

THE EFFECTS OF LANDSCAPE, HABITAT, AND COMMUNITY COMPOSITION ON
CANID OCCUPANCY

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ABSTRACT

Karen V. Root, Committee Chair

North American canid species have experienced major shifts in distribution and abundance since European settlement. These changes are often attributed to anthropogenic landscape modifications and associated habitat loss and fragmentation. Here we determine the response of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) to the altered landscape within the Oak Openings Region of northwestern Ohio. We identify occurrence patterns of local canids and their correlation with both fine-scale habitat variables and landscape-scale landcover data. A rapid assessment survey was conducted using scent-baited camera traps to generate coarse canid occurrence maps and identify optimal sites for the long-term monitoring phase of the study. Non-baited camera trap arrays that comprised the long-term monitoring portion of the study revealed widespread sympatry of red foxes and coyotes across the study area. This is in striking contrast to previous research that observed strong patterns of spatial partitioning in other regions. Fine-scale habitat variables were weakly associated with occurrence of either species, with the only significant correlation a positive relationship between coyote occurrence and percent bare ground. Landscape-scale variables, in contrast, were more predictive of canid occurrence. Red foxes were negatively associated with sand barrens and upland prairies, both open habitats where coyotes are known to be dominant. Both species demonstrated a negative association with dense urban landcover, which contrasts with other studies that suggest positive associations for both species at different scales. These findings suggest that reducing or strategically locating unsuitable habitats, such as upland prairies and sand barrens, and promoting forested refugia may help to conserve local red fox populations despite widespread coyote occurrence.

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INTRODUCTION

Modified Landscape

Humans began modifying the landscape of North America long before European settlement (Anderson and Moratto 1996). The increased conversion of natural areas to cropland and urban developments has resulted in widespread habitat loss and fragmentation. North America experienced a greater proportion of gross forest cover loss than any other continent between 2000 and 2005, with a 300,000 km² reduction in forest cover (Hansen et al. 2010). Prior to European settlement, nearly all of Ohio was forested (Gordon 1966); however, currently only 31% of the state's landcover consists of forests (Pfungsten et al. 2013). The glaciated region of Northwest Ohio has experienced some of the most dramatic changes in land use, with cropland currently being the dominant landcover. This expansive forest loss has had a large impact on local canid species, which are the focus of this study.

Northwest Ohio is home to the Oak Openings Region, which historically consisted of oak savanna and wet prairie habitats that were surrounded by Black Swamp Forest (Brewer and Vankat 2004). Forests and woodlands currently make up 15.0% of the region (a 5.4% decrease from 2011; Root and Martin 2020); however, the fragmented nature of these remaining forest patches makes them highly susceptible to the edge effect and therefore very little interior forest habitat remains. These fragmented forest patches have been demonstrated to have lower connectivity and dispersion than other habitats in the region, such as savannas and prairies (Martin and Root 2020). Of the remaining forest patches, only 34% are protected by parks and preserves, whereas 39% of oak savanna, 47% of shrubland, and 14% of prairie and meadow habitats have been put into protection (Schetter and Root 2011). This bias towards protecting oak savanna, shrubland, and prairie habitats is not without good reason and is driven by the

abundance of rare plant and animal species that require these habitats (Schetter et al. 2013). These early successional species benefit from this protection at the cost of species that require forest interior habitat.

Canid Responses to Landscape Modification

The response of mammals to landscape modification varies across species. Species that prefer edge and open habitats, such as coyotes (*Canis latrans*), have responded to current land use trends (likely in addition to other factors such as predator release and subsidization) with explosive population growth and range expansion. Coyotes have expanded well beyond the borders of their historic range within the Great Plains and now inhabit the vast majority of North and Central America (Gomper 2002). The Ohio Division of Wildlife's 2015 Bowhunter Survey Report documented a 3.5% annual increase in coyote abundance throughout Ohio between 1990 and 2015 (Ohio Division of Wildlife 2015). This population estimate is likely to have significantly underestimated the abundance of coyotes because of their marked success in urbanized (i.e., non-surveyed) areas, where bow hunting does not occur (Gehrt 2007).

In contrast, interior forest species have declined considerably. A 10.6% annual decline was observed for red foxes (*Vulpes vulpes*) between 1990 and 2015 (Ohio Division of Wildlife 2015). Similarly, gray foxes (*Urocyon cinereoargenteus*) experienced a 9.8% annual decline within the same period (Ohio Division of Wildlife 2015). Fox population declines due to habitat loss are exacerbated by the influx of coyotes which has drastically increased competition and predation on foxes (Farias et al. 2005). While no published studies have been conducted in Ohio, foxes in the Southeastern U.S. were found to avoid overlapping their home ranges with those of coyotes and have also been shown to temporally avoid coyote activity when possible (Chamberlain and Leopold 2005). In a study in California, most fox mortalities caused by

coyotes occurred on the periphery of fox home ranges (Farias et al. 2005). Thus, habitat loss and growing coyote populations likely increase the interactions between canid species, contributing to fox declines. The increased interactions may result in several outcomes (e.g., competitive exclusion, niche partitioning) that will change the community dynamics of these landscapes (Flagel et al. 2017).

Canid Interactions: Natural Areas

Coyotes are primarily adapted to open and semi-open habitats (Young and Jackson 1951). In these preferred habitats, their larger body size and territoriality enables coyotes to exclude foxes from areas, such as observed in a 1999 study in California (Crooks and Soule 1999). As a result, coyotes are the dominant canid in many open habitats. Although coyotes are also able to colonize forested areas (Messier and Barrette 1982), they tend to perform less than optimally in these habitats. Where coyotes have colonized forest habitats, they occur in much lower densities and have lower body reserves and reduced fecundity in comparison with those inhabiting more open areas (Richer et al. 2002). Vision plays a large role in coyote prey detection (Wells and Bekoff 1982), so it is thought that the increased vegetative cover in forest systems makes it more difficult for coyotes to capture their prey (Harrison 1992). It is probable that foxes benefit from increased vegetative cover because it obstructs coyote interactions and predation, thus providing a form of refuge. The ability of gray foxes to avoid predation by means of their semi-arboreal behavior (Wooding 1984) suggests that the presence of trees and debris piles may also help to reduce the negative impact of coyotes on gray foxes in areas of sympatry.

While numerous studies support the idea that densely wooded areas may contribute to fox persistence, none have quantitatively measured the environmental parameters required to promote fox survival and discourage use by the dominant coyotes. Given the highly fragmented

nature of natural areas in Northwest Ohio, there is considerable value in determining the landscape and habitat characteristics required for foxes to persist, so that the benefits can be maximized, and the costs minimized. Developing quantitative goals for beneficial vegetative structure within refugia is necessary to inform on-the-ground management.

Canid Interactions: Urban Areas

Coyotes and foxes have become established within urban and suburban areas from California to Chicago (Riley 2006, Gosselink et al. 2007, Gehrt 2007) and beyond. At intermediate and large spatial scales, urban coyotes and foxes are associated with a high degree of development; however, at a finer scale, differences in habitat association start to arise. In a study in Illinois, foxes were found to associate with high density urban landcover whereas coyotes inhabit urban development with increased forest cover at small spatial scales (Willingham 2008). Gosselink et al. (2003) suggest that urban foxes in Illinois may avoid conflicts with coyotes by taking refuge near humans. Additionally, coyotes may seek natural areas within urban landscapes because their presence is less tolerated by humans (Gosselink et al. 2003). In this light, dense urban development may be a form of fox refugia like that of dense forested habitat. Urban systems also foster an increased abundance of prey items and urban foxes have been found to consume a more varied diet and have increased body weight in some studies (Harrison 1997, Cypher and Frost 1999).

Despite these apparent benefits to urban living, coyotes have still been identified as a major source of predation on urban foxes in Chicago (Willingham 2008). Additionally, foxes inhabiting urban areas may face increased exposure to disease and thus have higher mortality (Riley et al. 2004). Increased vehicular traffic and road densities may also lead to higher probability of vehicular mortality in urban environments as found by Willingham (2008). For

these reasons, natural areas are likely ideal for long-term fox conservation.

Synopsis

Targeted management may be necessary to reverse fox population declines. While the threats of habitat loss and competition with coyotes are widely identified, other major factors may be contributing to fox declines. Studying the landscape, habitat, and community characteristics in areas where foxes persist can increase our understanding of canid ecology and inform future conservation efforts. In a larger context, this research will contribute to the current understanding of how ecological mechanisms govern species' ranges. Additionally, this study will investigate how variation in habitat characteristics can alter the outcome of competition between species (e.g., competitive exclusion or niche partitioning). These last strongholds (particularly for gray foxes) may possess certain characteristics that allow the foxes to persist in the face of numerous threats. For example, there may be a minimum patch size of densely vegetated habitat that effectively excludes, or significantly reduces use by coyotes and therefore provides a refuge for foxes. Additionally, there may be other landscape characteristics such as recreational path or road density, connectivity, or habitat heterogeneity that benefit foxes. Mammalian community composition may also play a large role in fox persistence. For example, foxes may persist in patches with reduced raccoon densities and therefore fewer vectors for disease transmission. In any of these cases, the common characteristics of remnant fox habitats could be replicated to conserve the species.

MATERIALS AND METHODS

Study Sites

This study took place in and around the Oak Openings Region in Lucas County, Ohio. The Oak Openings Region is a 48,000-hectare area of habitat that is particularly known for containing one of the largest oak savanna systems in the Midwestern United States (Schetter and Root 2011). This region's heterogenous landscape is comprised of forests and woodlands (swamp forest, floodplain forest, upland deciduous forest, and upland coniferous forest), shrublands (wet shrubland), prairies and meadows (wet prairie, upland prairie, sand barren, Eurasian meadow), water (perennial pond), built-up areas (dense urban, residential/mixed), and vacant land (turf/pasture, cropland) in addition to its namesake upland oak savanna habitat (Martin and Root 2020). The region is also a biodiversity hotspot containing many species of special conservation interest. Study sites spanned private and public land but were predominantly located within natural areas owned and managed by Metroparks Toledo, including Wildwood Preserve Metropark, Secor Metropark, Swan Creek Preserve Metropark, Oak Openings Preserve Metropark, and Blue Creek Metropark.

Rapid Assessment

A rapid assessment composed of 51 scent-baited camera traps was conducted in the spring of 2019 throughout natural areas in the region to generate a canid occurrence map and to identify suitable sites for long-term monitoring. Camera traps were placed in dense arrays of two camera traps per 120 hectares (Figure 1). This density was selected so that two camera traps would occur per estimated home range of the region's smallest ranging canid species, the gray fox (Follman 1973, Willingham 2008).

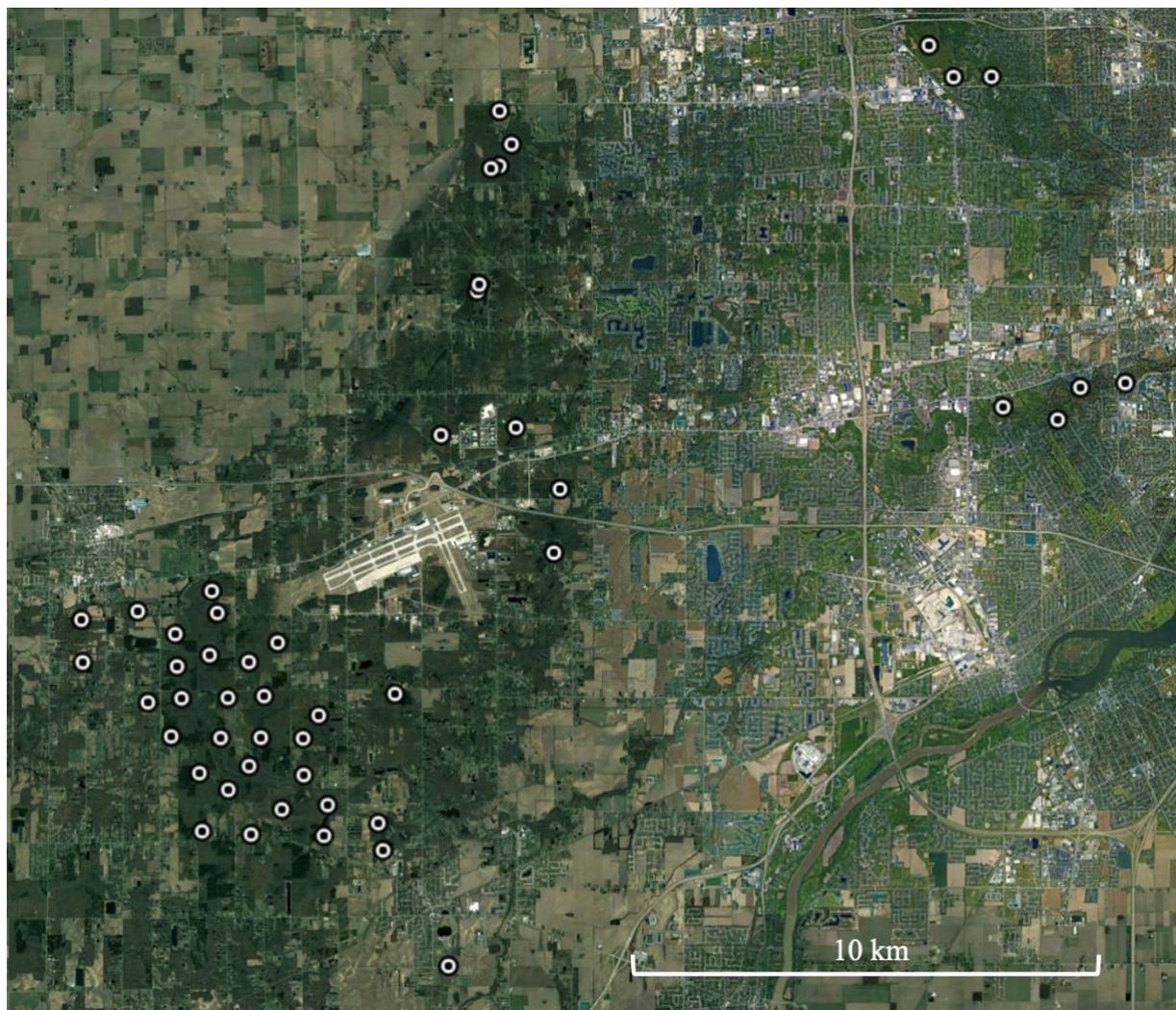


Figure 1. Locations of scent-baited camera traps (white circles) used for rapid assessment of canid occupancy in Northwest Ohio, in and around the Oak Openings Region.

Each scent-baited camera trap station was composed of a Moultrie M-40 Game Camera (Moultrie, Alabaster, AL, USA), secured to a tree at a height of 20cm above the ground, as per the World Wildlife Fund camera-trapping guidelines (Wearn and Glover-Kapfer 2017). A plaster disc impregnated with fatty acid scent (FAS, USDA Wildlife Services) was fixed to a nearby log or tree within view of the camera to prevent removal of the scent bait by wildlife (Figure 2). This fatty acid scent has been demonstrated to effectively attract all three local canid species (Iannarilli et al. 2021) and the standardized scent formulation reduces variance in attractiveness or detectability that may exist with other naturally sourced scent baits.



Figure 2. Example image from canid rapid assessment showing a coyote that was attracted to the fatty acid scent disc fixed to the log below.

Scent-baited camera traps were deployed for 10 consecutive trap-days. This period was informed by a 2012 study (Cove et al. 2012) that determined the latency to initial detection (LTD) of gray foxes, red foxes, and coyotes by baited camera stations to be 2.00, 3.11, and 4.90 days respectively. At more than twice the length of the longest canid LTD, the 10 trap-day sampling period ensured high detection confidence. Following the 10-day sampling period, we

compiled all camera trapping records to generate a binary detection history for each local canid species.

Long-term Monitoring Sites

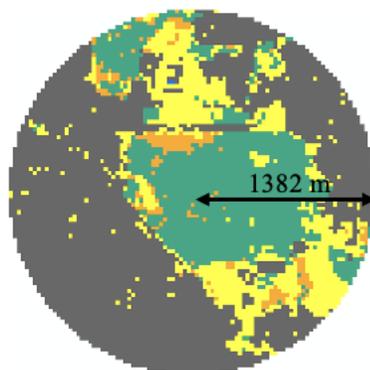
After reviewing the rapid assessment data, the locations of six scent-baited camera traps were selected for further investigation with long-term, non-baited monitoring techniques. The scent-baited camera traps were removed and circles with an area of 600 hectares were superimposed on the landscape with centers on the former camera trap locations. These circular regions, hereafter referred to as long-term monitoring sites, were representative of the average home range of red foxes (the focal species of this study going forward) based on previous studies in similar mixed-use landscapes (Carter et al. 2012).

Land cover maps of the region (with 15 and 7 landcover classes) produced by Martin and Root (2020) were analyzed in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California) to determine the percentages of each landcover type within the long-term monitoring sites (Figure 3). The landcover proportions were then used to stratify the placement of seven non-baited camera traps within each long-term monitoring site, with the number of cameras occurring within a given landcover type being proportional to the percentage of that landcover within the long-term monitoring site (Table 1). Dense urban, residential, and perennial pond landcovers were not incorporated into the camera stratification, as this study is focused on natural areas and these habitats were not feasible to survey with our methodology. Camera locations were simultaneously stratified by both 7-class and 15-class landcover types. In total, 42 camera traps were deployed across the six long-term monitoring sites. All camera traps were located no closer than 25m to the edge of an assigned land cover patch. An effort was made to space camera trap locations as evenly as possible throughout the long-term monitoring sites, but

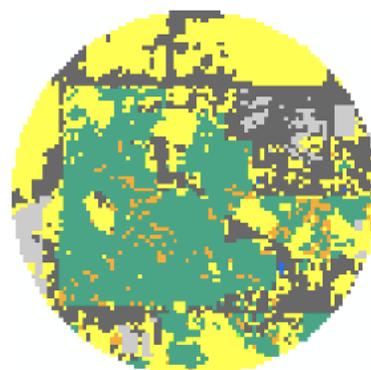
in some cases clustering of camera traps was required to achieve proper stratification while avoiding sensitive wildlife areas. Cameras were secured to trees or wooden stakes at a height of 20cm above ground level and focused on areas of suspected wildlife traffic, such as game trails in order to increase detection probability. All cameras were deployed in late December 2022 or early January 2023 and collected in early April 2023 before plants began to leaf out.

LANDCOVER

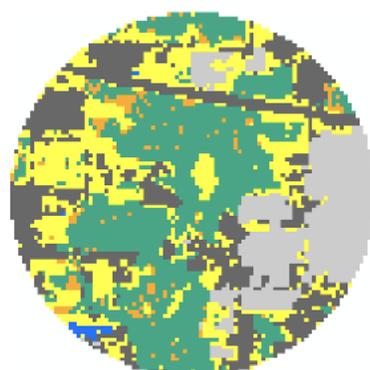
- Forests/Woodlands
- Savannas
- Shrublands
- Prairies and Meadows
- Water
- Built-Up
- Vacant



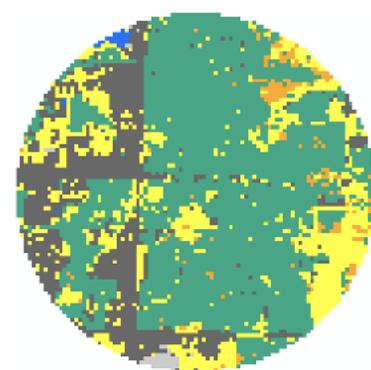
Wildwood Preserve Metropark



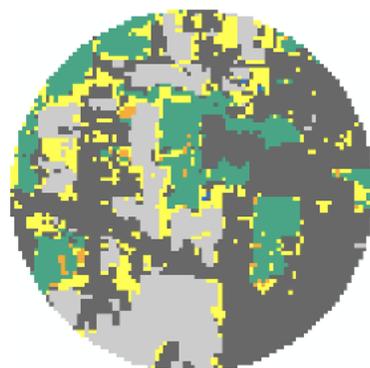
Secor Metropark



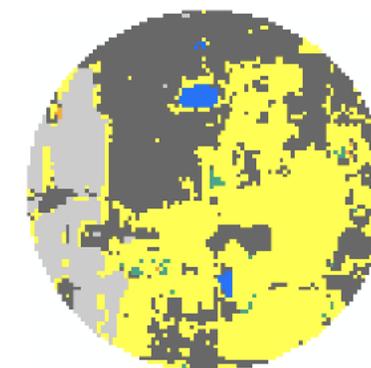
Metropark Corridor



Oak Openings Preserve Metropark



Private Parcel



Blue Creek Metropark

Figure 3. Long-term monitoring sites showing landcover within 600-hectare buffer zones.

Table 1. Example breakdown of 15-class landcover proportions and stratified camera trap placement at Wildwood Preserve Metropark.

15 Class Landcover	Pixel Count	Percent Coverage	Camera Count
Turf/Pasture	0	0.0	
Wet Prairie	21	0.7	
Residential/Mixed	3072		
Perennial Ponds	2		
Upland Savanna	245	8.1	1
Wet Shrubland	0	0.0	
Swamp Forest	42	1.4	
Upland Conifer Forest	4	0.1	
Upland Deciduous Forest	899	29.8	2
Floodplain Forest	628	20.8	1
Sand Barrens	224	7.4	1
Eurasian Meadow	50	1.7	
Upland Prairie	904	30.0	2
Dense Urban	694		
Cropland	166	3.3	

Fine Scale Habitat Variables

Fine scale habitat variables were recorded for each camera trap location within the long-term monitoring sites. Transects (25m) running in all four cardinal directions were established with their origins on each camera trap location, along which fine scale habitat variables were measured (Figure 4). The average canopy cover for each site was determined by taking photos of the sky vertically from 30cm above ground level (estimated red fox eye level) and calculating the percent of the sky covered by trunks, branches, and leaves using the ‘Percentage Cover’ application (Mignanelli, 2022). Measurements were taken at 15m and 25m in all four cardinal directions from the camera traps and the average of these eight measurements was recorded as the average canopy cover for a given camera trap location.

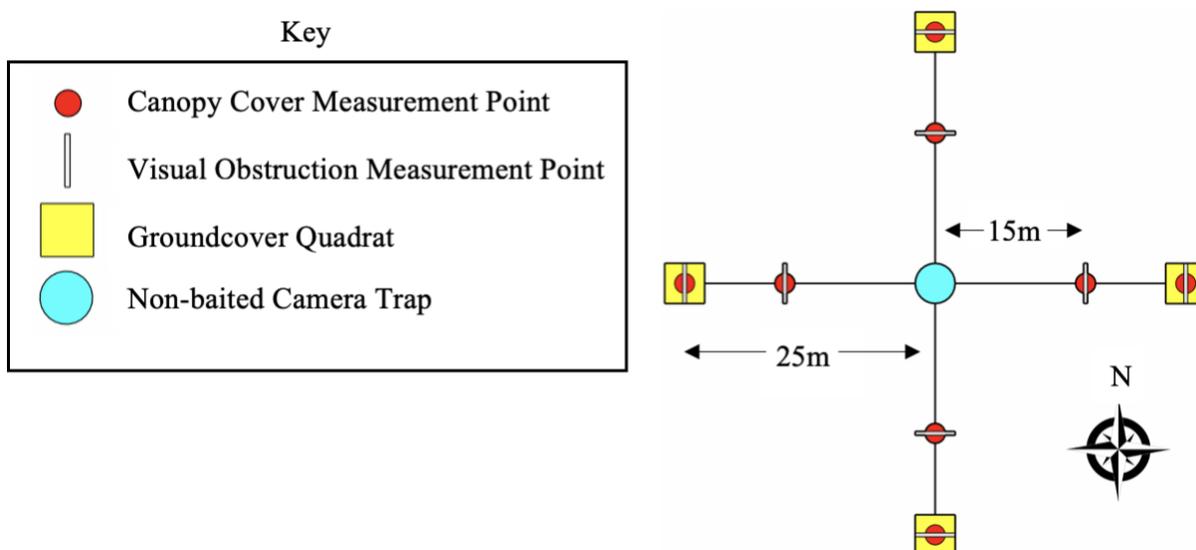


Figure 4. Diagram of a non-baited camera trap transects with measurement points for fine scale habitat data.

Similarly, the average horizontal visual obstruction was calculated for each camera trap location by standing at the camera trap and photographing a 1-meter square white board at distances of 15m and 25m and a height of 30cm (estimated red fox eye level) in all four cardinal

directions. The percentage of the board obstructed by vegetation and other habitat features was calculated using the ‘Percentage Cover’ application (Mignanelli, 2022) and the average of these four values was recorded as the average visual obstruction for each camera trap location at both distances (Figure 5).

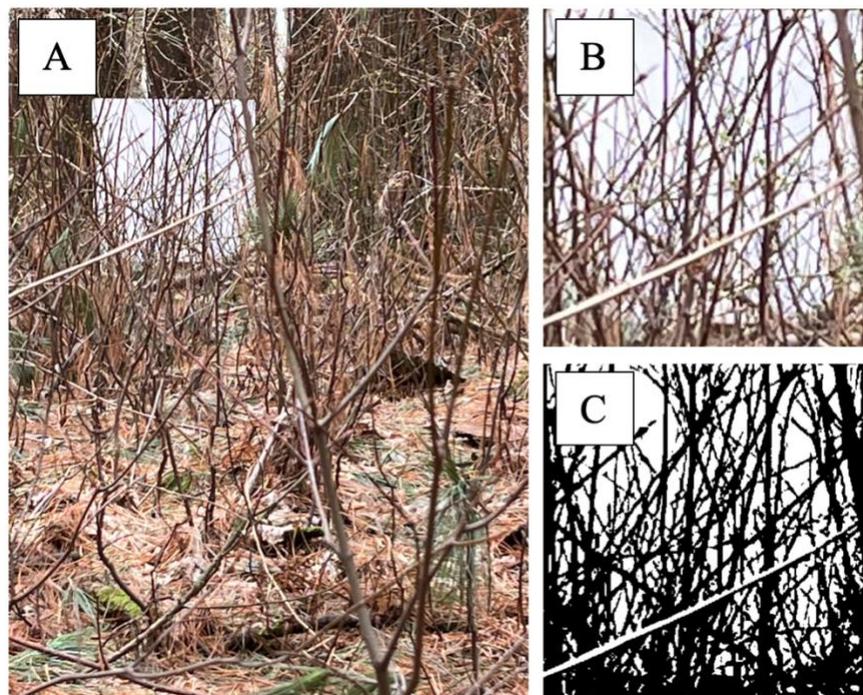


Figure 5. Example of the visual obstruction measurement process including (A) the original photo taken from 30cm above ground level at the non-baited camera location of 1m² white board 15m away, (B) the original image cropped to extent of the board, and (C) the processed image from ‘Percentage Cover’ application (Mignanelli, 2022).

Average ground cover percentages were calculated for each camera trap location by placing a 1-meter square quadrat at 25m from the camera trap in all four cardinal directions and visually estimating the percentage of each quadrat occupied by leaf litter, coarse woody debris greater than 15cm in diameter, small woody debris less than 15cm in diameter, grasses and forbs, woody vegetation basal coverage, and bare ground. The average percentage of each groundcover type across all four quadrats was recorded for each camera trap location.

The number of trees with a diameter at breast height (DBH) greater than 15cm was recorded within a 25m radius of each camera location as well. The landcover type within which each camera trap was located was also recorded. All fine scale habitat variables were measured while the camera traps were actively deployed. Given that the camera trapping period occurred during the winter and early spring (while plants were dormant), the exact date of measurement had little effect on the recorded values and these values should be considered highly comparable between all camera trap locations.

Statistical Analysis

Correlations between landscape and habitat variables and occurrence of red foxes and coyotes were tested in JMP, Version 17.1.0 (SAS Institute Inc., Carry, NC.). First, univariate logistic regression analysis was used to identify variables that were significantly associated with canid occurrence on their own. A cross correlation analysis was then conducted to identify sets of uncorrelated landscape and habitat variables that could be tested with multivariate analyses. Finally, multivariate logistic regression models were created (JMP Version 17.1.0, SAS Institute Inc., Carry, NC.) to determine which combinations of uncorrelated variables most strongly predicted the probability of occurrence of red foxes and coyotes.

RESULTS

Rapid Assessment

The scent-baited rapid assessment survey yielded observations of red foxes at 11 cameras and coyotes at 27 cameras. No gray foxes were detected as a part of this survey. Red foxes and coyotes were sympatric at six camera sites (Figure 6). Areas of sympatry were emphasized for the long-term monitoring portion of this study.

Long Term Monitoring

Red foxes were detected at eight non-baited, long-term monitoring camera stations (19% of cameras) across three of six long-term monitoring sites. Coyotes were detected at 26 camera locations (62% of cameras), with occurrences at all six long-term monitoring sites. Red foxes were sympatric with coyotes at seven of eight camera locations where they were detected (Figure 7).

Correlations between these non-baited occurrence data and both fine scale habitat variables and landscape scale variables were analyzed for red foxes and coyotes (Tables 2, 3, 4, 5, 6, and 7). No fine scale habitat predictor variables were significantly correlated with red fox occurrence (Table 2). Percent bare ground was the only fine scale habitat predictor variable significantly correlated ($p \leq 0.05$) with coyote occurrence, which indicated that coyote occurrence was more likely with increased bare ground coverage (Table 3). The average values for bare ground percentage at non-baited camera locations, grouped by canid occurrence, are displayed in Figure 8. Averages for all other fine scale habitat variable values are displayed in Appendix A.

Landscape scale predictor variables were more commonly correlated with red fox and coyote occurrence than fine scale habitat predictor variables. When analyzed using the 15-class landcover map, red fox occurrence was significantly and negatively correlated with percent sand

barrens, percent upland prairie, and percent dense urban landcovers (Table 4). With the 15-class landcover map, coyotes were nearly significantly ($p=0.0617$) and negatively correlated with percent dense urban landcover (Table 5). Red fox occurrence was significantly and negatively correlated with percent prairie and meadow when analyzed using the 7-class landcover map (Table 6). Percent vacant landcover was the only nearly significant variable identified for coyotes when the 7-class landcover was used (Table 7), which was a positive relationship with coyote occurrence more likely as the percent vacant landcover increased.

Prior to investigating these data further with multivariate methods, a correlation analysis was conducted in JMP Version 17.1.0 (SAS Institute Inc., Cary, NC.) to identify correlated predictor variable sets in order to minimize multicollinearity (Table 8). Variables with a correlation coefficient of ≥ 0.6 were considered strongly correlated and the use of strongly correlated predictor variables was avoided within a single multivariate model to reduce multicollinearity.

Combinations of non-correlated variables (with an emphasis on variables that were significantly correlated with canid occurrence in univariate tests [Tables 2, 3, 4, 5, 6, 7]), were then analyzed using multivariate logistic regression. Table 9 includes all significant ($p \leq 0.05$) models relating red fox occurrence to predictor variables in order of AIC score. The best multivariate model for predicting red fox occurrence included percent sand barrens and percent upland prairie as predictor variables (Table 9). There was a negative association between the percent of these two landcovers (sand barrens and upland prairie) and red fox occurrence. The best model for predicting coyote occurrence included percent bare ground and percent dense urban as predictor variables, highlighting a positive relationship with bare ground and a negative relationship with dense urban coverage (Table 10).

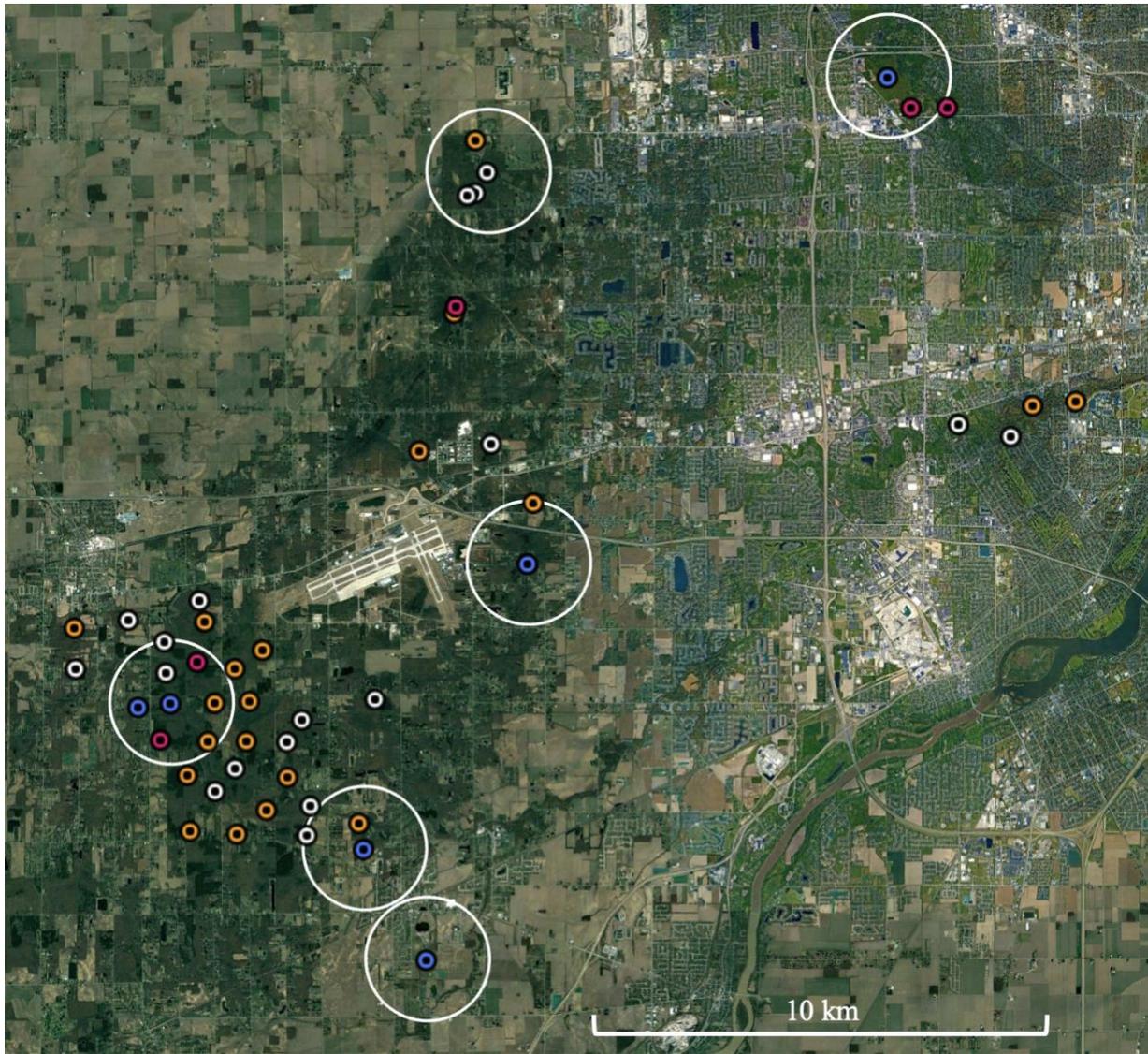


Figure 6. Scent-baited rapid assessment survey results showing camera stations with no detections (white), red fox only (magenta), coyote only (orange), and sympatric detection of both red foxes and coyotes (blue). Buffers representative of estimated red fox home ranges (600 ha) around the six sites selected for long-term monitoring are outlined in white.

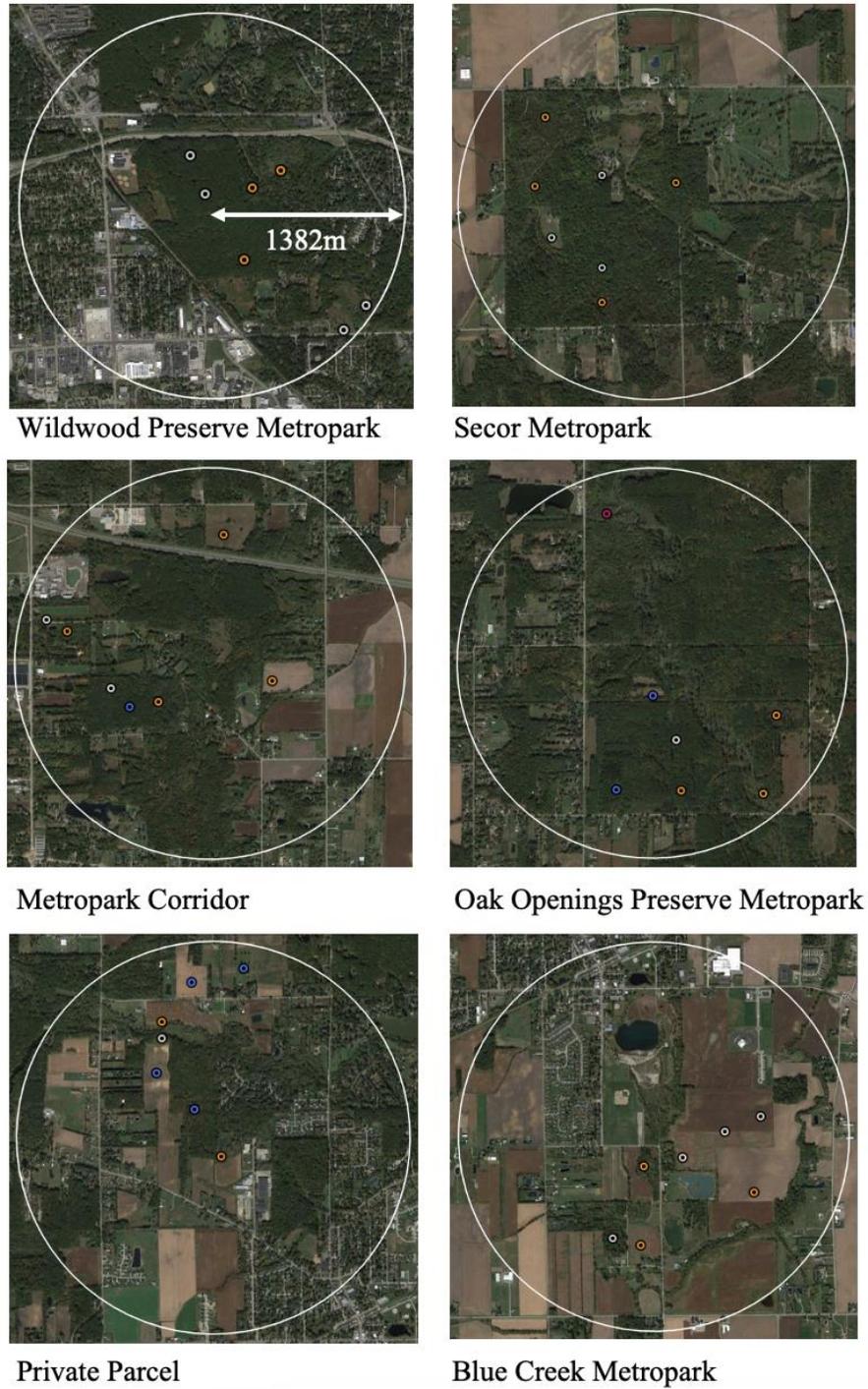


Figure 7. Long-term monitoring sites and landcover-stratified camera stations with no canid detections (white), red fox only (magenta), coyote only (orange), and sympatric red foxes and coyotes (blue). 600 ha buffers are outlined in white.

Table 2. Univariate logistic regression results for red fox occurrence in relation to fine scale habitat predictor variables at all camera stations.

Red Fox Fine Scale Predictor Variable	Parameter Estimate (Coefficient)	Standard Error	Wald Chi- Square	p-value	Odds Ratio	Whole Model Test p-value
Tree Density (>15cm DBH)	0.01	0.01	0.72	0.40	2.94	0.398
% Canopy Cover	-1.50	2.83	0.28	0.60	0.39	0.587
% Visual Obstruction (15m)	-1.29	1.41	0.83	0.36	0.28	0.344
% Visual Obstruction (25m)	-1.10	1.30	0.71	0.40	0.33	0.393
% Leaf Litter	-0.40	0.97	0.17	0.68	0.68	0.678
% Course Woody Debris (>15cm)	5.21	6.55	0.63	0.43	4.19	0.443
% Fine Woody Debris (<15cm)	-0.15	10.74	0	0.99	0.98	0.989
% Grasses and Forbs	-0.81	1.01	0.65	0.42	0.44	0.403
% Vegetation Basal Coverage	-0.07	7.17	0	0.99	0.98	0.992
% Bare Ground	1.83	1.16	2.49	0.11	6.25	0.123

Table 3. Univariate logistic regression results for coyote occurrence in relation to fine scale habitat predictor variables at all camera stations.

Coyote Fine Scale Predictor Variable	Parameter Estimate (Coefficient)	Standard Error	Wald Chi-Square	p-value	Odds Ratio	Whole Model Test p-value
Tree Density (>15cm DBH)	-0.01	0.01	0.38	0.54	0.52	0.538
% Canopy Cover	-0.19	2.12	0.01	0.93	0.89	0.929
% Visual Obstruction (15m)	-0.88	1.05	0.70	0.40	0.42	0.400
% Visual Obstruction (25m)	-0.89	1.05	0.72	0.40	0.41	0.391
% Leaf Litter	-0.23	0.78	0.09	0.77	0.80	0.767
% Course Woody Debris (>15cm)	5.31	7.72	0.47	0.49	4.30	0.454
% Fine Woody Debris (<15cm)	-2.76	8.53	0.10	0.75	0.66	0.748
% Grasses and Forbs	-0.68	0.74	0.86	0.35	0.51	0.354
% Vegetation Basal Coverage	5.11	7.40	0.48	0.49	4.64	0.443
% Bare Ground	4.53	4.66	0.94	0.33	92.41	0.050**

*p<0.1, **p<0.05

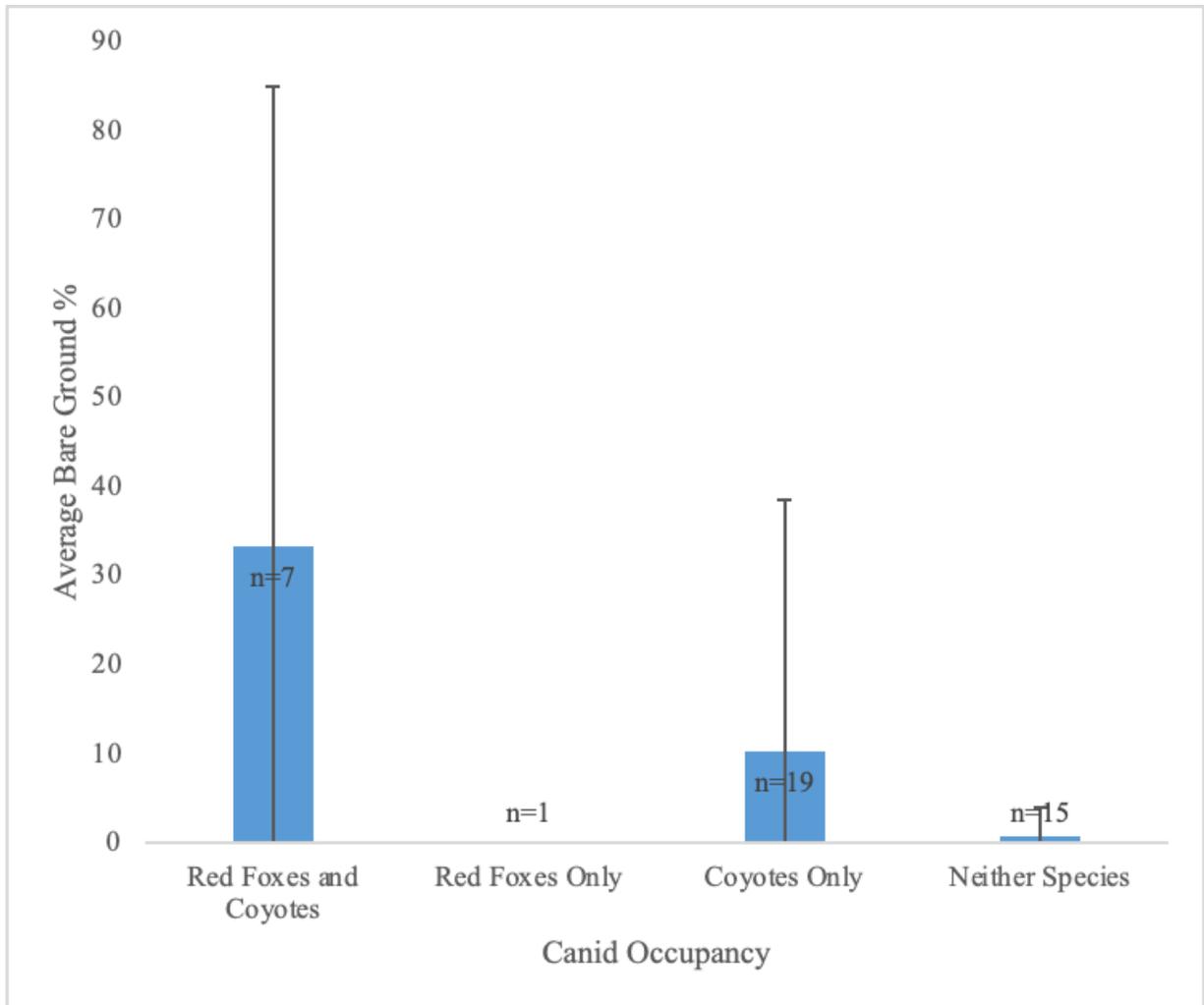


Figure 8. Average bare ground percentage at non-baited camera locations grouped by canid occurrence.

Table 4. Univariate logistic regression results for red fox occurrence in relation to landscape scale habitat predictor variables (15-class landcover) at all camera stations.

Red Fox Landscape Scale Predictor Variable - 15 Class Landcover	Parameter Estimate (Coefficient)	Standard Error	Wald Chi-Square	p-value	Odds Ratio	Whole Model Test p-value
% Turf and Pasture	-1396.50	149998.26	0.00	0.99	0.00	0.250
% Wet Prairie	-10.24	24.71	0.17	0.68	0.44	0.668
% Residential and Mixed Use	0.79	3.11	0.07	0.80	1.49	0.799
% Perennial Pond	124.84	81.71	2.33	0.13	3.48	0.119
% Upland Savanna	0.00	26.48	0.00	1.00	1.00	1.000
% Wet Shrubland	0.00	0.00	.	.	1.00	.
% Swamp Forest	3.69	4.67	0.62	0.43	2.61	0.429
% Upland Conifer Forest	10.65	9.90	1.16	0.28	3.23	0.299
% Upland Deciduous Forest	3.35	6.40	0.27	0.60	2.39	0.606
% Floodplain Forest	6.31	5.39	1.37	0.24	4.84	0.243
% Sand Barrens	-32.46	28.02	1.34	0.25	0.00**	0.013**
% Eurasian Meadow	-2.56	10.08	0.06	0.80	0.72	0.798
% Upland Prairie	-33.11	14.10	5.52	0.019**	0.01**	0.012**
% Dense Urban	-32.18	16.68	3.72	0.054*	0.01**	0.019**
% Cropland	8.12	5.50	2.18	0.14	7.61	0.139

*p<0.1, **p≤0.05

Table 5. Univariate logistic regression results for coyote occurrence in relation to landscape scale habitat predictor variables (15-class landcover) at all camera stations.

Coyote Landscape Scale Predictor Variable - 15 Class Landcover	Parameter Estimate (Coefficient)	Standard Error	Wald Chi-Square	p-value	Odds Ratio	Whole Model Test p-value
% Turf and Pasture	44.23	99.13	0.20	0.66	2.42	0.638
% Wet Prairie	2.37	18.28	0.02	0.90	10.65	0.897
% Residential and Mixed Use	-1.95	2.56	0.58	0.45	0.38	0.443
% Perennial Pond	-38.47	65.11	0.35	0.55	0.68	0.555
% Upland Savanna	23.29	22.01	1.12	0.29	4.05	0.283
% Wet Shrubland	0.00	0.00	.	.	1.00	.
% Swamp Forest	4.22	3.97	1.13	0.29	3.00	0.279
% Upland Conifer Forest	6.13	10.03	0.37	0.54	1.96	0.528
% Upland Deciduous Forest	4.54	5.85	0.60	0.44	3.26	0.424
% Floodplain Forest	0.27	4.54	0.00	0.95	1.07	0.952
% Sand Barrens	-3.32	3.37	0.97	0.32	0.31	0.323
% Eurasian Meadow	-3.10	7.98	0.15	0.70	0.05	0.698
% Upland Prairie	-3.99	11.22	0.13	0.72	0.02	0.720
% Dense Urban	-15.70	8.77	3.20	0.07*	0.11	0.062*
% Cropland	8.33	5.54	2.27	0.13	8.03	0.106

*p<0.1, **p≤0.05

Table 6. Univariate logistic regression results for red fox occurrence in relation to landscape scale habitat predictor variables (7-class landcover) at all camera stations.

Red Fox Landscape Scale Predictor Variable - 7 Class Landcover	Parameter Estimate (Coefficient)	Standard Error	Wald Chi- Square	p-value	Odds Ratio	Whole Model Test p-value
% Forest and Woodland	3.00	2.36	1.62	0.20	7.70	0.20
% Savanna	0.00	26.48	0.00	1.00	1.00	1.00
% Shrubland	-14.56	1956.62	0.00	0.99	0.00	0.13
% Prairie and Meadow	-10.78	6.04	3.18	0.07*	0.00	0.02**
% Water	124.84	81.71	2.33	0.13	3.48	0.12
% Built-up	-1.00	2.82	0.13	0.72	0.57	0.72
% Vacant	8.05	5.53	2.12	0.15	7.47	0.15

*p<0.1, **p≤0.05

Table 7. Univariate logistic regression results for coyote occurrence in relation to landscape scale habitat predictor variables (7-class landcover) at all camera stations.

Coyote Landscape Scale Predictor Variable - 7 Class Landcover	Parameter Estimate (Coefficient)	Standard Error	Wald Chi- Square	p-value	Odds Ratio	Whole Model Test p-value
% Forest and Woodland	1.93	1.99	0.94	0.33	3.72	0.321
% Savanna	23.29	22.01	1.12	0.29	4.05	0.283
% Shrubland	0.05	0.17	0.09	0.76	1.95	0.753
% Prairie and Meadow	-2.04	2.35	0.75	0.39	0.34	0.385
% Water	-38.47	65.11	0.35	0.55	0.68	0.555
% Built-up	-2.80	2.35	1.41	0.23	0.21	0.224
% Vacant	8.49	5.59	2.31	0.13*	8.35	0.102

*p<0.1, **p≤0.05

Table 8. List of predictor variables along with the other variables with which they are strongly correlated ($r \geq 0.6$).

Predictor Variable	Strongly Correlated ($r \geq 0.6$) Variables
Tree Density (>15cm DBH)	% Canopy Cover, % Leaf Litter, % Course Woody Debris (>15cm), % Grasses and Forbs
% Canopy Cover	Tree Density (>15cm DBH), % Leaf Litter, % Grasses and Forbs
% Visual Obstruction (15m)	% Visual Obstruction (25m)
% Visual Obstruction (25m)	% Visual Obstruction (15m)
% Leaf Litter	Tree Density (>15cm DBH), % Canopy Cover, % Grasses and Forbs
% Course Woody Debris (>15cm)	Tree Density (>15cm DBH)
% Fine Woody Debris (<15cm)	None
% Grasses and Forbs	Tree Density (>15cm DBH), % Canopy Cover, % Leaf Litter
% Vegetation Basal Coverage	None
% Bare Ground	None
% Turf and Pasture	None
% Wet Prairie	% Swamp Forest, % Shrubland
% Residential and Mixed Use	% Built-up
% Perennial Pond	% Eurasian Meadow, % Water
% Upland Savanna	% Upland Deciduous Forest, % Sand Barrens, % Eurasian Meadow, % Forest and Woodland, % Prairie and Meadow
% Wet Shrubland	None
% Swamp Forest	% Wet Prairie, % Built-up
% Upland Conifer Forest	% Upland Deciduous Forest, % Floodplain Forest, % Forest and Woodland
% Upland Deciduous Forest	% Upland Savanna, % Upland Conifer Forest, % Floodplain Forest, % Sand Barrens, % Eurasian Meadow, % Forest and Woodland, % Prairie and Meadow
% Floodplain Forest	% Upland Conifer Forest, % Upland Deciduous Forest, % Eurasian Meadow, % Forest and Woodland, % Prairie and Meadow
% Sand Barrens	% Upland Savanna, % Upland Deciduous Forest, % Eurasian Meadow, % Forest and Woodland, % Prairie and Meadow
% Eurasian Meadow	% Perennial Pond, % Perennial Pond, % Upland Deciduous Forest, % Floodplain Forest, % Sand Barrens, % Forest and Woodland, % Savanna, % Prairie and Meadow, % Water
% Upland Prairie	None
% Dense Urban	% Forest and Woodland
% Cropland	% Vacant
% Forest and Woodland	% Upland Savanna, % Upland Conifer Forest, % Upland Deciduous Forest, % Floodplain Forest, % Sand Barrens, % Eurasian Meadow, % Dense Urban, % Savanna, % Built-up
% Savanna	% Upland Savanna, % Upland Deciduous Forest, % Sand Barrens, % Forest and Woodland, % Savanna, % Prairie and Meadow
% Shrubland	% Wet Prairie
% Prairie and Meadow	% Upland Savanna, % Upland Deciduous Forest, % Floodplain Forest, % Sand Barrens, % Eurasian Meadow, % Savanna
% Water	% Eurasian Meadow, % Perennial Pond
% Built-up	% Residential and Mixed Use, % Swamp Forest, % Forest and Woodland
% Vacant	% Cropland

Table 9. Multivariate logistic regression results for red fox occurrence in relation to habitat predictor variables at all camera stations. Whole model test p-values were significant ($p \leq 0.05$)

for all included models.

Model 1: Red Fox Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	2.77	2.22		
% Sand Barrens	-25.93	0.89		
% Upland Prairie	-25.63	3.26		
Whole Model Test		9.88	0.2415	37.6563
Model 2: Red Fox Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	2.27	2.31		
% Upland Prairie	-26.31	3.58		
% Dense Urban	-28.26	2.38		
Whole Model Test		9.55	0.2334	37.9877
Model 3: Red Fox Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	3.10	2.34		
% Sand Barrens	-31.69	0.76		
% Upland Prairie	-20.66	2.00		
% Dense Urban	-21.54	1.38		
Whole Model Test		11.68	0.2855	38.3041
Model 4: Red Fox Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	2.39	1.46		
% Bare Ground	1.02	0.61		
% Sand Barrens	-29.74	0.83		
% Upland Prairie	-22.06	2.28		
Whole Model Test		10.49	0.2565	39.4892
Model 5: Red Fox Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	2.88	1.84		
% Bare Ground	0.71	0.3		
% Sand Barrens	-35.92	0.79		
% Upland Prairie	-18.32	1.47		
% Dense Urban	-20.11	1.17		
Whole Model Test		11.98	0.2928	40.5911

Table 10. Multivariate logistic regression results for coyote occurrence in relation to habitat predictor variables at all camera stations. Whole model test p-values were nearly significant ($p \leq 0.1$) for all included models.

Model 1: Coyote Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	0.90	2.54		
% Bare Ground	3.86	0.75		
% Dense Urban	-12.23	1.89		
Whole Model Test		5.86	0.1050	56.59
Model 2: Coyote Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	0.48	0.39		
% Bare Ground	3.60	0.76		
% Dense Urban	-9.22	0.92		
% Vacant	4.59	0.59		
Whole Model Test		6.49	0.1162	58.41
Model 3: Coyote Occurrence	Parameter Estimates (Coefficients)	Wald Chi-Square	R-Square	AIC
Intercept	0.50	0.43		
% Bare Ground	3.60	0.74		
% Dense Urban	-9.35	0.96		
% Cropland	4.46	0.57		
Whole Model Test		6.46	0.1158	58.44

DISCUSSION

Rapid Assessment

The scent-baited rapid assessment survey proved to be a valuable tool for identifying long-term study sites and optimizing camera placement to increase detections of the study species. While some literature supports the notion that scent-baited surveys can quickly and thoroughly detect all canid species that occur within a study site (Cove et al. 2012), it should be noted that a local wildlife rehabilitation clinic reported a gray fox that was involved in a vehicular collision within the study site during the rapid assessment period. Given that no gray foxes were detected in this study, this suggests that canids within the study site were not necessarily detected in all locations where they occurred. As such, despite the value of scent-baited rapid assessment surveys, absence data acquired by these methods should be interpreted cautiously.

Increased camera density and sampling duration may improve the accuracy of rapid assessment surveys, particularly regarding confidence in absence data. Although the camera density in this study was selected so that two cameras would occur per average home range of the smallest ranging local canid, the gray fox, local environmental conditions (i.e., topography, vegetation, wind, etc.) were uncontrolled and scent dispersal (and therefore the effective sampling radius) was likely highly variable between camera stations. It is possible that even if the scent-bait was detected by an animal, factors such as the presence of predators or habitat preferences may have discouraged the animal from investigating further and being detected by the cameras.

Long-term Monitoring

The detection of coyotes at 62% of non-baited camera stations and in all six study sites

speaks to their widespread occurrence across the landscape and is in line with the findings of previous research (Gomper 2002, Ohio Division of Wildlife 2015). Interestingly, the sympatric occurrence of red foxes with coyotes at 88% of the locations in which red foxes were detected contrasts with other studies that demonstrated strong spatial partitioning between the species (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989, Fuhrmann 1998, Gosselink et al. 2003). This deviation may be a result of the substantial loss and fragmentation of forested fox refugia in the region that would have historically been avoided by coyotes (Richer et al. 2002). With little suitable habitat remaining that is devoid of coyotes, red foxes may simply have no option but to co-occur with coyotes within the study area.

Given that coyote colonization of the region occurred decades or centuries ago (Heppenheimer 2017), the contemporary occurrence of red foxes alongside coyotes suggests that either foxes are successfully niche partitioning in ways that do not include avoiding home range overlap as observed in other studies (Chamberlain and Leopold 2005), or the foxes observed within the study site are members of a sink population that is supported by source populations in areas of low coyote density outside of the study area. If the latter is true, highly developed areas adjacent to the study site could function as urban refugia (Gosselink et al. 2003) that support source populations. While the demographic investigations required to identify fox population dynamics within the study site were outside the scope of this study, it is important to consider that areas inhabited by foxes are not necessarily preferred or adequate to sustain their populations. Further demographic research is recommended to most accurately interpret the habitat and landcover associations identified here. Nonetheless, the habitat and landcover associations identified in this study serve as a valuable foundation for future investigation.

Contrary to our a-priori hypothesis that local habitat characteristics (particularly visual

obstruction) would be strong predictors of canid occurrence, we found weak evidence to support this relationship. Possible explanations for the significant positive correlation between coyote occurrence and percent bare ground, the only significant fine scale variable, may include ease of travel or identification and capture of prey. We did anecdotally observe high percentages of bare ground in disturbed sites such as riparian corridors and in thickets of invasive honeysuckle (*Lonicera spp.*). Further investigation into the effects of these specific habitats on canid occurrence is recommended.

At the landscape scale, our observation that red foxes demonstrated significant negative associations with sand barrens and upland prairie habitats is aligned with the findings of prior studies (Gosselink et al. 2003). As mentioned previously, these open habitats are theorized to favor coyotes which are dominant and better adapted to these environments (Messier and Barrette 1982).

In contrast with other studies, we observed significant negative associations between the occurrence of both canid species and dense urban landcover. Previous research suggests that both species are positively associated with urban areas at large scales, whereas at small scale, coyotes most frequently occur in natural areas within the urban matrix and red foxes most commonly occur in close proximity to human developments (Willingham 2008). This discrepancy, in part, may be the result of varying definitions of “dense urban” landscapes between studies. The landcover maps used in this study (Schetter and Root 2013, Martin and Root 2020) classify dense urban landcover based upon impervious surface coverage. Other studies use human density for classification (Gehrt 2007) or do not offer a quantitative description of urban areas. Considering the difference in classification methods, data between studies should be compared with caution. The negative correlation between both red fox and coyote occurrence and

impervious surface coverage has not yet been described in other studies to our knowledge and is an interesting subject for future study. In particular, studying these relationships at various scales may offer more insight into these interactions.

It is interesting to note that of all landscape scale variables examined in this study, only those with strong negative relationships were significantly correlated with red fox occurrence. While our findings that red foxes avoid open habitats such as sand barrens and upland prairies is in line with previous research, we expected to find strong positive correlations with densely vegetated habitats, such as forests and woodlands (Weber and Meia 1996, White et al. 2006). This suggests that the presence of unsuitable habitats (sand barrens and upland prairies) is a stronger driver of red fox occurrence than habitats that are traditionally considered suitable such as forests and woodlands. Assuming red fox populations within our coyote dominated study sites are sustainable, this finding can inform land managers in natural areas on how to best support fox populations.

While red foxes may benefit from a reduction or conversion of sand barrens and upland prairies, this would come at a cost to many other species of special conservation concern within the Oak Openings Region. A land management approach that could serve both forest interior species and species that occupy open habitats may be to cluster similar habitat types together, rather than evenly scattering them throughout the landscape. This would result in larger blocks of habitat and reduce edge effect. Softening habitat edges by transitioning from open habitats like prairies or sand barrens to savannas or shrublands, and finally to forests would also help preserve forested interior habitats that may be utilized as refugia (Theberge and Wedeles 1988). Perhaps the simplest approach of all would be to avoid creating new open habitats in close proximity to forests where they may have the strongest negative impact on forest communities.

Conclusion

In summary, negative correlations with landscape scale variables appear to most strongly predict the occurrence of both canid species investigated in this study. In order to promote red fox conservation in the region, care should be taken to avoid saturating the landscape with habitat types that strongly reduce occurrence probability of red foxes, such as sand barrens and upland prairies. Additional demographic studies on red foxes in the region are suggested in order to determine if the species has sustainable populations despite a higher degree of sympatry with coyotes than observed in most other studies. Further research on the effects of landcover and fine scale habitat variables on canid occurrence may be facilitated by the use of radio telemetry or GPS collars which would provide more data points and allow for more robust and finer resolution analyses than camera traps alone. A comparison of both methods would be particularly valuable in generating an accurate cost-benefit analysis. If both methods lead to similar conclusions, a strong case would be made for replicating the methodologies of this study.

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APPENDIX A: AVERAGE FINE SCALE HABITAT VARIABLES AT LONG-TERM
MONITORING SITES GROUPED BY CANID OCCURRENCE

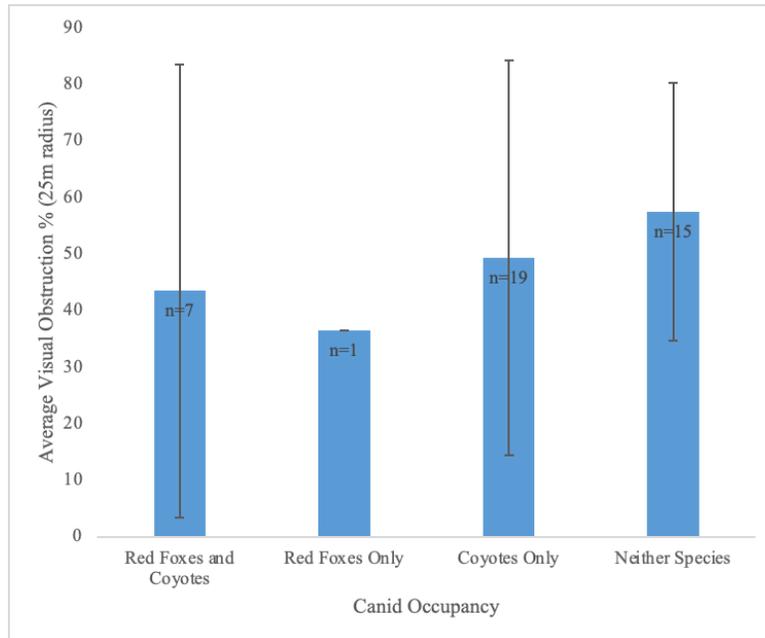


Figure A.1. Average visual obstruction percentage (25m) at non-baited camera locations grouped by canid occurrence.

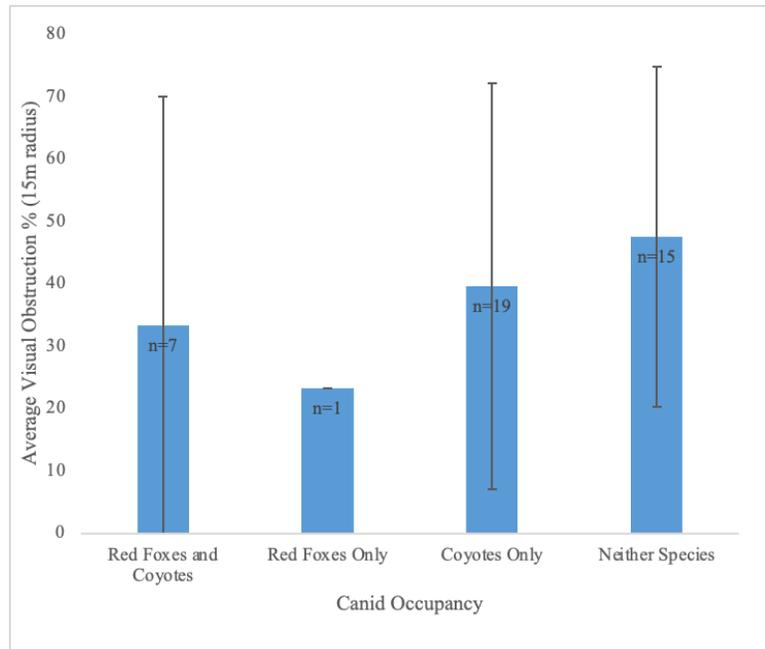


Figure A.2. Average visual obstruction percentage (15m) at non-baited camera locations grouped by canid occurrence.

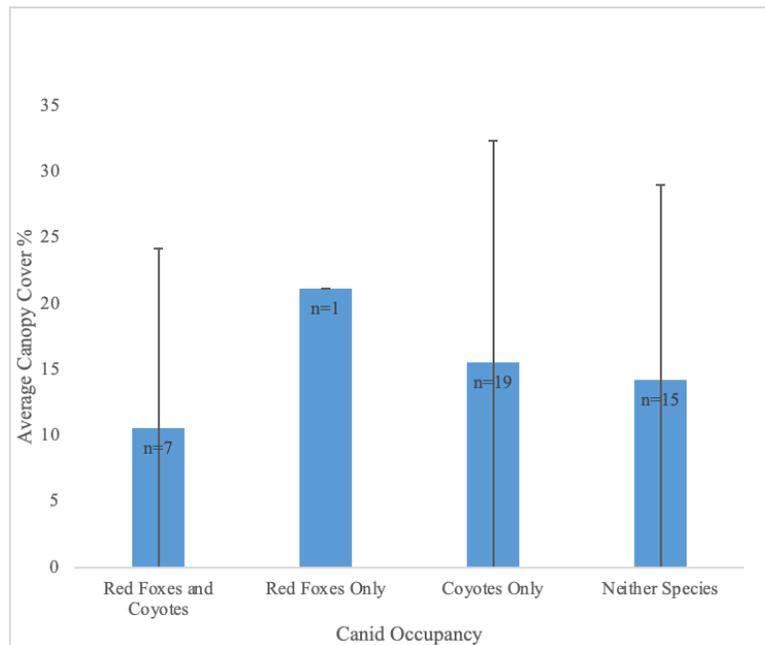


Figure A.3. Average canopy cover percentage at non-baited camera locations grouped by canid occurrence.

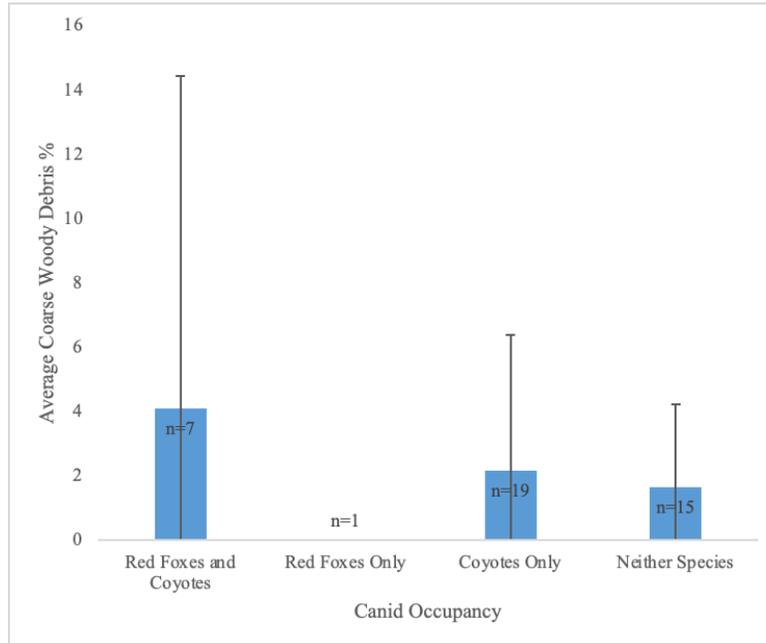


Figure A.4. Average coarse woody debris percentage at non-baited camera locations grouped by canid occurrence.

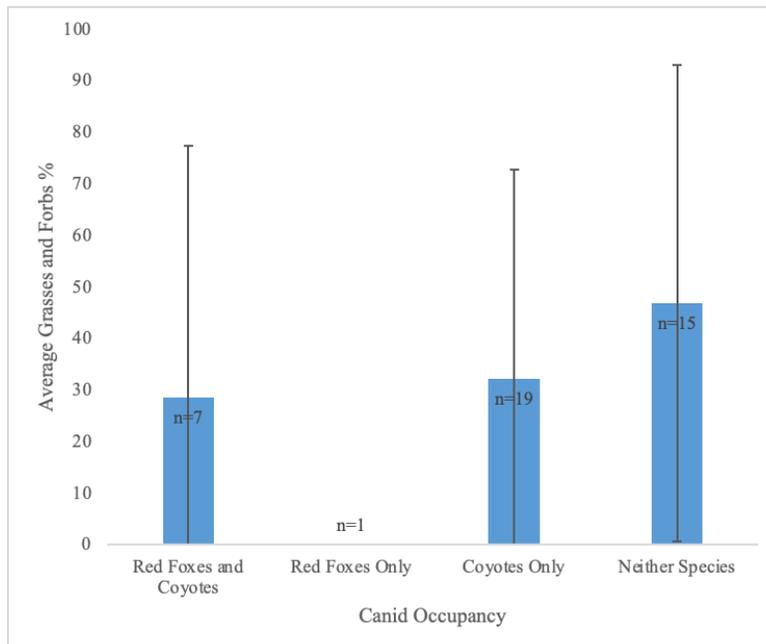


Figure A.5. Average grasses and forbs percentage at non-baited camera locations grouped by canid occurrence.

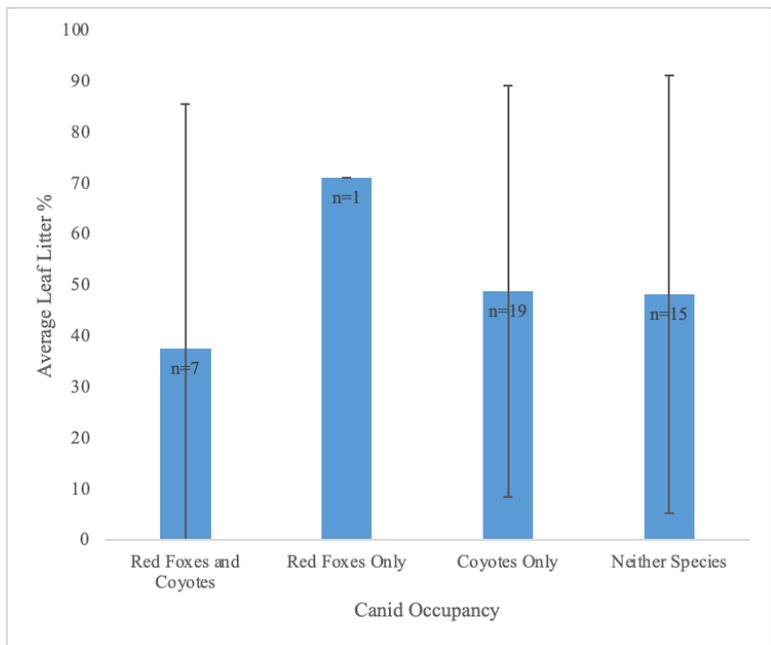


Figure A.6. Average leaf litter percentage at non-baited camera locations grouped by canid occurrence.

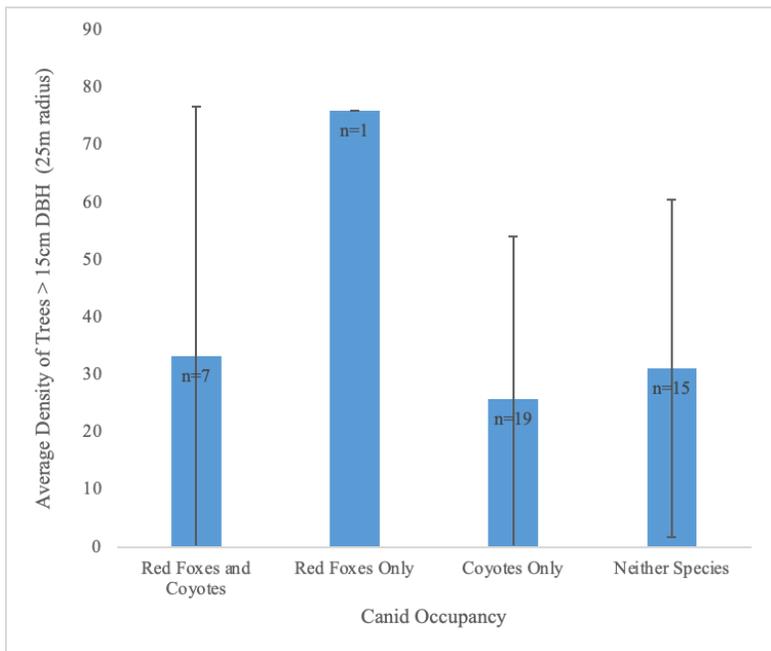


Figure A.7. Average density of trees at non-baited camera locations grouped by canid occurrence.

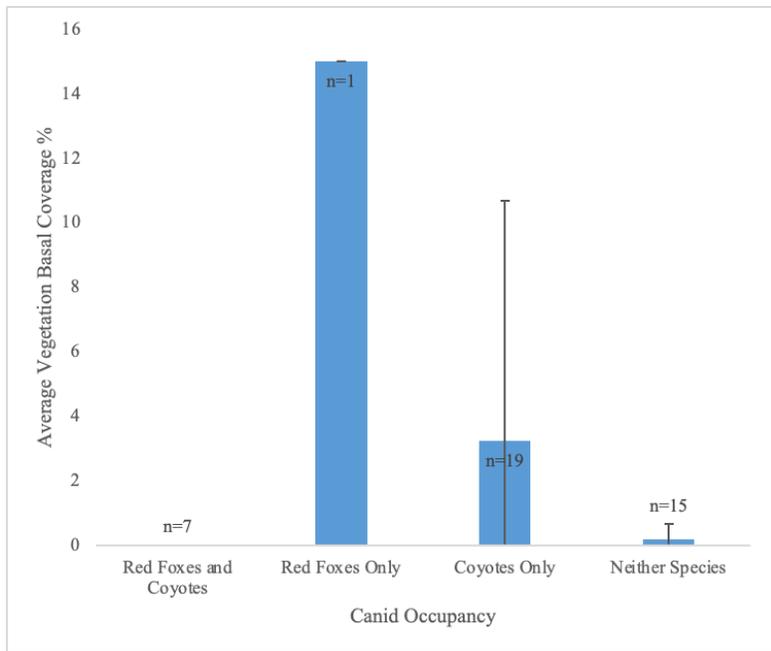


Figure A.8. Average vegetation basal coverage percentage at non-baited camera locations grouped by canid occurrence.

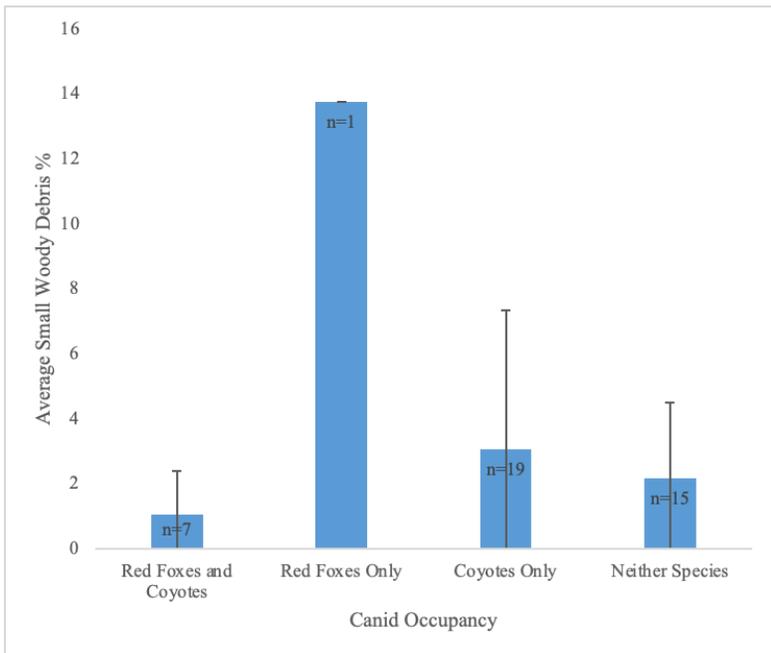


Figure A.9. Average small woody debris percentage at non-baited camera locations grouped by canid occurrence.

APPENDIX B: INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL



DATE: May 31, 2018

TO: Karen Root, PhD
FROM: Bowling Green State University Institutional Animal Care and Use Committee

PROJECT TITLE: [1231129-1] The Effects of Landscape, Habitat, and Community Composition on Canid Occupancy

IACUC REFERENCE #:
SUBMISSION TYPE: New Project

ACTION: APPROVED
APPROVAL DATE: May 29, 2018
EXPIRATION DATE: May 28, 2021
REVIEW TYPE: Designated Member Review

Thank you for your submission of New Project materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission.

Please make sure that all members of your research team read the approved version of the protocol.

Report all NON-COMPLIANCE issues regarding this project to this committee.

Please note that any revision to previously approved materials must be approved by this committee prior to initiation. Please use the Addendum Request form for this procedure.

This project requires Continuing Review by this office on an annual basis. Please use the Annual Renewal form for this procedure.

If you have any questions, please contact the Office of Research Compliance at 419-372-7716 or orc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.



DATE: June 11, 2019

TO: Karen Root, PhD
FROM: Bowling Green State University Institutional Animal Care and Use Committee

PROJECT TITLE: [1231129-2] The Effects of Landscape, Habitat, and Community Composition on Canid Occupancy

IACUC REFERENCE #:
SUBMISSION TYPE: Continuing Review/Progress Report

ACTION: APPROVED
APPROVAL DATE: June 11, 2019
EXPIRATION DATE: May 28, 2021
REVIEW TYPE: Designated Member Review

Thank you for your submission of Continuing Review/Progress Report materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission. Please make sure that all members of your research team read the approved version of the protocol.

The following modifications have been approved:

Continuing Review/Progress Report - IACUC.annual.reprt.Root.Schoen.xlsx (UPDATED: 05/20/2019)

Continuing Review/Progress Report - IACUCAnnualRenewal_1-16 (1).doc (UPDATED: 05/20/2019)

Report all NON-COMPLIANCE issues regarding this project to this committee.

Please note that any revision to previously approved materials must be approved by this committee prior to initiation. Please use the Addendum Request form for this procedure.

This project requires Continuing Review by this office on an annual basis. Please use the Annual Renewal form for this procedure.

If you have any questions, please contact the IACUC Administrator at 419-372-8753 or iacuc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.



DATE: June 16, 2020

TO: Karen Root, PhD
FROM: Bowling Green State University Institutional Animal Care and Use Committee

PROJECT TITLE: [1231129-3] The Effects of Landscape, Habitat, and Community Composition on Canid Occupancy

IACUC REFERENCE #:
SUBMISSION TYPE: Continuing Review/Progress Report

ACTION: APPROVED
APPROVAL DATE: June 15, 2020
EXPIRATION DATE: May 28, 2021
REVIEW TYPE: Designated Member Review

Thank you for your submission of Continuing Review/Progress Report materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission. Please make sure that all members of your research team read the approved version of the protocol.

The following modifications have been approved:

- Amendment/Modification - IACUC.annualreport_Schoen2020.xlsx (UPDATED: 05/20/2020)
- Amendment/Modification - IACUCAnnualRenewal_Schoen2020.doc (UPDATED: 05/20/2020)

If you have any questions, please contact the IACUC Administrator at 419-372-8753 or iacuc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.