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Relationship between Carnivore Distribution and Landscape Features in the Northern Highlands Ecological Landscape of Wisconsin

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ABSTRACT.—Residential development has been associated with habitat fragmentation and loss and declining diversity of indigenous species, especially when development occurs in ecologically sensitive environments such as wetlands and/or riparian zones. In recent decades, the upper mid-west region of the United States has experienced a dramatic increase in residential development along lakeshores. In northern Wisconsin, recent studies have documented negative effects of such development on local flora and certain fauna (avian and amphibian communities) but less is known about how mammal communities, especially carnivores, respond to housing development. To quantify the influence of lakeshore development on these taxa, we conducted snow track surveys on 10 pairs of low- and high-development lakes and deployed remote cameras at four lakes in Vilas County, Wisconsin, in 2008. Our results suggest that a higher diversity of carnivores ($P = 0.006$) were present on low-development lakes. Coyotes (*Canis latrans*) were detected most frequently ($n = 34$) especially on low-development lakes. Fishers (*Martes pennanti*), wolves (*Canis lupus*), bobcats (*Lynx rufus*), and northern river otters (*Lontra canadensis*) were exclusively detected on low-development lakes by snow track surveys. Raccoon (*Procyon lotor*) and red fox (*Vulpus vulpus*) detection was greater on higher-development lakes than low-development lakes. These results also were supported by 12 remote cameras on a subset of four lakes. We also investigated the influence of housing and road density in the surrounding landscape (500 m buffer) on carnivore community composition by means of a non-metric multidimensional scaling ordination. Significant associations were observed between community composition and landscape attributes associated with development. Our results suggest that residential development along lakeshores is having a negative impact on carnivore diversity in this region.

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INTRODUCTION

Rural landscapes in the Midwestern United States have experienced dramatic changes in recent decades due to residential development (Radeloff *et al.*, 2005). Residential development in rural landscapes causes fragmentation and loss of wildlife habitat (Theobald *et al.*, 1997) thus poses a serious threat to biodiversity (Wilcove *et al.*, 1998; Czech *et al.*, 2000). Humans are inclined to construct primary or secondary homes in and around natural areas because they provide amenity values such as recreation and scenery (Schnaiberg *et al.*, 2002). Freshwater ecosystems have attracted people and development for centuries (Naiman, 1996; Riera *et al.*, 2001). In northern Wisconsin, residential development has increased over 200% along lakeshores in recent decades [Wisconsin Department of Natural Resources (WDNR), 1996; Radeloff *et al.*, 2001; Gonzales-Abraham *et al.*, 2007].

In 1968, the State of Wisconsin attempted to protect lakeshore habitat by implementing ordinances that mandated vegetation cutting standards in a buffer zone along lakeshores. The Wisconsin Shoreland Management Program (WDNR Chapter NR 115) states that vegetation within a buffer zone must be left intact for 10.7 m (35 ft) inland from the ordinary high water mark and no more than 9.1 m (30 ft) for every 30.5 m (100 ft) of shoreline can be cleared of vegetation. This program recommended the remaining shoreline be left in a naturally vegetated state. However, many lakeshore owners routinely ignore or are unaware of these ordinances which often results in the removal of vegetation structure along shorelines (Christensen *et al.*, 1996; Elias and Meyer, 2003). Wildlife can be affected directly or indirectly by these actions (Ford and Flaspohler, 2010).

Recent studies comparing low- and high-development lakes in Vilas County, Wisconsin, documented declines in the flora and fauna on the more developed lakeshores. For example, species composition of breeding birds differed significantly (Lindsay *et al.*, 2002), abundance of green frogs was substantially lower (Woodford and Meyer, 2003), and vegetation structure and composition in riparian and littoral zones were dramatically different (Elias and Meyer, 2003) along low- and high-residential development lakeshores. In addition, wolf (*Canis lupus*) recovery in this area has been slow compared to other areas in Wisconsin. This may be related to human development, road densities, and habitat fragmentation (Mladenoff *et al.*, 1995, 1997). Very little is known about the effect of residential development on the mammalian carnivore community in this region, especially along lake riparian areas.

Human dominated areas can lead to the decline or extirpation of carnivores, either through competition for resources, direct persecution, or habitat loss (Woodroffe, 2000; Cardillo *et al.*, 2004). Crooks (2002) reported that certain species of mammalian carnivores are sensitive to human habitat fragmentation, and that the presence and abundance of carnivores can be an overall indicator of ecosystem health. Carnivores are related to ecosystem health because they play an important role in structuring communities (Eisenberg, 1989; Crooks and Soule, 1999; Schmitz *et al.*, 2000). For example, in southern California, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) were less common in landscapes with more residential development (Crooks, 2002). The absence of carnivores in an ecosystem can have a significant impact on the relative abundance of herbivores and small carnivores. In some localities, the loss of larger carnivores has allowed one or two smaller mammalian predator species to dominate a community and further reduce biodiversity (Crooks and Soule, 1999; Berger *et al.*, 2001; Hebblewhite *et al.*, 2005; Prugh *et al.*, 2009). Thus, maintenance of carnivore species diversity is an important consideration in managing healthy ecosystems (Eisenberg, 1989); however, management of natural habitats for carnivores is becoming one of the greatest challenges for conservation biologists and policy makers in North America (Noss *et al.*, 1996).

Carnivore conservation is challenging, in part, because many carnivore species are among the most elusive animals in the world, are nocturnal and secretive, live in low densities, and have large home ranges which make them difficult to detect and monitor (Hoffman, 1996). We used two non-invasive techniques, snow tracking and remote cameras, to determine the presence of carnivore species on low- and high- development lakeshores in northern Wisconsin. We choose these two monitoring techniques because certain mammal species have different seasonal behavior patterns. For example, black bears (*Ursus americanus*) hibernate and raccoons (*Procyon lotor*) are mostly inactive though the winter months and may not be detected by snow track surveys. Certain canid species that are wary of human scent may avoid cameras. In addition, vegetation and seasonality can produce species-specific differences in detectability and body size characteristics of species may influence detection (O'Connell *et al.*, 2006).

Many studies have investigated the effect of residential development on carnivore presence and abundance relative to patch size and isolation impacts on metapopulation dynamics (Crooks, 2002), trophic cascades (Crooks and Soulé, 1999; Hebblewhite *et al.*, 2005), species interactions (Gosselink *et al.*, 2003; McDonald *et al.*, 2008), and wildlife habitat (Theobald *et al.*, 1997). However, few studies have investigated the relationship between mammal diversity in lake riparian habitat and residential development. In one of the studies, Racey and Euler (1982) found a decrease in small mammal diversity with increasing development on lakeshores in Ontario, Canada. However, their study was conducted on lakes for which smaller seasonal cottages represented the typical development (Robertson and Flood, 1980).

The objectives of our research were to (1) determine if residential development on lakeshores is related to carnivore diversity and relative abundance and (2) establish baseline data for long-term monitoring of carnivores. Because residential development has been shown to have a negative impact on species richness and diversity for other taxa, we hypothesized that lakeshores with higher-development will have fewer carnivore species than lakeshores with lower-development.

METHODS

STUDY AREA

We conducted our study in Vilas County, Wisconsin, which is within the Northern Highland Ecological Landscape (Puhlman *et al.*, 2006). Vilas County encompasses a 2636 km^2 area along the Wisconsin's northern border with the Upper Peninsula of Michigan. Vilas County contains 1320 pitted outwash glacial lakes ranging in size from 0.1 to >1500 ha and covering 16% of the county's area (WDNR, 2005) and 53% of the area is privately owned (Schnaiberg *et al.*, 2002). The land cover is a mixture of bogs, northern wet forest, boreal forest, and northern dry to northern xeric forest (Curtis, 1959). Vilas County has undergone relatively high residential development with 61% occurring within 100 m of lakes in recent decades (Schnaiberg *et al.*, 2002).

Study lakes were systematically chosen from the University of Wisconsin, Trout Lake Limnology, North Temperate Lakes BioComplexity project data base as a function of their development density and morphometric characteristics (http://lter.limnology.wisc.edu). We paired 10 low-development lakes (<10 houses/km, mean = 2.10 ± SE 0.64) with 10 high-development lakes (≥10 houses/km, mean = 23.45 ± SE 2.69), controlling for surface

TABLE 1.—2008 snow tracking survey lake characteristics in Vilas County, Wisconsin (WDNR, 2005). Ten low-development lakes (<10 houses/km, mean = 2.10 ± 0.64) are matched with 10 high-development lakes (≥10 houses/km, mean = 23.45 ± 2.69) by surface area, lake type (drainage, seepage, spring fed), and perimeter of shoreline. Paired lakes are sequenced top to bottom (http://lter.limnology.wisc.edu)

Development	Lake	Surface Area ha	Type[b]	Perimeter m	House Density (homes km^{-2})
Low	Escanaba[a]	119	DG	8135	0.37
	Jag[a]	158	SE	4935	1.4
	White Sand	220	DG	9881	5.8
	Lac Du Lune	172	SE	13,724	2.0
	Erickson	106	DG	3570	0.5
	Nebish	40	SE	4295	0.2
	Palmer	257	DG	10,617	3.1
	Round	47	DG	3586	0.3
	Little John	67	SP	5369	2.1
	Laura	242	SE	8239	5.2
High	Found[a]	132	DG	6362	16.7
	Moon[a]	124	SE	3190	14.7
	Lost	297	DG	7537	26.2
	Carpenter	135	SE	5492	18.0
	Brandy	110	DG	3470	29.8
	Vandercook	38	SE	3257	13.8
	Eagle	231	DG	7490	30.2
	Johnson	32	DG	3546	26.2
	Towanda	59	SE	6119	18.7
	Stormy	211	SE	7595	40.2

[a] Lake with digital remote camera deployed
[b] Lake type: DG = drainage, SE = seepage, SP = spring fed (WDNR, 2005)

area and lake type (*i.e.*, drainage, seepage, spring fed; http://lter.limnology.wisc.edu Table 1).

SNOW TRACK SURVEYS

We conducted winter snow track surveys between Jan.–Feb. 2008 on all 20 lakes. Transect surveys were conducted 48 to 96 h following snowfalls of ≥2.5 cm, at temperatures above −17 C, and with winds less than 16 km/hour. Survey transects started at a point of lake access (*e.g.*, boat landing) and traveled (via snow-shoes or cross-country skis) 1500 linear meters on the frozen lake surface, along the shoreline. We identified all carnivore species according to methods described by Halfpenny (1986). If tracks were not immediatley identified, we backtracked the trail to suitable topography to record measurements and determine the species. We recorded all carnivore tracks encountered 10 m on each side of the survey transect. In addition, we tallied encounters with domestic dogs (*Canis familiarus*) and non-carnivore species including: microtine rodents (*e.g., Peromyscus sp., Myodes sp.*), snowshoe hares (*Lepus americanus*), eastern cottontail rabbits (*Sylvilagus floridanus*), tree squirrels (*Sciuridae* s*p.*), and white-tailed deer (*Odocoileus virginianus*). To quantify the difference in occurrence of non-carnivore species between high- and low-development lakes, we developed the following index to categorize the abundance of these species: 0 if no tracks were detected, 1 = 1 to 5 tracks, 2 = 6 to 10 tracks, 3 = >10 tracks for each transect

TABLE 2.—Mammals, other than carnivores, detected during snow track surveys on ten pairs of lakes in Vilas County, Wisconsin. Species were assigned categories based on average frequency detected on low- and high-development lakes. Categories are (0) absent, (0.1–0.4) rare, (0.5–1.4) uncommon, (1.5–2.4) common, (>2.4) abundant. Data were collected during the winter of 2008

Species		Development			
Common name	Scientific name	High	Low	Test stat	P
Domestic Dog	*Canis familiarus*	1.5	0.1	3.500*	**<0.001**
White-tailed Deer	*Odocoileus virginianus*	2.5	0.6	4.000*	**<0.001**
Squirrels	*Sciuridae* sp.	2.2	1.4	1.697	0.107
Microtine rodents	NA	0.7	1.1	−1.434	0.169
Eastern Cottontail	*Sylvilagus floridanus*	1.1	0.1	14.000*	**0.003**
Snowshoe Hare	*Lepus americanus*	0.2	1.4	79.000*	**0.017**

* Nonparametric Mann-Whitney Rank Sum *U*-test

(Table 2). Paired high- and low-development lakes, were surveyed sequentially the same day with no more than 30 min between surveys periods.

REMOTE CAMERAS

To augment the winter track surveys we deployed remote cameras to detect carnivore species. Twelve motion sensor, digital cameras (Cuddeback™ Expert, Non Typical, Inc., Park Falls, Wisconsin) with a ¾ second trigger speed were placed on the subset of four paired lakes, two low- and two high-development (Table 1). Six cameras were deployed on low-development and six cameras deployed on high-development lakes from 12 Jun. 2007 to 31 Aug. 2008 for 5700 camera nights. Camera sites were determined by dividing the shoreline into 50 m segments using Geographic Information System (GIS) software and segments were labeled sequentially (*i.e.*, 1, 2, 3 …). Sample segments were randomly picked; however, all cameras were placed ≥1 km from each other to increase sampling independence. The number of cameras per lake was determined by the length of the shoreline such that every 2 km of shoreline contained one camera, (*i.e.*, if the shoreline was 4 km in length, then two cameras were used on that lake). If cameras were disturbed by human activity, they were moved to another location. During the course of our study, there were 11 camera sites on the high- development lakes and eight camera sites on low-development lakes.

Cameras were placed within 10 m of the shoreline, positioned toward a game trail when present, and attached to a tree 50 cm above the ground. On high-development lakes, cameras were placed where some vegetation cover was present rather than in a resident's yard. A cotton ball saturated with lure (shellfish oil) was placed inside an empty plastic, perforated film canister and hung in a tree within 5 m of camera. Cameras were programmed to take photos 24 h/day, pause for one minute intervals between events, and record date and time of event on each image. Batteries and compact flash cards were examined every 2 to 4 wk.

DATA ANALYSES

Snow track survey.—We calculated Shannon's Index of species diversity and evenness (Magurran, 2004) for each lake within a group of ten lakes categorized as low- or high-development. We used a paired *t*-test to test the null hypothesis that low- and high-development lakes have equal species diversity. The abundance indices for non-carnivore species were averaged by treatment and interpreted by relative abundance (Table 2). A paired *t*-test was used to compare mean relative abundance of non-carnivore species between high- and low-development lakes. For paired *t*-tests, we determined if all test assumptions (normality and equal variance) were met. The Kolmogorov-Smirnov test was used to test for normal distribution of the samples. Data that violated assumptions were transformed using natural logarithms. When transformation of variables was unsuccessful in producing a normal distribution, the nonparametric Mann-Whitney Rank Sum *U*-test was used. Analyses were conducted using SigmaStat 3.5 software (Systat Software Inc., 2006) and significance levels were set at $\alpha = 0.05$.

Remote cameras.—Mean rate of occurrence (number of events/camera night) was calculated for each species, at each camera location, by development type (O'Connell *et al.*, 2006). We defined an occurrence event as a single species detection within a 24 h period. For instance, if six images of a raccoon were recorded in a 24 h period at a camera site, this was recorded as one occurrence event. We excluded data collected in the months of Jan. and Feb. 2008 because extreme cold temperatures and blowing drifting snow rendered some cameras inoperable.

Landscape feature.—We used (GIS) software to assess landscape features that contributed to carnivore presence. We used ArcGis version10 (ESRI, 2010) and 2006 National Land Cover Dataset (NLCD) to analyze landscape-feature patterns and to generate landscape indices of housing density, percent landuse/landcover for all lakes listed. Principle methods for each included the creation of two concentric buffers of a pre-determined distance from the edge or center (NLCD 10 km Hydro) of each lake which were then used to conduct Intersect analysis on county-derived address points, NLCD landcover units, and Wisconsin roads for geospatial analyses. To evaluate the influence of measured landscape feature variables on carnivore community composition, we used non-metric multidimensional scaling conducted with PC-ORD. The main matrix was composed of track observations by species for each lake. The second matrix contained lake attributes and landscape features within 150 and 500 m buffer zones. Lake attributes investigated included lake type (low- or high-development), lake surface area, lake perimeter, and housing density within 10 m of shoreline. Landscape feature investigated within each buffer included housing (number km^{-2}) and road (linear distance, km) density and percent cover of open water, forest, shrub and herbaceous vegetation, agriculture, and wetlands.

RESULTS

SNOW TRACK SURVEY

We recorded 83 encounters of tracks of nine carnivore species across all lakes sampled ($n = 20$). Five of the nine species were detected exclusively on low-development lakes (Fig. 1). Sixty-eight carnivore track detections accounted for 92% of all tracks recorded on low-development lakes, and 15 carnivore track detections accounted for 8% of all tracks recorded on high-development lakes. Coyotes were the most encountered species ($n = 34$) across all lakes. Red foxes (*Vulpes vulpes*) accounted for 14 encounters of which nine encounters were recorded on high-development lakes. Mink detections were four times higher on low-development than high-development lakes (Fig. 1). Shannon's index of species diversity was significantly higher ($t = 3.547$, df = 9, $P = 0.006$) on low-development (mean = 1.974 ± 0.438 SE) than on high-development lakes (mean = 0.277 ± 0.113 SE). Evenness was also significantly higher ($t = 7.321$, df = 9, $P = <0.001$) on low-development lakes (mean = 1.50 ± 0.282 SE) than on high-development lakes (mean = 0.40 ± 0.163 SE). Overall, there were twice as many carnivore species on low-development lakes ($n = 8$) than on high-development lakes ($n = 4$).

For non-carnivores species, white-tailed deer were abundant on all high-development lakes, but were detected on only 50% of low-development lakes. Snowshoe hare ($P = 0.017$) and eastern cottontail occurrence differed statistically ($P = 0.003$) between the types of

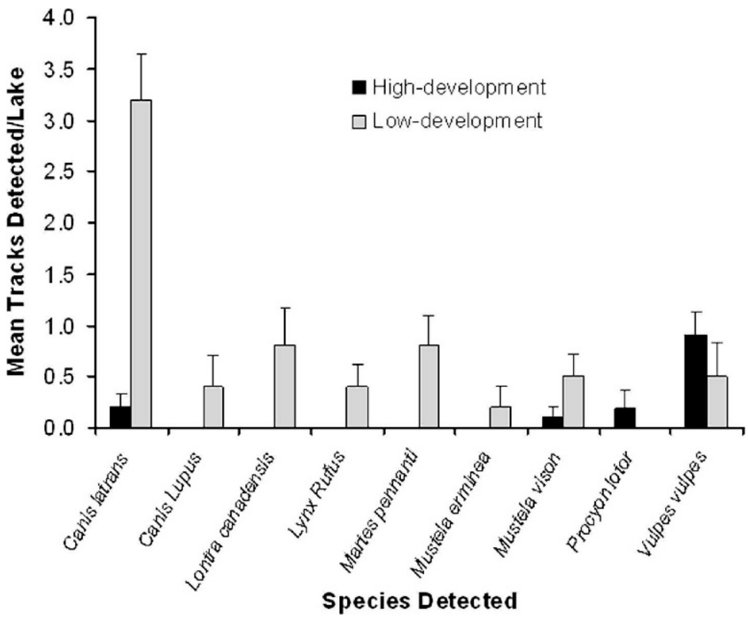

FIG. 1.—Mean and standard error of tracks detected by snow track surveys within pairs of ten lakes with each pair containing a low- and high-development lake, in Vilas County, Wisconsin. Data were collected in Jan. and Feb. of 2008

development. Hares were detected on 70% of low-development lakes and 20% of high-development lakes, whereas cottontails were recorded on 80% of high-developments lakes and 10% of low-development lakes. Domestic dogs were common on high-development lake and rare on low-development lakes (P = <0.001). There was no statistical difference of occurrence for *Sciuridae* (P = 0.107) and microtine rodents (P = 0.169; Table 2).

REMOTE CAMERAS

Nine carnivore species were detected by cameras (n = 12) across all lakes sampled (n = 4). Beavers (*Castor canadensis*), wolves, and fishers were photographed only on low-development lakes (Fig. 2). Rate of occurrence for raccoons was approximately 2.5 times higher on high-development (mean = 0.048 occurrence/camera night ± SE 0.036) than on low-development lakes (mean = 0.019 occurrence/camera night ± SE 0.012). Red fox rate of detection was nearly twice as high on high-development lakes (mean occurrence/camera night = 0.005 ± SE 0.003) than on low-development lakes (mean = 0.003 individual/camera night ± SE 0.002). Rate of detection for domestic dogs was over four times higher on high-development (mean = 0.037 occurrence/camera night ± SE 0.019) than low-development lakes (mean = 0.009 individual/camera night ± SE 0.004). Wolf and black bear detections were extremely low on all lakes sampled (Fig. 2).

For non-carnivore species, white-tailed deer were photographed ≥3 times more frequently on high-development (mean = 0.20 occurrence/camera night ± SE 0.09) than low-development lakes (mean = 0.06 occurrence/camera night ± SE 0.02). Snowshoe hares, *Sciuridae* species, and eastern cottontails had low detection rates on all lakes. Eastern

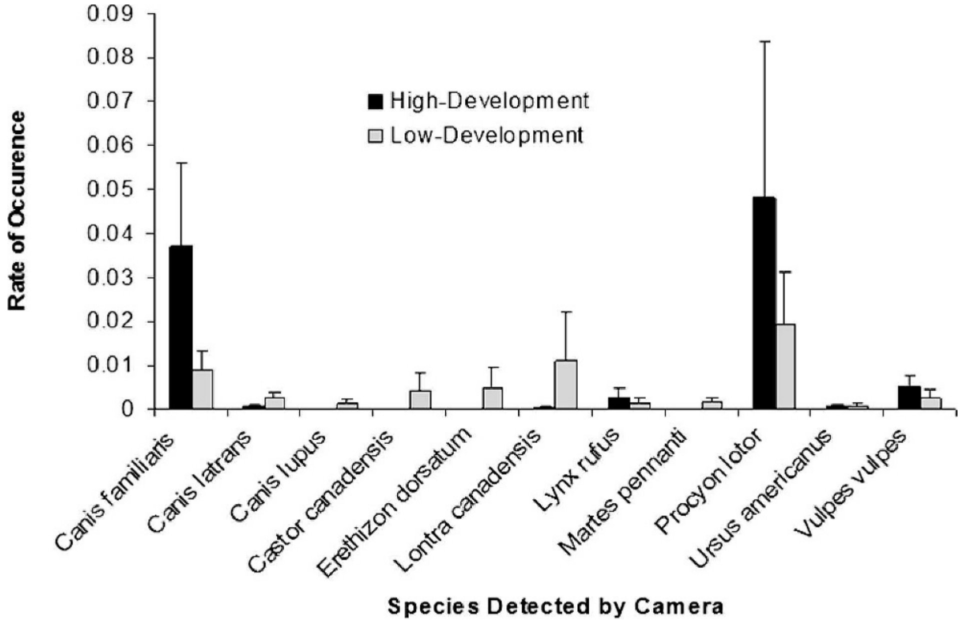

FIG. 2.—Mean rate of occurrence with standard error bars for carnivore species, domestic dogs, and beavers detected by remote camera on two pairs of low- and high-development shoreline lakes in Vilas County, Wisconsin. Data collected from Jun. 2007 to Aug. 2008 (excludes Jan. and Feb. 2008 due to technical problem with cameras)

cottontails were not detected on low-development lakes. *Sciuridae* species had similar rates of occurrence on both lake types and no micro-tine rodents were detected by remote cameras.

LANDSCAPE FEATURES

Landscapes surrounding high- and low- development lakes varied predictably at the 150 m buffer scale, with high-development lakes displaying housing densities an order of magnitude greater than those associated with low-development lakes (Table 3). The percent of land classified as developed within the 150 m buffer averaged 18.7 ± 2.5 for high-development lakes versus 5.9 ± 1.1 for low-development lakes. At the 500 m buffer scale there was less difference in percent of land developed and road density (Table 3), likely indicating the impacts to carnivores was related to changes to the riparian buffer or human impacts on the lakeshore, not some larger landscape scale effect.

The final nonmetric multidimensional scaling ordination solution was two dimensional with a final stress of 9.5 and explained 90.1% of the variation in the species matrix (Fig. 3). Axis 1 explained the most variation ($r^2 = 0.740$) and was most strongly associated with landscape attributes associated with a high level of residential development (Table 4). Axis 2 explained less variation ($r^2 = 0.161$) and was most strongly associated with the percentage of land area occupied by open water within the 500 m buffer (Table 4). Raccoons and foxes were most strongly associated with landscape attributes indicative of development, such as housing density (Fig. 3). The other carnivore species observed displayed repulsion in species space to environmental vectors associated with development (Fig. 3, Table 4).

TABLE 3.—Mean ± SE lake and landscape attributes of high- and low-developments along lakeshore of study lakes in Vilas County, Wisconsin

	High development (n = 10)	Low development (n = 10)
Lake		
Surface Area (ha)	135.9 ± 27.5	142.8 ± 25.2
Perimeter (m)	6029.2 ± 1015.5	7235.1 ± 1088.0
Houses km^{-1} shoreline	23.5 ± 2.7	2.1 ± 0.6
150 m buffer		
Housing Density (Homes km^{-2})	26.3 ± 3.2	2.3 ± 0.7
% Open Water	7.6 ± 0.9	8.2 ± 0.7
% Developed	18.7 ± 2.5	5.9 ± 1.1
% Forest	55.1 ± 3.8	67.9 ± 3.3
% Shrub/Herbaceous	1.6 ± 0.8	0.3 ± 0.2
% Agriculture	0.1 ± 0.1	0.0 ± 0.0
% Wetland	16.9 ± 3.3	17.6 ± 3.6
Roads (km)	3.7 ± 0.7	3.3 ± 0.9
500 m buffer		
% Open Water	8.0 ± 1.7	5.3 ± 1.6
% Developed	8.6 ± 1.3	12.9 ± 2.9
% Forest	63.6 ± 4.9	64.1 ± 5.2
% Shrub/Herbaceous	0.7 ± 0.4	3.2 ± 1.4
% Agriculture	0.2 ± 0.2	0.2 ± 0.2
% Wetland	18.8 ± 4.0	14.3 ± 3.2
Roads (km)	11.3 ± 1.8	10.3 ± 2.2

DISCUSSION

Our results suggest that carnivore diversity, evenness and species richness are higher on low-development than high-development lakes in our study region. Coyotes were by far the most frequently encountered carnivore species on low-development lakes in this study; bobcats were exclusively detected on low-development lakes during the snow tracking surveys. This suggests that these species may be sensitive to residential development or the various landscapes and stand-level changes associated with residential development (Crooks, 2002). Recent winter track surveys conducted by WDNR throughout the northern third of Wisconsin also found that coyotes were the most frequently encountered carnivore species (Wydeven *et al.*, 2004, 2007). In addition, Wydeven *et al.* (2007) reported a two-fold increase in coyote detections between his 2004 and 2007 surveys. Historical records indicate that coyotes were common to abundant throughout Wisconsin in the late 1800s and early 1900s but were considered vermin and were hunted vigorously, resulting in declining populations through the mid-1900s (Jackson, 1961). More recently, coyotes have become more abundant in the northern half of Wisconsin (Fruth, 1986) which corresponds with increasing populations throughout North America (Gompper, 2002).

Coyotes have adapted to suburban and urban landscapes across North American (Gompper, 2002; Gerht, 2004; Markovchick-Nicholis *et al.*, 2008) yet our data indicates they avoid high-development lakes in northern Wisconsin although they are present across the region (Wydeven *et al.*, 2007). Gehrt (2007) postulated that coyotes will avoid humans, both temporally and spatially, while still living in the immediate area.

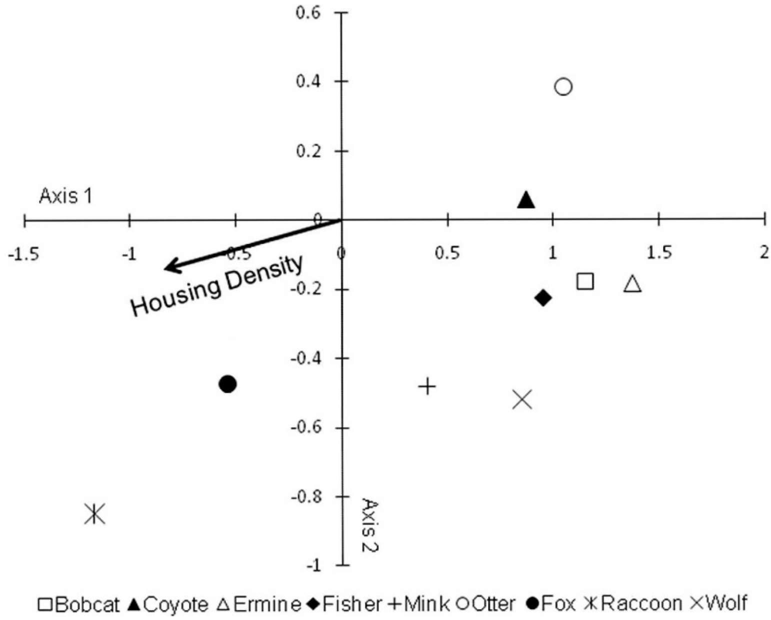

FIG. 3.—Nonmetric multidimensional scaling-ordination joint-plot of mammalian carnivore species composition derived from track surveys in sample space versus housing density within 150 m of lake shores for 20 lakes in Vilas County, Wisconsin in 2008. For a complete list of environmental variables examined and their associated correlations with the ordinations axes, *see* Table 4

Red foxes and coyotes can be sympatric (McDonald *et al.*, 2008), but foxes usually avoid coyotes by locating territories on the periphery of coyote territories (Voigt and Earle, 1983; Sargeant *et al.*, 1987) or by avoiding habitats frequented by coyotes (Dekkar, 1989). In rural east-central Illinois, red foxes selected human-associated habitats, which coyotes generally avoided (Gosselink *et al.*, 2003). It is common for these two canids to have inverse population densities in an area (Dekkar, 1989) which may explain the higher rate of red fox detections on high-development lakes in this study.

Remote cameras did not detect mink (*Mustele vision*) on any lakes, but they were encountered on snow track surveys primarily on low-development lakes. A similar study in Ontario, Canada, reported that mink occurrence and activity decreased with increasing levels of residential development (Racey and Euler, 1983).

The higher rate of detections for white-tailed deer on high development lakes is likely due to supplemental feeding by humans living on the lake (pers. obs.). Supplemental feeding can affect deer movement patterns by concentrating them around rich food sources (Ozoga and Verme, 1982). Such aggregations of deer can negatively affect natural vegetation at and adjacent to feeding sites (Doenier *et al.*, 1997). The higher rate of occurrence for white-tailed deer on high-development lakes is supported by both remote camera and snow tracking surveys. Numerous studies have investigated the ecological impact of deer over-abundance on landscapes. Deer herbivory can have strong negative effects on plant communities (Beals *et al.*, 1960; Russell *et al.*, 2001), lower recruitment of palatable species (Alverson and Waller, 1997; Holmes *et al.*, 2009; Witt and Webster, 2010), affect habitat of

TABLE 4.—Pearson correlations between nonmetric multidimensional scaling ordination (final stress = 9.5, cumulative r^2 = 0.901) axis scores for mammalian carnivore encounters along track surveys and lake and landscape attributes for 20 lakes in Vilas County, Wisconsin

	Axis 1 (r^2 = 0.74)	Axis 2 (r^2 = 0.16)
	r	r
Lake		
Surface Area (ha)	−0.016	0.021
Perimeter (m)	0.142	0.181
150 m buffer		
Housing Density (Homes km^{-2})	−0.821	−0.489
% Open Water	0.086	0.074
% Developed	−0.732	−0.590
% Forest	0.488	0.372
% Shrub/Herbaceous	−0.179	−0.149
% Agriculture	−0.251	−0.252
% Wetland	0.039	0.011
Roads (km)	−0.632	−0.362
500 m buffer		
% Open Water	−0.046	0.064
% Developed	−0.571	−0.416
% Forest	0.358	0.255
% Shrub/Herbaceous	−0.039	−0.066
% Agriculture	−0.365	0.350
% Wetland	−0.074	−0.053
Roads (km)	−0.666	−0.447

other species (deCalesta, 1994), and wreak havoc on habitat restoration projects (Opperman and Merenlender, 2000; Haskell, 2009).

Our snow tracking survey revealed an inverse relationship between snowshoe hare and cottontail detections with more snowshoe hares detected on low-development lakes compared to high-development lakes, and with cottontails showing the opposite pattern. Both species live sympatrically and utilize similar habitat types (Keith and Bloomer, 1993). Snowshoe hares inhabit conifer forest and areas of dense brushy understory, avoiding open areas (Pietz and Tester, 1983; Wise, 1986) and cottontails use a wide variety of disturbed habitat and human dominated landscapes (Chapman and Litvaitis, 2003). Furthermore, Bueller and Keith (1982) found that cottontails were associated with human development and were absent in extensive forests in northern Wisconsin.

Unlike the snow tracking survey, remote cameras detected snowshoe hares and bobcats at a higher rate on high-development than low-development lakes, suggesting that like coyotes, characteristics of camera location will influence the number of photo-captures (O'Connell *et al.*, 2006; Séquin *et al.*, 2007). However, no eastern cottontails were detected on low-development lakes with remote cameras, reinforcing our track survey finding that cottontails may be more abundant on high-development lakes.

As expected, raccoons were detected 2.5 times more often on high-development lakes compared to low-development lakes. Several studies from across North America (Oehler and Litvaitis, 1996; Crooks and Soule, 1999; Crooks, 2002) and throughout the world (Prugh *et al.*, 2009) have found that raccoon populations increase with increasing housing development and habitat fragmentation. It is well documented that raccoon densities are higher in urban and suburban areas compared to rural areas (Hoffman and Gottschang, 1977; Prange *et al.*, 2003). Prior to 1960, raccoons were not common in northern Wisconsin (Jackson, 1961). Raccoons have increased in abundance and expanded their distribution throughout the state in recent decades (J. Olson WDNR, pers. comm.). Furthermore, housing development may displace higher trophic level carnivores, thus removing or relaxing the top-down force on medium-sized carnivores such as the raccoons, resulting in a ''mesopredator release'' (Soulé *et al.*, 1988; Rogers and Caro, 1998; Crooks and Soule, 1999). A mesopredator release involves the increased density of a consumer species usually following a decline in predation by species at higher trophic levels.

In addition, raccoons have the most diverse diet of any carnivore in North America, which accounts for their success in human dominated landscapes (Gehrt, 2004). Raccoons have benefited more from human development than any other carnivore. Raccoons readily exploit human garbage, pet food, and other food resources related to human activities (Gehrt, 2004; Prange *et al.*, 2004). Therefore, it is plausible that decreased interspecific competition and increased energy sources have led to the increase in raccoon abundance measured on developed lakes. A higher predation rate on species in the lower trophic levels is a likely consequence, which can cause population decline among the prey of the mesopredator, and alter community structure (Crooks and Soule, 1999; Prugh *et al.*, 2009). For example, Raccoons can prey heavily on lake shore nesting bird eggs (McCann *et al.*, 2005).

Our results suggest the distribution of carnivores in our study area may be associated with the landscape scale matrix of development/fragmentation within which the high- and low-development lakes occur. Housing density was considerable higher within the 150 m buffer area on high-development compared to low-development lakes. This concentration of development can hinder movement (connectivity) of carnivores between lakes (Crooks, 2002), and carnivore presence (Randa and Yunger, 2006). Since 1937, road density has double in the region from 1.7 km/km^2 to 3.5 km/km^2 (Hawbaker *et al.*, 2006). However, we found relatively no difference in road density on this set of lakes sampled at the 150 and 500 m buffers (but *see* Wydeven *et al.*, 2001).

In summary, the landscape of northern Wisconsin is unique with over 12,000 glacial lakes scattered in a mixed deciduous-coniferous forest (WDNR, 1996). However, many lakes are ringed with residential housing, thus creating a suburban setting. Residential development can have an effect on the spatial and movement patterns of carnivore species and may differ based on a larger spatiotemporal scale with specific species (Gehrt, 2004). The displacement of apex carnivores and habitat conversion has created outbreaks of mesopredators throughout the world (Prugh *et al.*, 2009) and our study suggests that this phenomenon may also be occurring in northern Wisconsin.

In other areas of North American and Europe, carnivore populations have increased where favorable legislature was introduced (Linnell *et al.*, 2001). Thus, enforcement of current policies regarding habitat along lake riparian areas and carnivore conservation could provide sustainable populations or natural recolonization. In addition, efforts should be made to educate developers and property owners of the ecological importance of preserving a natural vegetation buffer zone adjacent to the lake shore. Furthermore, undeveloped lake shoreland should be protected via purchase, conservation easements, or other means of conservancy.

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