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Influence of Habitat on Presence of Striped Skunks in Midwestern North America

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Abstract: Striped skunks (*Mephitis mephitis*) are urban-adapted, generalist mesocarnivores widely distributed throughout North America. Although striped skunks have been studied extensively at small scales, knowledge of habitat influences on striped skunks at large scales is lacking. We developed a species distribution model (SDM) to examine potential striped skunk presence in a 16,058 km² portion of southern Illinois, USA. We built models using SDM Toolbox and MaxEnt, and incorporated known presence locations, 1 km² land cover data, and an index of human modification of the landscape. Land cover and human modification explained 98% and 2% of variation in our model, respectively. The highest presence of striped skunks existed in areas with forest cover and developed open space with moderate human modification. The striped skunk presence was lowest in areas with cultivated crops and woody wetlands with either low or high human modification. Forest cover provides natural food and shelter resources for striped skunks, but resources are likely augmented by human activity in developed open space. Cultivated crops only provide seasonal resources, and inundation limits denning in wooded wetlands. Our model indicated striped skunks are a synanthropic species that regularly inhabits both natural and anthropogenic habitats over a large scale.



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1. Introduction

Human activities such as exploitation, persecution, and habitat loss and fragmentation have led to the decline of large carnivores and the rise of mesocarnivores in many parts of the globe [1–4]. Mesocarnivores are medium-sized predators that are often more numerous and diverse than iconic large carnivores, yet their ecological role is comparatively less studied [4]. Though not typically viewed as a threat by humans, generalist mesocarnivores often persist near humans [4]. These species typically benefit from increased landscape diversity associated with human-induced landscape changes [5,6] and the variety of resources gained from multiple habitat types in one heterogeneous area [7]. Mesocarnivores are hosts to many parasites and diseases common in both wildlife and domestic animals, and may act as drivers of disease dynamics in habitats where they are prevalent [4]. However, individual specialization within species and the variety of habitat types that some generalist species use may make it difficult to establish broad scale patterns of habitat preferences or infer patterns from one region to another [8,9].

Certain mesocarnivore species thrive in the Midwestern United States (hereafter, Midwest) [10–12], a region dominated by agricultural and anthropogenic activity with remnant patches of native habitat scattered throughout [13,14]. In this region, southern Illinois maintains high interspersions of agriculture, urban development, and forest cover [15]. Lesmeister et al. [16] examined occupancy and co-occupancy dynamics of the mesocarnivore guild in southern Illinois and found habitat preferences, as opposed to interspecific interactions, to be the most important factor in determining the structure

of the community. However, determining habitat preference may be difficult for some members of the mesocarnivore guild. For instance, Virginia opossums (*Didelphis virginiana*) are steadily increasing their geographic range as anthropogenic resources become more readily available to support the species in previously marginal regions of habitat [17], and Lesmeister et al. [16] indicated that raccoons (*Procyon lotor*) were nearly ubiquitous throughout southern Illinois.

Striped skunks (*Mephitis mephitis*) are generalist mesocarnivores widely distributed throughout North America and especially so in the Midwest [18]. Striped skunks have exhibited varying habitat preferences across their geographical range, ranging from woodlands and fields [18] to marsh [19], farmland [20,21], and even anthropogenic or commercial/industrial areas [16,22,23]. Bixler and Gittleman [24] established striped skunks as an edge species, a trait often associated with urban-adapted species [25] given the increased edge effects caused by rapidly changing landscapes during the process of urbanization [26]. Studies of striped skunk ecology in Illinois indicated higher striped skunk occupancy in anthropogenic areas and along edges [16], but striped skunk densities did not appear to vary with urbanization [27]. Harvest records showed higher numbers of striped skunks in areas of Illinois with sufficient water resources and a mixture of farmland and timber [28,29], and striped skunks also reportedly used pasture and hay crops more frequently than expected [20]. Woodlands with open areas were important components of striped skunk habitat [18], and distance to forest was the most important contributor to habitat suitability for striped skunks [30].

Species distribution models (SDM) [30–32] can be used to predict wildlife presence and elucidate habitat factors affecting potential presence over large scales. Although several studies have examined striped skunk habitat use at small scales, broad-scale studies are limited to two prior efforts in Illinois: an SDM for the Chicago metropolitan area [30] and an occupancy-based spatial model created for southern Illinois [16]. Given stark differences between these two study areas and methodology (i.e., occupancy models depict the occupied niche of a species rather than the fundamental niche modeled by SDMs [33]), we developed an SDM of potential presence of striped skunks in a generally rural region of high habitat heterogeneity with varying degrees of human modification in southern Illinois. We hypothesized potential striped skunk presence in southern Illinois would generally be high because of the high habitat heterogeneity in the region and the benefits of habitat heterogeneity for generalist mesocarnivores such as striped skunks. Specifically, we expected forest cover and areas of high habitat interspersed created by human modification would have the highest predicted striped skunk presence due to abundant food and shelter resources. We anticipated high striped skunk presence in agriculture cover types because previous research indicated striped skunks may prefer agricultural cover. We further expected low striped skunk presence in wetlands because of poor denning opportunities in inundated areas.

2. Materials and Methods

2.1. Study Area

We studied striped skunks in the 16 southernmost counties of Illinois (16,058 km²). The region was a transition zone comprised of the Southern Till Plain, Wabash Border, Ozark, Lower Mississippi River Bottomlands, Shawnee Hills, and Coastal Plain divisions of Illinois [34]. Mean human population density was 50.3 persons/km² [35], with abundant stream (1.1 km/km²) [36] and road densities (1.2 km/km²) [37]. Mean annual temperature was 13.4 ± 0.2 °C (±standard error), and mean annual precipitation was 127.0 ± 2.0 cm [38]. The region was dominated by agriculture (45%), especially in the northern counties and along major rivers. The southern portion of the region was largely forest (34%), including the Shawnee National Forest, Crab Orchard National Wildlife Refuge, Cypress Creek National Wildlife Refuge, and multiple state parks and other state-managed public land. Grasslands and pastures (13%), wetlands (4%), urban development (2%), and open water (2%) were also present [15].

2.2. Striped Skunk Presence

Similar to other SDM studies [39,40], we utilized different sources of presence-only data collected at different scales and during different temporal periods to model species distribution. We incorporated 342 presence-only striped skunk locations recorded via camera traps ($n = 234$ locations) and radiotelemetry ($n = 108$ locations) into SDMs. Striped skunk populations in southern Illinois appeared to be stable [16], so we pooled occurrence data collected by two different methods over two different time periods, allowing us to address potential shortcomings of each method for creating SDMs. Camera traps are easily deployed across large spatial scales [16], but placement of the cameras may bias spatial models. In our case, cameras used to detect striped skunks were placed at a large scale ($16,058 \text{ km}^2$) on wildlife trails in randomly selected sites surrounded by forest cover; those areas with $>11\%$ forest cover were sampled [16]. However, radiotelemetry occurred at a much smaller scale (2650 km^2) within the study area that encompassed a gradient of forest-to-developed cover types. Furthermore, radiotelemetry allows for active gathering of location data depending on animal movements, as opposed to camera traps, which are placed at specific locations. We combined occurrences from both sampling methods and spatially rarefied data to address inherent sampling biases.

Camera traps ($n = 1188$ unique camera locations; Cuddeback Excite and Capture Models, Nontypical, Inc., Park Falls, WI, USA) were deployed during January to April 2008, 2009, and 2010 at randomly selected sites within 2.6 km^2 political sections with $>11\%$ forest cover throughout the region [16]. All cameras were baited with sardines and fatty acid scent disks (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, ID, USA) and placed 2 m from bait and 0.5 m from the ground in areas with woody or brushy cover [16]. All cameras were placed ≥ 250 m apart to maintain independence of sampling locations. Striped skunk ($n = 40$, 22 male and 18 female) locations were recorded via radiotelemetry during April 2018 to March 2020 as part of an ongoing study of striped skunk ecology in the region. All capture and tracking methods were approved by Southern Illinois University Carbondale's Institutional Animal Care and Use Committee (protocol number 18-021, approved 19 April 2018). Striped skunks were captured in wire Tomahawk traps (Tomahawk Live Traps, Hazelhurst, WI, USA) baited with cat food and fish sauce. Captured striped skunks were anesthetized with Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA) and fitted with VHF radiocollars (Wildlife Materials, Inc., Murphysboro, IL, USA). Collared striped skunks were located ≥ 3 times each week by nighttime triangulation (18:00–23:00) with a vehicle and daytime homing (7:00–17:00) on foot with a radio receiver (Communications Specialists, Inc., Orange, CA, USA) and Yagi antenna. We included both resting and active locations because striped skunks use many different den sites that are scattered throughout the home range and are an important resource for survival of the aposematic species [18]. We estimated triangulated locations with program LOAS (Ecological Software Solutions LLC) and discarded points with error polygons >1 ha. All radiotelemetry locations were rarefied to 250 m to ensure uniform scale throughout all presence data and to prevent bias due to clumping of locations.

2.3. Environmental Variables

We included two environmental data layers in the SDM: an index of human modification of the landscape at 1 km^2 scale (Figure 1) [41] and land cover data from the National Land Cover Database (NLCD; Figure 2) [15] resampled to 1 km^2 with ArcGIS, version 10.6 (ESRI, Redlands, CA, USA) with open water, wooded wetlands, and emergent herbaceous wetlands combined into one class. Land cover classes were water/wetland, developed open space ($<20\%$ impervious surfaces), developed low intensity ($20\text{--}49\%$ impervious surfaces), developed medium intensity ($50\text{--}79\%$ impervious surfaces), barren land, deciduous forest, evergreen forest, mixed forest, grassland/herbaceous, pasture/hay, and cultivated crops [15]. The index of human modification incorporates scores for human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure to create a human modification score ranging from 0.00 (no modification) to 1.00 (high modi-

fication) for each pixel [41]. The layer is at 1 km² spatial resolution because it incorporates 13 stressor datasets into the index and provides global coverage [41].

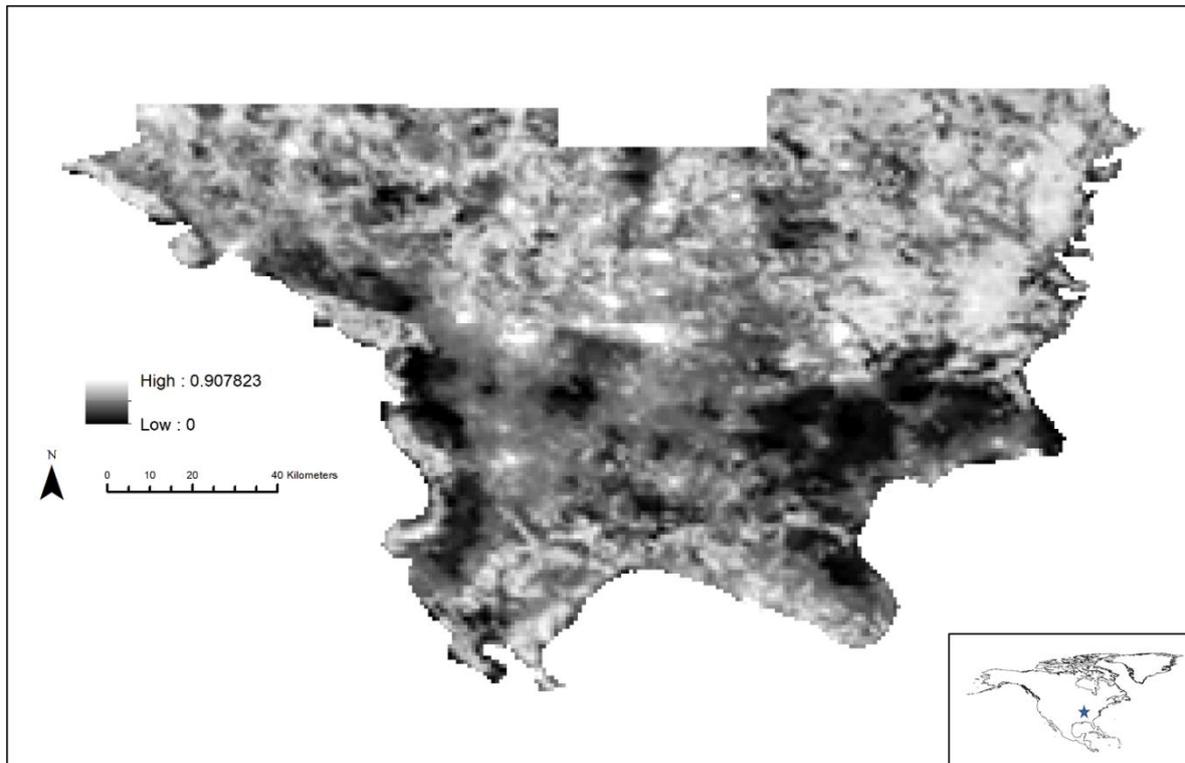


Figure 1. Human modification of southern Illinois, USA [41]. Modification score ranges from 0.0 (low) to 0.908 (high).

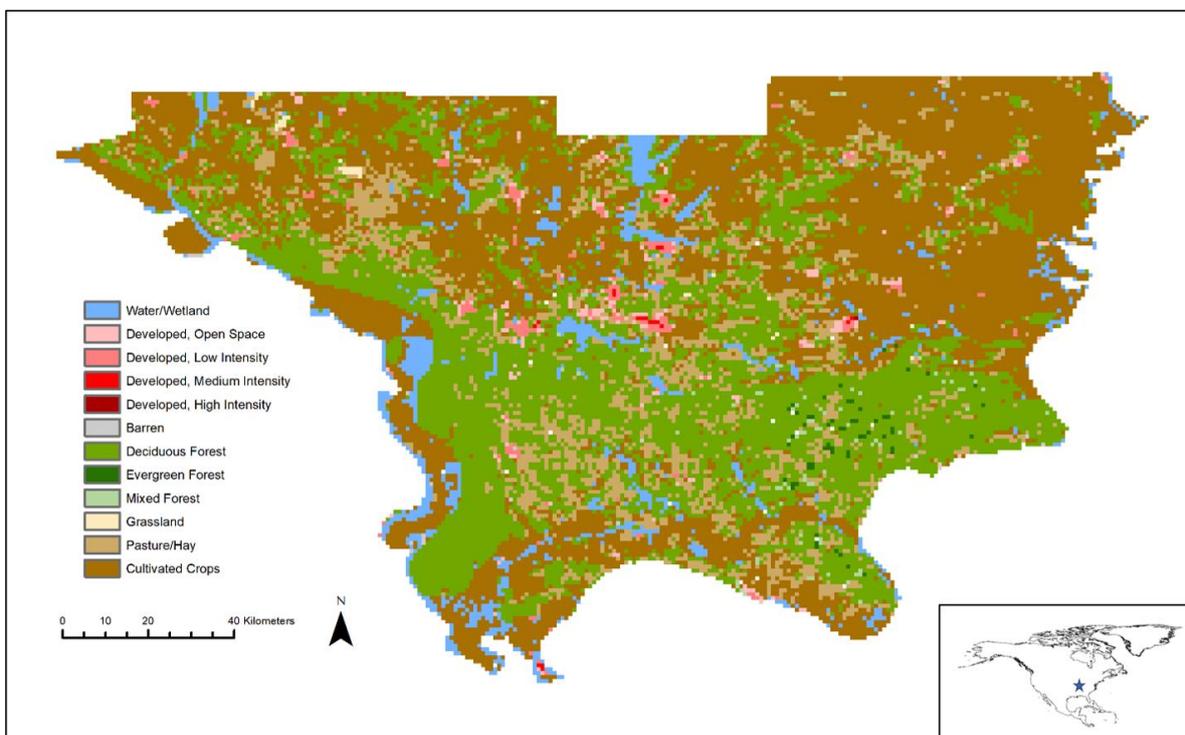


Figure 2. Land cover classes of southern Illinois, USA [15]. Classes were resampled to 1 km² and open water, wooded wetlands, and emergent herbaceous wetlands were combined to one class.

2.4. Species Distribution Modeling

We built spatial models of potential striped skunk presence using SDM Toolbox, version 2.4, [42] and MaxEnt, version 3.4.1 [32]. This method uses machine learning to evaluate presence-only data and environmental variables to model species distributions [32]. To do this, MaxEnt creates pseudo-absence locations to compare to recorded presences via random sampling [32,42]. The most informative models limit overfitting to the data while maintaining highest discriminatory ability [33,42]. We used SDM Toolbox to implement several techniques to create the most informative model for our data. We incorporated a buffered minimum convex polygon bias file to reduce overprediction by limiting pseudo-absences to the same region where striped skunk presence was recorded in this study [42]. We used spatial jackknifing ($k = 3$) rather than random sampling to evaluate presences and pseudo-absences, and we tested multiple regularization multipliers (e.g., 0.5, 1, 1.5, 2, 3, 5) and feature class types (e.g., linear, quadratic, hinge, product, threshold) to determine best model performance and to prevent overfitting [32,42–44]. We examined omission error rate (OER), then area under the curve (AUC), to determine model fit [33,42]. The top model had the lowest OER and highest AUC. We examined percentage contributions and response curve patterns of environmental variables to determine their impact on presence of striped skunks.

3. Results

The SDM model (Figure 3) was of reasonable fit (OER = 0.003, AUC = 0.629) and included a five-regularization multiplier and a hinge, linear, quadratic feature class. Land cover type (Figures 2 and 4) and human modification (Figures 1 and 5) explained 98% and 2% of variation in the model with 92% and 8% permutation importance, respectively. The model indicated high presence of striped skunks in central parts of the study area dominated by developed areas and forests, but relatively low presence in the northeast, which was comprised of primarily cultivated crops (Figures 2 and 3).

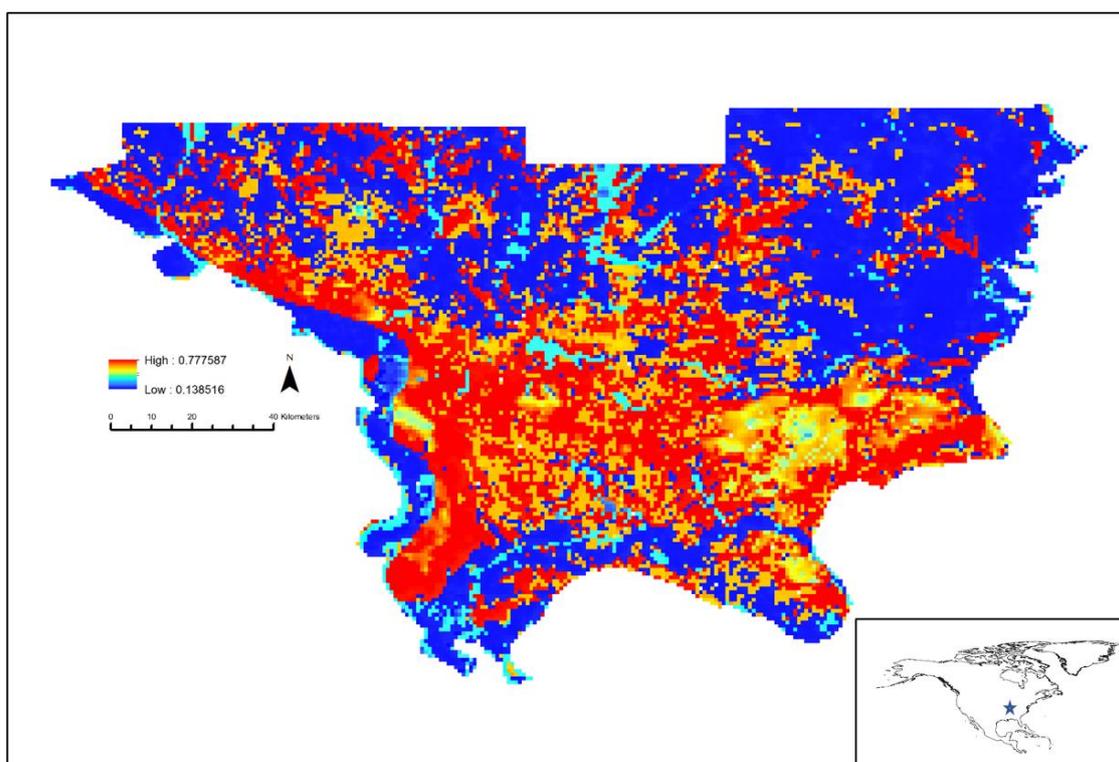


Figure 3. Spatial distribution model of predicted striped skunk presence in southern Illinois based on striped skunk occurrences collected during January to April 2008–2010 and April 2018–March 2020. Predicted presence score ranges from 0.0 (low) to 1.0 (high).

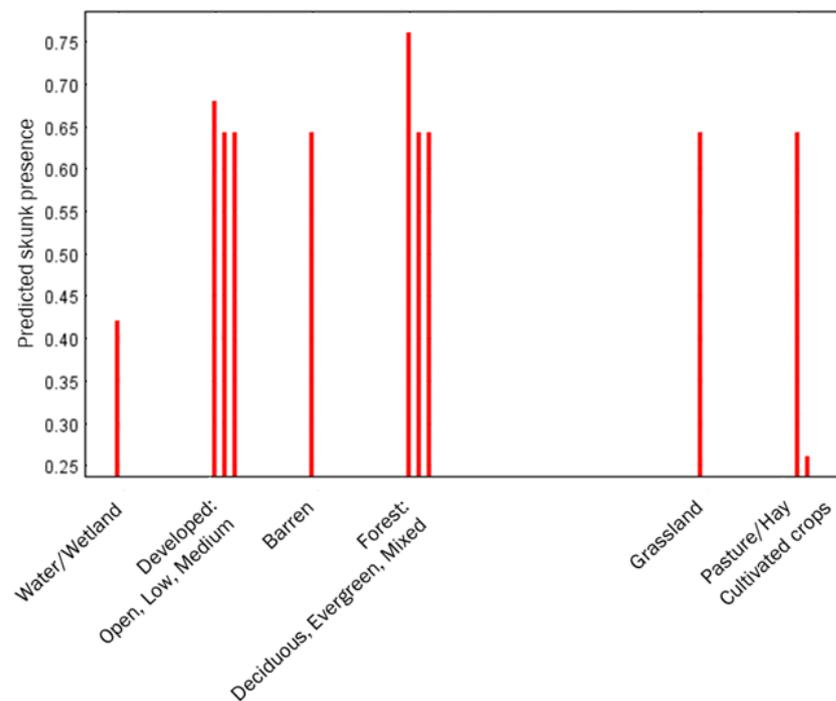


Figure 4. Predicted striped skunk presence as a function of land cover class as described by the NLCD [15] based on striped skunk occurrences collected during January to April 2008–2010 and April 2018–March 2020.

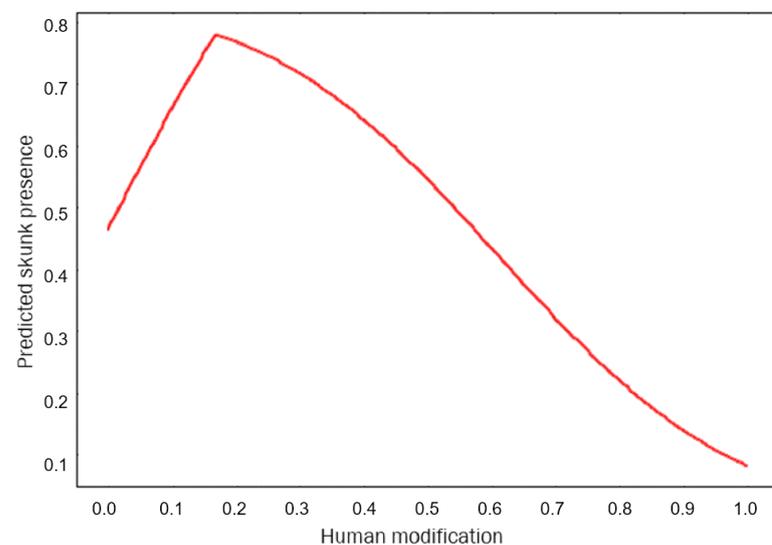


Figure 5. Predicted striped skunk presence as a function of human modification [41] based on striped skunk occurrences collected during January to April 2008–2010 and April 2018–March 2020.

Highest probability (>75%) of striped skunk presence was found in areas with deciduous and mixed forests, especially in large, contiguous patches in the central portion of the study area (Figures 2–4). Developed open space often associated with maintained lawns and golf courses in the central portion of the study area also had high (>65%) striped skunk presence (Figures 2–4). Striped skunk presence was also highest in areas of moderate (0.1–0.4) [41] human modification often associated with exurban and fragmented forest (Figures 1, 3 and 5).

Cultivated crops and water/wetlands were land cover classes least likely (<30% and <45%, respectively) to support striped skunk presence and were dominant in the north

and south (Figures 2–4). Areas of very high or very low human modification, present in northern regions (high) and some patches of the central region (low) were indicative of low striped skunk presence (Figures 1, 3 and 5). Urban centers with high human modification and forested areas with little human activity appeared to be less likely to support striped skunk presence (Figures 1–5). Extensive presence of cultivated crops also led to an elevated human modification score, and thus, low striped skunk presence (Figures 1–3).

4. Discussion

Our SDM indicated large areas of both low and high potential striped skunk presence despite our expectation that the study area would primarily support high striped skunk presence. Our model used striped skunk occurrences collected by camera traps that were also incorporated in the Lesmeister et al. [16] spatial model of striped skunk occupancy in southern Illinois. Predicted striped skunk occupancy in southern Illinois varied across the region [16], as did predicted striped skunk presence in our SDM. However, the occupancy-based model indicated different effects of environmental covariates on striped skunks than our SDM. The occupancy-based model detected a weak negative effect of anthropogenic features on striped skunks [16], but our SDM identified high striped skunk presence in developed open space and areas of moderate human modification. Striped skunk occupancy in southern Illinois was highest in agricultural cover [16], but our SDM predicted low striped skunk presence in these areas. Different findings between these two studies can be explained by the use of different datasets and modeling frameworks.

As expected in our SDM, highest potential presence of striped skunks occurred in developed open space and mixed and deciduous forest land cover classes. Striped skunks are often associated with forest cover, which provides many types of den sites (e.g., brush piles, hollow logs, and previously excavated holes) and diverse forage (e.g., insects, fruits, and carrion) [18,30,45]. However, these resources may also be available in other land cover types. Developed open space is defined by NLCD as <20% impervious surfaces and typically consists of maintained lawns and golf courses near human structures [15]. These greenspaces have previously been identified as preferred striped skunk habitats [16,22,23] that provide supplemental food and den resources for striped skunks [46] but may also bring them into closer contact with other species and alter behaviors and interactions [47]. Roads, yards, and other manmade structures fragment previously forested landscape in the central part of our study area [48], increasing habitat heterogeneity and providing opportunities for generalist mesocarnivores such as striped skunks to forage and seek shelter in several land cover classes within a small area [5–7].

We predicted agricultural cover would support high striped skunk presence and wetlands would support low striped skunk presence, but both wetlands and cultivated crops had the lowest predicted striped skunk presence in our SDM. Previous research indicated that striped skunks avoided denning in the woody wetlands associated with the Mississippi River floodplain, likely due to inundation [49]. Our model identified low presence of striped skunks along major rivers within the study area where woody wetlands often occur. During some seasons, crop cover may provide suitable protection for denning striped skunks, but cover is not consistent throughout the year. Furthermore, cultivated crops are often treated with insecticides, which limit forage for striped skunks, who are primarily insectivores. Previous research identified higher striped skunk presence in agricultural landscapes interspersed with forest cover where resources could be easily obtained from more than one land cover class [7].

Areas of extensive cultivated crops are also highly modified by humans [41], and striped skunk presence was lowest in areas of very low or very high human modification. We predicted striped skunk presence would be higher near human modification, but our SDM indicated low striped skunk presence in highly agricultural areas and urban centers. Though some development may provide supplemental resources for striped skunks, highly modified urban centers put striped skunks further from other land cover classes, such as forest cover, that may contribute additional food and shelter resources. Striped skunks in the

Chicago metropolitan area followed a similar trend, with predicted striped skunk presence closer to forest cover within the highly modified landscape [30]. However, our SDM also indicated low predicted striped skunk presence in areas of forest cover with very low human modification. Sparse striped skunk populations were also detected in large, contiguous forests of the Missouri Ozarks and attributed to minimal food resources [49]. Striped skunks appear to benefit from habitat heterogeneity, whether natural or human-induced.

5. Conclusions

Spatial distribution models can elucidate large-scale trends in species presence that may otherwise be difficult to quantify, as is the case with the striped skunk. Knowledge of distributional patterns of striped skunk presence are important for wildlife managers given the widespread distribution of the species; the tendency to use den sites created and used by other species [50]; and the wide array of diseases (e.g., canine distemper virus, leptospirosis, tularemia, and rabies) striped skunks may carry that can be passed to other wildlife, domestic animals, and humans [45]. Our SDM indicated that striped skunks are most likely present in open developed and forested spaces moderately impacted by humans. Thus, wildlife managers should note that supplemental resources provided by anthropogenic activity may attract striped skunks and increase their interactions with other wildlife, domestic animals, and potentially humans [47].

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Informed Consent Statement: Not applicable.

Data Availability Statement: Data available on request from the corresponding author.

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