early successional habitat and is the primary habitat for massasaugas during most of the active season. Agriculture included all fields that were tilled or plowed for row crops as of 2021. Forest consisted of all habitats dominated by trees with notable canopies but excluded shrublands. Anthropogenic encompassed all human-dominated areas such as mowed lawns, driveways, and buildings. The road covariates are as they appear, with the difference between road-paved and road-busy being my subjective evaluation of whether they were low traffic (paved) or high traffic (busy) based on how I experienced them during the field season. All busy roads were also paved. Finally, “other” was included as a way to examine how marginal open habitats like infrequently mowed ditches and field edges, field margins, unknown fields that appeared in aerial imagery but that I never visited, and isolated wetland patches impacted massasauga occupancy.

I also created three additional land cover covariates by altering or supplementing some of the original covariates. Field 2-total area consisted of the same herbaceous dominated early successional habitat as the original field covariate, except that all shrubby vegetation within 100 m of the survey point was removed. Herbaceous-total area was much the same as field 2-total area except that it also included all habitat contained in the covariate “other”. Woody-total area included all woody vegetation/shrub-dominated habitat within 100 m of the survey point.

I included edge density-forest, edge density-field, total edge-forest, and total edge-field to assess whether the amount of edge within 100 m of the survey point predicted massasauga occupancy. Finally, I included crop year in order to determine whether the number of years since a field was last in agricultural production predicted massasauga occupancy. I created the crop year covariate by determining the last year each field at the wildlife area was planted in row crops based on aerial imagery and conversations with management staff and subtracting that year from 2022, the year the data was collected.

In addition to the occupancy covariates, I also examined a series of detection predictor covariates, as occupancy models include both. The detection predictors for visual encounter surveys came from the environmental information I collected prior to each survey (**Table 1**). I assessed day of year, survey start time, survey end time, air temperatures in the sun and shade, ground temperatures in the sun and shade, and visibility. Visibility is a categorical descriptor of how easy it was to see through the vegetation in a field; fields could be classified as having “good”, “moderate”, or “poor” visibility. Only day of year was examined as a predictor variable for AHDriFT arrays as day of year was the only quantifiable information provided by the array cameras.

While I did have presuppositions about which covariates would best predict massasauga occupancy based on my observations from the field and general knowledge of the species, the model selection process for this study was more exploratory than it was the testing of specific hypotheses. I created a global model using all possible occupancy predictor variables and used this model to remove variables based on individual performance and model WAIC until arriving at a final model (**Table 3**). Detection predictor covariates were evaluated in much the same way, but they were pruned prior to fitting the global model based on whether they had any effect on uncertainty in early models. I created four separate versions of the global model, one for each connectivity covariate, as this was one of the covariates I thought would predict occupancy well and they could not be evaluated simultaneously. Ultimately, none of the connectivity measures impacted uncertainty or improved the model so they were all removed. To simplify the global model in Table 3, I only included a single connectivity covariate with a footnote indicating that all four were examined. To fit Model 2, in addition to the connectivity covariates, I removed all soil moisture covariates, and all edge covariates from the global model, as none showed meaningful effects on uncertainty or improved support for the model; this model retained the primary land cover covariates, crop year, and the additional land cover covariates of field 2-total area, woody-total area, and herbaceous-total area. Beginning with Model 2, I also began generating and comparing WAIC for each model. Models 3-6 all included “other” and crop year, as they consistently and significantly impacted uncertainty. In addition to “other” and crop year, the models included field, field 2-total area, herbaceous-total area, and woody-total area respectively to evaluate how each covariate behaved when separated from the others. Model 7 included only field 2-total area and crop year to assess the effect of a simplified model on WAIC. I ultimately selected the model with the lowest WAIC as the final model.

Results

I conducted 107 visual encounter surveys in 44 unique fields. Two surveys were removed from the final count due to inconsistent survey methods or data collection, for a total of 105 surveys of 44 fields. All fields were surveyed at least twice, with some surveyed up to five times, and I detected massasaugas in 19 of 44 visually surveyed fields. I placed a single AHDriFT array in each of 43 fields and detected massasaugas at 24 of the 43 arrays. Of the 23 fields surveyed using both methods, AHDriFT arrays detected massasaugas in four fields where they were not detected during visual encounter surveys.

The model that best predicted massasauga occupancy at the northern Ohio wildlife area based on model support determined by lowest WAIC was Model 4, which consisted of the occupancy predictor covariates field 2-total area, “other”, and crop year. It also included the quadratic of ground temperature in the shade for the visual survey predictor covariate, and the quadratic of day of year for AHDriFT predictor covariate (**Table 4**). The chi-square Bayesian p-value for visual encounter surveys was .3442, and .2037 for AHDriFT. All three occupancy covariates had positive effects on occupancy and none of their credible intervals overlapped zero (**Figures 3, 4, and 5**). Ground temperature in the shade and day of year both had non-linear relationships with detection (**Figures 6 and 7**).

The inclusion of field 2-total area in the final model suggests that massasaugas are more likely to occupy fields with greater proportions of herbaceous-dominant, early successional habitat and minimal woody vegetation (**Figure 3**). Crop year's inclusion implies that massasaugas are more likely to occupy a field the longer it has been out of agricultural production (**Figure 4**). The presence of "other" in the final model means that massasaugas are predicted to occupy fields more frequently as the proportion of marginal, otherwise-unclassified open habitat such as field edges and infrequently mowed ditches increases (**Figure 5**).

The detection predictor covariates included in the final model were the quadratic of ground temperature in the shade for visual encounter surveys, and the quadratic of day of year for AHDriFT. The inclusion of the quadratic terms for both covariates means that both ground temperature in the shade and day of year have non-linear relationships with detection for their respective survey methods. The quadratic of ground temperature indicates that detection likelihood during visual encounter surveys increases with more moderate temperatures, as opposed to particularly high or low temperatures (**Figure 6**). The quadratic of day of year has a much less straightforward interpretation and its credible intervals do have some overlap with zero (**Figure 7**). This means that the model is uncertain how day of year impacts detection for AHDriFT arrays.

Discussion

With the objective of determining which habitat features and land use practices best predict massasauga occupancy for a robust population in northern Ohio, I used occupancy data collected during the 2022 field season to create a series of non-spatial single species integrated occupancy models. My best-fitting model predicted that massasaugas were more likely to occupy sites with more open, early successional habitat, more marginal open habitat including infrequently mowed ditches and field margins, and those sites that were not recently in agricultural production. These results align with previous studies that indicate massasaugas preferentially select open, herbaceous habitats and avoid dense, woody environments with more canopy cover (Lipps 2017). Bailey et al. (2012) found that massasaugas in a Michigan population made use of areas with predominantly herbaceous vegetation and largely avoided habitat with mature trees or forest even though forests were the dominant landcover in the area. Szymanski (2000) noted that while there is considerable variation in habitat use among populations throughout the range, massasaugas generally used open canopy habitats comprised of sedges and grasses and avoided shrubby or wooded areas. Although massasaugas are known to sometimes utilize forested habitats, they prefer and likely are reliant on early successional, open-canopy habitats. The most likely explanation for this preference is that open, herbaceous-dominant areas provide optimal conditions for thermoregulation, as well as other needs like hunting and avoiding predators (Lipps 2017).

Before Ohio was colonized by Europeans near the end of the 17th century, only about 2.5% of the state was comprised of open, early successional habitat in the form of prairie or grassland, much of which was located in the area that is now my study site (Ohio Division of Wildlife 2015). Over time, advances in agricultural technology allowed this poorly drained area to be converted into large-scale row crop production. The wildlife area was purchased by the state of Ohio beginning in 1952, at which time many fields were removed from agricultural production and restored to grassland or prairie (Ohio Division of Wildlife brochure, unknown year). Former agricultural fields, provided they contain suitable vegetative structure, are commonly used as habitat by massasaugas during the active season according to the USFWS Species Status Assessment (Szymanski 2016). Elsewhere in Ohio, massasaugas have been observed in fallow and abandoned farm fields to the extent that field abandonment may have historically constituted an important means of habitat creation for them (McCluskey et al. 2017). I detected massasaugas at numerous sites with known histories of agricultural use ranging from 11 years ago to 100 years ago, reinforcing the importance of habitat restoration as a means to conserve this species. The probability of field occupancy, as predicted by my model, increases with field age, but it is worth noting that the majority of occupied fields are located in close proximity to one another in the center of the wildlife area where most fields have likely been out of agricultural production since around when the wildlife area was purchased. Thus, my model may inflate the true time lag between site restoration and recolonization. Previous work with massasaugas in Ohio suggests that fields may be recolonized as quickly as one to two years following removal from production even absent significant restoration efforts, provided the removed fields are adjacent to already occupied fields (Lipps 2017, McCluskey et al. 2017).

Restoring an agricultural field to prairie can be as easy as sprinkling seeds in soil, depending on the time of year and what crop was last planted in the field. Unfortunately, the transition from early successional habitat back to shrubland and forest can also occur easily when newly open habitat is not managed aggressively. Using historical imagery, McCluskey observed this transition (from open field to forest) occurring in as little as ten to twenty years (McCluskey et al. 2017). Habitat loss and fragmentation remains the single greatest threat to massasaugas as a species (Szymanski 2016), and vegetative succession is one of the primary ways habitat becomes non-functional for these snakes. Late-stage vegetative succession has been cited as the greatest risk factor for extirpation of many massasauga populations (Szymanski 2016, Faust et al. 2011). Maintaining open, early successional habitat is difficult and labor intensive for land managers, but it represents the most clearly supported and straightforward conservation tool for securing and restoring massasauga populations throughout most of their range.

Although it is arguably more labor intensive than maintaining open areas, removing forest is also a valid way to create and expand early successional habitat. Mechanical removal of trees and prescribed burns have been used successfully in northeast Ohio to maintain and expand open, massasauga-compatible habitat (McCluskey). Given my study site's prairie and grassland history, few if any of the forested areas are likely original to the landscape. Since late-stage vegetative succession creates closed-canopy habitat that is no longer functional for massasaugas, it stands to reason that depending on their size, forested portions of the wildlife area could also impose significant barriers to massasauga movement. Removing large, forested patches between areas known to contain significant numbers of massasaugas would not only create habitat, but would also improve gene flow (McCluskey et al. 2017). The negative effects of removing forest from a landscape surrounded on all sides by agriculture must also be considered, however, and the confirmed presence of populations of two endangered bat species at the wildlife area significantly limit the feasibility of woodland removal as an option.

The ability to move between habitat or resource patches in order to overwinter, thermoregulate, hunt, and find mates is as vital to massasaugas as it is to most other organisms and although none of the connectivity covariates predicted occupancy in my model, the ecological significance of connected landscapes cannot be overstated. There are several possible reasons connectivity could have underperformed in my model. First, it could be that connectivity was simply a difficult metric to quantify at a meaningful scale for this analysis. A telemetry study from Ontario found that most massasauga habitat selection and use occurs on a very small scale (Harvey and Weatherhead 2006). I used relatively large, discrete field polygons to determine the source and receiving patch areas in my incidence function models which, while convenient for calculation purposes, were probably ecologically arbitrary and incompatible with the scale at which massasaugas interact with their surroundings. It is also conceivable that the massasauga population at the wildlife area is largely stable such that extinction and colonization events are not occurring regularly enough to be modeled with incidence functions (Hanski 1994). Once last consideration is that the covariate “other”, which did predict occupancy, plays some role in connectivity as well. While massasaugas are almost certainly not traveling the length of the wildlife area via ditch, the presence and relative abundance of marginal habitat features like these infrequently mowed ditches, field margins, berms, and tree lines could be providing snakes with relatively safe passage between close fields that allow them to avoid dangerous and frequently impassible areas like agricultural fields and roads. “Other” classified features are largely and very notably free of frequent human disturbance, which is typically only beneficial for snakes.

Even after accounting for its challenges, the wildlife area in northern Ohio is among the largest remaining interconnected landscapes inhabited by eastern massasauga rattlesnakes anywhere in their range. Understanding the patterns that determine occupancy at this site will help ensure that future management of this population is adaptive and data driven. In addition to benefitting these massasaugas, the results of this analysis can be used elsewhere in the state and in similar landscapes across the range to evaluate suitability of potential sites for restoration and conservation. Conserving and creating massasauga habitat will not only benefit snakes, but the myriad other grassland bird and mammal species that were displaced as a result of the conversion of historical grassland and prairie for agricultural production at this wildlife area and across Ohio.

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Tables

Table 1. Table of environmental variables collected at the beginning of each visual encounter survey, their units of measure and how each variable was measured.

Environmental Variable	**Unit of Measure**	**Measurement Device**
Air Temperature (sun)	degrees Celsius	Kestrel 5500 Weather Meter
Air Temperature (shade)	degrees Celsius	Kestrel 5500 Weather Meter
Ground Temperature (sun)	degrees Celsius	Kestrel 5500 Weather Meter
Ground Temperature (shade)	degrees Celsius	Kestrel 5500 Weather Meter
Relative Humidity	percentage	Kestrel 5500 Weather Meter
Wind Speed	meters per second	Kestrel 5500 Weather Meter
Cloud Cover	percentage	surveyor estimate
Visibility	poor, moderate, good	surveyor estimate

Table 2. Table of occupancy predictor covariates included in models along with a basic description of the covariate.

Occupancy Covariate	Description
connectivity 1	incidence function- distance to all fields
connectivity 2	incidence function- distance to occupied fields only
connectivity 3	incidence function- distance to occupied fields, area of occupied field and source field
connectivity 4	incidence function- distance to occupied fields, area of occupied field, source field and destination field
clay	total area of clay soil (aggregated all 3 types) within 100m of survey point
topographic wetness	average topographic wetness within 100m of survey point
field	total area of field within 100m of survey point
agriculture	total area of agriculture within 100m of survey point
water	total area of semi-permanent standing water or wetland within 100m of survey point
anthropogenic	total area of anthropogenic land use within 100m of survey point
forest	total area of trees with a notable canopy within 100m of survey point
other	total area of other marginal habitat within 100m of survey point (e.g. infrequently mowed ditches, field margins)
road-rail	total area of railroad within 100m of survey point
road-gravel	total area of gravel road within 100m of survey point
road-paved	total area of paved road within 100m of survey point
road-busy	total area of busy/high traffic road within 100m of survey point
edge density- forest	density of forest edge within 100m of survey point
edge density- field	density of field edge within 100m of survey point
total edge- forest	total forest edge within 100m of survey point
total edge- field	total field edge within 100m of survey point
crop year	years since a field was last in agricultural production
field 2- total area	total area of field within 100m of survey point, shrubby habitat removed
herbaceous- total area	total area of field and other within 100m of survey point, shrubby habitat removed
woody- total area	total area of woody vegetation dominated areas within 100m of survey point

Table 3. Table of model formulas. All covariates were scaled before being used in models. The detection formula for visual encounter surveys was the quadratic of the ground temperature in the shade term in every model, and the detection formula for AHDriFT was the quadratic of day of year in every model.

Model	Occupancy Formula	WAIC- Visual	WAIC- AHDriFT
Global	connectivity* + clay + topographic wetness + field + forest + anthropogenic + agriculture + other + water + edge density-forest + edge density-field + total edge-forest + total edge-field + crop year + field 2-total area + herbaceous-total area + woody-total area	Not calculated for global model	Not calculated for global model
Model 2	field + forest + agriculture + anthropogenic + other + water + crop year + field 2-total area + herbaceous-total area + woody-total area	112.9817	360.0665
Model 3	field + other + crop year	111.775	353.007
Model 4	field 2-total area + other + crop year	111.5815	352.0987
Model 5	herbaceous-total area + other + crop year	114.9412	353.9739
Model 6	woody-total area + other + crop year	115.7639	354.7178
Model 7	field 2-total area + crop year	111.2925	356.2526

*Four different connectivity measures were assessed.

Table 4. Table of the parameters included in the final occupancy model along with mean estimates and credible intervals.

Model Parameter	Mean	0.025 Quantile	.975 Quantile
Occupancy:			
field 2-total area	0.8981	0.0573	1.9068
crop year	1.2509	0.3898	2.3374
other	1.427	0.128	3.0177
Detection (VES):			
temperature	-0.1284	-0.7545	0.4515
temperature (quadratic)	-0.5324	-1.1024	-0.0382
Detection (AHDriFT):			
day of year	0.1526	-0.1477	0.4833
day of year (quadratic)	-0.2245	-0.5981	0.1087

Figures

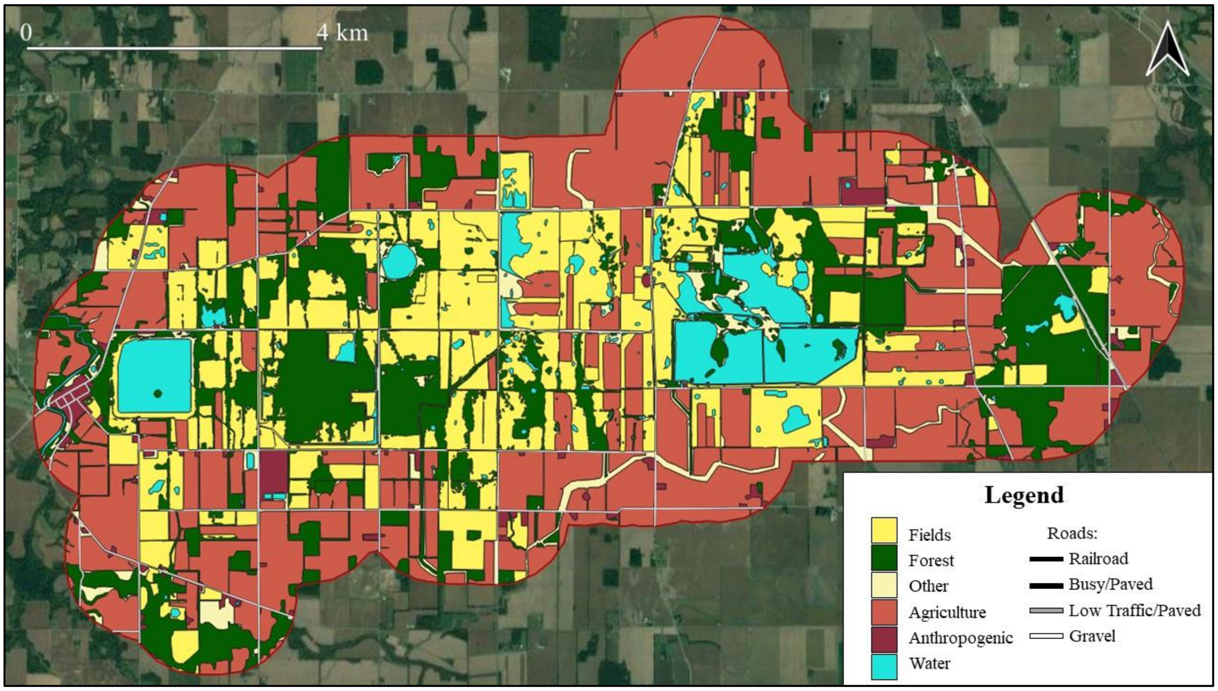

Figure 1. Map of the major land cover classes at the northern Ohio wildlife area. There is a 1 km buffer around all the edges of the property so additional land cover features within potential massasauga dispersal distance can be visualized.

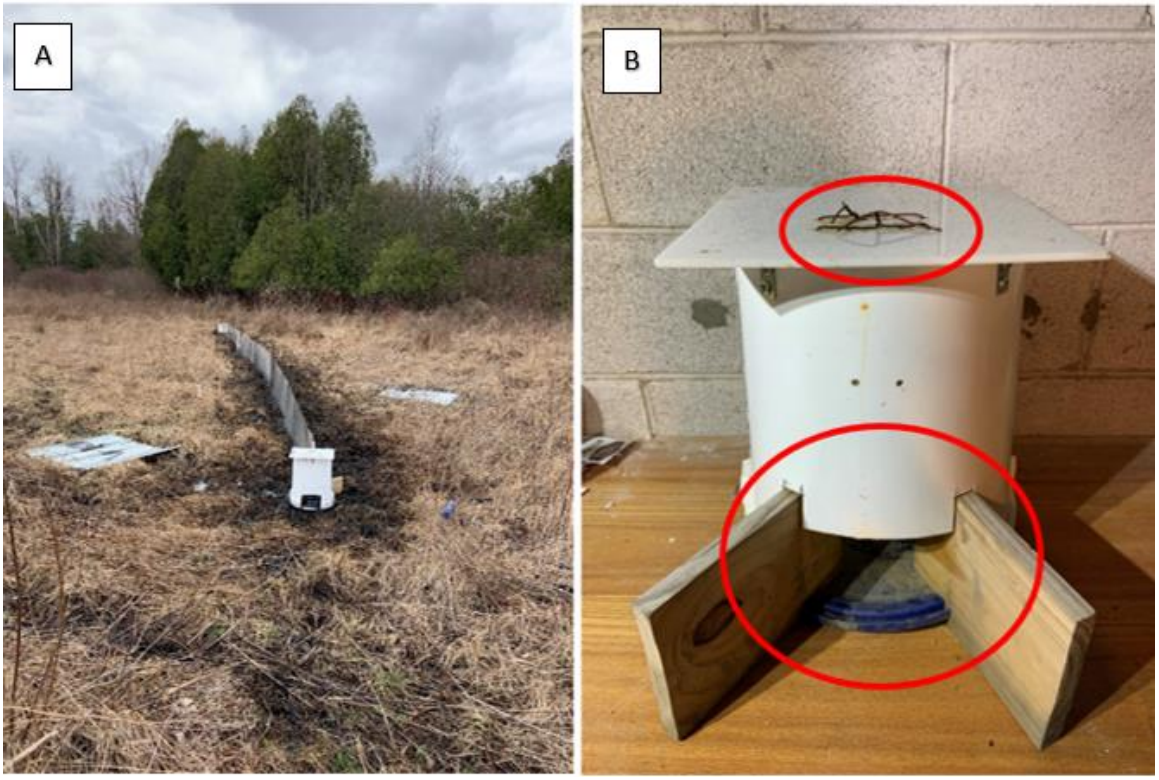

Figure 2. Alterations to the AHDriFT array design used by Amber et al. (2021). Image A shows the linear array construction using only two cameras; Amber et al. (2021) used a Y-shaped array with three cameras. Image B highlights changes to the camera housing unit, including the use of black annealed wire to attach cameras to the acrylic top and the use of slotted guideboards instead of the permanently affixed boards used by Amber et al. (2021).

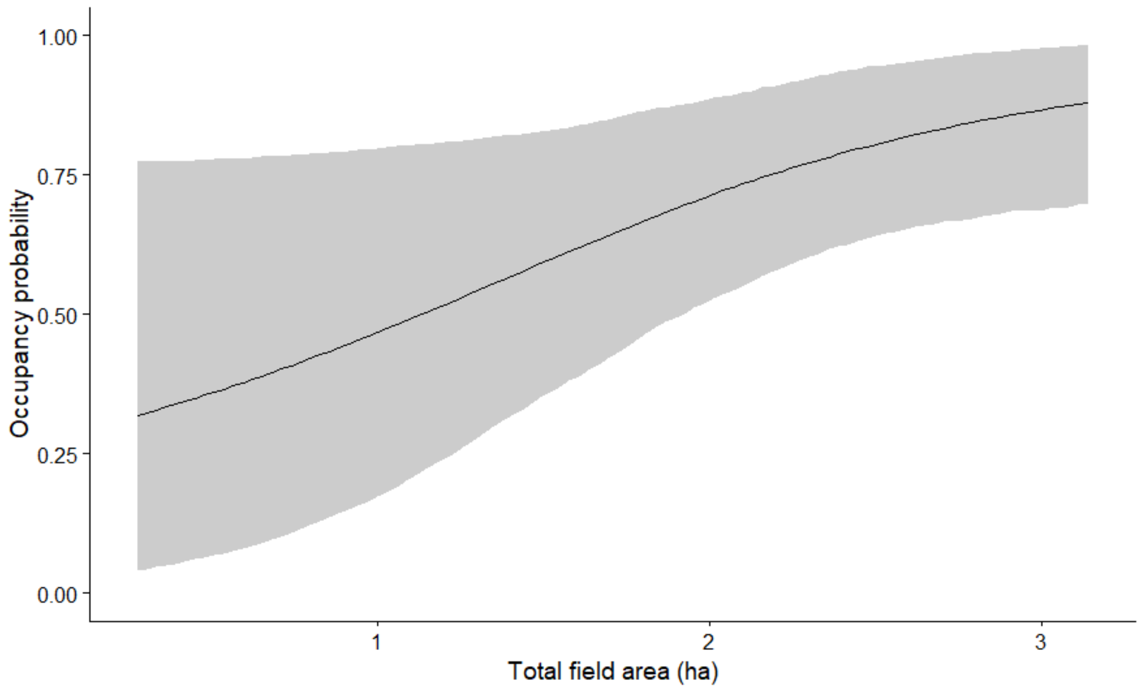

Figure 3. Marginal effects plot for occupancy predictor covariate field 2-total area. Field 2 had a positive effect on massasauga occupancy, meaning that massasaugas are more likely to occupy a space as the total area of field within 100 m of the survey point increased.

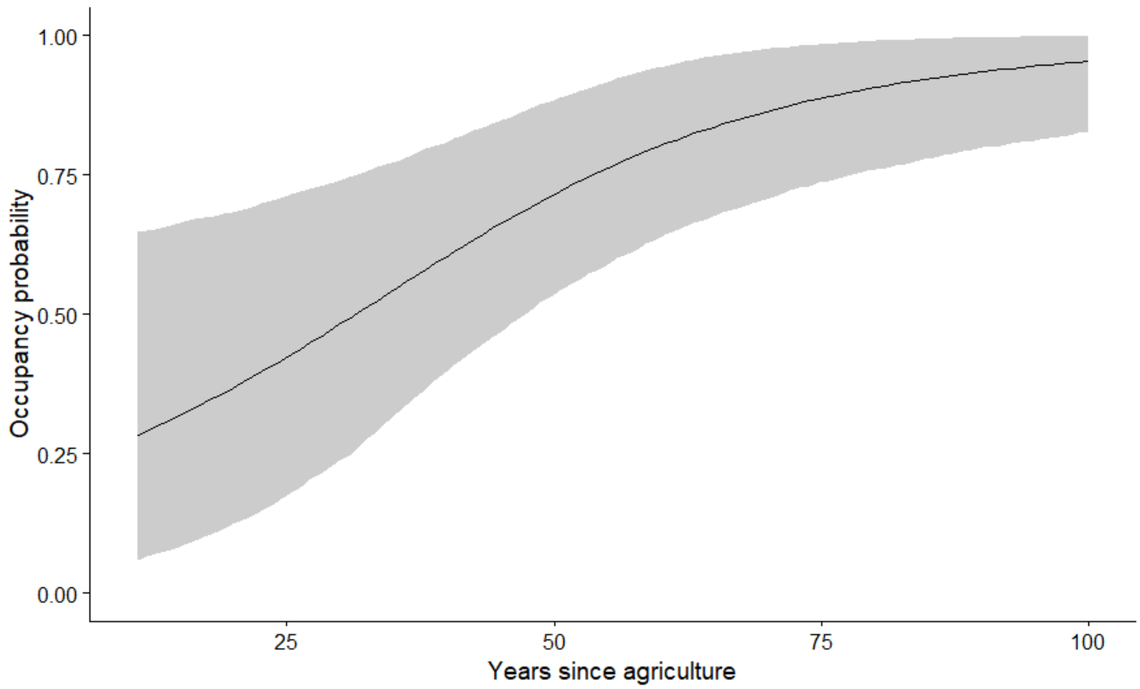

Figure 4. Marginal effects plot for occupancy predictor covariate crop year. Crop year had a positive effect on massasauga occupancy, meaning that massasaugas are more likely to occupy a field the longer it has been out of agricultural production. Crop year performed consistently well across all scales and models.

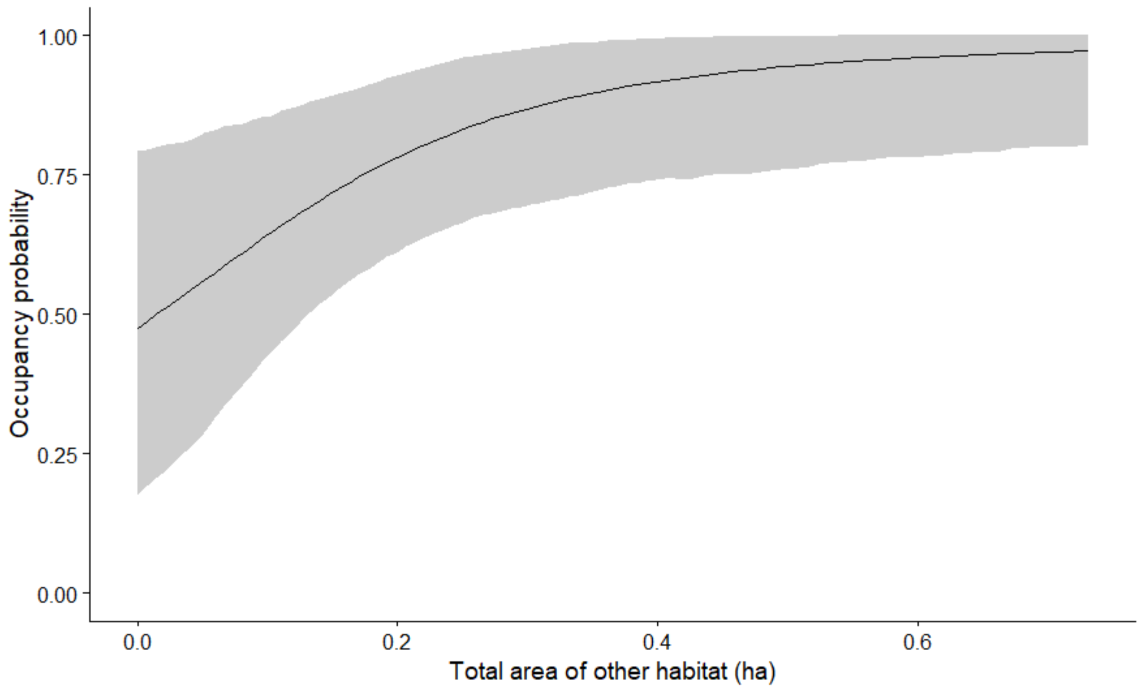

Figure 5. Marginal effects plot for occupancy predictor covariate “other”. “Other” had a positive effect on massasauga occupancy, meaning that massasaugas are more likely to occupy a field as the total area of “other” habitat within 100 m of the survey point increased. “Other” was used to describe otherwise unclassified marginal open habitats like infrequently mowed ditches and field edges, field margins, unknown fields that appeared in aerial imagery but were never visited and isolated wetland patches.

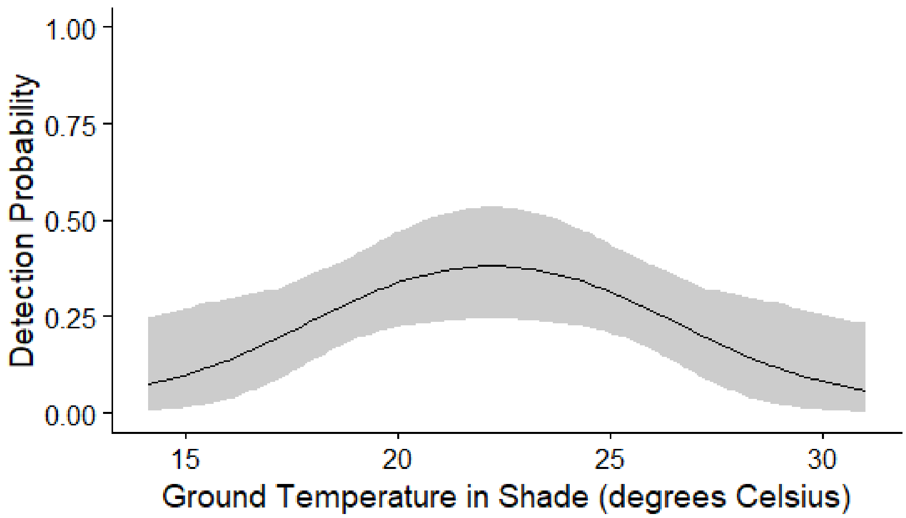

Figure 6. Marginal effects plot for visual survey detection predictor covariate ground temperature in the shade. Ground temperature had a non-linear effect on massasauga detection, meaning that massasaugas are more likely to be detected when temperatures are more moderate, as opposed to especially high or low.

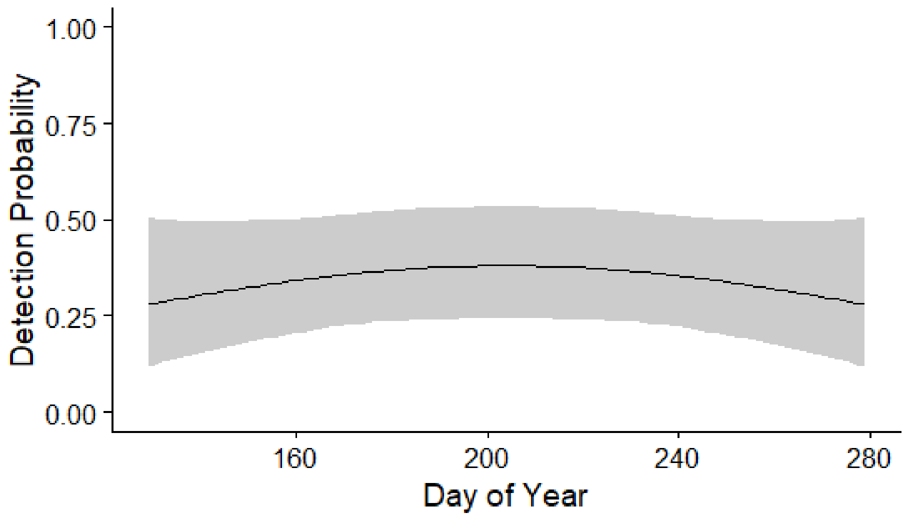

Figure 7. Marginal effects plot for AHDriFT detection predictor covariate day of year. Day of year had a non-linear effect on massasauga detection, but its credible intervals overlapped zero meaning that the model was not certain about the effect of this covariate.

Chapter 2. Evaluating functional connectivity for eastern massasaugas (*Sistrurus catenatus*) across an agricultural-prairie landscape in northern Ohio

Abstract

Movement is an essential part of life for most organisms. To be considered functionally connected, a landscape must be structured in a way that facilitates the movement of the organisms that use it. As human activity leaves natural ecosystems progressively more fragmented around the world, there is an increasingly urgent need to understand animal movement in order to restore and maintain functional connectivity of critical habitats.

The federally threatened eastern massasauga rattlesnake (*Sistrurus catenatus*) occurs across the Great Lakes region of the United States and Ontario, Canada in increasingly small and fragmented populations. One of the most robust remaining populations inhabits a wildlife area in northern Ohio. My goal for this study was to determine how the wildlife area is functionally connected for massasaugas given the amount of agricultural production still taking place on the landscape and the movement characteristics of the species. I used a series of cumulative kernel density surfaces with differing dispersal kernels derived from a resistance surface to analyze connectivity at the wildlife area. I also examined the potential impact of agriculture on connectivity by using multiple resistance values for agriculture in the resistance surface.

The results of this study will help facilitate the effective management of the northern Ohio wildlife area massasauga population now and into the future and will offer valuable insight into how massasaugas traverse heterogeneous landscapes.

Introduction

The ability of organisms to move across a landscape depends on how that landscape is connected. Habitat connectivity is the way a landscape enables or hinders the movement of an organism among resource patches, and it can be evaluated in terms of both its structure and function. A structurally connected landscape is connected by its physical features, but whether or not it is functionally connected is relative to the behavior, ecology, and movement patterns of each species in the ecosystem (Diniz et al. 2020). Restoring habitat and maintaining ecologically meaningful connections requires a holistic understanding of connectivity as it applies to individual organisms and populations (Cushman et al. 2014).

Habitat connectivity modeling allows us to understand and predict how processes like animal movement and gene flow are likely to occur on various landscapes (Landau et al. 2021). Connectivity models often require the input of a resistance surface, wherein researchers assign relative movement costs incurred by a species moving through each land cover type (Dutta et al. 2022). Resistance surfaces offer a more refined alternative to traditional binary habitat/nonhabitat surfaces (Zeller et al. 2012). They are often used with connectivity frameworks like least cost paths and circuit theory, but these methods are of limited utility as they do not incorporate the biology of the focal organism in a meaningful way. Cumulative kernel density also models connectivity, but while simultaneously accounting for the dispersal ability of a focal organism in addition to landscape resistance (Bauder et el. 2022). The output of a resistant kernel density analysis is a probability surface of the predicted relative density of dispersing organisms in each cell of a landscape (Cushman et al. 2013).

Understanding how critical habitats are functionally connected is key in conserving rare species at the landscape level. The eastern massasauga rattlesnake (*Sistrurus catenatus*) is a federally threatened snake species with remaining populations in the Great Lakes region of the United States and Canada, the majority of which are small and highly fragmented (Lipps 2017). Massasaugas have been the subjects of previous connectivity analyses examining genetics (e.g. Martin et al. 2022, Kudla et al. 2021) and urban corridor planning (Choquette et al. 2020), but many massasauga populations, particularly in the southern portion of the range, exist in rural landscapes surrounded by or interspersed with agricultural fields (Szymanski 2016). This necessitates a more thorough understanding of how they might move across diverse and fragmented landscapes.

One of most robust remaining populations of eastern massasaugas inhabits a wildlife area located in the former Sandusky Plains region of northern Ohio. The wildlife area is a large, heterogeneous landscape consisting primarily of restored prairie and grassland, as well as forest, managed wetland complexes, and active agricultural fields. Given the limited available data on the ability of massasaugas to move through agricultural landscapes (Dreslik 2005), understanding how and where movement is likely to occur is valuable information with the potential to benefit this and many other massasauga populations. My goal was to determine how the northern Ohio wildlife area, which will not be explicitly named to protect rare snakes and sensitive locations, is functionally connected for massasaugas and how connectivity can vary based on movement and dispersal ability, as well as the presence and seasonal status of agricultural fields in the wildlife area. Additionally, my will analyses provide land managers with data to inform which fields or portions of the wildlife area may be most critical for massasauga connectivity, as well as how to proceed with subsequent field removals from crop production based on the likelihood of massasauga colonization.

Methods

Study Site

The wildlife area the focal massasauga population inhabits is a 3,735 ha state-owned wildlife area in the former Sandusky Plains region of northern Ohio and it is made up of 154 management units that vary in size and management history. Approximately two thirds of these management units are in grassland, restored prairie, or agricultural production. The remaining units are a mixture of mature forest, early successional forest, shrubland, and open water or wetland complexes. The management units known to be occupied by massasaugas are predominantly early successional herbaceous fields and restored prairie and many are located near the center of the property.

Data Collection

I categorized major habitat types at the wildlife area using manually digitized landcover assessments created in Google Earth and QGIS using aerial imagery from September 2021. These landcover designations were informed heavily by ground-truthed observations and conversations with land managers on site. I imported all landcover polygon layers into R (v4.1.2, R Core Team 2021) as spatial objects using the "sf" R package (Pebesma 2018) and reprojected them to WGS 84/UTM 17N. I rasterized the layers using the "raster" R package at a resolution of 3 m and then created SpatRasters that could be used with the "terra" R package (Hijmans 2022).

I relied on expert opinion and a critical review of the literature to create resistance values for all land cover types (**Table 5**). I assigned three separate resistance values for agriculture to reflect uncertainty about how massasaugas interact with agricultural fields both seasonally, and in general. The resistance value of 1.8 presumes that agricultural fields do not present a significant barrier for snakes to traverse. This value would be most likely reflective of conditions during the summer, as agricultural fields are typically not being actively managed during that time and have grown enough to provide adequate cover for a traversing snake. The resistance value of 5 presumes that a slightly higher cost is incurred by traversing an agricultural field, but fields are not impassable. This value would be most likely reflective of the late spring and early summer when row crops have not emerged enough to provide effective cover, or after crops are harvested in the fall assuming some crop debris is left in the field. The field is still traversable, but a moving snake would be much more visible and susceptible to predation. The resistance value of 50 assumes that agricultural fields represent a significant barrier to movement and that massasaugas are unlikely to cross them successfully. This value is meant to account for conditions during spring field preparation and planting, as well as during the fall harvest season and assigns a resistance value equal to that of a paved road. I reclassified all raster layers and their corresponding resistance values using the “terra” R package (Hijmans 2022) and summed all layers to create the resistance surface. I assigned most other resistance values based on VHF telemetry movement data from Dreslik (2005) in Carlyle Lake, Illinois, as that site is climatically and vegetatively similar to the northern Ohio wildlife area. Dreslik radio-located 48 massasaugas classified as either males, non-gravid females, or gravid females over the course of 3 years. He located snakes daily between egress in the spring and ingress in the fall on a state-owned property consisting of woodlands and grasslands intermixed with agriculture and some development, which is very similar to the landscape at the northern Ohio wildlife area.

Data Analysis

I used the “gdistance” R package (van Etten 2017) to create a series of cumulative resistant kernel surfaces using the aforementioned resistance surface. I created a hexagonal grid of points with a minimum interpoint distance of 300 m. 322 of these points fell within the boundaries of fields occupied by massasaugas. Occupied fields for this analysis included both the fields found to be occupied during the occupancy surveys from Chapter 1 of this study and those identified as occupied based on sightings from management staff since approximately the year 2000. The mean number of points within a field was 6 (range = 1–27). I created a cost map of movement from each point using the ‘accCost’ function in “gdistance” (van Etten 2017). I then applied a Gaussian kernel function to model the probability of dispersing across the landscape from each point given the cost distance.

$$\frac{1}{\pi\sigma^2}\exp\left(-\frac{dist^2}{\sigma^2}\right) \qquad \text{(eq. 1)}$$

In this kernel function, σ is a scale parameter that determines how dispersal probability declines with distance. To reflect uncertainty surrounding the movement and dispersal tendencies of massasaugas at the wildlife area, I selected dispersal kernels of 250 m, 500 m, and 750 m which equate to 95% of dispersal kernel density being within 500, 1000, or 1500 m, respectively. Distances of 500 m and 1000 m likely account for the majority of daily massasauga movement and even many dispersal events at this site, based on the results of a genetic analysis of landscape resistance by Martin et al. (2022). The 1500 m distance was included to account for additional rare long-range movements. I then summed the dispersal kernel surfaces to create a cumulative kernel surface depicting the relative likelihood of massasaugas dispersing across the landscape surface. I created nine separate versions of this probability surface using the three different values for agricultural resistance with each of the three alternative dispersal kernel distances (**Table 6**).

I used the "terra" R package (Hijmans 2022) to extract the maximum value of the cumulative resistant kernel from each agricultural field for each of the nine different probability surfaces. Next, I determined the rank order of cumulative kernel density for each field across the nine scenarios. Finally, I calculated the average rank value for each of the 45 agricultural fields to determine which agricultural fields, regardless of dispersal ability or effect of agriculture on movement, would have the highest probability of being colonized by massasaugas if they were removed from production.

Results

There was considerable variation between the probability surfaces created across the nine scenarios, meaning that functional connectivity likely varies based on the distances massasaugas move at the wildlife area and the seasonal status of the active agricultural fields (**Figure 8**). The surface that most closely matched the order of the mean ranked agricultural fields was the combination of the moderate values for both dispersal distance (500 m kernel) and agricultural resistance (resistance value of 5); it will hereafter be referred to as the "moderate surface".

The 15 agricultural fields most likely to be encountered by dispersing massasaugas based on this analysis were those in close proximity to the occupied fields in core of the wildlife area, which appear as red-orange on the map (**Figure 9**). These are the fields that, if removed from production and restored, would most benefit functional connectivity for this massasauga population. The fields that are located outside the central core are nearly all adjacent to other occupied massasauga fields.

The next 15 fields most likely to be encountered by dispersing massasaugas based on the analysis are located just to the south of the heavily occupied core of the wildlife area, as well as in several more peripheral parts of the property, but still close to known occupied fields (**Figure 10**). Several of the peripheral fields are on the opposite side of paved and high-traffic roads from occupied fields, which presents a significant barrier to colonization for massasaugas (Martin et al. 2022).

With few exceptions, the remaining 15 fields are not located in close proximity to other occupied fields (**Figure 11**). For massasaugas to even encounter these fields would likely necessitate multi-generational movement and dispersal, or connectivity created through the restoration of a series of fields between presently occupied fields and these isolated fields.

In addition to identifying the parts of the wildlife area with the highest probability of being encountered by dispersing massasaugas, the moderate surface also highlights a series of areas that may act as corridors between occupied areas. On the moderate surface map, these areas are generally narrow and extend off the edges of the red, high kernel density cores. They represent relatively low resistance parts of the landscape and are partially comprised of features classified as “other” on the resistance surface. Maintaining these areas and expanding them where possible will keep snakes functionally connected until such time as the agricultural fields can be removed from production and restored.

Discussion

The primary goal of this study was to determine how a northern Ohio wildlife area is functionally connected for massasaugas and how connectivity might vary based on massasauga movement and dispersal ability, as well as the presence and seasonal status of agricultural fields located within the wildlife area. My analysis ranked the 45 agricultural fields at the wildlife area based on each field's likelihood of being encountered by dispersing massasaugas. These fields would be most beneficial to improving connectivity if removed from agricultural production restored. I also found that the probability of dispersing massasaugas was greatest in the central core of the wildlife area and that there are several areas that likely act as corridors for this population. The core area where the probability of dispersing massasaugas is highest contains much of the open, herbaceous dominated early successional habitat at the wildlife area. Identified by Szymanski (2016) as primary habitat for massasaugas, this landcover type had the lowest value on the resistance surface from which the cumulative resistant kernel density surfaces were derived. Almost immediately outside the high-probability-density core areas are several land cover types with significantly higher resistance values including busy and paved roads, forested areas, and large amounts of open water. Martin et al. (2022) and DiLeo et al. (2013) identified these as land cover features that inhibit landscape connectivity for massasaugas. When roads, forests and open water occur on the landscape alongside active agriculture, snakes in the central part of the wildlife area can be effectively isolated from the rest of the property.

While even seasonal isolation is not ideal, massasaugas may be well equipped to deal with the genetic implications of living in isolated populations (Martin et al. 2022). Limited dispersal by both adults and neonates, as well as very restricted daily movement, seem to have always been a part of massasauga spatial ecology (Gibbs and Chiucchi 2010). There is limited data pertaining to natal or juvenile dispersal, so most discussion of dispersal in the literature refers to dispersal by adults. A simulation study by DiLeo et al. (2013) found that variable juvenile dispersal might contribute to differences in massasauga population structure regionally, but more research is needed on this topic. The results of a genetic kinship analysis completed at my study site by Martin et al. (2022) found that the most spatially distant pair of related snakes from the sample, a grandparent and grandchild, were only separated by a straight-line-distance of about 1.1 km. Martin determined that this was the result of a single dispersal event and was not representative of the majority of daily movement for massasaugas at the wildlife area. These findings support my modeled kernel distances selected for this analysis, as well as the decision to average the rankings across scenarios to weight favor closer to more intermediate dispersal distance, while also not discrediting the potential for longer distance movements.

Martin's (2022) aforementioned kinship analysis at the wildlife area examined landscape resistance and massasauga population connectivity from a genetic perspective. He selected six sample sites withing six km^2 of each other and collected genetic data from 109 snakes. Martin was able to determine that there was no significant genetic structure in the massasauga population at the wildlife area, meaning all individuals came from a single genetic population. This also means that there is a sufficient amount of functional connectivity between the members of this population. Gibbs and Chiucchi found the population at the same wildlife area to exhibit some of the highest genetic diversity in Ohio (2010). Both of these sets of results highlight the importance of understanding and maintaining functional connectivity at this site.

In stark contrast to the results from Martin’s (2022) analysis at the northern Ohio wildlife area are his results from a previous genetic analysis of 86 massasaugas from five geographically close but fragmented sites in northeast Ohio. The sites existed on the same approximately six km^2 of land as the wildlife area, with some being separated by as little as 1.2 km. The massasaugas from the fragmented sites were determined to make up five separate genetic units, with only one possible instance of movement between sites. These results are a perfect example of how important it is that functional connectivity be maintained for the population at the wildlife area and reinforces just how unlikely massasaugas are to disperse long distances.

From historical aerial imagery, we know the landscape at the wildlife area has changed significantly over the course of the last half century, with fields being put into and taken out of production and other fields being restored to native prairie or allowed to transition to closed canopy forest. By extension, this means that functional connectivity for massasaugas has changed as well. While there are other potential habitat fields scattered across the wildlife area, results like those from Martin’s (2022) northeast Ohio genetic analysis make it clear that much of the suitable but unoccupied massasauga habitat scattered across the wildlife area will remain unoccupied until it is functionally connected to presently occupied fields. Massasaugas are able to colonize fields taken out of agricultural production relatively quickly when the fields are connected to existing occupied fields (Lipps 2017). McCluskey et al. (2018) also found anecdotal evidence to suggest massasaugas will move into adjacent fields within a year or two of the fields being removed from agricultural production.

There are ways to improve connectivity that do not entail waiting for fields to be removed from agricultural production; most notably, removing or significantly reducing forest patches to connect massasauga occupied fields. While Martin (2022) found forest to have the lowest resistance value based on his genetic analysis, it was assigned a slightly higher resistance value in my own analysis. Having viewed historical imagery of the wildlife area, I know most of the forested areas now present on the landscape were not there even 80 years ago. This is a relatively short amount of time on a genetic timescale, so it is likely that while the forests appeared to Martin to provide low resistance for massasaugas, his results were in fact a relic of the grassland that was present before the forest. In addition to removing agricultural fields from production and removing forested patches between occupied fields, the potential landscape corridors discussed in the results section can be improved and expanded. These corridors likely play an outsized role in keeping different parts of the massasauga population at the wildlife area functionally connected when their movement is otherwise limited by agriculture or other high resistance land cover features.

Maintaining functional connectivity and restoring connections between fragmented populations is increasingly important as humans continue to fragment and destroy natural landscapes. Massasaugas, like all organisms, must be able to travel between resources patches and when patches are separated by roads or large agricultural fields, the snakes are left effectively isolated. The results of this connectivity analysis detailing where and how massasaugas are predicted to move will help improve functional connectivity and gene flow among this important population of rattlesnakes and will help inform management and habitat restoration for other populations located on heterogeneous landscapes across the range.

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Tables

Table 5. Major land cover types present at the northern Ohio wildlife area, along with descriptions and resistance values for each. Field represents typical massasauga habitat and has the lowest resistance value. Busy roads, which massasaugas are effectively unable to cross, have the highest resistance value.

Land Cover Type	Description	Resistance Value
Field	early successional habitat, herbaceous	1
Other	miscellaneous marginal habitat (i.e. field margins, infrequently mowed ditches)	1.2
Forest	dominated by trees with a notable canopy	1.5
Agriculture Low	tilled and plowed for row crops as of 2021, low movement cost, likely traversable	1.8
Agriculture Medium	tilled and plowed for row crops as of 2021, moderate movement cost	5
Anthropogenic	buildings, parking lots and driveways, mowed lawns	10
Water	all semi-permanent standing water	25
Agriculture High	tilled and plowed for row crops as of 2021, high movement cost, traversal success unlikely	50
Road-rail	rail road tracks	50
Road-gravel	low traffic, gravel	50
Road-paved	low traffic, paved	50
Road-busy	large, busy paved roads	100

Table 6. Nine alternative cumulative resistant kernel surfaces with descriptions. Resistance values of 1.8, 5, and 50 were chosen to examine different scenarios for agricultural resistance. A resistance value of 1.8 indicates that agricultural fields do not present a significant barrier for snakes to traverse. This value would be most likely reflective of summer, as agricultural fields are typically not being actively managed then and have grown enough to provide adequate cover for a traversing snake. A resistance value of 5 indicates that a slightly higher cost is incurred by traversing an agricultural field, but that fields are not impassible. This value would be most likely reflective of the early summer when row crops have not emerged enough to provide effective cover, or after crops are harvested in the fall assuming some crop debris is left in the field. The field is still traversable, but a moving snake would be much more visible and susceptible to predation. A resistance value of 50 assumes that agricultural fields represent a significant barrier to movement and that massasaugas are unlikely to cross them successfully. This value is meant to reflect spring field preparation and planting, as well as the fall harvest season and assigns a resistance value equal to that of a paved road. Dispersal kernels of 250, 500 and 750 equate to 95% of dispersal kernel density being within 500, 1000, or 1500m respectively.

Surface Name	**Description**
Ag1Low	agriculture resistance value of 1.8, dispersal kernel of 250
Ag1Med	agriculture resistance value of 5, dispersal kernel of 500
Ag1High	agriculture resistance value of 50, dispersal kernel of 750
Ag2Low	agriculture resistance value of 1.8, dispersal kernel of 250
Ag2Med	agriculture resistance value of 5, dispersal kernel of 500
Ag2High	agriculture resistance value of 50, dispersal kernel of 750
Ag3Low	agriculture resistance value of 1.8, dispersal kernel of 250
Ag3Med	agriculture resistance value of 5, dispersal kernel of 500
Ag3High	agriculture resistance value of 50, dispersal kernel of 750

Figures

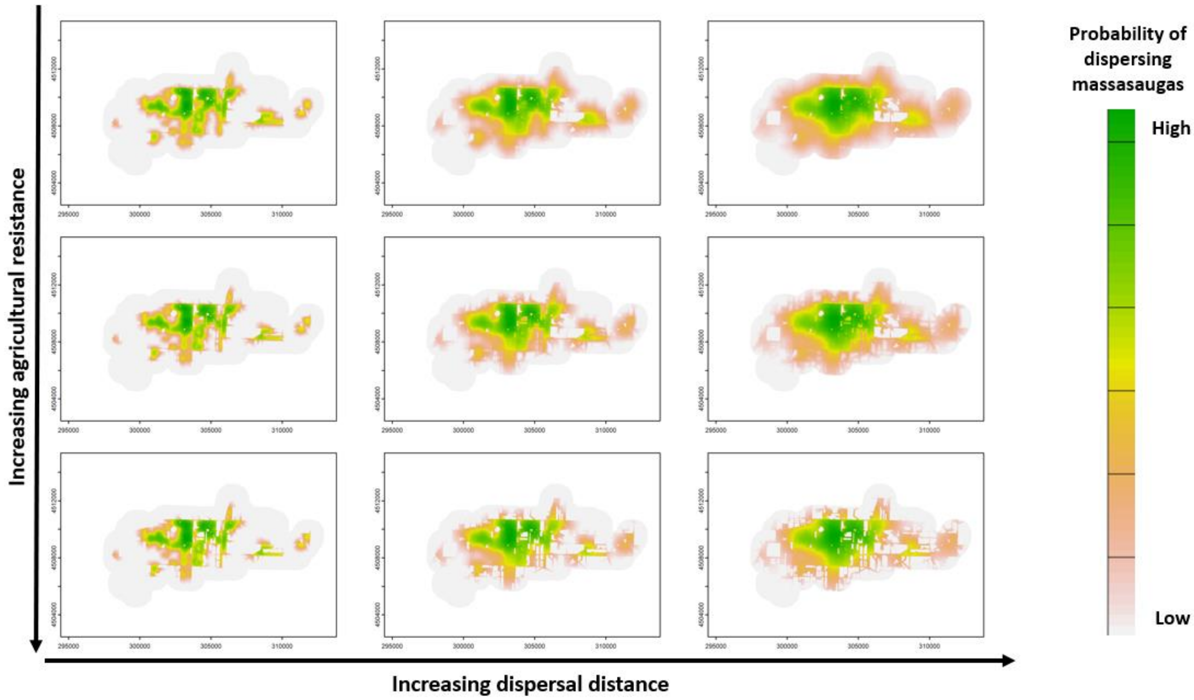

Figure 8. Nine cumulative resistant kernel surface outputs. Dispersal distance as determined by the dispersal kernel increases by column from left to right. Agricultural resistance increases by row from top to bottom. The color green indicates a high probability of dispersing massasaugas being present. The color red indicates a low probability of dispersing massasaugas being present. The color white/grey indicates approximately zero probability of dispersing massasaugas.

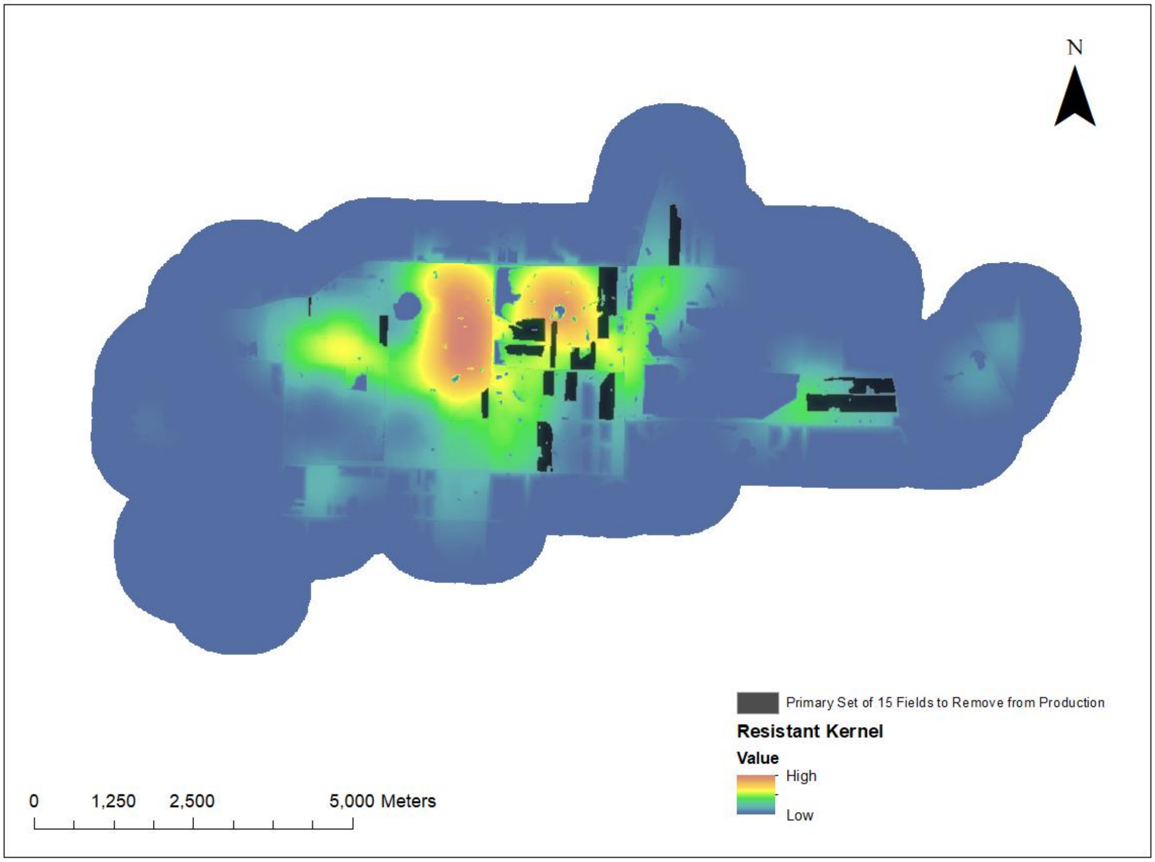

Figure 9. 15 fields that if removed from agriculture and restored would most increase functional connectivity based on my models. These fields represent the fields most likely to be colonized by massasaugas. This image shows the effective 1000 m dispersal distance and a resistance value of 5 for agriculture.

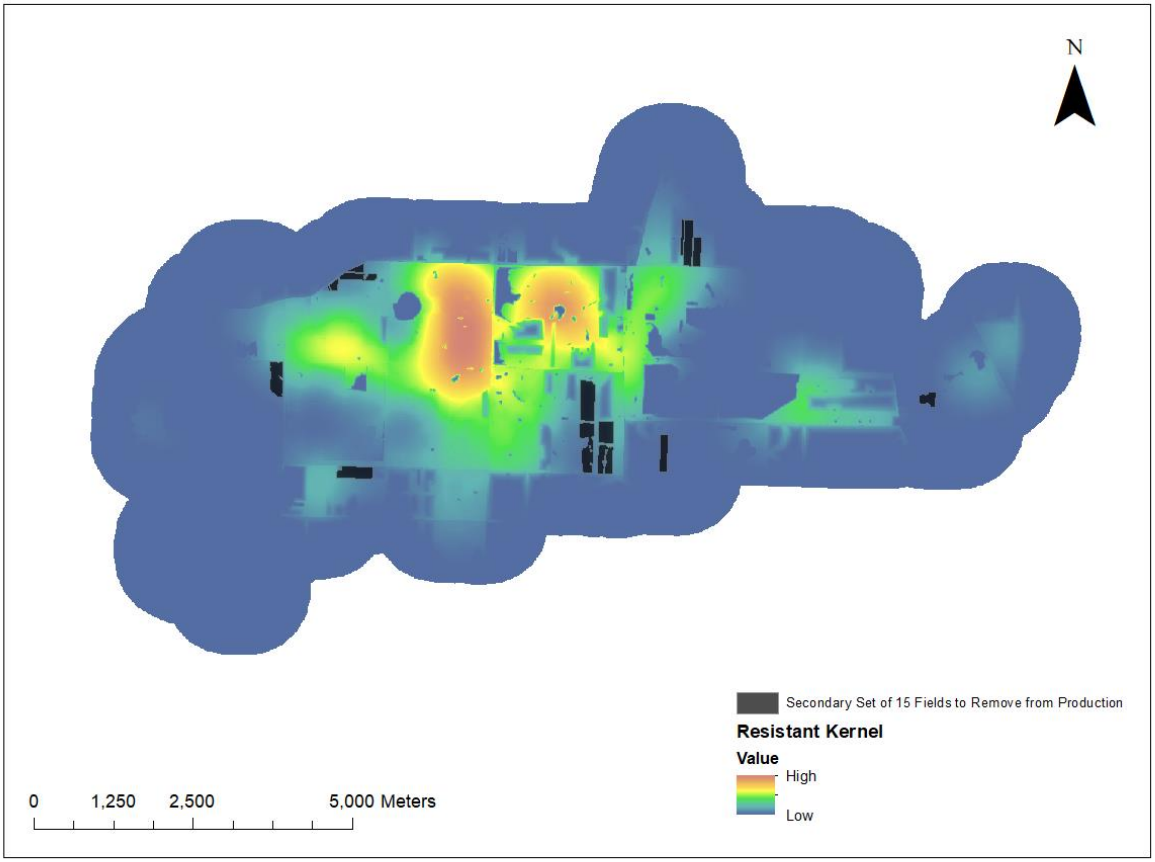

Figure 10. Secondary set of 15 fields that if removed from agriculture and restored would most increase functional connectivity for massasaugas based on my models. Most of these fields are located in close proximity to other occupied fields, or in areas that could be colonized by removing the initial 15 fields from production. This image shows the effective 1000 m dispersal distance and a resistance value of 5 for agriculture.

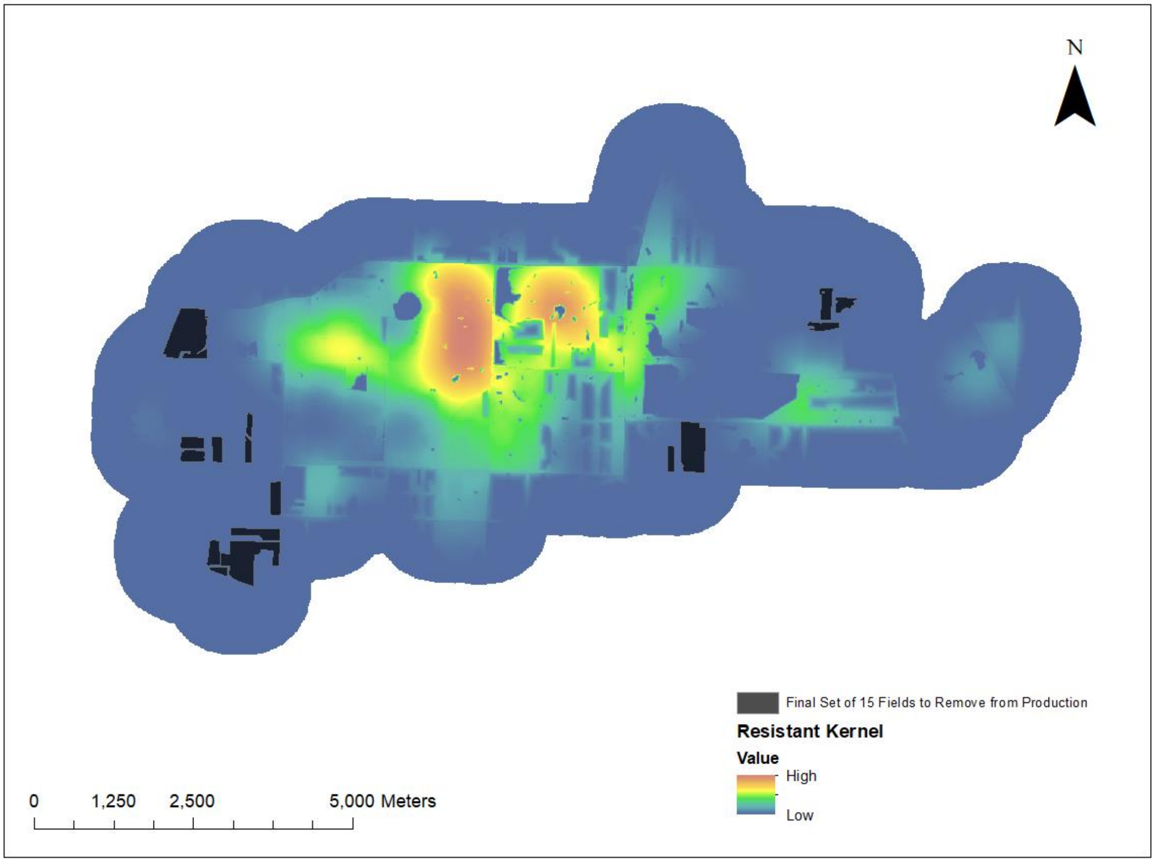

Figure 11. Tertiary set of 15 fields that if removed from agriculture and restored would increase functional connectivity based on my models. Colonization of these fields would likely necessitate multi-generational movements and dispersals, or connection via other suitable habitat. This image shows the effective 1000 m dispersal distance and a resistance value of 5 for agriculture.

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