Scale-dependent Responses by White-tailed Deer to Habitat Configuration and Fragmentation

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Introduction

The choice of scale plays a key role in the design of ecological studies. However, this is often overlooked or misunderstood, particularly when examining wildlife. Both components of scale, extent and grain, can have profound effects on how interpretations are made about wildlife populations (Sayre, 2005). Even when scale is considered, it is likely for researchers to completely miss the scale of effect—the scale that describes the population most accurately (Chase & Knight, 2013). This can be due to a variety of factors, such as scales that are too different in magnitude, where the scale of effect between scales and is undetected due to being too far from any one chosen scale, and due to minimum and maximum extents that do not include scales of effect within them (Jackson & Fahrig, 2015; Miguet et al., 2016). Further complicating this is the possibility of multiple scales of effect for a landscape metric, as well as differing scales for others (Holland et al., 2004).

Each species has unique behavioral responses to their environment that can manifest at a variety of scales (Powell & Michell, 2012). Most commonly, this is seen through impacts on home ranges, which have been used as the basis of measurement scale in ecological studies. Other times, this choice is not well justified or linked to any clear ecological process (Jackson & Fahrig, 2015). Changes in habitat configuration such as an increase in fragmentation can result in altered food availability and limited access to watering sites, causing individuals to search larger areas for these resources (Holland et al., 2004). As a result, home ranges and the closely related scales of effect seen in the population can become drastically different (Jackson & Fahrig, 2015; Powell &

Michell, 2012). Populations must be assessed individually as they are fundamentally different, leading to extensive and costly field efforts. In response to this, wildlife practitioners have embraced the use of camera traps (i.e., trail cameras) as a more practical method to monitor populations (Burton et al., 2015).

The scale at which camera trap datasets measure wildlife abundance is largely up to debate. Camera traps are often used to describe a wide range of environmental factors from the microhabitat to landscape scale, but the true scale they examine is still inconclusive (Wheatley & Johnson, 2009). In some ways, cameras act similar to simple point counts, but due to their ability to continuously record wildlife for entire seasons, they have the potential to gather more detailed information on local ecological processes. While the relationship between camera trap sampling and spatial scale are still not well defined, it is clear that they have potential as an effective tool for wildlife practitioners, especially with the increased presence of camera trap data that can be used for reanalysis.

Some species appear to experience larger changes to their behavior due to changes in habitat configuration compared to others due to their specific habitat selection behavior. White-tailed deer (*Odocoileus virginianus*) in particular have been shown to have complex interactions with their environments due to their relatively large daily movement ranges compared to other North American mammals, and the use of forest, forest edge, and open (non-forested) habitats for differing purposes (Beier & McCullough, 1990). Understanding habitat selection and behavior in white-tailed deer has become of high interest due to the species’ wide range, relative overabundance, and role as a game species across the eastern United States. Current high deer abundances now pose issues for agriculture and habitat restoration through browsing, increased disease transmission rates such as with chronic wasting disease, and through increased roadkill accidents leading to danger for drivers (Côté et al., 2004). These factors have led to large-scale efforts to control deer populations across the United States, ranging from local community cooperatives to legislation from the federal government. These management actions often fall short due to limitations in our understanding of deer populations compounded with their ubiquity in landscapes of the eastern United States (McCance et al., 2017).

Previous research on the relationship between deer populations and fragmentation in landscapes have shown mixed results. In general, deer are cited as preferring fragmentation due to the higher proportion of edge, but this is not shown clearly in practice. However, some studies have found relationships between deer abundance and low fragmentation (Stephens et al., 2014; Walter et al., 2018), high fragmentation (Walter et al., 2009), and insignificant relationships (Koen et al., 2017). While these studies did assess scale to some degree, there were no significant scales of effect found. The range of results produced related to this subject shows a great need for further research into both the ecology of white-tailed deer in general and the effects of habitat configuration on the species. These studies have also exclusively used GPS collaring as their primary methodology. While this can provide high-precision movement data, GPS collaring is one of the most costly field methodologies for large mammals presenting an issue for practitioners that have limited resources for wildlife monitoring (Lahoz-Monfort & Magrath, 2021).

As an alternative to the standard collaring method, I present an approach using camera trapping data, which is typically less resource intensive and can be used to collect a larger amount of total data points for analyses in a single season. Camera traps are commonly deployed for other, unrelated studies which have the potential to be reanalyzed to better understand scale effects of landscape configuration on deer populations. With increasing efforts related to open science, availability of research data, and collaboration in the past decade, camera trap datasets are readily available for reanalysis in this way (Powers & Hampton, 2019). No dataset seems to exemplify this as well as Snapshot USA, a novel collaborative camera trapping survey encompassing the entire United States. The images captured during this period can be used to characterize animal communities across larger geographic areas with high accuracy because of the minimized temporal variation and standardized protocols (Cove et al., 2021; Kays et al., 2022; Shamon et al., 2024). As a result, this dataset is ideal for characterizing deer populations in relation to scale, which benefits from sampling across a large area with differing habitat configurations.

Due to the high number of camera placements across the three years of released Snapshot USA data (2019–2021) and high relative deer densities, North Carolina was chosen as the ideal study area for characterizing responses to landscape variables in relation to scale (Hanberry & Hanberry, 2020). Deer population abundance was modeled from image observance data using occupancy models. Occupancy is a statistical measure used to estimate the probability that a particular species is occupying an area at any given time (MacKenzie et al., 2002). This method has become increasingly common in wildlife management along with the increased popularity of camera traps (Lahoz-Monfort & Magrath, 2021). Occupancy is also well favored by practitioners because it can be estimated with minimal data inputs and does not require identification and differentiation of individual animals (MacKenzie et al., 2002). Base occupancy models were converted into extended models by including landscape variables measured at five different spatial extents. Model performance was compared using Akaike Information Criterions (AIC) to determine the extent with most explanatory power for each landscape variable (Aho et al., 2014).

Landscape variables measured at different extents showed differing distributions and generally increased as extent sizes became larger, despite being normalized by area. Responses by deer to habitat were highly variable between different years and scale classes. Road density dominated model groups for 2019 and had the highest explanatory power for deer abundance. For 2020 and 2021, patch area was the dominating variable. There was a strong indication that scales of effect were different for each landscape variable. No models showed a peak in performance at intermediate extents, leading to the conclusion that all variables are being responded to at extents outside of those examined here (Jackson & Fahrig, 2015; Miguet et al., 2016). Despite this, the trends between extents display the general direction extents should be shifted to locate the scale of response. Both patch area and road density showed positive relationships with scale class, indicating a scale of response larger than the largest scale class. Inversely, stream density showed a negative relationship and likely has a scale of response smaller than those examined here.

Despite some limitations, camera trapping datasets represent a trove of data waiting to be analyzed for scale effects. Data from Snapshot USA were able to display clear patterns between scales indicating that camera traps can accurately assess species at larger scales. While true scales of effect could not be determined, general directions of scale-landscape relationships were present and could guide future research endeavors. Camera traps show a large amount of promise as a method of examining scale effects in a less intensive way than other standard methods, while being much easier to coordinate at large across large geographic areas.

Methods

Study Area

This study was conducted using camera trap data within the state of North Carolina, USA. This region is home to a unique set of geographic features divided between the Blue Ridge Mountains to the west, the central Piedmont Plateau, and the eastern Tidewater coastal plain (Figure 1). Across these three regions exists a large elevational gradient in relation to these primary regions that provides a wide variety of forest ecosystem types from pine to hardwood (Pinder et al., 1999; Brown et al., 2014). The main land cover type in the state is forests, covering 41.3% of its total area and encompassing 59.5 thousand square kilometers across all three National Land Cover Database (NLCD) forest types. Agriculture has historically been and still is a major export of the state, accounting for 19.6% of its total land area between both pasture and cropland (Dewitz, 2023; Table 1). Between the three major regions, the Blue Ridge Mountains contain majority forest cover types, while the Tidewater coastal plain is composed of a forest-agricultural matrix.

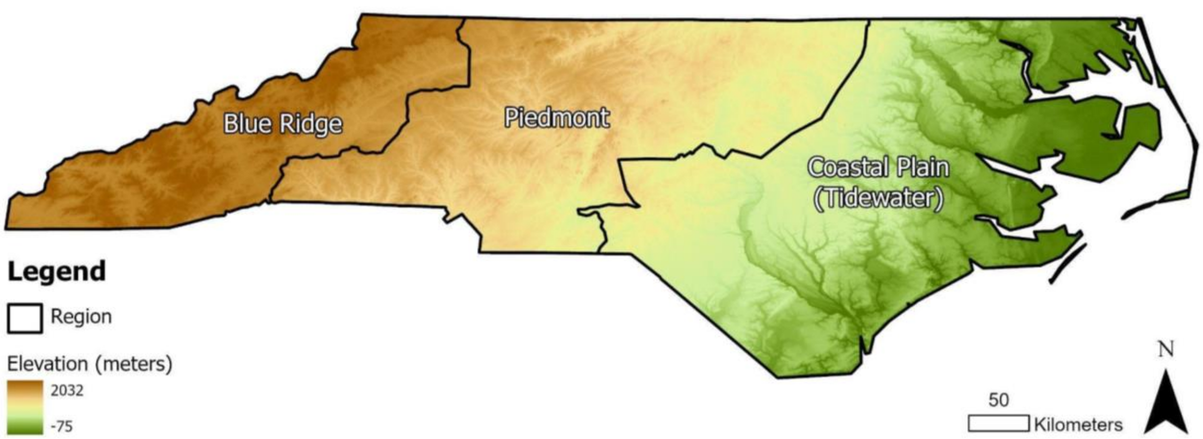

Figure 1. Major regions of North Carolina overlaid with elevation. Regions are defined using county borders based on the U.S. Forest Service's survey areas.

Table 1. Total area and percent cover of NLCD land classes across North Carolina.

Land Class	**Area (km^2)**	**Percent Cover**
Open Water	10,766.5	7.5%
Developed, Open Space	96,72.4	6.7%
Developed, Low Intensity	4,789.6	3.3%
Developed, Medium Intensity	2,127.8	1.5%
Developed, High Intensity	712.1	0.5%
Barren Land	338.1	0.2%
Deciduous Forest	25,954.3	18.0%
Evergreen Forest	18,712.6	13.0%
Mixed Forest	14,852.3	10.3%
Shrub/Scrub	3,724.2	2.6%
Herbaceous	3,228.7	2.2%
Hay/Pasture	10,301.3	7.2%
Cultivated Crops	17,961.3	12.5%
Woody Wetlands	18,923.6	13.1%
Emergent Herbaceous Wetlands	1,997.4	1.4%
TOTAL	**144,062.2**	**100.0%**

The ecological history of North Carolina is a story shared with most other early European settlement areas in North America. Starting in the 16th century, the region underwent the early stages of development seen in the colonial United States, which brought mass deforestation and the large-scale adoption of agriculture, especially in the coastal plains region (Pinder et al., 1999). Across the Eastern United States, deforestation often takes a patchwork, mosaic pattern, resulting in a net decrease in forested area with an increase in fragmentation. In North Carolina this pattern can be seen especially strongly in the coastal plain and Piedmont as the result of human settlements and agricultural land use. In recent decades, the total amount of forest land cover in the state has increased, but composition has been permanently altered. Forest patches are still relatively small compared to pre-Columbian estimates with the continued presence of roadways and agricultural fields splitting habitats, despite increasing total areas (Cowell, 1998; Riitters et al., 2002). Forests are also much earlier in their successional cycle, with many forest stands being composed of individuals mostly <100 years in age. For North Carolina, the loss of late-successional individuals has allowed the encroachment of early-successional species and the loss of a large portion of late-successional pine and oak species, which compose the majority of virgin forests (Cowell, 1998).

Until the early 1900s, white-tailed deer populations were declining as settlement of eastern North America expanded along with increased hunting and harvest due to exponentially increasing human populations. Recognizing the risks deer and other species then faced, measures for conservation began in the early 1900s, slowly creating the overabundance we see today. Previous measures have removed predators from the landscape, increased the availability of food through successional change and the presence of agriculture, provided preferable edge habitats through fragmentation, and increased the power of hunting regulations (Côté et al., 2004; Hanberry & Hanberry, 2020). Recent assessments have placed deer densities in North Carolina at an average of nine individuals per square kilometer, over thirty times estimates for 1940 (Hanberry & Hanberry, 2020).

Datasets

Camera Traps

Snapshot USA is a novel collaborative wildlife sampling effort encompassing the entire United States. Using camera traps researchers coordinate a yearly wildlife monitoring period between September and October across the country. With standardized protocols and minimized temporal variation, the images captured during this period can be used to characterize animal communities across larger areas with more accurate results than disparate projects (Cove et al., 2021; Kays et al., 2022; Shamon et al., 2024). Between 2019 and 2021, North Carolina had more cameras deployed for Snapshot USA than any other state, making it ideal for assessing the efficacy of large-scale camera trap networks on white-tailed deer (2019: 212, 2020: 128, 2021: 131). Snapshot data was subset to only North Carolina, with the exception of one camera array in South Carolina that was included in the final dataset due to its proximity to the states' shared border being less than five kilometers. This resulted in a total of 28 arrays covering 485 cameras that were used for analyses. Cameras were primarily located within patches of forest cover types, but some individual cameras were placed within "Open, Developed" (typically neighboring forest patches) and "Herbaceous" land cover types. Between the three years, locations for 2020 and 2021 are highly similar, with many locations being resampled (Figure 2).

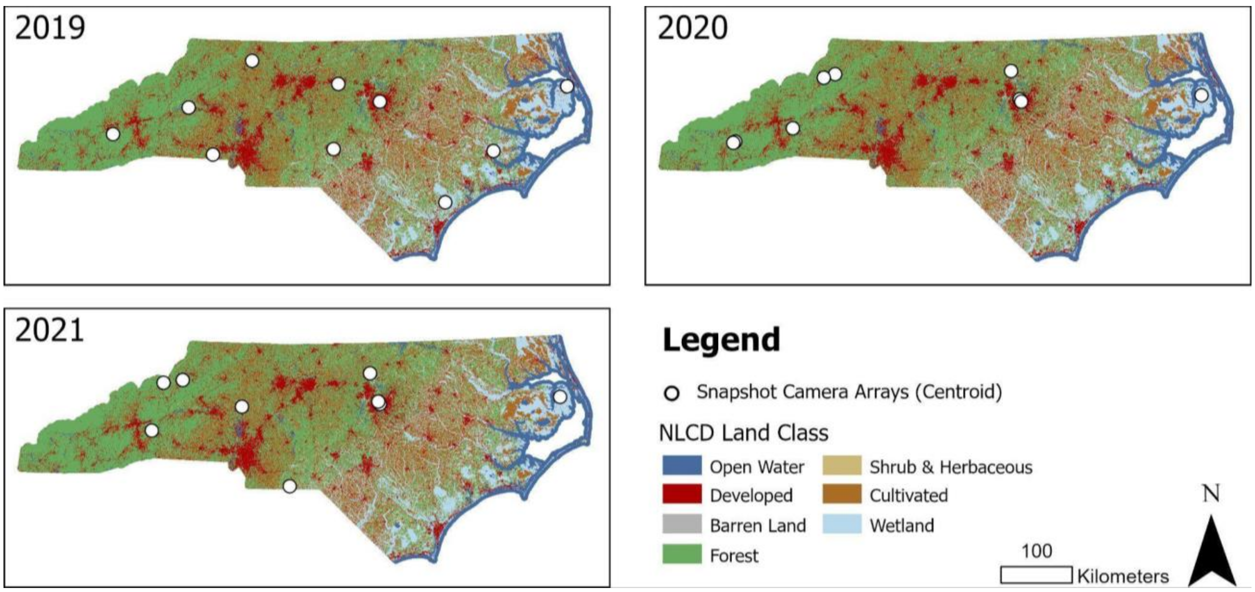

Figure 2. Snapshot camera locations by year. Points represent centroids of camera arrays. NLCD land classes are simplified and reclassified from 15 to 7 classes and clipped to the state border with a 5 km buffer. Cameras within arrays are spatially clustered near the centroid point.

Land Cover

The National Land Cover Database (NLCD) is an authoritative, Landsat-based, 30-meter resolution land cover dataset developed by the United States Geological Survey. NLCD data products are produced roughly every three years, with the most recent representing the state of the United States during 2021. Land cover is divided between 17 classes, representing both developed and human created land cover types, as well as natural cover types (see Table 1 for a list of land cover classes). Land cover types for a given cell are determined using decision trees based on a variety of remotely sensed physical and biological data, with an estimated average accuracy of 91% across the United States (Dewitz, 2023).

Roads & Streams

The National Hydrography Dataset (NHD) is a comprehensive dataset representing the surface waters of the United States. The dataset covers streams, rivers, canals, lakes, ponds, and dams all at a 1:24,000 scale. The NHD is maintained by the United States Geological Service as part of the National Map Program, which provides authoritative spatial data for federal agencies. Data within the NHD is often provided by a mix of state and federal agencies. The NHD is widely used for stream network analyses by agencies such as the Environmental Protection Agency, but also acts as one of the primary sources for estimates of stream density and aquatic surface area (U.S. Geological Survey, 2023).

The Topologically Integrated Geographic Encoding and Referencing system (TIGER) is the United States Census Bureau’s primary spatial dataset. TIGER provides a variety of datasets including legal boundaries, roads, address information, water features, and demographic data. TIGER datasets are updated annually and represent the most up-to-date version of many common types of geospatial data. Data is compiled primarily by the U.S. Census for demographic data, but information on road networks, water features, and legal boundaries are provided by a combination of federal agencies. Features such as road networks are provided at multiple scales and levels of detail such as primary, secondary, and local roads (U.S. Census, 2023).

Analysis

Four landscape variables were chosen to characterize fragmentation and habitat configuration: patch area, forest edge, road density, and stream density. Patch area and forest edge are normalized by extent area. Variables are sourced from the NLCD (patch area and forest edge), TIGER (road density), and NHD (stream density). Each variable attempts to characterize a different aspect of the local environment in relation to fragmentation. Patch areas are typically lower when fragmentation is high, while forest edge lengths tend to be higher. Both road and stream networks split habitat patches, but both may not be viewed the same way by wildlife.

Landscape Variables

Habitat configuration data were extracted and summarized for every camera placement at five different extents. Extents were organized into classes with values of 1–5, relating to the relative area covered by the extent. Extents were chosen with roughly one square kilometer (0.98 km^2) as the central extent area (Table 2). This aligns with previous estimates of deer home ranges that have been found in the coastal plains region estimated at roughly 1.2 km^2 (Byrne et al., 2014). Home ranges in this area are expected to be larger than in the other regions within the state due to higher deer densities seen in the coastal plains (Hanberry & Hanberry, 2020). In general, high densities contribute to lower availability of resources in the local environment and increased competition that in turn increase the total area an animal must traverse for resources (i.e., their home range; Kjellander et al., 2004; Walter et al., 2018).

Table 2. Extent classes used for analyses.

Extent Class	Side Length (m)	Area (km^2)	Cell Dimensions
1	630	0.40	21 x 21
2	810	0.66	27 x 27
3	990	0.98	33 x 33
4	1170	1.37	39 x 39
5	1350	1.82	45 x 45

Landscape variables were extracted from data sources using a combination of ArcGIS Pro's Python API (*arcpy*) and Fragstats 4.2 (McGarigal et al., 2023). Extent areas were generated using *arcpy* and data within was summarized. For road density and stream density, the total length of line segments within each extent was determined. Patch area was calculated with a custom geoprocessing tool that extracts patch areas based on input points, with a specified extent (see *Data & Code Availability*; Figure 3). Forest edge was calculated using Fragstats with points exported from ArcGIS Pro as raster cell locations. Covariance between all landscape variables was calculated to examine potential relationships between model performance and real-world similarity in the distribution of features.

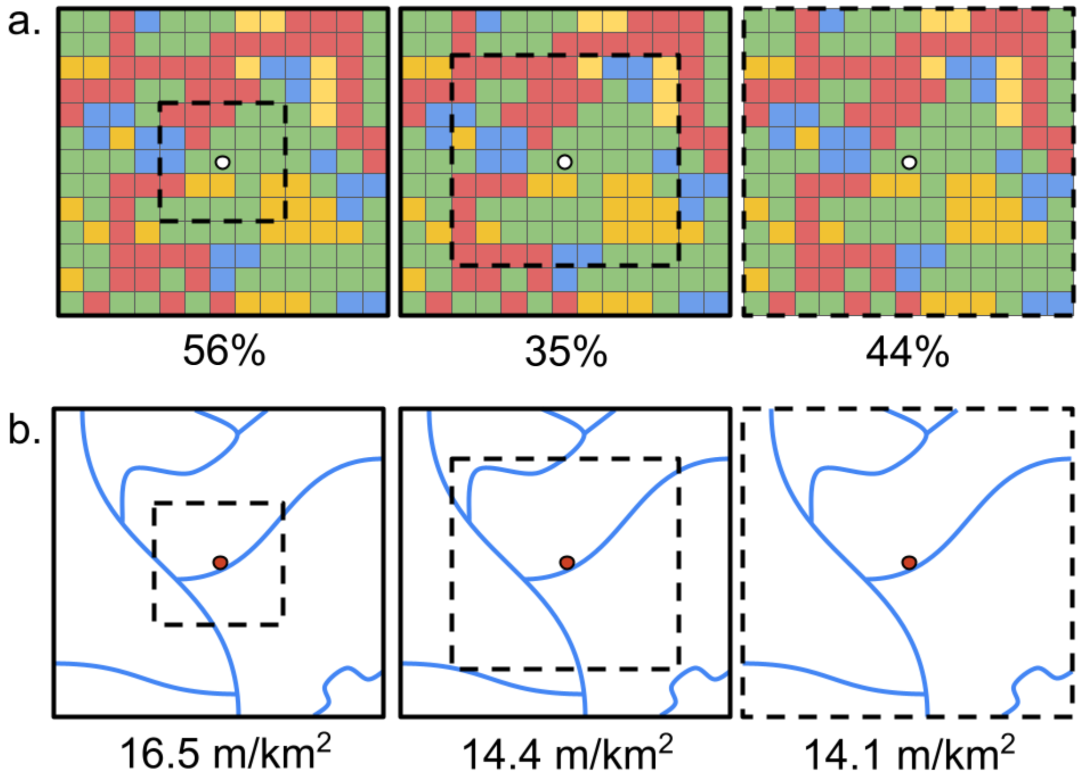

Figure 3. Conceptual diagram of measuring landscape variables across three extent classes for proportion of (a) forest cover and (b) stream density. Dashed lines represent the extent being examined in each panel. (a) White and (b) red points represent a central sampling point all extents center on (i.e., camera locations). Proportion of forest cover shows a nonlinear relationship with extent area, while stream density shows a more linear negative relationship with extent area.

Occupancy Models

White-tailed deer abundance was calculated using single-season occupancy models in R with the *camtrapR* package (Niedballa et al., 2016; R Core Team, 2021). Snapshot data was transformed from image records to detection histories representing presence/absence at each site during each day using Python. Detection histories were input into *camtrapR* with covariate data to create base (null) occupancy models. All three years of Snapshot USA data were modeled separately as their own base model. Extended models were created from base models with each including one landscape variable measured at a specific scale class. All variables were standardized before modeling to improve computational efficiency and performance.

After models were created, they were compared using model selection with the Akaike Information Criterion (AIC) using the *MuMIn* package in R (Bartoń, 2024). AIC is a measure of the overall fit of models in relation to others in a model selection group. Models with the lowest AIC values display the best fit to the original data and those with a difference in AIC (ΔAIC) greater than two are significantly different from the next best performing model. Using model selection, the AIC metrics of multiple models can be compared and those with the best performance can be determined (Aho et al., 2014). Model groups were created as combinations of either (1) multiple variables assessed at the same scale class during a year or (2) a single variable assessed across all scale classes during a year. It can be assumed that the model with the best performance in a group is the most likely to be related to deer behavior in the group. However, having a high performance does not necessarily signal an overt significant relationship between the two.

Results

Occupancy Models

I constructed a total of 65 occupancy models to assess the relationship between measurement extent and deer abundance. Models were organized into 27 groups for model selection. Model groups 1–15 were organized to compare multiple variables at a given scale class, while groups 16–27 were organized to examine the differences between scale classes of a single variable. All model groups included an appropriate null model for comparison. Each model group only used data from a single year, as attempting model selection between different datasets is generally not possible due to the influence of the number of records and data distribution on AIC scores (Aho et al., 2014).

Within model groups 1–15, the best performing models included road density for all 2019 groups and patch area for all 2020 and 2021 groups. Null models consistently ranked in the bottom half of all models in all groups. Road density showed the most variable performance, being the highest ranked in 2019, similar to the Null model in 2020, and higher at low and high scales in 2021. As extent area increased, model groups showed more drastic differences between the best performing model and others. Road density, stream density, and patch area showed clear changes in performance over scales, while forest edge did not. Depending on the year, the relationship between performance and scale was different, with road and stream density having alternating positive-negative patterns (Figure 4).

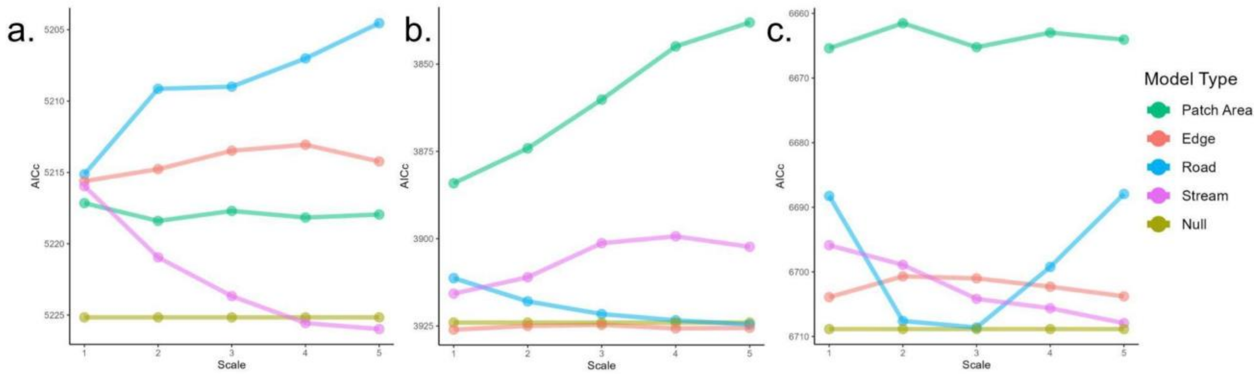

Figure 4. Visual representation of model rankings with AIC_c in model groups 1–15. (a) model groups for 2019: 1–5, (b) model groups for 2020: 6–10, and (c) model groups for 2021: 11–15.

In groups 16–27, rankings were much more inconsistent. ΔAIC_c values were overall lower and no single scale class dominated model groups. Model groups focused on forest edge showed the least amount of variability in ΔAIC_c between all three years, although this was also the only variable to have a null model as the best performing model, in 2019. Groups focused on patch area also had less variability, but only in 2019 and 2020. While the spatial distribution of camera locations and the results of model groups 1–15 showed similarities between 2020 and 2021, groups 16–27 had high similarity in ΔAIC_c between 2019 and 2020. The best performing scale class for each landscape variable did not have a clear pattern, but scale classes 1 and 5 were the most common high ranked models (Table 3).

Table 3. Best performing extent class of each variable by year for model groups 15–27. Models with significantly greater performance than the next best performing model (ΔAIC_c > 2) are indicated with an asterisk.

Year	Patch Area	Road Density	Stream Density	Forest Edge
2019	1	5*	1*	4
2020	5*	1*	4	Null
2021	2	5	1*	2

Landscape Variables

All landscape variables were significantly different between scales, even after adjusting for total extent area (Table 4). As extent area increased, the range and maximum value of landscape variables also increased despite values being normalized with extent area. Values clustered near zero at small scale classes but as extent areas got larger, they tended to cluster at larger values. Both patch area and stream density showed somewhat bimodal distributions at small scale classes that were no longer present at larger ones (Figure 5). There were no strong correlations found between landscape variables (Table 5).

Table 4. Linear regression results for landscape variables in relation to extent class. F-statistics all reported with degrees of freedom of 4 and 2420.

Variable	F-statistic	P-value	Adjusted R^2
Stream Density	46.58	<0.001	0.070
Road Density	53.20	<0.001	0.079
Forest Edge	42.62	<0.001	0.064
Patch Area	4.09	<0.001	0.007

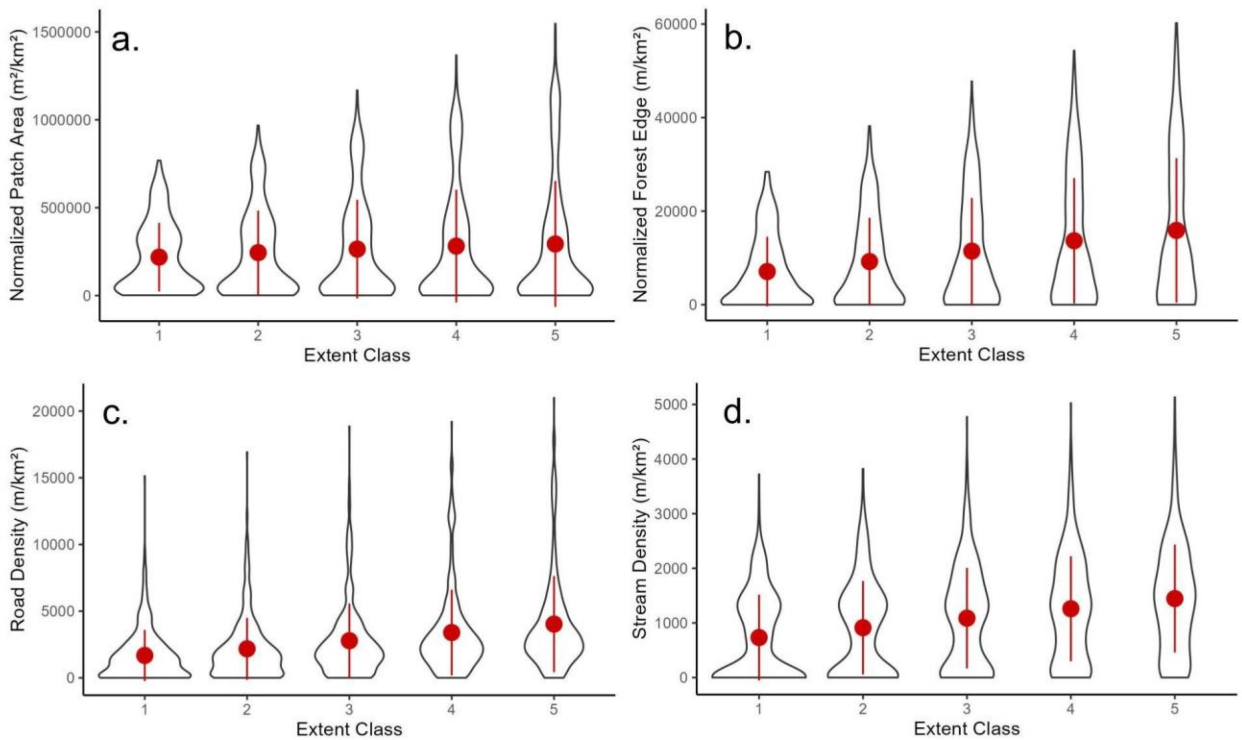

Figure 5. Violin plots displaying variation in landscape variables across five extent classes. Width of plots at each location is related to the density of data points. Variables shown include (a) patch area, (b) forest edge, (c) road density, and (d) stream density. Red points and lines represent mean values and standard deviations respectively.

Table 5. Correlation matrix for landscape variables and scale class.

	Scale Class	Patch Area	Forest Edge	Roads Density	Stream Density
Scale Class	1.000	0.092	0.257	0.284	0.267
Patch Area	0.092	1.000	-0.092	-0.147	-0.188
Forest Edge	0.257	-0.092	1.000	0.069	0.041
Roads Density	0.284	-0.147	0.069	1.000	0.046
Stream Density	0.267	-0.188	0.041	0.046	1.000

Discussion

Landscape variables were significantly different between scale classes and showed little to no correlation with each other. Although all variables were normalized based on extent area, larger scales always showed higher maximum values. I theorize that this is the result of multiple factors that each uniquely affect landscape variables. Forest edge is calculated based on the side lengths of cells in a raster grid, which is not directly related to area. Thus, this had a different, almost exponential scaling factor for even simple square patches, which have the smallest amount of edge per area (Guthery & Bingham, 1992; Riitters et al., 2002). For both road and stream densities, values were likely higher at larger extents due to there being an increased probability that areas of high density would be found within the extent area. Many sampling locations were moderately close to urban areas, which naturally have higher road density and may have higher stream density that were included within large extents. The relationship seen with patch area was somewhat surprising, as increasing the extent past the full size of a patch should lower the normalized patch size. With this in mind, it is assumed that patches never covered the entirety of a single extent as extent increased and that a few patches managed to increase in area as more of that patch was included. Patch areas overwhelmingly did not exceed extent areas in total span, as indicated by the clustering of values near zero at all scales. The majority of cameras were placed within forest land cover types, but some were placed in “Developed, Open” patches. These patches were almost always small and adjacent to forest patches indicated that cameras were within forests, but the 30-meter resolution of the NLCD did not accurately capture the location of edges. These cameras were also noted as being within forest areas in the raw Snapshot USA datasets.

Deer responses to habitat displayed high variability between years but showed more support for large extents. Each landscape variable displayed a unique pattern during different years, showing fundamental differences in the three Snapshot USA datasets. Surprisingly, data for

2020 and 2021 were not overly similar in terms of scale class, despite having similar spatial distributions and the dominance of patch area. Occupancy models are highly affected by their input datasets, so differences in deer activity during camera deployments likely account for much of the difference between 2020 and 2021. Both road density and patch area were strong comparative predictors of deer abundance as seen by their substantially higher AIC_c values during respective years.

Based on model results, there is a strong indication that each landscape variable had a differing scale of effect, though the actual scale this was at differs by year. Road density was consistently not important or displayed a positive relationship with extent and likely has a scale of effect that is or larger than the largest scale class. Patch area was consistently important and likely has a scale of effect larger than the largest scale class. Stream density had little importance, but did have a strong negative relationship with extent and likely has a scale of effect smaller than the smallest scale class. Forest edge did not show a clear relationship, so it may have no specific scale of effect, or this scale could be so far from those used here that it was not detected. No models showed a peak in performance at intermediate extents, leading to the conclusion that all variables are being responded to at extents outside of those examined here (Jackson & Fahrig, 2015).

The directions of these relationships appear to align with the ecological phenomena they represent and support the idea that multiple scales of effect can be at play for a single species (Holland et al., 2004). Stream density performed well at smaller scales likely because of deer gathering near water sources. Water availability acts as an inherent limiter to deer abundance in a given area, with individuals clustering near water sources. Water availability at a more local scale (i.e., at smaller extents) therefore is more likely to accurately describe the local abundance (Beier & McCullough, 1990). Road density and patch sizes at larger extents may be effective predictors simply due to the similarity in area between average home ranges and extent areas, allowing the overall configuration of their entire home range to be considered. Both patch areas have previously been shown to have large effects on mammal abundance estimates with camera trap occupancy studies (Niedballa et al., 2015; Norris et al., 2010), as has the presence of roadways (Di Bitetti et al., 2014). Neither variable has been directly assessed in terms of scale, but previous research has linked scales of effect and home ranges. While scales of response for deer may not always follow home range sizes, it is very likely for there to be similarity between the two (Allen & Singh, 2016; Burton et al., 2015).

Even with the relatively small differences in extents (0.35 km^2 on average), the scales chosen for this study showed a great amount of variability. A true scale of effect could not be determined due to the range of scales chosen, which is a commonly seen downfall of multiscale studies (Jackson & Fahrig, 2015; Miguet et al., 2016). It is often suggested to test more spatial extents within a wider range to alleviate these issues. While this does provide a solution to missing the scale of effect, finding significant relationships within data that do not exist becomes much more common when so many hypotheses are tested. With the goal of assessing populations at the correct scale while also avoiding type II errors and accidental p-hacking behavior, scales should be purposefully chosen and have a clear connection to ecological processes (Fraser et al., 2018; Head et al., 2015; Jackson & Fahrig, 2015).

The choice to work with camera trap data in relation to scale comes with many challenges, especially because of there being limited understanding of the scale camera studies actually assess (Kays et al., 2021; Kolowski et al., 2021). Wildlife occupancy metrics have become a standard method of determining relative wildlife abundance but unfortunately eliminates the possibility of utilizing certain statistical measures. With models being compared using AIC or similar criterion metrics, a Bayesian approach is always required to analyze occupancy model results. However, these do not afford users the same certainty in results as frequentist approaches. Applications of Bayesian methods more advanced than AIC for occupancy models also require priori information related to the ecology of the species being examined, but these can be difficult to determine with the deep complexity of scaling in ecology (Aho et al., 2014; Jackson & Fahrig, 2015). A final layer of complexity created from camera trap data is the presence of unmarked species. Recent methods have been developed that allow populations to be partially marked from images alone to create better occupancy measures, but these are still in their infancy and require exponentially more effort than simply identifying the species in an image (Chandler et al., 2013; Macaulay et al., 2020). Without individual wildlife IDs, occupancy models must operate under the assumption that each capture is a different individual. As a result, the estimations drawn about abundance from occupancy can become extremely skewed if a single individual is sampled repeatedly during multiple time periods (MacKenzie et al., 2002). Despite the issues imposed by the type of data being used, this study has shown that camera trap data has the potential to be used as an assessor of scales of effect, while being a cost-effective and increasingly common method of sampling wildlife.

Data & Code Availability

All datasets used in this paper are publicly available. The code and directions for re-running these analyses are available through GitHub using the following link: https://github.com/oxyppgyn/deer-scale-frag-response.

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Supplemental Materials

Table S1. Model selections statistics for all model groups. Model names are composed of the variable type, extent class, and year the model was created with.

Model Name	Model Group	Rank	AIC_c	ΔAIC_c	Model Weight
Road1_19	1	1	5215.13	0.00	0.36
Edge1_19	1	2	5215.61	0.48	0.28
Strm1_19	1	3	5215.96	0.83	0.23
PA1_19	1	4	5217.15	2.02	0.13
Null_19	1	5	5225.16	10.03	<0.01
Road2_19	2	1	5209.14	0.00	0.93
Edge2_19	2	2	5214.77	5.63	0.06
PA2_19	2	3	5218.40	9.27	<0.01
Strm2_19	2	4	5220.95	11.81	<0.01
Null_19	2	5	5225.16	16.02	<0.01
Road3_19	3	1	5208.99	0.00	0.89
Edge3_19	3	2	5213.48	4.49	0.09
PA3_19	3	3	5217.70	8.71	0.01
Strm3_19	3	4	5223.67	14.67	<0.01
Null_19	3	5	5225.16	16.16	<0.01
Road4_19	4	1	5207.01	0.00	0.95
Edge4_19	4	2	5213.06	6.05	0.05
PA4_19	4	3	5218.16	11.15	<0.01
Null_19	4	4	5225.16	18.15	<0.01
Strm4_19	4	5	5225.56	18.55	<0.01
Road5_19	5	1	5204.54	0.00	0.99
Edge5_19	5	2	5214.23	9.69	<0.01
PA5_19	5	3	5217.95	13.41	<0.01
Null_194	5	4	5225.16	20.62	<0.01
Strm5_19	5	5	5225.98	21.44	<0.01
PA1_20	6	1	3884.12	0.00	1.00
Road1_20	6	2	3911.29	27.18	<0.01
Strm1_20	6	3	3915.73	31.61	<0.01
Null_20	6	4	3924.02	39.90	<0.01
Edge1_20	6	5	3926.05	41.93	<0.01
PA2_20	7	1	3874.11	0.00	1.00
Strm2_20	7	2	3911.04	36.93	<0.01
Road2_20	7	3	3917.94	43.83	<0.01
Null_20	7	4	3924.02	49.91	<0.01

Edge2_20	7	5	3924.97	50.86	<0.01
PA3_20	8	1	3860.15	0.00	1.00
Strm3_20	8	2	3901.28	41.13	<0.01
Road3_20	8	3	3921.58	61.44	<0.01
Null_20	8	4	3924.02	63.87	<0.01
Edge3_20	8	5	3924.66	64.51	<0.01
PA4_20	9	1	3844.92	0.00	1.00
Strm4_20	9	2	3899.31	54.39	<0.01
Road4_20	9	3	3923.37	78.45	<0.01
Null_20	9	4	3924.02	79.10	<0.01
Edge4_20	9	5	3925.68	80.77	<0.01
PA5_20	10	1	3838.07	0.00	1.00
Strm5_20	10	2	3902.32	64.25	<0.01
Null_20	10	3	3924.02	85.94	<0.01
Road5_20	10	4	3924.56	86.48	<0.01
Edge5_20	10	5	3925.52	87.45	<0.01
PA1_21	11	1	6665.39	0.00	1.00
Road1_21	11	2	6688.25	22.87	<0.01
Strm1_21	11	3	6695.87	30.49	<0.01
Edge1_21	11	4	6703.91	38.52	<0.01
Null_21	11	5	6708.85	43.46	<0.01
PA2_21	12	1	6661.51	0.00	1.00
Strm2_21	12	2	6698.91	37.40	<0.01
Edge2_21	12	3	6700.69	39.17	<0.01
Road2_21	12	4	6707.60	46.08	<0.01
Null_21	12	5	6708.85	47.34	<0.01
PA3_21	13	1	6665.23	0.00	1.00
Edge3_21	13	2	6701.00	35.77	<0.01
Strm3_21	13	3	6704.17	38.93	<0.01
Road3_21	13	4	6708.61	43.37	<0.01
Null_21	13	5	6708.85	43.61	<0.01
PA4_21	14	1	6662.97	0.00	1.00
Road4_21	14	2	6699.23	36.26	<0.01
Edge4_21	14	3	6702.29	39.32	<0.01
Strm4_21	14	4	6705.62	42.65	<0.01
Null_21	14	5	6708.85	45.88	<0.01
PA5_21	15	1	6664.06	0.00	1.00
Road5_21	15	2	6687.94	23.88	<0.01
Edge5_21	15	3	6703.78	39.72	<0.01

Strm5_21	15	4	6707.93	43.87	<0.01
Null_21	15	5	6708.85	44.79	<0.01
PA1_19	16	1	5217.15	0.00	0.28
PA3_19	16	2	5217.70	0.55	0.21
PA5_19	16	3	5217.95	0.79	0.19
PA4_19	16	4	5218.16	1.00	0.17
PA2_19	16	5	5218.40	1.25	0.15
Null_19	16	6	5225.16	8.01	<0.01
PA5_20	17	1	3838.07	0.00	0.97
PA4_20	17	2	3844.92	6.84	0.03
PA3_20	17	3	3860.15	22.07	<0.01
PA2_20	17	4	3874.11	36.03	<0.01
PA1_20	17	5	3884.12	46.04	<0.01
Null_20	17	6	3924.02	85.94	<0.01
PA2_21	18	1	6661.51	0.00	0.48
PA4_21	18	2	6662.97	1.46	0.23
PA5_21	18	3	6664.06	2.55	0.14
PA3_21	18	4	6665.23	3.72	0.08
PA1_21	18	5	6665.39	3.87	0.07
Null_21	18	6	6708.85	47.34	<0.01
Road5_19	19	1	5204.54	0.00	0.67
Road4_19	19	2	5207.01	2.47	0.19
Road3_19	19	3	5208.99	4.46	0.07
Road2_19	19	4	5209.14	4.60	0.07
Road1_19	19	5	5215.13	10.59	<0.01
Null_19	19	6	5225.16	20.62	<0.01
Road1_20	20	1	3911.29	0.00	0.95
Road2_20	20	2	3917.94	6.65	0.03
Road3_20	20	3	3921.58	10.29	<0.01
Road4_20	20	4	3923.37	12.08	<0.01
Null_20	20	5	3924.02	12.72	<0.01
Road5_20	20	6	3924.56	13.26	<0.01
Road5_21	21	1	6687.94	0.00	0.54
Road1_21	21	2	6688.25	0.31	0.46
Road4_21	21	3	6699.23	11.29	<0.01
Road2_21	21	4	6707.60	19.66	<0.01
Road3_21	21	5	6708.61	20.67	<0.01
Null_21	21	6	6708.85	20.91	<0.01
Strm1_19	22	1	5215.96	0.00	0.89

Strm2_19	22	2	5220.95	4.99	0.07
Strm3_19	22	3	5223.67	7.70	0.02
Null_19	22	4	5225.16	9.19	<0.01
Strm4_19	22	5	5225.56	9.60	<0.01
Strm5_19	22	6	5225.98	10.01	<0.01
Strm4_20	23	1	3899.31	0.00	0.63
Strm3_20	23	2	3901.28	1.98	0.23
Strm5_20	23	3	3902.32	3.02	0.14
Strm2_20	23	4	3911.04	11.74	<0.01
Strm1_20	23	5	3915.73	16.42	<0.01
Null_20	23	6	3924.02	24.71	<0.01
Strm1_21	24	1	6695.87	0.00	0.80
Strm2_21	24	2	6698.91	3.04	0.18
Strm3_21	24	3	6704.17	8.29	0.01
Strm4_21	24	4	6705.62	9.75	<0.01
Strm5_21	24	5	6707.93	12.05	<0.01
Null_21	24	6	6708.85	12.98	<0.01
Edge4_19	25	1	5213.06	0.00	0.33
Edge3_19	25	2	5213.48	0.42	0.26
Edge5_19	25	3	5214.23	1.17	0.18
Edge2_19	25	4	5214.77	1.71	0.14
Edge1_19	25	5	5215.61	2.56	0.09
Null_19	25	6	5225.16	12.10	<0.01
Null_20	26	1	3924.02	0.00	0.28
Edge3_20	26	2	3924.66	0.64	0.20
Edge2_20	26	3	3924.97	0.95	0.17
Edge5_20	26	4	3925.52	1.51	0.13
Edge4_20	26	5	3925.68	1.67	0.12
Edge1_20	26	6	3926.05	2.03	0.10
Edge2_21	27	1	6700.69	0.00	0.37
Edge3_21	27	2	6701.00	0.32	0.31
Edge4_21	27	3	6702.29	1.61	0.16
Edge5_21	27	4	6703.78	3.10	0.08
Edge1_21	27	5	6703.91	3.22	0.07
Null_21	27	6	6708.85	8.16	<0.01