

DIET AND HUNTING BEHAVIOR OF COYOTES IN AGRICULTURAL-FOREST
LANDSCAPES OF NEW YORK STATE

by

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Abstract

Boser, Christina, L. Diet and hunting behavior of coyotes in agricultural-forest landscapes of New York State. Wordprocessed and bound thesis/dissertation, 113 pages, 12 tables, 15 figures, 6 appendices, 2009.

Coyotes (*Canis latrans*) have recently become widespread and abundant throughout New York State, which likely has broad implications for prey such as white-tailed deer (*Odocoileus virginianus*). I studied coyote diet and selection for deer, and the searching behavior and resource selection of coyotes in two study areas, representing low and high deer densities in agricultural/forest matrix. Deer was the dominant prey item in each season and area. Coyote use of fawns was similar between study areas, indicating selection in the area of lower deer density. Evaluation of searching behavior suggested that GPS-collared coyotes did not selectively move through nor alter their search intensity in open areas where fawns may be more vulnerable. Individual resource selection functions indicated coyotes avoided rugged terrain and human encounters by avoiding areas near roads, crossing roads, and open habitats. My results suggest that movement costs and mortality risks influence coyote movement choices more so than prey availability and that coyotes are not selectively hunting for fawns.

Key Words Diet selection, deer density, energetic cost, mortality risk, path tortuosity, percent biomass consumed, resource selection function, selection ratio, step selection, white-tailed deer (*Odocoileus virginianus*).

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Prologue

Following extirpation of wolves (*Canis lupus*) and cougars (*Felis concolor*) from the northeastern United States at turn of the 20th century, ungulate populations such as the white-tailed deer (*Odocoileus virginianus*) were largely unchecked by natural predators for decades (Boitani 1995, McCullough 1997). Between 1920 and 1930 coyotes (*Canis latrans*) entered New York State and found a landscape almost free of competitors (Parker 1995). Except where they co-exist with black bears (*Ursus americanus*), coyotes have become the most abundant, and largest predator throughout much of the state (Gompper 2002). The arrival of coyotes to the ecological communities of New York State is likely to have direct effects on prey populations in the form of predation, and indirect effects as both prey and predator alter resource selection to maximize fitness (Creel et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005). This thesis explores the potential impact of coyote predation on deer populations in central New York State, as well as the role of deer in sustaining coyote numbers.

Quantifying the direct effects of predation on prey populations is a difficult task, requiring knowledge of the functional response (number of prey killed per predator per unit time) and numeric response (number of prey converted to new predators; Holling 1959, Abrams 1994) of predators to prey as well as the proportion of compensatory predation-related of mortality. When predators consume many prey species (as do coyotes), it is more difficult to isolate the direct effects of predation on one prey species (Lyver et al. 2000, Joly and Patterson 2003). Simply identifying the shape of the functional response curve (type I being linear, type II being hyperbolic, and type III being sigmoidal; Holling 1959) may require years of data. Some studies have attempted

to describe the functional responses of a predator for a given prey by estimating kill rates at varying prey densities (Trexler et al. 1988, Patterson et al. 1998, Joly and Patterson 2003), however distinguishing between a type II and type III curve may only be possible if the curvature is extreme (Marshall and Boutin 1999).

Lacking sufficient data to define the shape of a functional response curve, we can make inferences about the importance of a given prey species to a predator and surmise potential effects of predation on prey populations by examining predator diet and selection (Joly and Patterson 2003). Diet composition can inform us of the importance of the prey to the predator; which fundamentally drives functional and numerical responses. Joly and Patterson (2003) argue that the Manly et al. (2002) selection indices can be used to evaluate the form of the functional response. If we assume that prey consumption correlates with kill rates, and we evaluate selection under varying prey densities, then we may infer information about how predation changes under the studied ecological conditions.

Evaluating diet and diet selection as a component of coyote predation research is important because coyote hunting behavior is extremely variable and responsive to changes in resource availability. Previous studies have described coyotes as both general and selective foragers depending on the particular conditions of the study site (Young and Jackson 1951, Bekoff 1977, O'Donoghue et al. 1998, Patterson et al. 1998). Although there may be advantages to selecting medium-size prey during denning (Harrison and Harrison 1984), coyotes have been found to be selective for a variety of prey items such as white-tailed deer fawns, snowshoe hares (*Lepus americanus*), microtine rodents

(*Microtus* spp.), and porcupines (*Erethizon dorsatum*; Hamlin et al. 1984, O'Donoghue et al. 1998, Patterson et al. 1998, Prugh 2005).

Predation may not be proportional to prey availability for many reasons. The predator may exhibit preference for one prey item, and delay switching to an alternative prey item if that preference is strong (Murdock 1969), or if the prey item is extremely profitable (Charnov 1979). Moreover, the predator may have developed a search image and may not immediately switch to alternative prey items when primary prey density begins to decline (Cornell 1976). Apparent competition may result when the abundance of a primary prey increases the number of predators in the area, which causes secondary prey items to be consumed in greater proportion to their availability (Holt 1977, Courchamp et al. 2003). This may have substantial consequences for management of both predator and prey.

Indeed, if predator density increases as a result of high prey abundance as described by the numerical response (Solomon 1949), then other ecological consequences may occur as a consequence of increased predator numbers. Coyotes are mid-sized predators that have relatively low daily energetic requirements. If their diet consists mostly of large prey items such as white-tailed deer, then coyotes must consume fewer individuals to maintain their population size. Thus the importance of deer to coyote diet may influence the numerical response of coyotes. The resulting number of predators on the landscape could affect alternative prey species density and distribution and alter human-coyote interactions.

Given the recent entrance of coyotes to New York State, and the importance of deer populations to the people of New York State, coyote predation on deer and the

resulting impacts of that predation is of primary interest to deer managers, landowners and the public. In my first chapter, I report coyote diet and explore selection for adult deer and fawns in 2 areas differing in overall deer density.

Coyote hunting behavior

The indirect effects of coyote predation may be observed by studying animal movements. Techniques to analyze movement paths are advancing as Global Positioning System (GPS) collars become widely used; enabling greater spatio-temporal resolution in the analyses of animal movements. Common techniques of analyzing large-scale movements include path tortuosity (Haskell 1997, McIntype and Wiens 1999), fractal dimension (Bascompte and Vilá 1997, Mårell et al. 2002, Fritz et al. 2003), and first-passage time (Fauchald and Tveraa 2003). The random walk (Turchin 1998), or components of the random walk (step lengths and turn angles), are used to compare actual movement paths to expected paths (Fortin et al. 2005) to determine how ecological constraints influence movement paths. Moreover, these tools can be used to identify types of movement, be it resting, foraging, or migrating (Frair et al. 2005, Fryxell et al. 2008). Foraging movements are typically characterized by circuitous paths within resource patches (Bell 1991). Path tortuosity should increase within a patch that is selected for by a preferred prey, or where a predator has increased hunting success (Bell 1991). Foraging movements in areas or circumstances known to engender successful predation for a specific prey may indicate searching behavior for a preferred prey (Doerr and Doerr 2004). In this way predator movement is altered by prey behavior, which may in turn engender changes in prey behavior – an indirect effect of predation.

Resource selection evaluates movement at small spatial and temporal scales and can be used to determine how multiple ecological factors combine to constrain movement behavior (Manly et al. 2002). In areas where predators are hunted, they are subject to the same types of movement constraints as prey species; (which have been more commonly studied in movement literature), a need to forage, avoid predators (humans) and maximize energetic efficiency to increase fitness (Roy and Dorrence 1985, Rettie and Messier 2000, Hebblewhite et al. 2005). Resource selection functions (Manly et al. 2002) can be used to evaluate how animals balance these ecological trade-offs. Many studies have evaluated resource selection at the population level; however, recent studies suggest that the large variation typical among individuals may indicate that animals should be considered individually (Forester et al. 2007). Resource availability inevitably differs for each individual, and considering those differences in light of model results may better inform us of how ecological constraints alter population dynamics.

My second chapter explores coyote movement patterns on the scale of nightly hunting paths in summer, where I expected increased tortuosity in areas of higher fawn hunting success, and, further, considers the relative effects of prey availability, mortality risks, and movement costs on seasonal coyote movement decisions over the course of 20-min and 6-hr windows. Both chapters are formatted in a manuscript style following the Journal of Wildlife Management convention.

When analyses of the diet and movement behaviors coalesce, researchers may arrive at a parsimonious and cohesive description of predator/prey interactions. Further, researchers should be cognizant of the influence of factors other than prey density on predation; factors such as predator density, mortality risk, and energetic cost. In my brief

epilogue I provide comments to synthesize my study results and elaborate on the resulting management implications.

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Chapter 1

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RH: Boser • Diet and Selection by Coyotes

Coyote diet and selection for deer in central New York State

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ABSTRACT Within the last few decades, coyotes (*Canis latrans*) have become widespread and abundant throughout the northeastern United States. This likely has broad implications for prey populations and the ecosystem processes dependent upon them. Of particular interest in New York State is the magnitude of predation on white-tailed deer (*Odocoileus virginianus*). I studied coyote diet and selection for white-tailed deer in 2 study areas representing relatively low and high deer densities in the agricultural-forest matrix of New York. Seasonal diets and deer densities were quantified June 2007-August 2008, to determine whether seasonal selection for adult deer and fawns was influenced by differences in deer availability. In coyote scats collected in both study areas, deer dominated coyote diets (46-74% depending upon season), and percentages of deer consumed were similar among study areas. Coyotes selected for fawns 2.2 to 4.8 times more in the low deer density site compared to the high density site when considering differences in deer density. Estimates of deer consumption were similar between sites and

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comparable to previous studies. Thus the magnitude of predation and resulting impact on deer populations is determined by factors other than deer density.

KEY WORDS Diet selection, deer density, percent biomass consumed, selection ratio, white-tailed deer (*Odocoileus virginianus*).

INTRODUCTION

In the 20th century, coyotes have steadily increased their range and density in northeastern North America (Parker 1995). Coyotes became the largest canine predator in many areas of the Northeast after Eastern wolves (*Canis lycaon*) were locally extirpated from the region around 1910 (Parker 1995). Coyotes typically show a variable diet, perhaps facilitating range expansion. Previous studies conducted in Quebec, New Brunswick, and the Adirondack Mountains of New York found that coyotes hunted snowshoe hares (*Lepus americanus*) and white-tailed deer almost exclusively in winter (Messier 1986, Parker and Maxwell 1989, Moore and Parker 1992, Brundige 1993, Poulle et al. 1993). This unusual prey specialization by a generalist predator may be explained by low prey diversity or low densities of alternative prey relative to more southern habitats. Additionally, these studies found a significant correlation between harsh winter conditions and the number of deer killed by coyotes. For example, Parker and Maxwell (1989) observed coyotes switching between primary prey (hares) and secondary prey (deer) when deer vulnerability was high due to deep snow conditions. Farther south, in the southern tier of New York State, coyote foraging behavior is likely different from these studies due to greater prey diversity, the lack of a single abundant mid-sized prey item such as the snowshoe hare, and a lower average snow depth that may make killing large prey more difficult. However, similar to previous studies, these

northeastern coyotes are 10-15% larger on average than western coyotes (Gompper 2006), and thus have the potential to kill large prey items like white-tailed deer.

There is growing demand for information about coyote predation on deer in the rural agricultural-forest matrix of the Northeast where coyote diet and ecology have not been thoroughly studied. Predator diets provide critical information on the importance of different prey items to the predator, and, along with information on prey populations, can also yield insight into predation patterns structuring prey populations. For example, MacCracken and Hanson (1987) reported increased amounts of black-tailed rabbits (*Lepus californicus*) in coyote diets with increasing rabbit abundance. Predation patterns may be influenced by many factors, among them, primary prey density, alternative prey availability, and inter- and intra-specific competition. Of these, primary prey density is most likely to directly affect consumption (Holling 1959, Abrams 1993, Abrams 1994, Fryxell and Lundberg 1994), and is perhaps the easiest to derive empirically.

Diet selectivity ratios quantify how prey consumption deviates from expectations based on prey availability, and allow us to infer the shape of functional response (Joly and Patterson 2003). Selectivity ratios are defined as the ratio between prey consumption and prey availability (or density; Savage 1931, Cock 1978, Manly et al. 2002), with selection occurring when prey is consumed disproportionately to its availability. If prey is consumed as a function of encounter rate, consumption should increase proportionally with increasing prey densities (until kill rate becomes constant when consumption becomes limited by handling times at high prey densities; Holling 1959). It follows that prey consumption by an opportunistic predator like coyotes should largely reflect differences in prey densities (Fryxell and Lundberg 1994).

Herein I report the summer and winter diet of coyotes in central New York State, and evaluate whether consumption of deer is proportional to deer abundance. I studied coyote diet in 2 areas chosen to represent similar habitat types (agricultural-forest matrix), but that captured variation in deer densities typical for New York State.

STUDY AREAS

Coyote populations were monitored in 2 study areas in central New York State, Steuben County and Otsego County from June 2007 to August 2008. Steuben County (42.31° N, -77.27° W.; Figure 1.1.) and Otsego County (43.03° N., -76.13° W; Figure 1.1) are rural landscapes comprised mostly of agriculture (25-31%) and forest (59-71%) land-cover (National Land-Cover Data; NLCD 2001, www.epa.gov/mrlc/nlcd-2001.html; Table 1.1; Figure 1.1). The agricultural land-cover class is used to propagate soybeans (*Glycine max*), corn (*Zea mays*), hay, cattle (*Bos taurus*) and goats (*Capra hircus*). Forested areas are intermixed with agricultural areas and contain mixed hardwood and softwood species. Predominant forest species include beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), white oak (*Quercus alba*) and yellow birch (*Betula alleghaniensis*). Terrain in both areas is gently rolling, with elevation ranging between 250 - 750 m. Mean yearly temperatures (30 year average of -5° C in January and 20° C in July; 1971-2000, NOAA National Weather Service 2008) and snow depth (mean = 5 cm in 2008, C. Boser, unpublished data) are similar between sites. The Steuben County study site is located in the west central portion of the state where agricultural lands are located primary on the high elevation hill tops and valleys remain forested. The Otsego County study site, at roughly the same latitude is located in the southeastern portion of New York State, where agricultural lands tend to

occur in the valleys between forested hills. Potential prey items in both study sites (listed in order of increasing body size) include deer mouse (*Peromyscus maniculatus*), jumping mouse (*Zapus* spp.), red-backed vole (*Myodes* spp.), a variety of small songbirds, Eastern chipmunk (*Tamias striatus*), Northern flying squirrel (*Glaucomys sabrinus*), American red squirrel (*Tamiasciurus hudsonicus*), Eastern grey squirrel (*Sciurus carolinensis*), Eastern cottontail (*Sylvilagus floridanus*), striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), Eastern wild turkey (*Meleagris gallopavo*), river otter (*Lutra canadensis*), woodchuck (*Marmota monax*), raccoon (*Procyon lotor*), American beaver (*Castor canadensis*), white-tailed deer, and domestic livestock (such as cows, goats, pigs; *Sus scrofa scrofa* and chickens; *Gallus domesticus*). American black bears (*Ursus americanus*) are potential predators on fawns in both areas, and harvest records suggest black bear populations are considerably larger in Steuben County than Otsego County (harvest records 34:1; New York State Department of Environmental Conservation 2008). Bowhunter sighting logs and (2000-2007) and coyote harvest levels (pelt sealing data 1990-2000) indicate potentially greater coyote densities in Otsego County versus Steuben County ((New York State Department of Environmental Conservation 2008).

METHODS

Quantifying coyote diet

From June-Aug 2007, Jan-Apr 2008, and May-Aug 2008, coyote scats were collected on deer trails, farm lanes and while back-tracking collared coyotes. Fresh scat samples (considered to be < 2 weeks old based on consistency and cohesiveness), and those most likely to be coyote scats based on a diameter ≥ 2 cm, were used to estimate coyote diet (Gompper et al. 2008). Samples were dried at 50° C for 48 hours, placed in nylon bags

and washed twice in a clothes washing machine using a delicate hot water rinse cycle to remove fecal material (Baker et al. 1993, Prugh 2005, Morey et al. 2007). A single observer separated scat contents by hand, identified hairs macroscopically by texture and thickness, and when necessary, microscopically examined the medulla and scale patterns of hair and compared them with keys and slides from known species (Adjoran and Kolenosky 1969, Brundige 1993). Hair scale impression slides were created for deer hair in summer to differentiate adults from fawns, which can be done reliably until the end of August (Brundige 1993). Impression slides were created by applying a thin layer of clear nail polish to a microscope slide, and pressing the hair into the polish for 60 seconds (Brundige 1993). These slides were compared with scale impressions from known summer adult and fawn deer hair. Microtine rodents were not identified to species, but considered collectively. A blind identification test ($N = 80$ hair samples by C. Boser) indicated 96% accuracy of known hair samples. The relative volume of prey remains in each scat was estimated in increments of 5%, with trace amounts of prey items recorded as 5% (Prugh 2005). Unknown prey species and species that occurred in fewer than 10 scats were included in the “other” category.

For comparison with previous studies conducted in the region, I report prey occurrence as the frequency of scats, percent occurrence, and percent biomass consumed (Kelly 1991). The frequency of scats containing a given prey item was calculated by dividing the number of scats containing the prey item by the total number of scats surveyed. The percent occurrence of a prey item (relative to all other prey items consumed), summed the total number of scats containing prey item i across all scats surveyed (O_i), then divided O_i by the total number of all occurrences of all prey items (

$\sum_{i=1}^n O_i$; e.g., a scat with 4 different prey items yields 4 prey occurrences). The frequency

of scats and percent occurrence methods are known to bias large prey items low because unequal surface:volume ratios make smaller items less digestible than larger items, and consequently a greater percentage of solid material of small-bodied animals are present in the scat. To correct for this, I estimated the percent biomass consumed for each prey item using information on the number of scats produced and differential digestibility of prey items as described in the section to follow.

Percent biomass consumed. – The relationship between the fresh mass of prey items consumed and the number of scats excreted was used to correct for the differential digestibilities of prey. I used data from a feeding trial conducted by Kelly (1991) wherein captive coyotes were fed prey ranging in mass from 0.03 kg to 45 kg. Kelly (1991) reported the relationship between the weight (kg) of prey recovered per collectible scat and corresponding prey weight (kg). Kelly (1991) originally fit a power function to these data, which generally underestimated small prey recoveries and overestimated large prey recoveries. I fit a piecewise linear regression (Toms and Lesperance 2003) to the original data, which I felt better reflected the underlying pattern in the data (Figure 1.2). From these lines I derived a correction factor for a given prey item based on its average body mass (Table 1.2). The live mass of prey items consumed by coyotes in my study were assigned using data from field studies in the area (A. Dechen, deer, unpublished data) or published documents describing Northeastern species when field data were not available (Preston 1966, Kays and Wilson 2002). I reduced the prey mass of birds by 25% before calculation following Johnson and Hanson (1979; Table 1.2). The correction factor for plants and insects was assigned a correction value at the y-intercept because I assumed

that a high proportion of the volume consumed would be excreted. The “other” category was assigned a prey weight of 10 kg because the items largely included raccoons, beaver, otter, and opossum.

The estimated volumetric percent of prey item i in each scat was summed across scats and multiplied by the correction factor (Table 1.2) to find the fresh mass of ingested prey i . The percent biomass of prey item i (B_i) is defined as the average fresh mass of prey item i divided by the total ingested mass of all prey items:

$$B_i = \frac{\sum_{j=1}^{l_i} V_{ij}R_i}{\sum_{i=1}^n \sum_{j=1}^{l_i} V_{ij}R_i} \quad [1]$$

where i is the individual prey item, j is the individual scat, l_i is the number of scats containing prey item i , n is the number of scats, V is the percent volume of prey item i in scat j , and R is the correction factor estimated from the curve fit to the data in Figure 1.2

I averaged B_i for each prey item separately for the winter and summer seasons. However, unequal numbers of scats were collected in early and late summer, thus, in summer 2007 and 2008 I calculated B_i for early and late summer (June 1 - July 14, July 15 - August 28 respectively), and took a weighted average of B_i to represent the entire summer. This was necessary because fawn vulnerability decreases 8-wks post-partition which may prompt a change in predation rates (Carroll and Brown 1977, Huegel et al. 1985, Nelson and Woolf 1987, Long et al. 1998, Vreeland et al. 2004).

Estimating deer density

I used a standardized distance sampling protocol (Underwood et al. 1989) to calculate the density of deer within my study sites. Data was collected in September 2007, March

2008 and August 2008. A total of 7, 2.5-10 km transects were established in each study site on seasonally accessible roads. Random starting locations were identified using Hawth's Tools (Beyer 2004) in ArcMap 9.1 (ESRI, Redlands, California, USA) based on a road layer acquired from the seamless data distribution (USGS 2008; seamless.usgs.gov). Transects were further stratified between forest and agricultural lands using the NLCD database (NLCD 2001; www.epa.gov/mrlc/nlcd-2001.html). To ensure that deer were sighted in both habitat types, i.e. agricultural and forest, and calculate an accurate probability of detection (\hat{p}) for both habitat types, transects were routed to include primarily agricultural or forest habitat. New York State law prohibits spotlighting 500 yards from any structure and thus transect lengths were affected by housing density. I attempted to minimize the effects of road proximity on deer behavior by routing transects onto roads with the lowest traffic volume.

In September 2007 distance sampling was conducted between 1 hour and 3 hours after sunset. The protocol was adjusted in March 2008 and August 2008 to sample between 1 hour prior to sunset and up to 3 hours after sunset. This increased daily sampling duration, decreased overall sampling period and increased the certainty that \hat{p} was constant within that sampling period. Observers drove at 5 mph with a non-driving observer on each side of the vehicle locating deer. After dark, observers used 1 million candlepower spotlights (Vector VEC134) to search for deer. Observers surveyed between 2-4 routes each night, randomizing order of routes and direction of travel. Observations continued in each season until at least 40 deer groups were recorded in forest transects and 60 groups in agricultural transects. Deer were considered to be “grouped” if they appeared to be socially cohesive based on similar behaviors and occurred < 50 m apart.

Observers recorded the habitat where the deer occurred, the number of deer in the group, and age class and sex of each deer when it could be identified. The distance of the group was recorded to the nearest meter using a range finder (Bushnell Yardage Pro[®]), and the angle of the group relative to the road was determined using a protractor.

Observers used a handheld GPS unit (Garmin eTrex Venture[®]) to mark locations ~500 m on each side of a structure where spotlights could not be used. The total distance not surveyed was removed from the total transect length. I also excluded sections of transects where the slope of the landscape was $> 70^\circ$ immediately adjacent to the road. These areas usually occurred when the road had been cut into a steep hillside which was not representative of the landscape such that \hat{p} was artificially lowered by assuming that a larger area was searched.

I assumed that \hat{p} differed between agricultural and forest habitat, but did not differ between seasons and study sites. Further, I expected density to vary between sites, and perhaps by season, but not by habitat type. I fit alternative models for \hat{p} using program DISTANCE 5.0 (Thomas et al. 2006), and compared models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Specifically I used the multiple covariates distance sampling function, truncated the observations at 500 m, and used 7 cutpoints of equal length. I selected the most parsimonious model from a candidate set of half-normal models. Within a study site, seasonal density estimates were within ± 1 deer/km², thus I ultimately stratified density estimates only by study area.

Selection of Deer

I hypothesized that adult deer and fawn consumption by coyotes would be proportional to local deer densities, thus I calculated the ratio between deer consumption and availability for each study site (w) following Savage (1931), Cock (1978), and Manly et al. (2002) as:

$$w = B/\delta \quad [2]$$

where B is the percent of adult deer or fawn biomass consumed (Equation 1), and δ is deer density (deer/km²). I computed this ratio separately for adult and fawn deer in summer 2007 and 2008, and for all deer (not differentiating young of year) during winter 2007-08. Due to the lack of annual replication of diet and deer density estimates, I induced variation in selection ratios using 1000 Monte Carlo simulations in PopTools (version 3.0.6) assuming a normal distribution for percent deer biomass consumed (with a 5% standard deviation) and a lognormal distribution of observed error in deer density. If error bars overlapped between sites within time periods I concluded that coyotes used deer in proportions equal to their availability.

RESULTS

I identified prey items in 523 coyote scats collected in summer 2007, winter 2007-2008 and summer 2008 ($N = 89$ -108 scats per season per area; Table 1.3). Regardless of how prey item importance was calculated, deer was consumed as much or more than any other prey item in both study areas, seasons, and years (Table 1.3). As expected, the percent biomass method inflated the relative importance of deer by 15% (7% SD) on average compared to the frequency of scats and percent occurrence methods (Table 1.3). Fawn biomass consumed was 9-31% greater in early summer than in late summer. From early to late summer the standard deviation of percent biomass of deer consumed decreased

2.7% on average across study sites and years (Table 1.4), indicating a decrease in the relative dominance of major prey items. Moreover, prey diversity increased in late summer, with 2 additional plant species (cherry; *Prunus* spp. and raspberry; *Rubus* spp.) and 1 additional insect (grasshopper) detected (Table 1.3). White-tailed deer comprised between 53-74% of coyote diet, except in late summer when alternative prey items were likely to be most abundant and consumption of deer dropped to 29-50% of coyote diet (Table 1.4).

Deer Density Estimates

The AIC selected detection model estimated $\hat{p} = 0.35$ (3.15 %CV). Deer density was significantly greater in Steuben County than Otsego County (Table 1.5). Recorded sampling effort also indicated a difference in deer density between sites in that observers sampled Otsego County for 13 nights and Steuben County for 7 nights in August 2008, but recorded comparable numbers of deer and deer groups.

Selection of Deer as a Function of Deer Availability

On average, use of adult deer between the 2 study sites differed by only 5-11% in summer and winter despite large differences in deer availability between sites (Figure 1.3). Selection for adult deer (w ; Equation 2) was not different between sites in summer 2007 based on the overlapping error distribution estimated by Monte Carlo simulations, but in winter 2007-08 and summer 2008 selection was nearly 3 times greater in Otsego County compared to the Steuben County (Table 1.6). Moreover, in Otsego County the average use of fawns was 8% greater (Figure 1.4) and selection for fawns was 2.2-4.8 times greater (Table 1.6) in 2008 and 2007, respectively, compared to Steuben County.

Selection was apparently different both summers after evaluating induced variation in selection indices.

DISCUSSION

I had expected coyotes to largely consume adult deer and fawns in proportion to their availability. However, coyotes were selective for deer, with deer consumed roughly equally in two areas that differed markedly in deer density. Importantly, consumption alone may not indicate predation *per se*. Backtracking efforts conducted concurrently to this study in winter identified only three coyote-killed adult deer (out of 39 known fate carcasses visited by coyotes), each of which had pre-existing injuries (R. Holeyvinski, unpublished data). Likewise, a previous study conducted in northwestern New York State indicated that most deer consumed by coyotes in winter were scavenged (Chambers et al. 1974). Thus, it is reasonable to assume that the great majority of adult deer consumed by coyotes in this study was scavenged. Moreover, all livestock consumed during our study also was scavenged based on landowner reports and the concurrent back-tracking study. As a result, carrion (adult white-tailed deer and domestic livestock) comprised upwards of 40% of coyote diets in summer and 74% in winter in both areas. In contrast to predation, scavenging likely requires less energy to search for and subdue prey, but potentially carries higher mortality risks when carcasses occur near roads and farms (Roy and Dorrance 1985, Prugh 2005). Although scavenging provides an important source of food for coyotes, it does not directly influence deer population growth rates. Therefore, despite adult deer being a large and important source of food for coyotes in my study sites, initial evidence indicates that coyotes may not be an important mortality factor for

deer (whether coyotes may influence deer population growth rates is the subject of continued investigation in these areas).

In contrast to adult deer, fawns consumed by coyotes were most likely killed because the concurrent backtracking study reported no evidence of coyotes scavenging on fawns killed either by cars or farm equipment (R. Holevinski, unpublished data). Coyotes are often reported to be the top predator of fawns (Cook et al. 1971, Huegel et al. 1985, Nelson and Woolf 1987, Whittaker and Lindzey 1999, Vreeland 2002), and coyote predation on fawns has been shown to limit growth of deer populations under some conditions (Stout 1982, Kie and White 1985, Ballard et al. 2001). For example, Smith and LeCount (1979) manipulated deer density within enclosures and observed that coyote predation on fawns limited population growth when deer populations were below the habitat's carrying capacity. Although deer carrying capacity is unknown in my study sites, the relatively mild winters of this region (compared to areas such as the Adirondacks), relatively constant deer harvest levels, and low conception rate by fawn deer in both study regions (Department of Environmental Conservation 2008) leads me to assume that these populations are not well below carrying capacity at this time.

Previous studies of eastern coyote predation have concluded that deer vulnerability exerts a greater influence than deer density on deer consumption rates (Messier 1986, O'Donoghue et al. 1998, Patterson and Messier 2000). In a review of 6 years of data collected in the Adirondacks over 3 decades, Brundige (1993) found no correlation between deer consumption and changing deer densities although he did observe increased deer kill rates as a function of more severe winter conditions. Likewise, Parker and Maxwell (1989) found that coyotes switched selection from hares

to deer as deer vulnerability increased due to increased snow depth. Fawn vulnerability varies in summer as well; and predation levels on fawns tend to decrease approximately 60 days post-partition (Carroll and Brown 1977, Huegel et al. 1985, Nelson and Woolf 1987, Long et al. 1998, Vreeland et al. 2004), consistent with observations of fawn consumption in this study.

That coyotes consumed similar amounts of fawns in areas of markedly different deer density may result from high overall deer density, high alternate prey density, predator swamping, or even competition for fawns by black bears. Perhaps deer density in my study sites fell at the far right of the functional response curve wherein kill rates plateau despite increasing prey density (Holling 1959). This plateau could indicate predator satiation or the equilibrium point when prey handling time restricts a predator's ability to increase their kill rate. Alternatively, reduced kill rates with decreasing deer densities may be undetectable because fawns are not the dominant prey item in coyote diet (accounting for between 18-41% of biomass ingested in June and July). Moreover, populations exhibiting concurrently timed parturition may benefit because fawn density is greatest during the short window when fawns are vulnerable to coyote predation, limiting overall mortality (Ims 1990). Indeed, I observed declines in fawn consumption rates from early to late summer, which may reflect either reductions in fawn density or their vulnerability. Finally, while black bear densities in my study sites are unknown, harvest numbers suggest densities in Steuben County are much higher than in Otsego County (34:1; New York State Department of Environmental Conservation 2008). Black bears and coyotes are responsible for the majority of fawn predation in the northeastern United States, while predation by other predators such as bobcats and fishers account for less

than 4% of fawn mortality (Cook et al. 1971, Mathews and Porter 1988, Fuller 1990, Ballard et al. 1999, Pojar and Bowden 2004). If black bears in Steuben County are predating on fawns, this could decrease the relative availability of fawns in that area and equalize fawn encounter rates by coyotes between study sites. It is likely that these different mechanisms each play a role in influencing coyote consumption of deer fawns, but additional study is necessary to evaluate the effects of each.

White-tailed deer appear to be an important factor in sustaining coyote populations in New York State, as this species is consistently the dominant prey item in coyote diets from a variety of eco-regions (this study; Brundige 1993, Chambers et al. 1974). The percentage of coyote scats containing deer was 37-63% between January and August, with the greatest percentage of scats containing deer occurring in winter when alternative prey items were considered most scarce. A study conducted in the northern Adirondack region of New York State found that deer occurred in 46-95% of scats year-round, with winter having the greatest number of scats containing deer (Brundige 1993). These higher numbers may reflect a lower diversity of prey, or lack of domestic livestock carrion in the Adirondacks in comparison to the southern tier of New York (Brundige 1993). In my study sites, livestock carrion represented a large portion of coyote diet in some seasons. Further north, Patterson et al. (1998) studied prey switching between hare and deer in 4 study areas in Quebec and observed that 35-63% of annual coyote diet was deer (consistent with my values of 46-74%). In those study areas, hares accounted for between 8-45% of diet, with hare consumption inversely related to deer consumption. In my study areas, livestock carcasses and microtine rodents ranked second and third in importance, yet at their peak comprised only 27% and 15% of coyote diet. The lack of a

single abundant mid-sized predator in the southern tier of New York State, such as the hare, or, alternatively, readily available carrion may prevent coyotes from prey-switching as they do in higher latitudes.

Assuming predation mortality is at least partially additive, then increases in predator density without reductions in primary prey consumption (as I observed here), could have important effects on prey populations. Telemetry data of coyotes trapped for a concurrent study (C. Boser, unpublished data) and bow-hunter's sighting logs (New York State Department of Environmental Conservation 2008) indicate coyote densities to be approximately 2 times greater in Otsego County than Steuben County. Higher coyote densities may be explained by delayed juvenile dispersal instigated by high prey availability (Person and Hirth 1991, Harrison 1992). Bekoff and Wells (1980) found a correlation between delayed dispersal and a high proportion (75%) of carrion in the winter diet of coyotes. Both Otsego and Steuben County coyotes had high amounts of carrion in their diet (34-43%, in summer and 69-78% in winter), suggesting a large available food subsidy in both areas. This food subsidy may maintain high coyote numbers despite fluctuating prey populations, although the discrepancy in consumption rates between study areas does not appear to be large enough to explain the variation in coyote density that I observed. Alternatively, differences in coyote harvest levels may influence density-dependent responses in population vital rates (Knowlton et al. 1999). In response to higher harvest levels in Otsego County, coyotes may increase fecundity or recruitment rates (Knowlton et al. 1999), and the carrion subsidy may allow offspring to remain in their natal range resulting in higher coyote densities. I postulate that if coyotes have an effect on deer population growth rates, that effect would be greater in Otsego

County than in Steuben County given that deer consumption was similar between sites but deer density was lower and coyote density higher in Otsego County.

This study found constant fawn consumption across 2 areas that vary in deer density. This may be explained in part by variation in predator densities, or abundant alternative prey and scavenging opportunity. Alternatively, coyotes in Otsego County may be modifying movement behaviors to increase their encounters with fawns. In the second chapter of this thesis I evaluate coyote paths to determine if movement decisions tend to increase encounter rates with fawns, or if other ecological constraints impact movement choices more so than prey availability.

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FIGURE CAPTIONS

Figure 1.1 Focal study areas in Steuben and Otsego Counties, New York State, USA.

Figure 1.2 Relationship between the amount of prey eaten per collectible scat (kg) and prey weight (kg) as determined by feeding trials using captive coyotes (adapted from Kelly 1991). The Kelly (1991) power function is shown along with the break-line regression used for this study.

Figure 1.3 Average percent biomass of adult deer consumed relative to average deer density (km^2) in summer (2007 and 2008) and winter 2007-08 in Steuben and Otsego Counties, New York State, USA. Vertical error bars reflect differences in consumption values between summer 2007 and 2008, whereas horizontal error bars reflect the 95% CI around deer density data.

Figure 1.4 Average percent fawn biomass consumed relative to average deer density (km^2) in summer (2007 and 2008) in Steuben and Otsego Counties, New York State, USA. Vertical error bars reflect differences in consumption values in 2007 and 2008, whereas horizontal error bars reflect 95% CI around deer density data.

Table 1.1 Percent land-cover in the Steuben (867 km²) and Otsego County (832 km²) study sites, New York State, USA acquired from NLCD 2001 (www.epa.gov/mrlc/nlcd-2001.html).

Habitat	Steuben County	Otsego County
Forest	56.9	71.22
Row crops	17.12	18.56
Pasture	19.76	7.95
Wetland	1.01	0.53
Residential areas	1.6	1.05
Other	3.61	0.69

Table 1.2 Fresh mass based on equation 1 (see methods) and correction factor of prey items in coyote scat based on regression shown in Figure 1.2.

Prey item	Mass (kg)	Correction
Domestic livestock	65 ^a	0.496
Adult white-tailed deer	47.2 ^b	0.434
Deer fawn (early summer)	8.5 ^c	0.299
Deer fawn (late summer)	19.5 ^c	0.337
Other	10 ^d	0.304
Wild turkey	7 ^d	0.293
Woodchuck	5.5 ^d	0.288
Grey Squirrel	3.5 ^d	0.141
Cat	3 ^d	0.279
Eastern cottontail	1.2 ^d	0.186
Small bird	0.3 ^d	0.138
Rodents	0.03 ^d	0.124
Insect	-	0.123
Plant	-	0.123

^a Preston 1966.

^b A. Dechen, unpublished data.

^c Robbins and Moen 1975.

^d Kays and Wilson 200

Table 1.3 Percent of each prey item found in coyote scat collected summer 2007, winter 2007-08 and summer 2008 in Steuben and Otsego Counties, New York State, USA. The results from 3 methods, frequency of scats, percent occurrence and percent biomass (see methods for details) are given.

Site	Period	N	Method	Livestock	Adult					Small						
					deer	Fawn	Turkey	Woodchuck	Squirrel	Cat	Rabbit	bird	Rodent	Insect	Plant	Other
Steuben	Sum. 2007	89	Frequency	1	27	11	4	11	8	-	4	9	34	7	10	1
			Occurrence	1	21	9	4	9	6	-	4	7	26	5	8	1
			Biomass	1	42	15	4	13	3	-	3	2	11	2	2	2
	Win. 2008	108	Frequency	5	51	-	-	3	2	1	17	-	38	-	4	4
			Occurrence	4	41	-	-	2	2	1	14	-	31	-	3	3
			Biomass	6	63	-	-	2	1	1	10	-	13	-	1	3
	Sum. 2008	65	Frequency	12	11	26	-	5	12	2	14	5	14	9	12	3
			Occurrence	10	9	21	-	4	10	1	11	4	11	7	10	2
			Biomass	15	19	27	-	5	5	2	9	2	5	3	5	3
Otsego	Sum. 2007	94	Frequency	10	21	31	2	3	7	4	12	9	22	1	6	2
			Occurrence	7	16	24	2	2	6	3	9	7	17	1	5	2
			Biomass	12	28	32	1	2	3	3	7	2	7	0	1	2
	Win. 2008	70	Frequency	3	63	-	-	1	-	-	17	-	23	-	9	1
			Occurrence	2	54	-	-	1	-	-	15	-	20	-	7	1
			Biomass	4	74	-	1	1	-	-	8	-	6	-	2	4
	Sum. 2008	101	Frequency	14	18	30	-	6	6	2	11	12	14	5	11	8
			Occurrence	10	13	22	-	4	4	1	8	9	10	4	8	6
			Biomass	19	23	26	-	7	2	2	5	3	4	1	3	5

Table 1.4 Percent biomass consumed of adult deer, fawns, mice, livestock and total deer in winter (Jan. 1 - Apr. 17) and early (Jun. 1-Jul. 14) and late (Jul. 15-Aug. 28) summer in Steuben and Otsego Counties, New York State, USA.

Site	Time period	N	Adult deer	Fawn	Rodent	Livestock
Steuben	Early summer 2007	27	47.22	18.95	5.78	0.00
	Late summer 2007	58	38.03	11.95	15.85	2.49
	Winter 2007-2008	47	63.90	-	12.70	6.45
	Early summer 2008	34	11.03	41.85	4.92	3.02
	Late summer 2008	31	27.80	10.79	5.40	27.07
Otsego	Early summer 2007	70	31.04	36.70	5.51	10.03
	Late summer 2007	24	18.69	10.00	15.43	17.89
	Winter 2007-2008	27	73.96	-	6.36	4.32
	Early summer 2008	65	25.25	32.80	5.35	10.90
	Late summer 2008	36	20.35	19.75	1.70	27.00

Table 1.5 Deer densities estimated using distance-sampling in Steuben and Otsego Counties, New York State, USA (see methods for sampling details).

Site	Observations	δ (km ²)	%CV	Lower 95% CI	Upper 95% CI
Steuben	400	5.56	21.28	3.58	8.63
Otsego	301	2.49	13.86	1.88	3.31

Table 1.6 Selection ratios for percent deer biomass consumed versus deer density in summers and winter 2007-2008 in Steuben and Otsego Counties, New York, USA. Errors were calculated by inducing variation in deer consumed ($\pm 5\%$) and deer density estimates (95% CI).

Prey item	Site	Time period	Selection ratio	Lower error	Upper error
Adult deer	Steuben	Summer 2007	7.66	4.99	11.27
		Winter 2007-2008*	11.70	7.57	16.95
		Summer 2008*	3.59	2.26	5.40
	Otsego	Summer 2007	11.47	8.62	14.63
		Winter 2007-2008*	30.15	22.96	38.87
		Summer 2008*	9.40	6.99	12.40
Fawn	Steuben	Summer 2007*	2.71	1.76	4.04
		Summer 2008*	5.13	3.32	7.57
	Otsego	Summer 2007*	13.04	9.97	16.89
		Summer 2008*	11.75	8.81	15.49

* Induced variation is different between study areas within seasons.

Figure 1.1

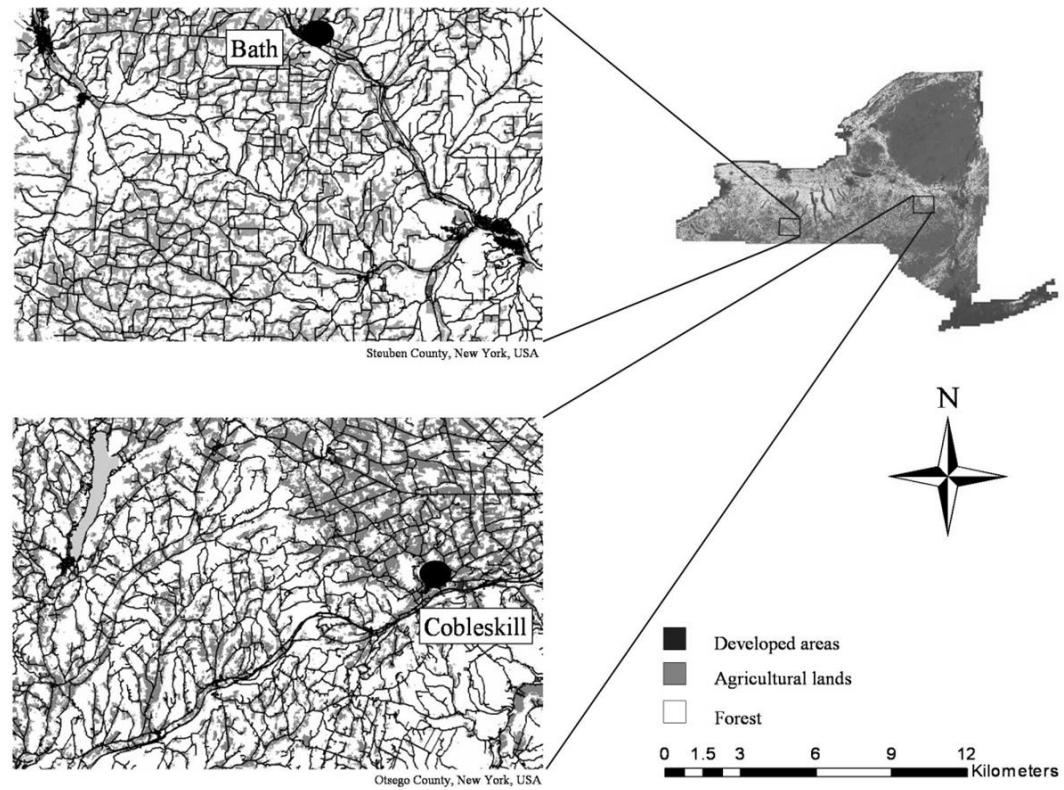


Figure 1.2

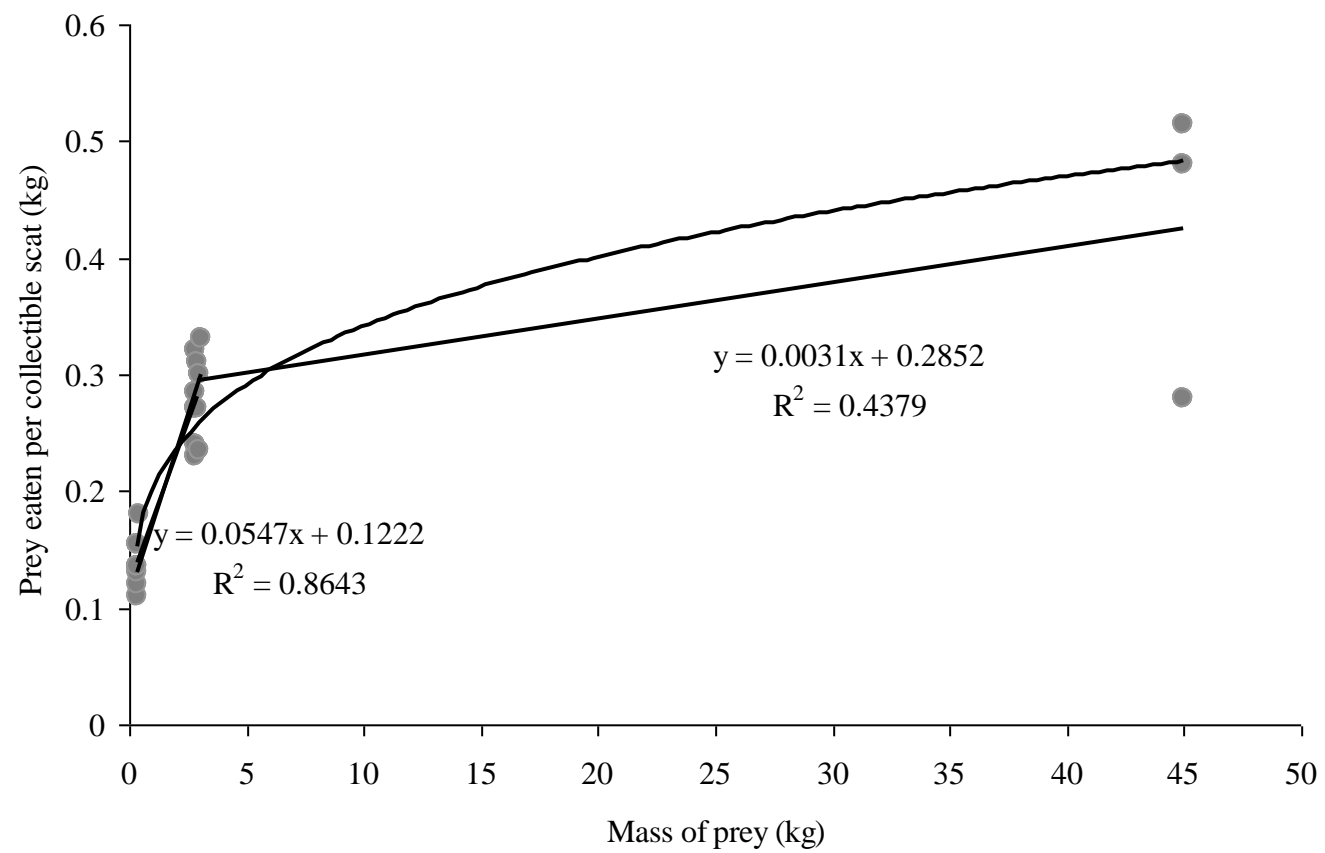


Figure 1.3

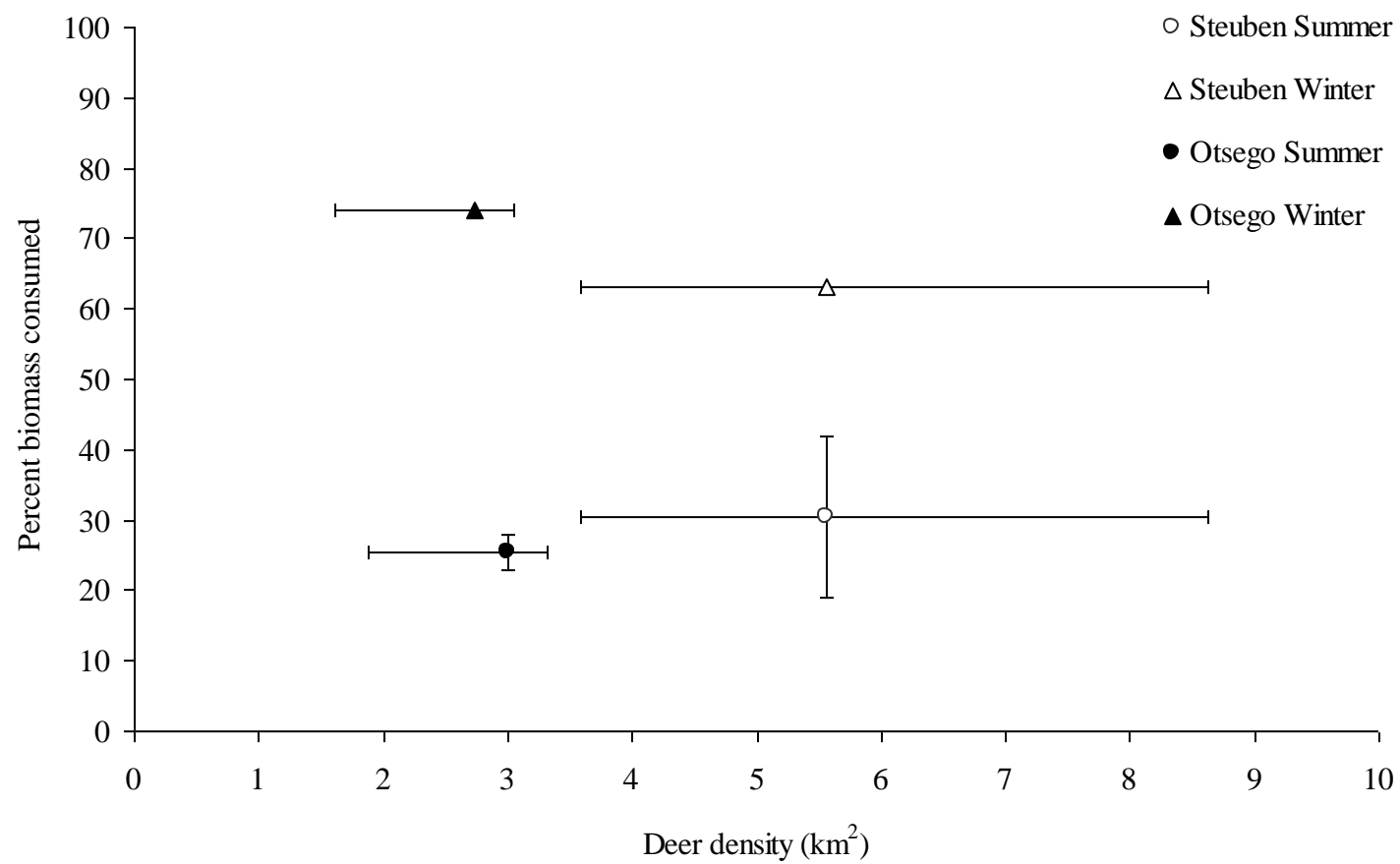
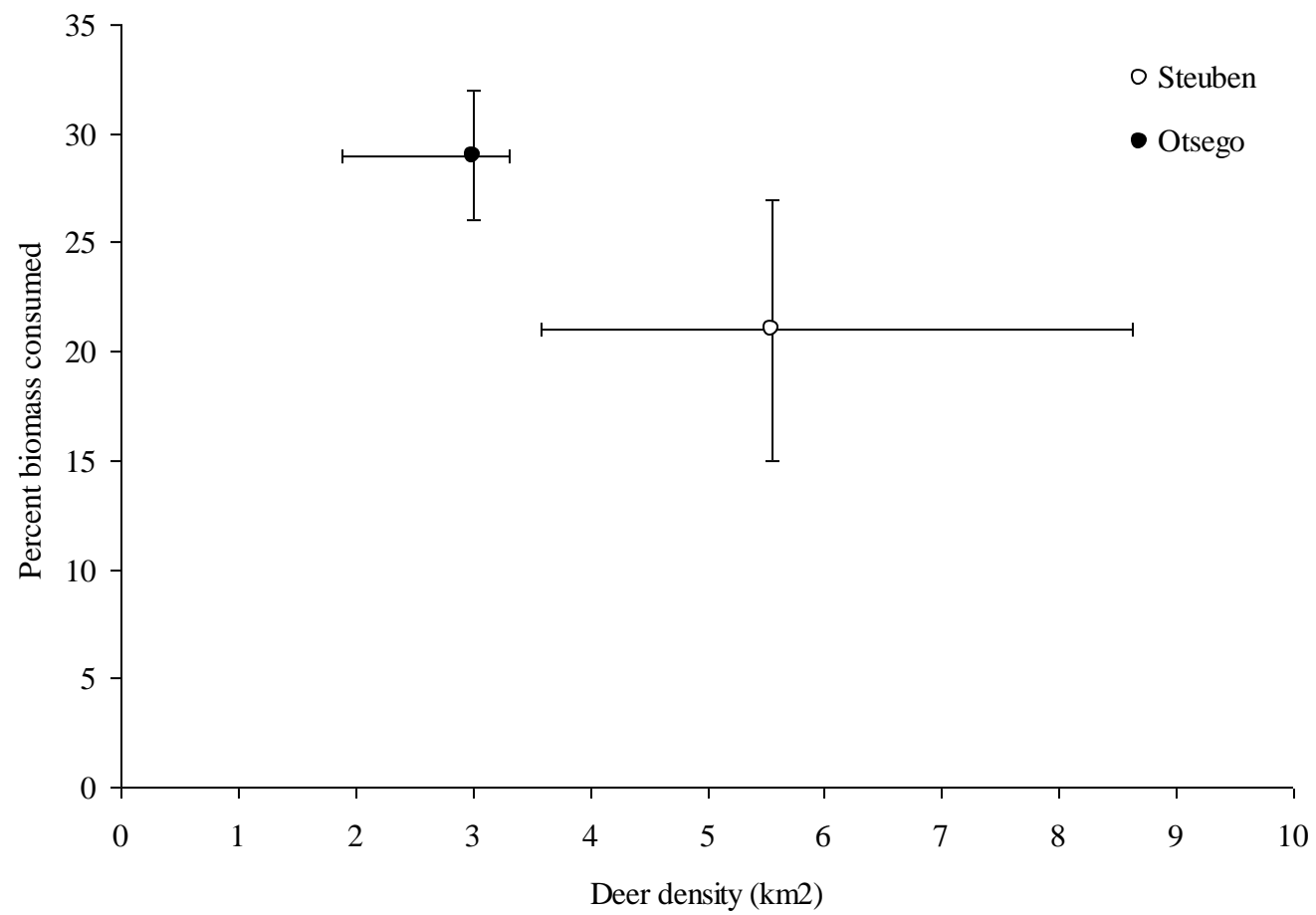


Figure 1.4



Chapter 2

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RH: Boser • Searching Behavior and Resource Selection by Coyotes

Searching behavior and resource selection by coyotes in central New York State

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ABSTRACT Predator movements may be driven primarily by the distribution of their preferred prey, but may be mediated to varying degrees by movement costs and mortality risks. I examined how such trade-offs affected the movement decisions of a generalist predator, the coyote (*Canis latrans*), in 2 areas that varied in prey abundance and coyote mortality rates. Specifically, I evaluated how habitat types, terrain, and roads influenced coyote path tortuosity and local movement decisions using coyote location data collected by global positioning system (GPS) collars. Although coyotes are known to kill fawns disproportionately in open habitats in this region, they did not selectively move through open habitats nor alter their search intensity in those habitats. Individual step selection functions indicated that coyotes moved over less rugged terrain, avoided being near or crossing roads, and also avoided open habitats (agricultural lands). My results indicate that constraints such as movement costs and mortality risks underlie coyote distribution and movement choices in this region more so than prey availability. Impeded only by

mortality risk and energetic costs, coyote populations may continue to increase in this region.

KEY WORDS Energetic cost, mortality risk, resource selection function, path tortuosity, step selection, white-tailed deer (*Odocoileus virginianus*).

INTRODUCTION

Animal movements and resource selection are driven by fundamental fitness requirements such as securing food, avoiding mortality sources, and minimizing energetic costs. Each fitness requirement imposes a constraint on individuals, and the trade-offs animals make relative to these constraints informs us of their relative importance (Lima 1998, Rettie and Messier 2000; Fortin et al. 2005). Trade-offs should be apparent in movement patterns, specifically in foraging movements as they are influenced by spatial variation in ecological constraints (Mills and Knowlton 1991, Jepsen et al. 2002, Hebblewhite et al. 2005, Bergman et al. 2006, Ciarniello et al. 2007). Ranking the influence of those constraints on animal movements and resource selection can reveal which ecological factors substantially alter individual decisions, and by extension, the population at large (Johnson 1980, Hebblewhite et al. 2005).

Habitat selection should reflect those influences that are most limiting to individuals (Rettie and Messier 2000), thus individuals in populations limited by food should select for high forage areas, whereas those sustaining high harvest pressure should minimize risk. Predators of large ungulates primarily select for areas of high prey abundance or vulnerability (Hopcraft et al. 2005, Hebblewhite et al. 2005, Hopcraft et al. 2005, Krebs et al. 2007). For example, wolves (*Canis lupus*) may select for edge habitat where elk (*Cervus canadensis*) are most vulnerable to predation (Bergman et al. 2006).

Conversely, for grizzly bears (*Ursus americanus*), a large generalist predator, harvest risk was more influential than prey abundance in predicting bear density outside of protected park areas (Ciarniello et al. 2007).

Patch contrast, defined as the difference between forage quality in resource patches versus matrix, and patch aggregation, is expected to relate to the intensity of search effort for a prey item (Stephens and Krebs 1986, Kotliar and Wiens 1990, Bell 1991). In an experimental study, de Knecht et al. (2007) found that movements of goats became slower and more tortuous when patch density increased, thus the goats increased search effort in areas of high-reward. When food patch quality is greater than that of the matrix, foragers should adopt tortuous movement paths so as to effectively search and exploit patch resources (Bell 1991, Haskell 1997, Vernes and Haydon 2001, Nolet 2002, de Knecht et al. 2007). Predators may perceive high patch quality if preferred prey is abundant within that habitat or if predators experience greater hunting success in that habitat type (Hopcraft et al. 2005). Conversely, predators foraging opportunistically for diverse prey items distributed among multiple habitat types may perceive low patch contrast and search for prey less intensively within discrete resource patches.

Coyotes are mid-sized predators, whose behavior, diet and habitat use is often considered to be adaptable and contingent upon resource availability (Young and Jackson 1951, Bekoff 1977, Parker 1995). They may hunt either selectively or opportunistically depending on available prey diversity, vulnerability, or abundance (Windberg and Mitchell 1990, Brundige 1993, O'Donoghue et al. 1998, Prugh 2005). For instance, coyotes specialize on white-tailed deer (*Odocoileus virginianus*) and snowshoe hare (*Lepus americanus*) in the northern regions of the eastern United States and Canada

where harsh winters make these prey vulnerable to predation (Parker and Maxwell 1989, Patterson et al. 1998, Patterson and Messier 2000) yet show greater diet breadth in more southerly, and prey rich regions (e.g., Morey et al. 2007, Schrecengost et al. 2008).

Coyote habitat use has been described as non-selective (Crete et al. 2001), selective for habitats that provide food and cover (Litvaitis and Shaw 1980, Kamler et al. 2005), or selective for habitats that reduce harvest risk independent of food abundance (Roy and Dorrance 1985, Atwood et al. 2004). However, many of these studies did not report estimates of prey abundance or the causes or magnitude of coyote mortality, and thus conclusions about general patterns underlying coyote resource use remain unclear.

Where coyotes and deer coexist, coyotes are nearly always the dominant predator of fawns, killing 8-58% of fawns produced (Hamlin et al. 1984, Ballard et al. 1999, Whittaker and Lindzey 1999, Vreeland 2002). In contrast to other prey items (Metzgar 1967), newborn fawns have little odor and remain immobile unless they are accompanied by dams (Faatz 1976, Halls 1984). Hunting for cryptic and immobile fawns should engender a more intensive search process than that associated with scavenging or flushing prey. Fawn resting areas typically have dense vegetation (Bryan 1980, Huegel et al. 1985, Kunkel and Mech 1994) in which neonate fawns hide to avoid predation (Carroll and Brown 1977, Nelson and Woolf 1987). Coyotes tend to rely on visual cues to find fawns (Wells and Lehner 1978), and may need to search for fawns in a systematic manner because they must be in close proximity to a fawn before detecting it. Where coyotes selectively hunt for fawns, I would expect their hunting paths to be tortuous in habitats where they are likely to encounter fawns (indicating an intensive search effort; Doerr and Doerr 2004). Previous studies indicate that white-tailed deer fawns use open

and forest land-cover types largely in equal proportion to their availability (Vreeland 2002 unpublished data analyzed by C. Boser with permission, Burroughs et al. 2006), however coyotes may have greater success finding and killing fawns in open habitats (Gese et al. 1996, Richer et al. 2002). As a result, I would expect that coyotes would select for open habitats where fawns may be more vulnerable to predation, and further, that coyote movements would indicate greater search intensity in open habitats. Additionally, fawn survival may be higher in more complex habitats; those containing more edges where fawns may be less detectable or accessible (Rahm et al. 2007). Thus, I would expect coyotes to intensively search open areas but to reduce their search intensity in more fragmented landscapes containing high amounts of edge habitat. Previous work in my study areas indicated fawn consumption peaked in June and waned thereafter (C. Boser, Chapter 1, 2009); thus I expected that coyote selection for open habitats would decrease as summer progressed.

My first objective was to evaluate coyote movement decisions with respect to fawn availability and vulnerability. I calculated a metric of search intensity integrated over nightly hunting paths and related that to the amount of open and edge habitat encountered by coyotes. I also evaluated variation in coyote selection of open habitats among individuals and across the summer months.

Should prey not be limiting to coyotes in these areas, then their movement decisions may not relate habitat types (a surrogate measure of prey availability) as much as to variables representing mortality risk or energetic cost of movement. Thus, my second objective was to determine the relative influence of habitat type, perceived mortality risk, and energetic cost of movement on coyote movement decisions.

STUDY AREAS

Coyote populations were monitored in 2 study areas in central New York State, Steuben County (42.31° N, 77.27° W) and Otsego County (43.03° N., 76.13° W) in 2 summers (June-August 2007 and 2008) and the intervening winter. Both sites represent rural landscapes comprised mostly of upland deciduous forest (59-71%) and agricultural land (25- 31%) based on National Land-Cover Data (NLCD, 2001, www.epa.gov/mrlc/nlcd-2001.html; Table 2.1). Predominant forest species include beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*). Agricultural lands are comprised of row crops (soybeans; *Glycine* spp., corn; *Zea mays*, and hay) and pasture (cattle; *Bos taurus* and goat; *Capra hircus*). Terrain in both areas is gently rolling, with elevation ranging between 250-750 m. Mean yearly temperatures are similar between sites with a 30-year average of -5° C in January and 20° C in July (1971-2000, NOAA National Weather Service 2008). The Steuben County study site is located in the west central portion of the state while the Otsego County study site is located at roughly the same latitude and located in the southeastern portion of New York State. Dominant prey items occurring in both study sites (listed in order of percent occurrence in summer diet) include white-tailed deer, deer mouse (*Peromyscus maniculatus*), jumping mouse (*Zapus* spp.), red-backed vole (*Myodes* spp.), Eastern chipmunk (*Tamias striatus*), Eastern grey squirrel (*Sciurus carolinensis*), Eastern cottontail (*Sylvilagus floridanus*), and domestic livestock (such as cows, goats, pigs; *Sus scrofa scrofa*, and chickens; *Gallus domesticus*; C. Boser, Chapter 1, 2009). American black bears (*Ursus americanus*) are potential competitors for fawns in both areas; but harvest records indicate black bears populations are considerably

larger in Steuben County than Otsego County (harvest records 34:1 respectively; New York State Department of Environmental Conservation 2008). Deer density was 5.56 deer/km² (21.28 %CV) and 2.49 deer/km² (13.86 %CV; C. Boser, Chapter 1, 2009) in the Steuben and Otsego study sites, respectively. Bow hunter's sighting logs and pelt sealing records (New York Department of Environmental Conservation 2008) indicated that that coyote density may be at least 2 times greater in Otsego County than Steuben County.

METHODS

Coyotes were trapped in both areas using offset laminated leghold traps and non-locking cable restraint devices, and handled following an approved Institutional Animal Care and Use Committee protocol (SUNY ESF #2007-07) and collection permit by New York State (NYS-DEC #1112). Captured animals were restrained with a catchpole and sometimes immobilized with Telazol (10mg/kg- Ballard et al. 1991; Fort Dodge, Iowa, USA). Coyotes were fitted with GPS (Lotek GPS4400s; Lotek Wireless, Ontario, Canada) collars prior to their release. Collars were programmed to record location fixes in 20-min and 6-hr intervals. Based on 90 collar trials in 5 dominant habitat types, the upper 95% CI of collar positional error was < 18 m in forest and shrub habitat, and < 6 m in open habitat. Fix rate was >97% in all habitat types. These errors were smaller than the 30 m resolution of habitat data, and thus no correction for bias or accuracy were conducted. Crude survival estimates using data on GPS collared coyotes and an additional sample of VHF collared animals (N = 22, 11 in Otsego and Steuben County, respectively) indicate higher mortality rates in Otsego County (50%) than in Steuben County (27%), with all mortalities being human-caused (C. Boser, unpublished data).

Search intensity and selection of open areas

I assumed that when coyotes were moving, they were hunting and thus evaluated 1) the tortuosity of nightly paths when coyotes were most active, and 2) selection for open habitat. A related backtracking study indicated that 28 of 33 coyote-killed fawns were killed in open or shrub habitat, largely consisting of agricultural lands (R. Holevinski, SUNY ESF, personal communication). I tested for intensive search effort in open habitats by evaluating the tortuosity (or fractal dimension) of nightly hunting paths using 20-min fix intervals. I first determined if nightly paths had a higher fractal dimension than expected at random. Next, I tested whether individual hunting paths were more tortuous (higher fractal dimension) in either the study area having higher overall deer density (Steuben County) or the area where coyotes selectively foraged for fawns (Otsego County; C Boser, Chapter 1, 2009). Finally, I tested whether the tortuosity of nightly hunting paths was a function of the percentage of time (based on 20-min GPS fixes) coyotes spent 1) in open habitat, or 2) within edges between forest and open habitat. A positive relationship between path tortuosity and the amount of open area encountered during the night would be consistent with my expectation that coyotes intensively searched for fawns where their hunting success was greater. I also evaluated whether coyotes selected for open habitats, and whether their selection of open habitats declined throughout the summer. To do so I calculated a resource selection function (RSF; Manly et al. 2002) using 6-hr fix interval data and fit the model as described in detail later.

Path tortuosity.- Twenty-minute locations were recorded for 3 individuals for 14 nights (May 27-June 24, 2008) in Otsego County and for 4 individuals for 7 nights (June 10-23, 2008) in Steuben County. I identified nightly hunting paths as locations between

1600 hrs and 800 hrs because coyote movement rates dropped a few hours after sunrise, and began to increase a few hours before sunset mid-day (Figure 2.1). Based on positional error in collar locations, consecutive locations occurring < 18 m apart in forest habitat and < 6 m apart in open habitat were considered to reflect resting bouts, and were combined so as not to bias the fractal dimension metrics (Bascompte and Vila 1997). I used program VFracal (Nams 2006; Version 5.18) to calculate the fractal dimension (fractal D) of each nightly path, which scales between 1 (linear) and 2 (plane-filling).

Correlated random walk.-To test whether coyote paths were more tortuous than expected at random, I created a correlated random walk (Turchin 1998) for comparison to coyote paths using HawthTools (H. Beyer 2004) and ArcMap 9.1 (ESRI, Redlands, California, USA), and restricted the correlated random walk by the boundaries of each coyote's home range (100% minimum convex polygon). Potential step lengths (linear distance between consecutive 20-min locations) and turn angles (change in move direction between 2 consecutive lengths) were independently drawn from distributions derived from 20-min coyote locations (Figure 2.2). To minimize circularity in comparisons of actual coyote paths to simulated paths, the step length and turn angle distributions used to create random paths for each individual were derived from data from every animal ($N = 7$) except the focal animal under consideration (Fortin et al. 2005). Step lengths were binned every 50 m until 2000 m; and turn angles were binned every 15° (between -180° and 180°). Starting from 100 random locations within each animal's home range, successive steps were created by randomly drawing from the step length and turn angle distributions. After a burn-in period of 25 steps, the random walk locations were recorded. When the selected step and turn angle would position the location across

the home range boundary, that step was rejected and a new step length and turn angle was chosen until the predicted location fell inside the home range. I averaged the fractal D of each of the 100 simulated nightly paths for 7 or 14 days as appropriate (Nams 2006; Version 5.0.11). The mean and 95% CI of fractal D values for the 100 random paths were compared to the empirical mean observed across individual animals ($N = 7-14$).

Correlating tortuosity with percentage of locations recorded in open and edge habitat.- To determine if coyotes increased path tortuosity in open habitats I compared the fractal D of coyote paths to the amount of foraging time spent in open areas during that night of foraging (using the number of GPS locations in open habitat as a surrogate for time). To define the GPS fixes located in “open” and “other” habitat I used NLCD 2001 data at a resolution of 30-m grid cell size. I merged all open and shrub areas into an “open” class and each of the other cover types into “other” in ArcMap 9.1 (Table 2.2). For each path I plotted fractal D against the percent of locations in open habitat and fit a linear regression to each individual.

I defined how much coyotes used edge habitat in a nightly foraging path by buffering the boundaries between open and forest habitat by 30 m, a buffer which should include most vegetation differences linked to increased fawn survival (Rochelle et al. 1999), and determined the percentage of GPS fixes that fell within that area. As was done for open habitat, the percentage of locations recorded in edge habitat throughout a nightly hunting path was plotted against the fractal D of that path.

Selection for open habitat.- To determine if coyotes selected for open habitat on the scale of 6-hr movements, I created a step selection function (Fortin et al. 2005) as described in detail in the next section. In contrast to the more comprehensive selection

model, here I specifically examined whether selection for open habitat changed as fawn vulnerability decreased from early to late summer. Data on individual coyotes was grouped into 7, 4-week intervals beginning May 1, May 15, June 1, June 15, July 1, July, 15, and August 1 to determine if selection of open habitat declined from early to late summer.

Trade-offs among encountering prey, avoiding mortality and minimizing energy expenditure

Resource selection functions (RSF; Manly et al. 2002) can be used to effectively observe the relative and interactive effects of multiple variables, operating on different scales or in different currencies. For each individual, I fit an RSF to coyote locations collected at 6-hr intervals in winter 2008 and summer 2007-2008. As done previously with 20-min data, I created a step length and turn angle distributions based on the 6-hr locations (Figure 2.3), and used random draws from these distributions to identify potential steps available to coyotes conditional on a starting location (Fortin et al. 2005). Step lengths were binned at 100 m intervals to 2000 m, then every 500 m to 6000 m. Excluding the data collected from a focal individual, 5 conditional points (potential steps) were created for each location for that individual (Fortin et al. 2005; Figure 2.4).

Covariates measured at each used and available location were compared in Program R (2008) using conditional logistic regression (Project survival; T. Therneau version 2.34-1, 2008). The function estimates coefficients for the RSF of Manly et al. (2002):

$$\hat{w}(\mathbf{x}) = \exp (\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_n x_n) \quad [1]$$

where β_1 to β_n are the estimated coefficients for the variables x_1 to x_n respectively and $\hat{w}(\mathbf{x})$ is proportional to the probability of use. Steps with a higher \hat{w} value have higher odds of being chosen by coyotes. Models were created for each individual, and step length was included as a covariate to account for autocorrelation between steps (Forester et al. 2007).

Covariates.- The NLCD layer was reclassified to merge residential locations with open cover instead of with forest as in the previous logistic regression targeting selection for fawns (Table 2.2). Merging residential areas with open cover was necessary because a small portion of the landscape was classified as residential areas (2-4.8%), and models that did not merge residential classes failed to compute due to singularities in the conditional logistic regression.

I assumed that coyotes were more likely to encounter humans in open habitat, when crossing roads, or when near roads in open habitat, owing to their greater visibility. To calculate the distance to roads and the number of roads crossed in a step, I used a road layer acquired from seamless data distribution (USGS 2008; seamless.usgs.gov). I included only all-season roads because seasonal roads are less frequently used by humans, and thus unlikely to facilitate encounters with humans or provoke changes in coyote movement (Thurber et al. 1994). I assumed risk from roads to be negligible beyond a 500 m distance and assigned proximities > 500 m and all cells in forest habitat (which provide screening cover) a value of 500 m, hypothetically corresponding to low risk. The number of road crossings along observed and potential coyote steps were counted using HawthTools (H. Beyer 2004). There is a cost to moving over variable terrain, so I calculated a terrain ruggedness index for each potential step, defined as the

coefficient of variation in elevation. Terrain ruggedness was expressed on a per 100 m of step length basis to increase the biological relevance of the movement cost. I assumed the energetic cost of movement was similar in winter and summer due to little average snow accumulation in winter (mean snow depth = 5 cm; January 5-March 26; C. Boser, unpublished data).

Model selection

I created 11 competing models to analyze coyote resource selection in winter (January-April) and summer (May-August; Table 2.3). I analyzed all plausible combinations of the 4 covariates (habitat type, adjusted road proximity, number of road crossings, and terrain ruggedness) and did not consider models that combined land-cover and distance to roads because the 2 were correlated. I used Akaike's information criterion (AIC_c) with a small-sample size correction (Burnham and Anderson 1998) to rank candidate models for each individual. The odds ratios for each of the estimated coefficients in the best model were plotted for each coyote to determine trends in selection across individuals for each landscape by season and between study sites.

RESULTS

Search intensity and selection of open areas

Nightly hunting paths of coyotes were more tortuous than expected at random (Table 2.4) however, the fractal D of coyote paths averaged 1.12 ± 0.250 indicating movements that were closer to the straight line end of the fractal D spectrum. Search intensity of nightly forays did not correlate to the percent of time spent in open or edge habitat ($R^2 < 0.45$, $p > 0.05$, Figures 2.5 and 2.6). The largest and most variable fractal D values corresponded to 2 male coyotes in Steuben County, each of which killed at least 5 fawns during the

time this GPS data was being recorded (R. Holevinski, unpublished data). However, the paths of even these individuals did not vary across the percent of open habitat along a given path (Figure 2.5). In fact, there tended to be a negative relationship between the percent of time spent in open cover and fractal D, although the average slope was low (-0.07, 0.07 SD).

Also contrary to my expectations, coyotes became more selective for open habitat as summer progressed, tending to use open habitats in proportion to their occurrence or even avoid open habitat in May (Figures 2.7 and 2.8). This trend was especially strong in Otsego County. In both sites, I also observed greater variation in selection later in summer.

Trade-offs along a movement path

In summer, the top three models across all individuals included the number of road crossings and terrain ruggedness, and the top 2 models also included either proximity to roads in open areas or land-cover; although there was considerable selection uncertainty indicating that these variables were not always strong contributors (Table 2.5). When choosing steps, in summer coyotes generally avoided either crossing or being in close proximity to roads, moving over variable terrain, or moving through open habitats. The odds of coyotes selecting a step that crossed a single road were 40% less than steps that did not cross roads (Figure 2.9). Similar patterns were observed in winter (Table 2.6), except that steps were not chosen so as to avoid open areas (Figure 2.10).

DISCUSSION

Analysis of coyote movement patterns suggest that coyotes do not alter their movements in response to variations in prey abundance or vulnerability as I have interpreted them,

either on a landscape level (nightly movement paths) or local level (6-hr movements). In fact, foraging patterns were only slightly more tortuous than expected from a random walk, suggesting that randomly searching for prey may be an efficient search process in these landscapes. However, resource selection models indicate that coyotes select against areas of increased mortality risk or energetic cost in their movement decisions, indicating that movement choices are not completely random.

Coyotes may not energetically benefit from intensively searching for fawns because fawns are not likely to be spatially aggregated into high density resource patches. More so than in other deer species, white-tailed deer dams do not tend bed their fawns in close proximity to other fawns (Bartush and Lewis 1978, Ozoga et al. 1982, Schwede et al. 1993). Although studies of fawn land cover selection are rare, we expected fawn distribution among habitat types to occur in proportion to the availability of habitat types within a dam's home range (Vreeland 2002 unpublished data analyzed by C. Boser with permission, Burroughs et al. 2006), or perhaps weighted towards use of open or 'non-forested' habitats where we have observed the majority of coyote-killed fawns in this region. If fawns are randomly distributed on the landscape and not aggregated into patches, then high path tortuosity will not necessarily produce higher encounter rates (Bell 1991). Instead, foraging success should increase with directional persistence for some time before eventually decreasing at which point the coyote would likely change course (Bell 1991). This course change may explain the small differences between the fractal D values of the random walk and the observed values. Although coyotes appear to experience higher kill rates in open cover than forest (R. Hlevinski, unpublished data),

they do not appear to be altering their search paths in a systematic manner in open habitat.

My fractal D results are similar to unpublished data by H. Brodie who reported a value of 1.11 ± 0.04 for coyotes (unpublished data cited originally by Nams 1996).

Bascompte and Vila (1997) found that wolves had higher values of fractal D, averaging 1.497 ± 0.275 ($N = 75$). The difference in fractal D values between coyotes and wolves may result from differences in foraging selectivity. Wolves prey selectively on large and medium-sized ungulates, which tend to occur in groups and select for specific habitats that wolves may perceive as high quality forage patches (Bascompte and Vila 1997).

Previous studies modeling ungulate and wolf habitat selection have found that wolves select for specific habitats and increase the duration of foraging in patches where ungulates are most vulnerable (Krunkle and Pletcher 2001, Bergman et al. 2006).

Atwood et al. (2004) proposed that coyotes in a fragmented landscape perceive landscape-level heterogeneity, which enables their use of patchily distributed resources. This body of literature and my results suggest that coyotes follow a more “coursing” search trajectory rather than exhibiting exhaustive search within resource patches.

In my study sites, coyotes consumed a broad array of prey items, which were not necessarily aggregated, and not restricted to one cover type (C. Boser, Chapter 1, 2009). After deer, small mammals such as mice, squirrels and rabbits were consistently the second most dominant prey item in June diets. Thus, while coyotes have incentive to hunt open areas where fawn vulnerability may be great, they also have high foraging opportunity in forest cover where small mammal populations are more abundant than in open areas (C. Boser, unpublished data). The percent of open habitat along coyote paths

was not correlated with the percent of open habitat within a coyote's home range (100% minimum convex polygon), thus availability of open habitat was not likely driving these patterns. Low path tortuosity combined with little to no selection by cover type, (or, for some coyotes, avoidance of open areas), is evidence of a more generalist or opportunistic foraging strategy, rather than specialization on fawns.

Deviations from completely random movement may occur due to trade-offs between avoiding areas perceived as risky, and limiting energetic costs, as well as being influenced by prey availability. There was greater variation among individuals in their selection patterns during summer than winter, potentially because the environment is more diverse in summer (a greater number of prey items are available), encounters with humans are more likely, and vegetation height in agricultural areas fluctuates, influencing screening cover and thus prey vulnerability and coyote mortality risk. All but one coyote avoided roads, with the strongest avoidance observed for coyotes in Otsego County where hunting mortality is higher. In winter, there was also a greater selection against more energetically costly paths by coyotes in Otsego County but not in Steuben County where this covariate was not included in most AIC-selected models.

Mortality risk, rather than prey abundance, appears to be driving cover type selection and coyote movement decisions in my study areas. Indeed, land-cover selection results may be confounded in part because of the inherent correlation between mortality risk and prey abundance in open habitats. Open habitats in my study regions are predominantly human-cleared areas (for agriculture and pasture). Such human-use areas represent both high energetic benefits and high mortality costs making it difficult to assess the internal motivations of coyotes selecting (late summer) or avoiding (early

summer) such areas. It may be that differences in spatial, temporal and ecological conditions, such as the exact placement of carcass piles relative to roads, or the current height of hay fields, dictated coyote movements, yet occurred at a resolution below what I could quantify. Assuming that the relative density of prey between open and forested habitats remains constant throughout the year (although overall levels may fluctuate), then the seasonal differences in land-cover selection that I observed likely reflects changes in the spatial distribution of mortality risk rather than in prey availability. Coyotes may readily perceive changes in mortality risk between seasons because most farm roads are impassable in winter and humans decrease their activity in farm fields. In this study, coyotes responded to low human-use of open areas in winter by using such areas in proportion to their occurrence rather than avoiding them as observed in summer.

Time of day may influence coyote selection of habitat and thus model results, especially when comparing models between seasons with varying daylight hours. Previous studies indicate that predator activity levels decrease in daylight hours, perhaps in response to perceived increases in mortality risk as human activity increases (Roy and Dorrance 1995, Atwood et al. 2004). I have some evidence that use of open habitat by coyotes differed as the day length (and duration of visibility) increased. From winter to summer, day locations in open habitat decreased from 40 to 32% and 58 to 47% in Otsego and Steuben County, respectively, indicating decreased use of open habitat as daylight hours increased. Alternatively, greater use of open habitat in winter may not be due to a time-of-day bias, but to a decrease in human-use of open areas and thus a perceived decrease in mortality risk.

Previous researchers have arrived at conflicting assessments of coyote selection of open and forest cover type (Roy and Dorrance 1985, Bogan 2004). Crete et al. (2001) and Richer et al. (2002) concluded that dense forest habitat was unsuitable to support high densities of coyotes; however Kays et al. (2008) found that coyote density was positively correlated with the amount of forest cover. Kays et al. (2008) also suggested that in areas dominated by forest cover, small scale metrics such as edge and percent canopy closure may increase coyote densities by increasing prey abundance. Yet Rahm et al. (2007) showed that fawn survival is higher in more fragmented areas with higher edge density, perhaps because fawns benefit from greater screening cover in those areas. In my study sites coyotes relied heavily on carrion (C. Boser, Chapter 1, 2009), which, combined with this study, suggests that foraging opportunity is not limiting coyote movements in this region. Thus, I suspect that differences in cover type selection in my study areas are not be explained by prey availability as Kays et al. (2008) hypothesized, because foraging opportunity is high. Instead, perceived mortality risk is likely to be influencing cover type selection in summer.

Mortality risk may be altered by availability of cover and distance to roads which may influence coyote movements and habitat use in areas where most coyote mortality is caused by humans (Riley et al. 2003, Atwood et al. 2004, Bogan 2004). In a suburban study area, Bogan (2004) found that coyotes that had larger open patches in their home range were more likely to be harvested. Those coyotes also selected for natural areas relative to developed land, potentially to avoid risky areas within their home range. Researchers have hypothesized that road avoidance is a learned behavior in coyotes (Roy and Dorrance 1985, Riley et al. 2003, Bogan 2004). This may explain the individual

variation in covariates representing mortality risk. Coyotes in Otsego County, where annual mortality is twice that of Steuben County, may have a greater probability of having had a negative interaction with humans, and thus associate increased risk of mortality with human encounters. All individuals in Steuben County (M6, F3, M5, F4, F10) slightly avoided roads (odds ratios > 0.56) whereas individuals in Otsego County indicated either strong (odds ratios > 0.28 ; F5, F20) or mild (odds ratios > 0.71 ; F4, M2, M6) avoidance of roads. The number of individuals that indicated a reluctance to cross roads decreased in winter relative to summer. Additionally, 20% of coyote steps crossed 3 or more roads in winter, while in summer this was only 6% of steps. This may be due to difference in daylight hours between seasons because most of these steps did not occur in full daylight. However while the number of daylight hours doubles between winter and summer, the number of steps crossing 3 or more roads decreased nearly three times. Alternatively, this may be the result of home range sizes increasing 2.4 times in winter relative to summer, which may lead to longer movement distances, thus increasing the number of road crossings. Interestingly, the percentage of locations close to roads (7% within 100 m) did not change between winter and summer, indicating that perhaps coyotes perceive locations near to roads as a threat in both seasons, and further suggesting that increased home range size in winter is responsible for increasing road crossings. Only one coyote selected for crossing roads, because she apparently frequented a carcass pit that required her to cross many roads (Figure 2.11). She selected for crossing roads more strongly in winter than in summer, possibility demonstrating greater reliance on the carcass pit.

Terrain ruggedness was important in summer and winter models, and selection for steps across more uniform terrain was stronger in Otsego County than in Steuben County in winter, suggesting a greater need (or ability) to conserve energy. This is consistent with analysis of conditional steps which indicated that terrain ruggedness was greater in Otsego County. Previous research in more rugged terrain has indicated that predators utilize energetically efficient movement paths (Hebblewhite et al. 2005, Neufeld 2006). That coyotes in central New York, where elevation generally varies by only 500 m, consistently selected for more uniform terrain is consistent with the expectation of choosing less costly moves. In fact, only 1% of coyote steps recorded at a 6-hr interval had a standard deviation of mean elevation (weighted by step length) of greater than 15 m. Alternatively, coyotes may have a natural tendency to follow contours such as streams and low lying areas which dominates their motivation to choose uniform terrain (Bergman et al. 2006). However the stronger selection for uniform terrain exhibited by coyotes in Otsego County (where conditional steps were more rugged than in Steuben County), may indicate that energetic cost does, in part, influence coyote movement decisions.

There were not pronounced differences between sites in the foraging behaviors I studied, suggesting foraging opportunity may not be biasing home range size and coyote population structure which would be consistent with the resource dispersion hypothesis (MacDonald 1981, 1983). Coyotes show no evidence of intensively searching in resource rich patches possibly because distribution of potential prey is not aggregated or confined to one cover type. Foraging behaviors and diet were similar between sites so I do not suspect that coyotes in either study site were limited by foraging opportunity (C. Boser,

Chapter 1, 2009). Instead, mortality risk appears to exert the largest influence on coyote movements, and thus may have a larger impact than foraging opportunity on coyote demographics. I may expect coyote movements and habitat selection to be altered if prey resources decreased and coyotes became limited by forage availability, and not mortality risk.

Coyote resource use has been linked to pack size, home range size, density and mortality rates in addition to prey size and availability (Carmenzind 1978, Bekoff and Wells 1980, Bowen 1982, Roy and Dorrance 1985, Mills and Knowlton 1991). Due to the variable nature of these animals, no one combination of these factors has sufficiently described the individual or regional variation observed in coyote behavior. My study is no different, reporting individual variation but nevertheless consistent trends in avoidance of areas of high mortality risk.

Combined with concurrent research on coyote diets (C. Boser, Chapter 1, 2009), this research indicated that prey resources do not appear to be limiting to coyote populations in central New York State, and thus coyote populations may continue to increase. Coyote numbers must ultimately respond to limits in prey abundance (O'Donoghue et al. 1997), however competition with wolves is the only top-down control that has been shown to limit coyote numbers (Berger and Gese 2007, Berger et al. 2008). My study suggests that coyotes alter their movements to avoid high humans-use areas; although the energetic sacrifices coyotes sustain to avoid those areas may not be substantial enough to reduce individual fitness. The persistence of large populations of urban and suburban coyotes (Grinder and Krausman 2001, Tigas et al. 2002) indicate that the constraints imposed by responses to perceived mortality risk combined with human

harvest will not, itself, act to limit coyote populations. In rural areas with abundant scavenge material made available by agricultural activities or human encounters with deer (C. Boser, Chapter 1, 2009), predator populations will be constrained only by their own behavioral tendencies. While coyotes have been shown to adapt to human populations and will scavenge on deer and livestock carcasses, other predators have shown a greater reluctance to co-exist with humans (Woodroffe 2000, Ripple and Beschta 2004). Thus, increased risk of human encounters may disproportionately affect predators, and thus indirectly shape predator community composition.

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FIGURE CAPTIONS

Figure 2.1 Coyote daily activity cycles between January and August 2008, represented by the average displacement (m) within a one hour period for GPS collared coyotes (N = 9) in Otsego and Steuben Counties, New York State, USA. Error bars represent 95% CI of displacement.

Figure 2.2 Distribution of the average percent of a) step lengths and b) turn angles of coyote paths (N= 9) at 20-minute intervals recorded using GPS collars placed on coyotes in June 2009, in Otsego and Steuben Counties, New York State, USA. Error bars represent 95% CI of step length.

Figure 2.3 Distribution of the average percent of a) step lengths and b) turn angles of coyote paths (N= 15) at 6-hour intervals recorded using GPS collars placed on coyotes in January 2008-August 2009, in Otsego and Steuben Counties, New York State, USA. Error bars represent 95% CI of step length.

Figure 2.4. Diagram of conditional logistic regression using step selection function (Fortin et al. 2005).

Figure 2.5 Relationship between fractal D values of a given path and the percent of locations in open cover in that path for a) Steuben County female coyotes b) Steuben County male coyotes, c) Otsego County female coyotes, and d) an Otsego County male coyote, May 27-June 24 2008, New York State, USA. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.6 Relationship between fractal D values of a given path and the percent of locations in edge habitat (defined as the area within a 30 m buffer between the intersection of forest and open habitat) cover in that path for a) Steuben County female

coyotes b) Steuben County male coyotes, c) Otsego County female coyotes, and d) an Otsego County male coyote, May 27-June 24 2008, New York State, USA. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.7 Selection for open habitat in 7, 4-week time periods in summer 2008 (May 1-August 28) for a) female coyotes and b) male coyotes in Steuben County, New York State, USA. The description on the x-axis indicates the beginning of the 4-week interval. Odds ratios above one indicate selection for open cover, and values less than one indicate avoidance. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.8 Selection for open habitat in 7, 4-week time periods in summer 2008 (May 1-August 28) for a) female coyotes and b) male coyotes in Otsego County, New York State, USA. The description on the x-axis indicates the beginning of the 4-week interval. Odds ratios above one indicate selection for open cover, and values less than one indicate avoidance. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.9 Odds ratio values for the AIC selected best resource selection model for summer 2007 and 2008 (June 1-August 28) in Steuben and Otsego Counties, New York State, USA. Potential covariates include open land-cover, distance to roads in open cover, number of roads crossed on movement path, and path ruggedness (measured as the percent coefficient of variation in the path). Odds ratios above one indicate selection for the covariate, and values less than one indicate avoidance. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.10 Odds ratio values for the AIC selected best resource selection model for winter 2008-2009 (February 15-March 31) in Steuben and Otsego Counties, New York State, USA. Potential covariates include open land-cover, distance to roads in open cover, number of roads crossed on movement path, and path ruggedness (measured as the percent coefficient of variation in the path). Odds ratios above one indicate selection for the covariate, and values less than one indicate avoidance. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Figure 2.11 Den site of coyote F19 and cow carcasses pit and the paths traveled directly between these locations June 5th-June 17th, 2008, Otsego County, New York State, USA.

Table 2.1 Percent land-cover in the Steuben (867 km²) and Otsego County (832 km²) study sites, New York State, USA acquired from NLCD 2001 (www.epa.gov/mrlc/nlcd-2001.html).

	Steuben County	Otsego County
Forest	56.9	71.22
Row Crops	17.12	18.56
Pasture	19.76	7.95
Wetland	1.01	0.53
Residential areas	1.6	1.05
Other	3.61	0.69

Table 2.2 Re-classification of National Land-Cover Database 2001 cover types for fawn selection analyses in summer 2008, and classifications used in resource selection functions (RSF), in summer 2007 and 2008 and winter 2008-2009 in Steuben and Otsego Counties, New York State, USA (www.epa.gov/mrlc/nlcd-2001.html).

NLCD Classification	Fawn selection analyses	RSF
Water	Other	Absent
Low Intensity Residential	Other	Open
High Intensity Residential	Other	Open
Commercial/Industrial/Transportation	Other	Open
Bare Rock/Sand/Clay	Other	Open
Quarries/Strip Mines/Gravel Pits	Other	Open
Transitional	Other	Open
Deciduous Forest	Other	Forest
Evergreen Forest	Other	Forest
Mixed Forest	Other	Forest
Shrubland	Open	Open
Orchard/Vineyards/Other	Other	Open
Pasture/Hay	Open	Open
Row Crops	Open	Open
Urban/Recreational Grasses	Open	Open
Woody Wetlands	Other	Forest
Emergent Herbaceous Wetlands	Open	Open

Table 2.3 Candidate set of models tested to predict coyote resource selection in Steuben and Otsego Counties, New York State, USA.

Candidate Models
Ruggedness
Roads crossed
Open land-cover
Distance to roads in open cover
Ruggedness + # Roads crossed
Ruggedness + Open land-cover
Ruggedness + Distance to roads
Roads crossed+ Open land-cover
Roads crossed + Distance to roads in open cover
Ruggedness + # Roads crossed + Open land-cover
Ruggedness + # Roads crossed + Distance to roads in open cover

Table 2.4 Fractal dimension of nightly coyote paths using GPS location fixes at 20-min intervals in May 27-June 24 2008 in Steuben and Otsego Counties, New York State, USA. Also shown is expected fractal D based on 100 random walkers within each animals home range (see text for details).

	Sex	N	Mean Tortuosity	SD	RW 95%CI
Steuben	Female	7	1.108	0.028	1.029-1.034
	Female	7	1.112	0.044	1.032-1.041
	Male	7	1.153	0.099	1.026-1.029
	Male	7	1.134	0.063	1.024-1.034
Otsego	Female	14	1.109	0.044	1.030-1.044
	Female	14	1.113	0.027	1.031-1.041
	Male	14	1.121	0.046	1.026-1.035

Table 2.5 Summary of support for candidate models across individuals in summer 2007 and 2008 in Steuben and Otsego Counties, New York State, USA. See Table 2.3 for the specific variables included in each model. Values indicate the number of parameters (K), and AICc model weight for each individual. Bolded values indicate the highest ranked models (those within $\Delta\text{AICc} < 2$ of the top model). The number of times each model is ranked among the top models is also given. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Model	Model variables	K	Steuben County					Otsego County							Rank
			F3	F4	F10	M5	M6	F4	F5	F19	F20	M2	M6	M21	
1	Terrain ruggedness (R)	3	0.000	0.057	0.000	0.007	0.025	0.000	0.000	0.291	0.000	0.044	0.000	0.000	1
2	Road crossings (C)	3	0.001	0.000	0.032	0.115	0.031	0.000	0.044	0.048	0.001	0.152	0.000	0.001	1
3	Percent open land-cover (O)	4	0.000	0.000	0.001	0.002	0.204	0.002	0.000	0.068	0.000	0.014	0.007	0.000	1
4	Mean road proximity (P)	3	0.000	0.000	0.000	0.002	0.010	0.000	0.000	0.048	0.000	0.055	0.000	0.000	0
5	R + C	4	0.199	0.465	0.019	0.341	0.035	0.000	0.121	0.107	0.481	0.180	0.000	0.392	6
6	R + O	5	0.000	0.024	0.001	0.004	0.152	0.086	0.000	0.163	0.000	0.017	0.072	0.000	2
7	R + P	4	0.000	0.036	0.000	0.004	0.009	0.000	0.000	0.119	0.000	0.072	0.000	0.000	1
8	C + O	5	0.003	0.000	0.535	0.076	0.273	0.049	0.016	0.030	0.000	0.055	0.085	0.001	2
9	C + P	4	0.003	0.000	0.039	0.055	0.012	0.000	0.384	0.021	0.000	0.147	0.000	0.000	1
10	R + C + O	6	0.323	0.176	0.348	0.225	0.234	0.863	0.045	0.061	0.336	0.068	0.836	0.169	10
11	R + C + P	5	0.472	0.242	0.024	0.171	0.013	0.001	0.389	0.044	0.182	0.193	0.000	0.437	7

Table 2.6 Summary of support for candidate models across individuals in winter 2008 in Steuben and Otsego Counties, New York State, USA. See Table 2.3 for the specific variables included in each model. Values indicate the number of parameters (K), and AICc model weight for each individual. Bolded values indicate the highest ranked models (those within $\Delta AICc < 2$ of the top model). The number of times each model is ranked among the top models is also given. Individuals are labeled by sex (M = male, F = female) and animal identification number.

Model	Model variables	K	Steuben County					Otsego County				Rank
			F3	F4	M5	M6	F7	F5	F19	M21	F26	
1	Terrain ruggedness (R)	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.161	0.087	1
2	Road crossings (C)	3	0.000	0.303	0.012	0.000	0.036	0.002	0.019	0.098	0.000	2
3	Percent open land-cover (O)	4	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0
4	Mean road proximity (P)	3	0.385	0.000	0.000	0.091	0.000	0.000	0.000	0.023	0.000	1
5	R + C	4	0.000	0.120	0.004	0.000	0.042	0.503	0.483	0.229	0.034	4
6	R + O	5	0.001	0.000	0.000	0.000	0.000	0.000	0.011	0.082	0.030	0
7	R + P	4	0.353	0.000	0.000	0.310	0.000	0.000	0.000	0.069	0.600	3
8	C + O	5	0.001	0.097	0.006	0.000	0.010	0.002	0.011	0.055	0.000	0
9	C + P	4	0.136	0.319	0.699	0.226	0.416	0.001	0.009	0.037	0.000	4
10	R + C + O	6	0.000	0.037	0.002	0.000	0.011	0.319	0.251	0.132	0.011	3
11	R + C + P	5	0.121	0.123	0.276	0.370	0.484	0.174	0.228	0.082	0.237	7

Figure 2.1

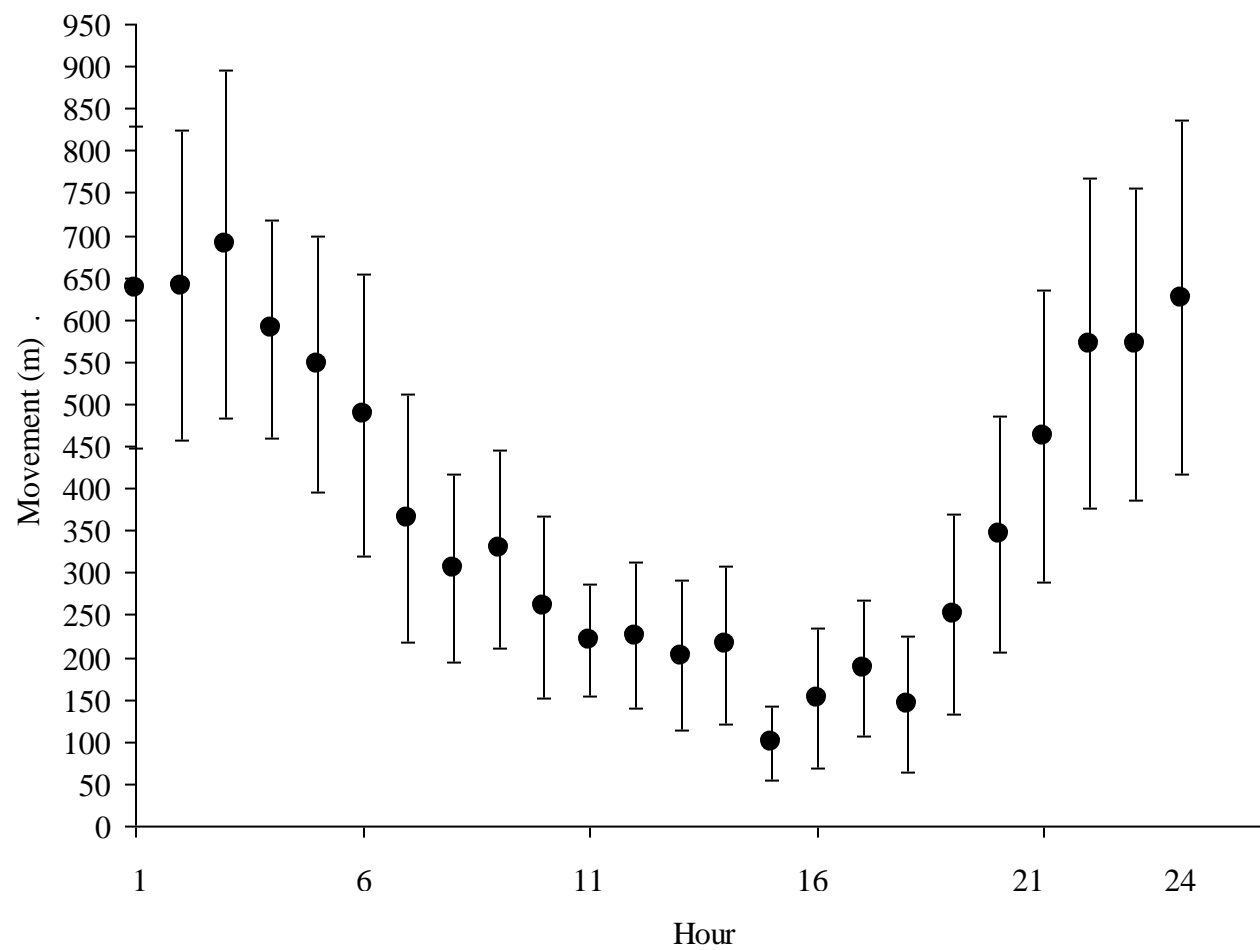


Figure 2.2a

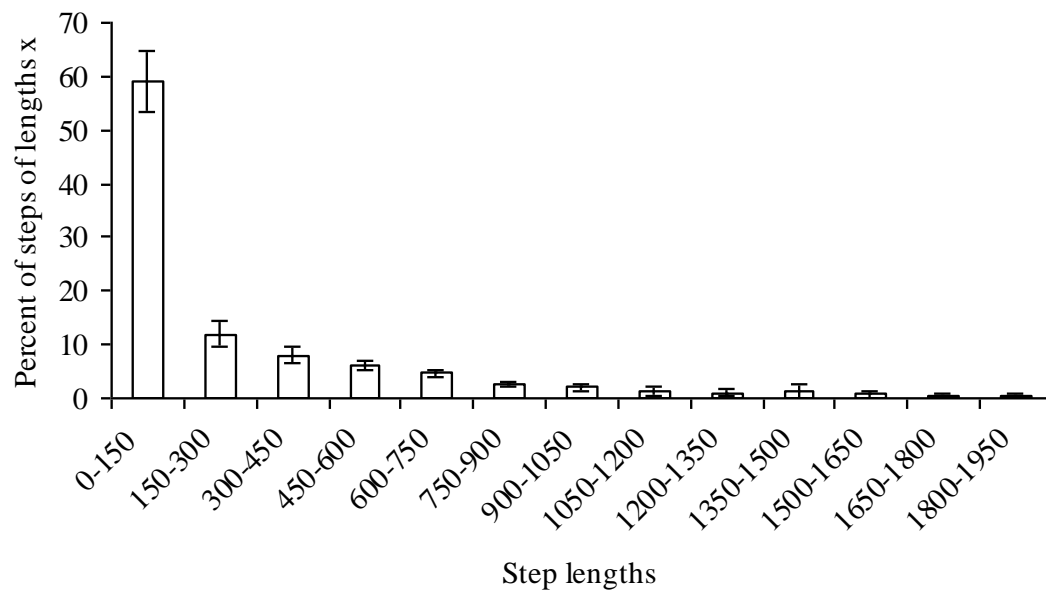


Figure 2.2b

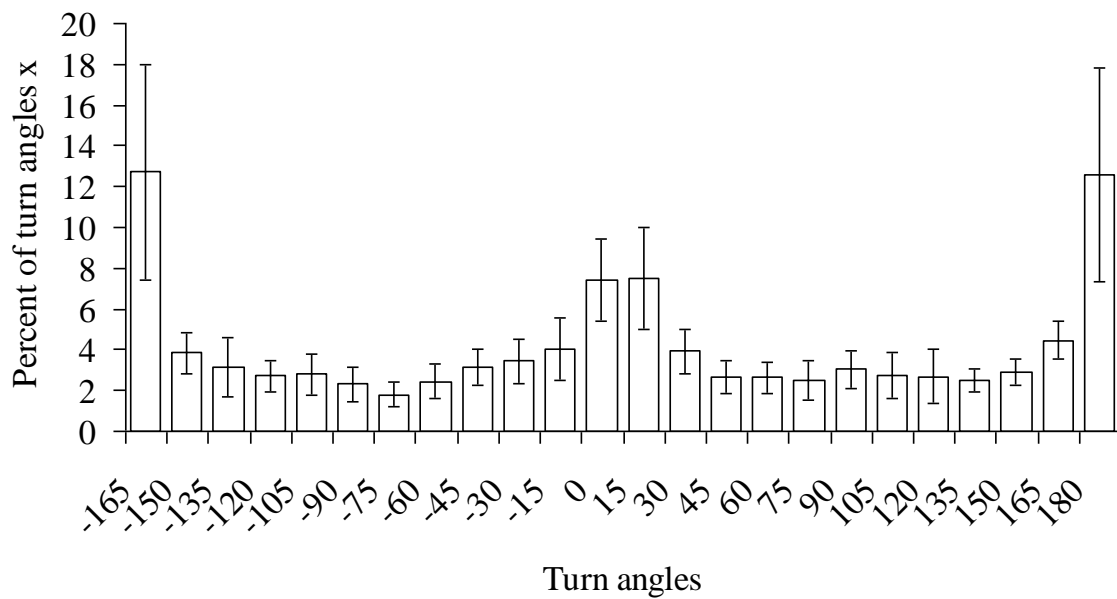


Figure 2.3a

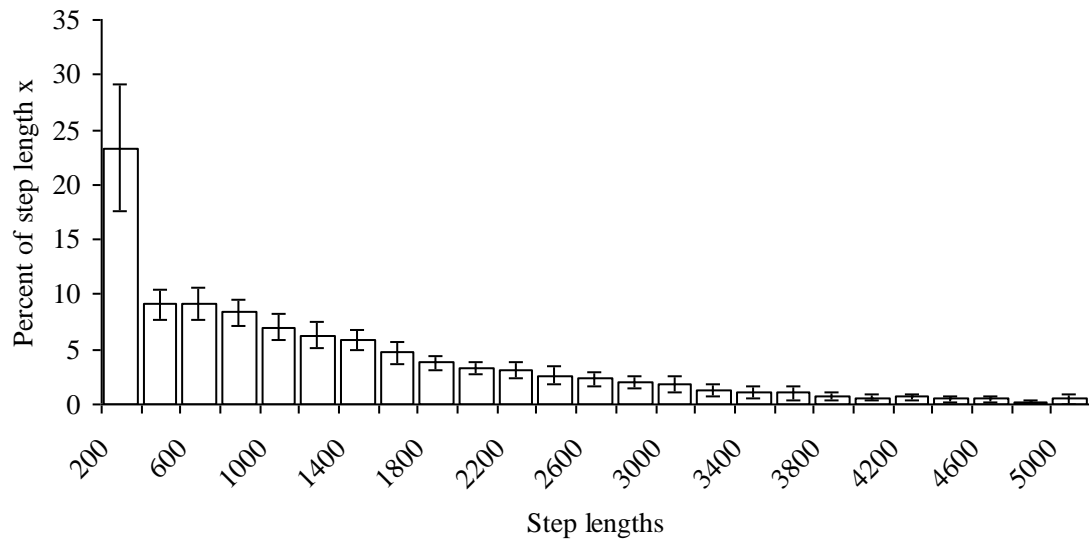


Figure 2.3b

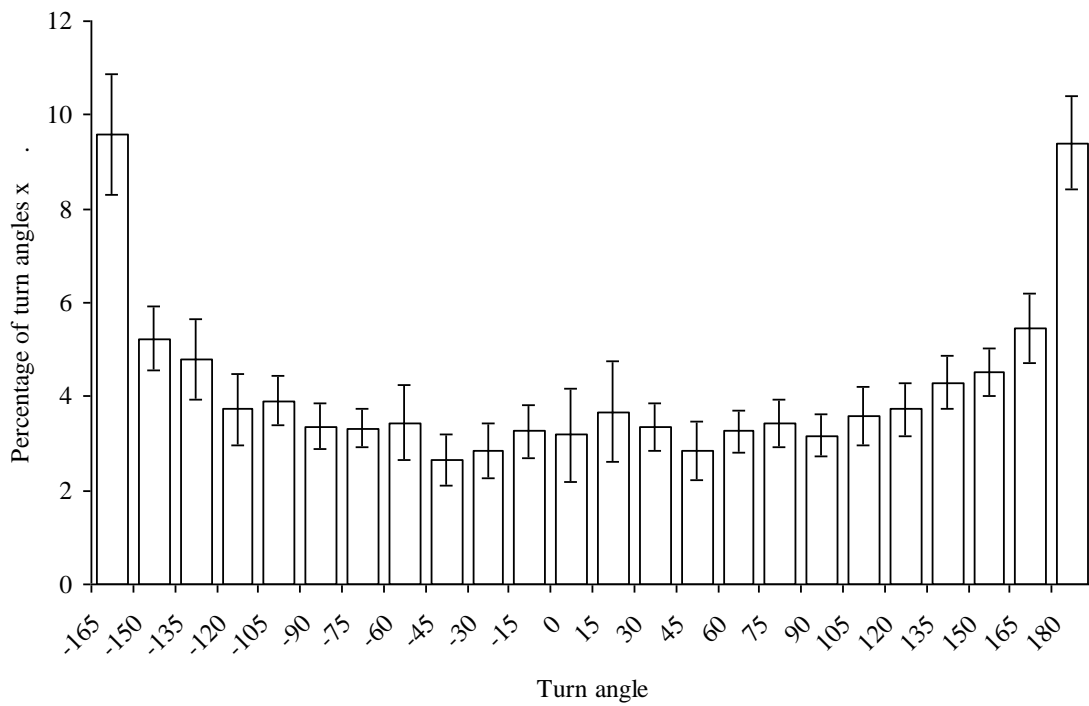


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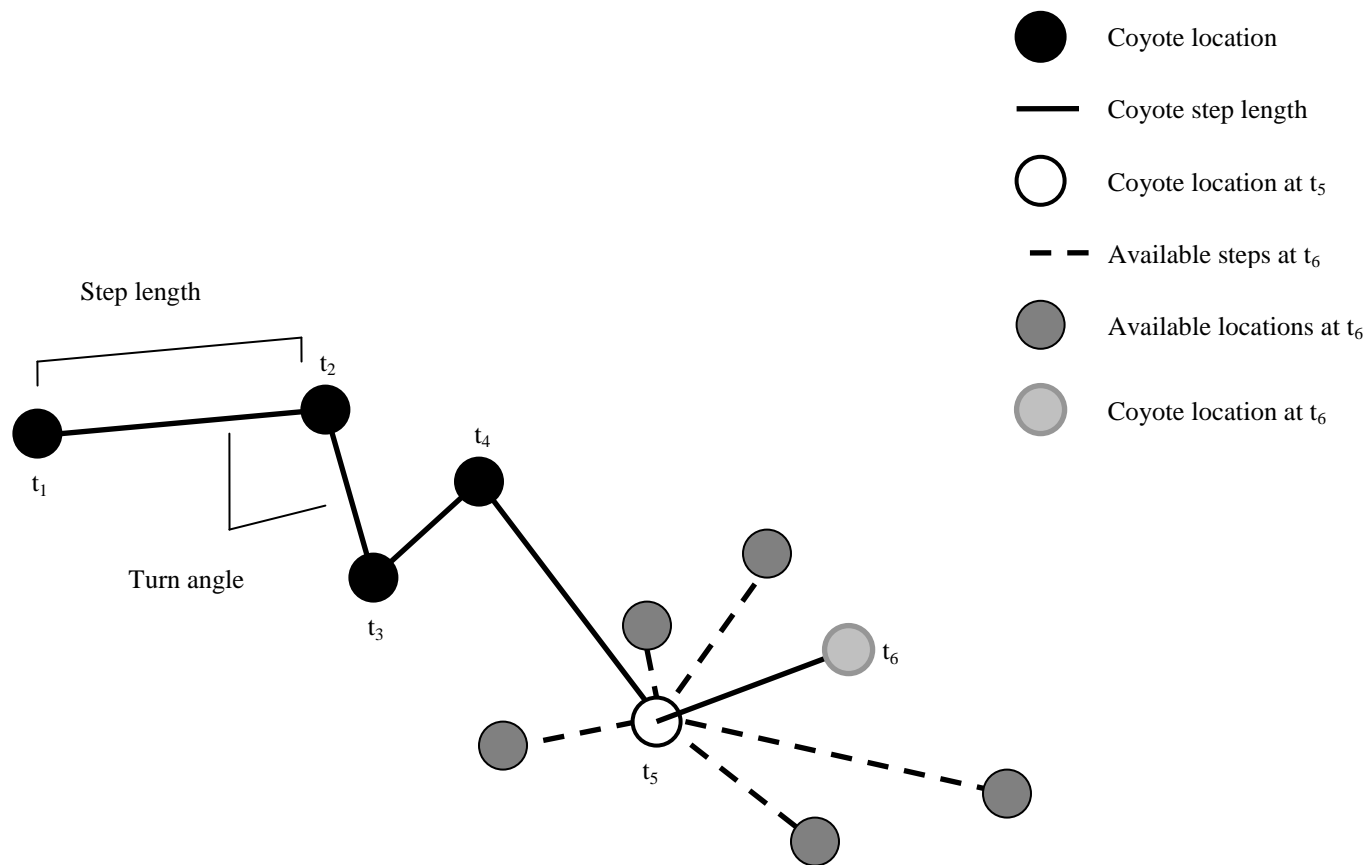


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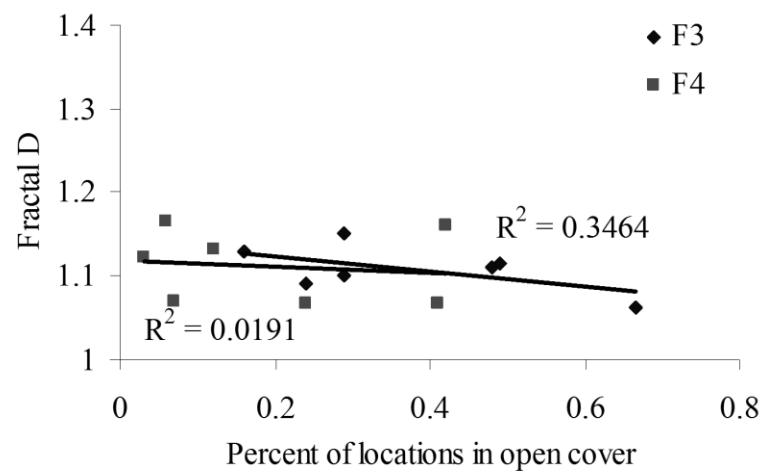


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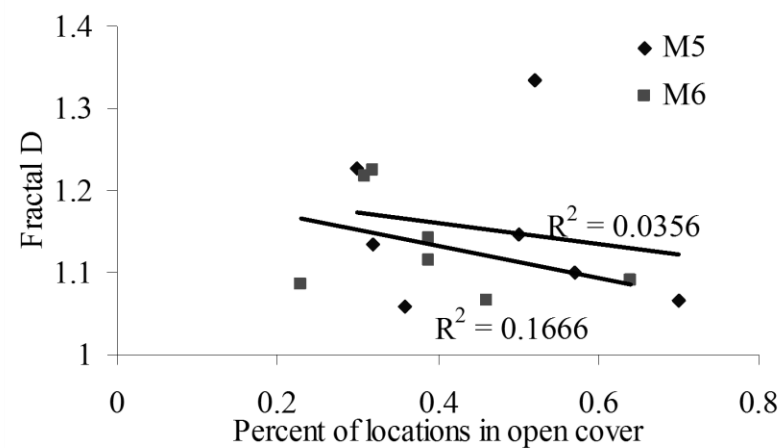


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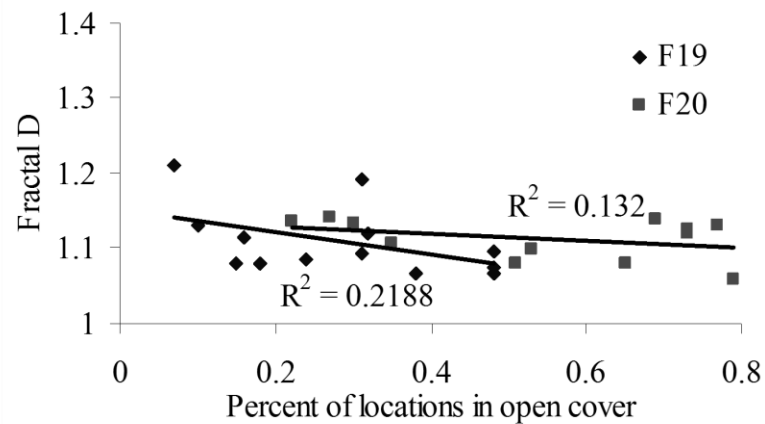


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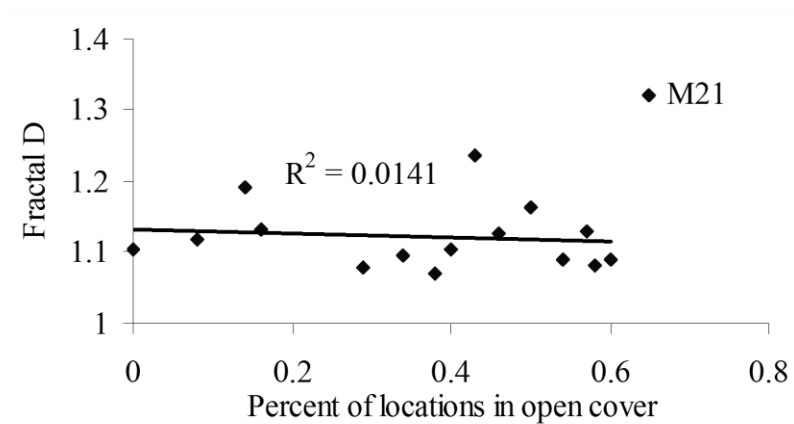


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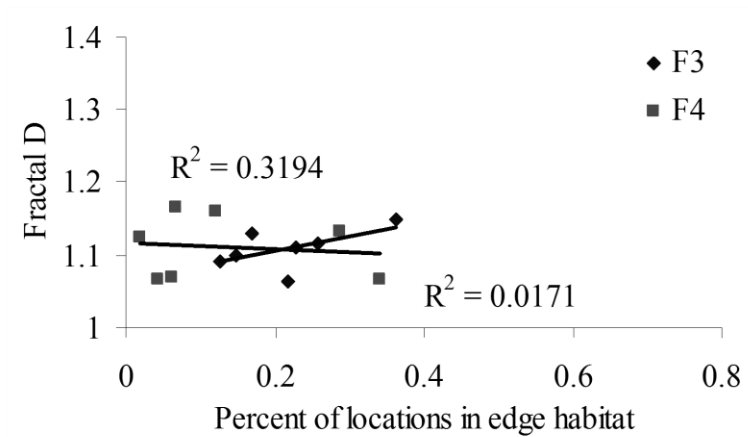


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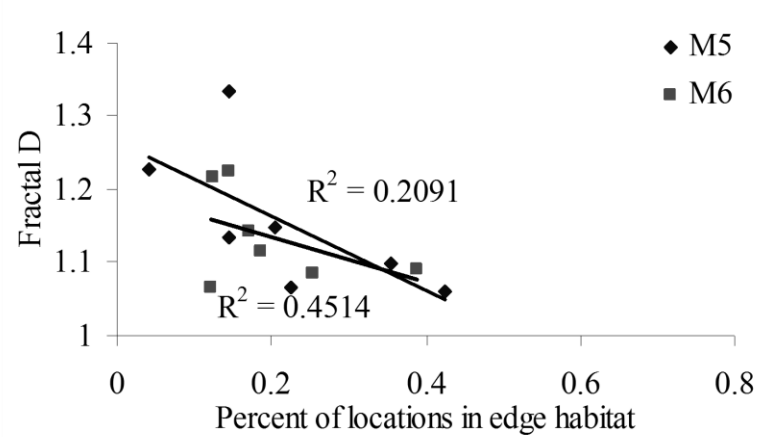


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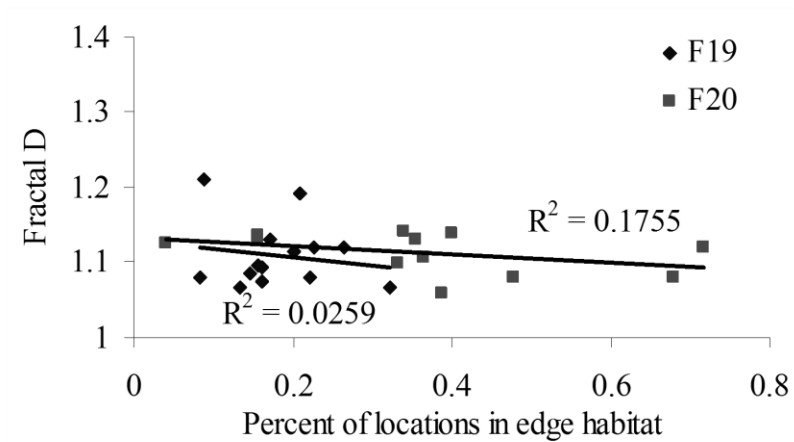


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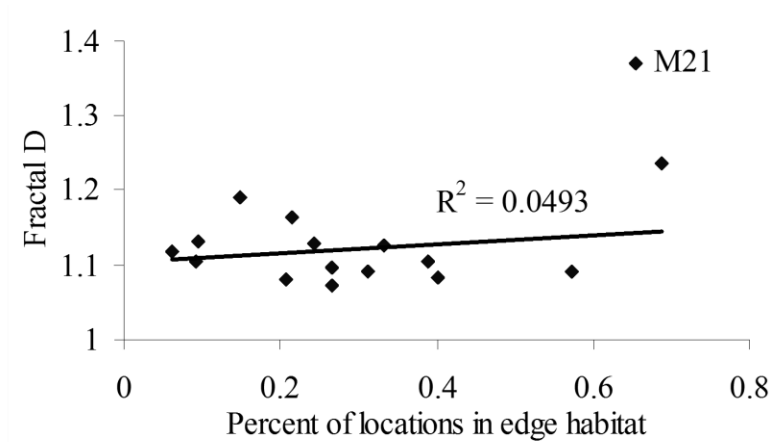


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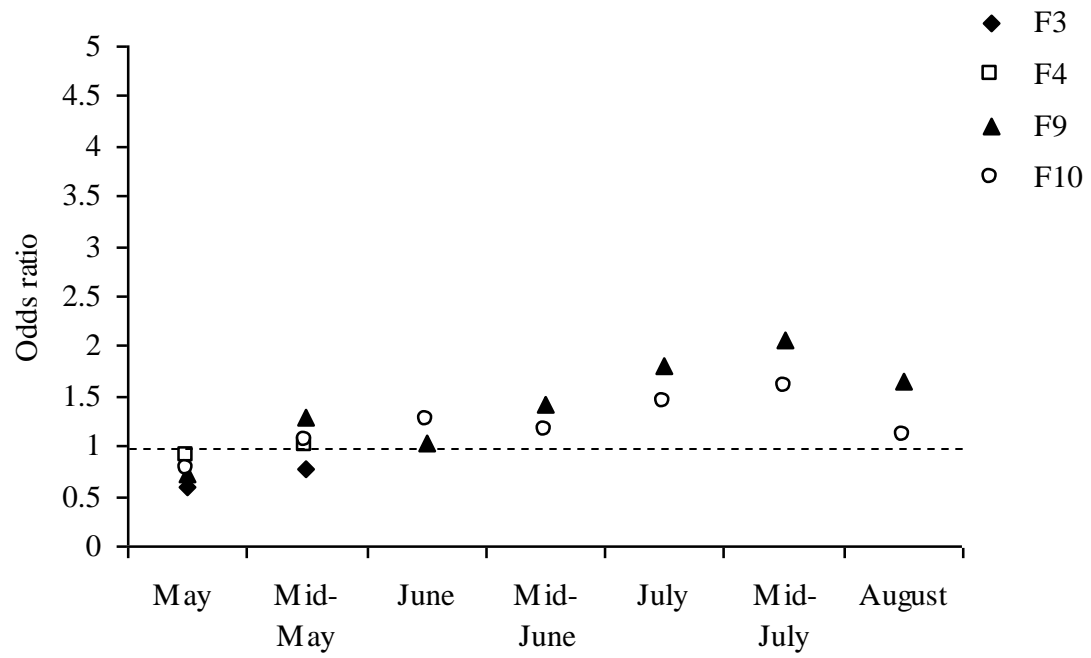


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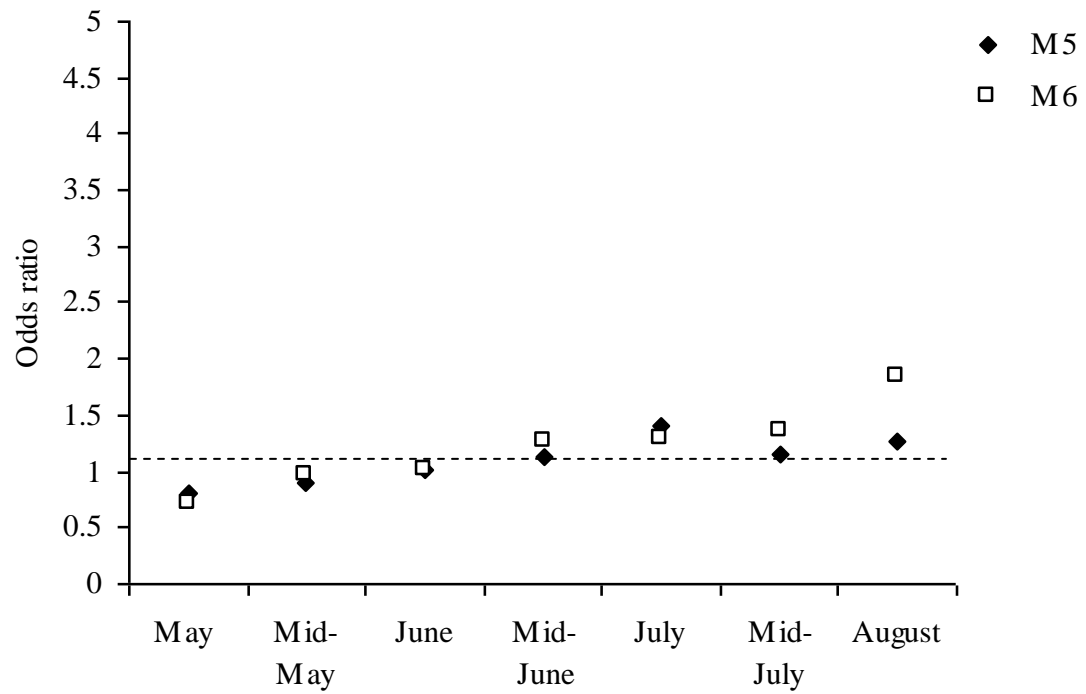


Figure 2.8a

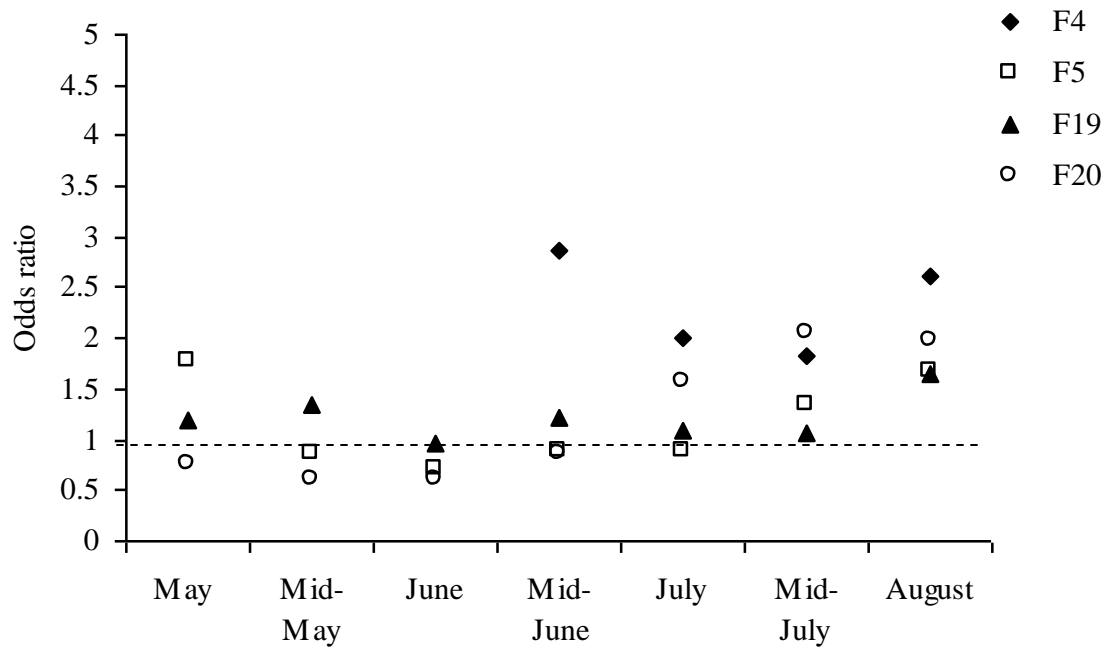


Figure 2.8b

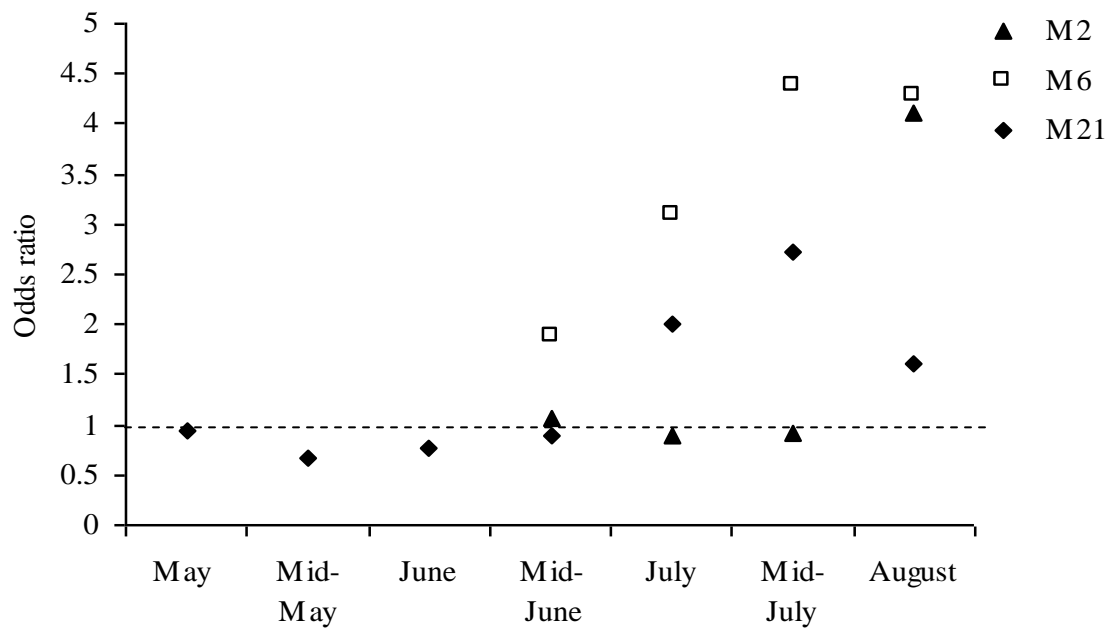


Figure 2.9

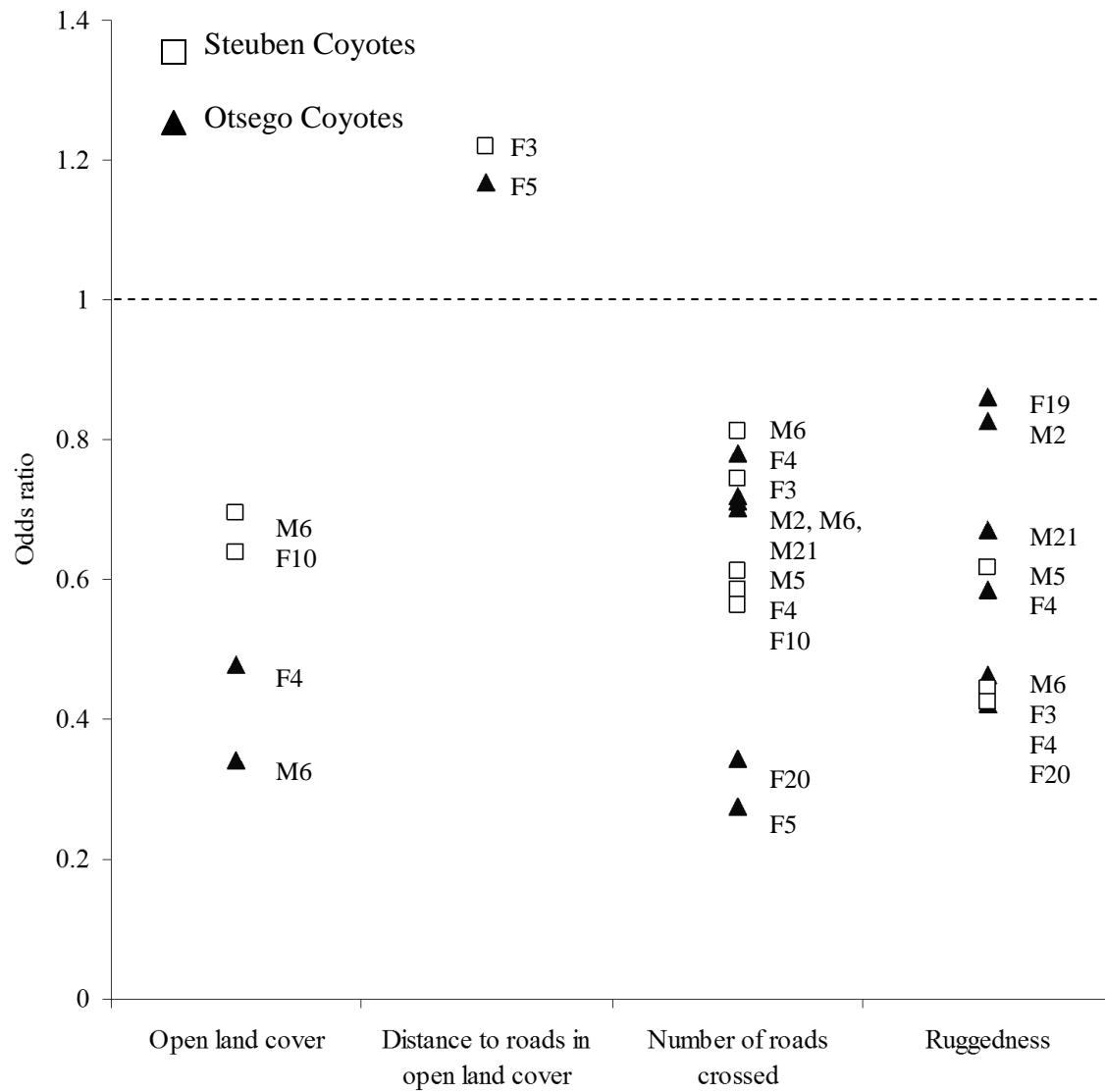


Figure 2.10

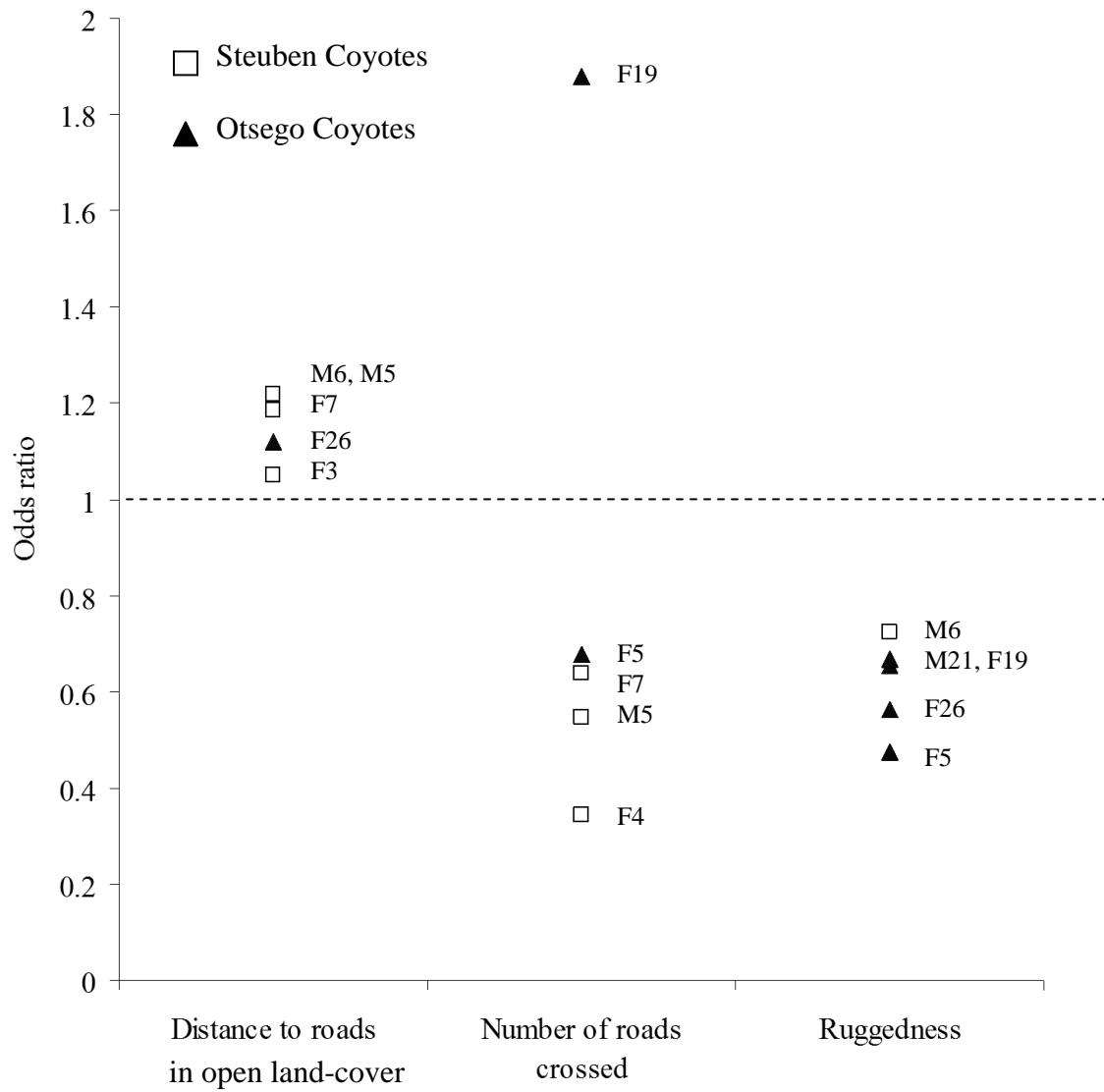
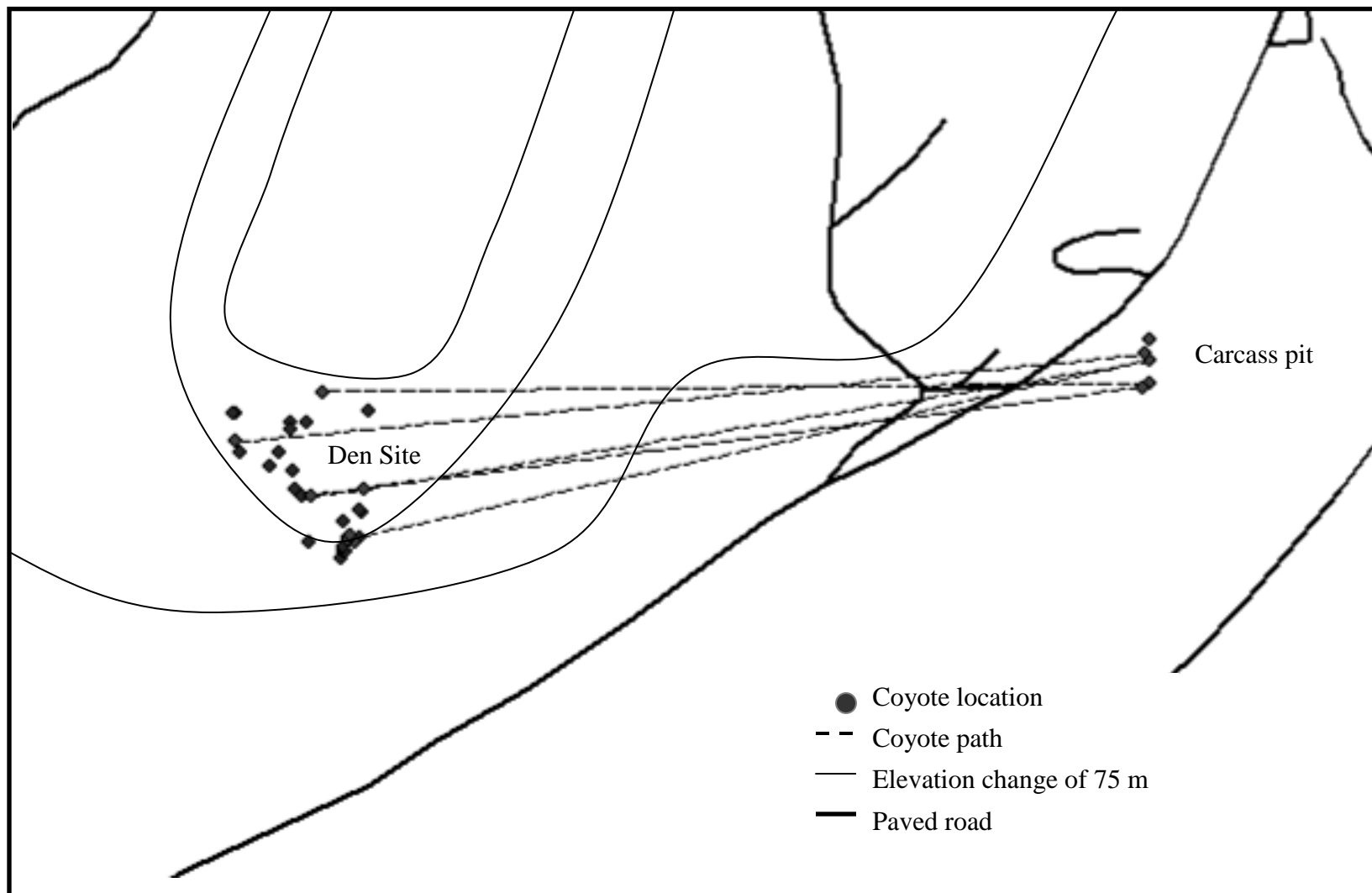


Figure 2.11



Appendix

Appendix A.1 Metrics describing conditional points created for individual coyotes in Steuben County, New York State, USA in summer using a step selection function. Columns describe the percent of locations in open cover, the average distance to roads in open cover, the average number of roads crossed on a conditional movement path and the average energetic cost of a conditional movement paths calculated by the percent coefficient of variation of the length weighted mean of elevation. Individuals are labeled by sex (M = male, F = female) and animal identification number.

	Percent open land-cover	Distance to roads	Number of roads crossed	Energetic cost
F3	37.28	413.97	0.89	0.93
F4	17.82	446.08	0.72	1.07
F10	37.82	391.60	0.95	0.91
M5	53.88	410.65	0.99	0.59
M6	43.95	371.43	1.53	0.56
Average (95%CI)	38.14 (11.55)	406.75 (24.36)	1.02 (0.27)	0.81 (0.19)

Table A.2 Metrics describing conditional points created for individual coyotes in Otsego County, New York State, USA in summer using a step selection function. Columns describe the percent of locations in open cover, the average distance to roads in open cover, the average number of roads crossed on a conditional movement path and the average energetic cost of a conditional movement paths calculated by the percent coefficient of variation of the length weighted mean of elevation. Individuals are labeled by sex (M = male, F = female) and animal identification number.

	Percent open land-cover	Distance to Roads	Number of roads crossed	Energetic cost
F4	47.28	382.51	1.02	0.76
F5	37.38	439.60	0.54	1.03
F19	39.93	353.76	1.39	1.54
F20	58.91	357.17	0.82	0.72
M2	49.42	373.24	0.75	0.95
M6	49.51	355.27	1.13	0.56
M21	57.04	313.73	1.62	1.13
Average (95%CI)	48.45 (5.91)	367.90 (28.35)	1.040 (0.28)	0.96 (0.23)

Appendix A.3 Metrics describing conditional points created for individual coyotes in Steuben County, New York State, USA in winter using a step selection function. Columns describe the percent of locations in open cover, the average distance to roads in open cover, the average number of roads crossed on a conditional movement path and the average energetic cost of a conditional movement paths calculated by the percent coefficient of variation of the length weighted mean of elevation. Individuals are labeled by sex (M = male, F = female) and animal identification number.

	Percent open land-cover	Distance to Roads	Number of roads crossed	Energetic cost
F3	38.20	404.94	1.02	0.75
F4	22.82	415.94	1.01	0.85
F7	40.85	375.38	1.16	0.57
M5	46.48	383.24	0.98	0.47
M6	40.85	375.38	0.97	0.57
Average (95%CI)	37.84 (7.82)	390.98 (16.19)	1.03 (0.06)	0.64 (0.13)

Appendix A.4 Metrics describing conditional points created for individual coyotes in Otsego County, New York State, USA in winter using a step selection function. Columns describe the percent of locations in open cover, the average distance to roads in open cover, the average number of roads crossed on a conditional movement path and the average energetic cost of a conditional movement paths calculated by the percent coefficient of variation of the length weighted mean of elevation. Individuals are labeled by sex (M = male, F = female) and animal identification number.

	Percent open land-cover	Distance to Roads	Number of roads crossed	Energetic cost
F5	38.30	387.08	2.42	0.94
F19	32.79	370.50	1.29	1.49
F26	39.46	349.82	2.54	1.15
M6	50.42	317.88	1.97	1.12
Average (95%CI)	40.24 (7.23)	356.32 (29.22)	2.05 (0.55)	1.17 (0.22)

Appendix B.1 Best model results for individuals in Steuben County (S) and Otsego County (O) New York State, USA, in summer including the coefficients, the standard error of coefficients, and the odds ratios. Labels include sex and identification number.

	Covariate	Coefficients	SE	Odds ratio
SF10	Open land-cover	-0.45	0.16	0.64
	Number of roads crossed	-0.57	0.16	0.56
SF3	Distance to roads in open cover	0.20	0.11	1.22
	Number of roads crossed	-0.30	0.23	0.74
	Ruggedness	-0.81	0.24	0.44
SF4	Ruggedness	-0.86	0.18	0.42
	Number of roads crossed	-0.54	0.23	0.59
SM5	Number of roads crossed	-0.49	0.16	0.61
	Ruggedness	-0.48	0.24	0.62
SM6	Open land-cover	-0.36	0.14	0.70
	Number of roads crossed	-0.21	0.13	0.81
OF19	Ruggedness	-0.15	0.08	0.86
OF20	Number of roads crossed	-1.07	0.13	0.34
	Ruggedness	-0.87	0.23	0.42
OF4	Open land-cover	-0.74	0.16	0.48
	Number of roads crossed	-0.25	0.10	0.78
	Ruggedness	-0.54	0.20	0.59
OF5	Distance to roads in open cover	0.16	0.07	1.17
	Number of roads crossed	-1.29	0.24	0.28
OM2	Number of roads crossed	-0.33	0.15	0.72
	Ruggedness	-0.19	0.13	0.83
OM6	Open land-cover	-1.07	0.18	0.34
	Number of roads crossed	-0.34	0.13	0.71
	Ruggedness	-0.77	0.31	0.46
OM21	Number of roads crossed	-0.35	0.08	0.70
	Ruggedness	-0.40	0.11	0.67

Appendix B.2 Best model results for individuals in Steuben County (S) and Otsego County (O) New York State, USA, in winter including the coefficients, the standard error of coefficients, and the odds ratios. Individuals are labeled by sex (M = male, F = female) and animal identification number.

	Covariate	Coefficients	SE	Odds ratio
SF3	Distance to roads in open cover	0.05	0.07	1.05
SF4	Number of roads crossed	-1.07	0.16	0.35
SF7	Distance to roads in open cover	0.17	0.07	1.19
	Number of roads crossed	-0.45	0.10	0.64
SM5	Distance to roads in open cover	0.20	0.06	1.22
	Number of roads crossed	-0.60	0.14	0.55
SM6	Ruggedness	-0.32	0.16	0.73
	Distance to roads in open cover	0.20	0.05	1.22
OF5	Ruggedness	-0.75	0.22	0.47
	Number of roads crossed	-0.39	0.09	0.68
OF19	Ruggedness	-0.42	0.15	0.66
	Number of roads crossed	0.63	0.07	1.88
OF26	Ruggedness	-0.57	0.15	0.56
	Distance to roads in open cover	0.11	0.05	1.12
OM21	Ruggedness	-0.41	0.20	0.67

Epilogue

Coyotes, being one of the top predators in New York State, adaptable and able to exploit a variety of ecological landscapes, have the potential to substantially alter the prey communities of New York State. Alternatively they may mostly scavenge on carrion, or embody Errington's (1956) description of a predator; one that kills the "doomed surplus". My research suggests that coyotes are utilizing carcasses, but also likely killing and consuming fawns. Given that consumption of fawns was equal between sites, the ratio of predators to prey will, in part determine the impact of predation on prey populations if at least some predation additive. I have no evidence that coyotes altered their foraging paths to intensively search for fawns during time periods and in locations where their diet was selective for fawns. Instead, changes in anti-predator behaviors by fawns and fawn vulnerability likely influences coyote foraging success, such that coyotes consumed about 72- 90% more fawn biomass in early summer when fawn vulnerability is greatest, relative to late summer.

Coyote foraging path tortuously was low; only slightly higher than that calculated from a random walk, and consistent between individuals. The fractal D values of foraging paths and individual habitat selection indicate that coyotes may not intensively search for prey in resource patches. Instead, coyotes appear to move in nearly straight paths, perhaps because they tend to rely on visual cues to detect prey (Wells and Lehner 1978) and nearly straight movement paths increase the likelihood of flushing prey.

Resource selection functions indicated that landscape attributes representing mortality risk and energetic cost more strongly altered movements than landscape proxies representing prey acquisition. This may be because prey opportunity on a landscape was

inadequately represented in this study. Coyotes consume a diversity of prey, and the densities of those prey items may respond to differences in microhabitat that are difficult to map at the scale at which coyotes perceive the landscape. Alternatively, prey opportunity may be so great that perceived mortality threats and energetic costs may influence coyote movements more so than prey availability.

While trends in the resource selection function models were apparent between seasons and study areas, model variation among individuals justified examining resource selection on the individual level. For example, Forester et al. (2007) examined individual movement models for elk (*Cervus elaphus*) and found that the most parsimonious model for an individual elk rarely well-predicted the movements of any other animal. Coyotes are highly adaptable and responsive to available resources so individual models may provide more informative data resolution than population-level analyses. In this study, the movements of a few animals inhabiting home ranges with a unique spatial distribution and availability of resources may have diluted model results if one model had been created for the all study animals.

That there were no differences in foraging path tortuosity or significant differences in fawn consumption between sites suggests that fawns may not be a preferred prey item; even when vulnerability greatest in early summer. While deer fawns may potentially benefit from predator swamping, the low percentage of fawns in coyote diet (< 32%) suggests that this resource is not fully exploited by coyotes. Throughout the summer when fawns were available and most vulnerable, coyotes fed on carcasses of livestock and adult deer in equal proportion to fawns. Foraging at carcasses may be

profitable and desirable to coyotes because these foods are inert and do not require search, chase, or capture effort.

Livestock carcass piles and deer carcass are available year-round, may carry little risk (depending on location) and consumption requires low energetic input. Adult white-tailed deer, which were not often killed by coyotes in my study areas (R. Holevinski, unpublished data), and are likely to be killed in traffic collisions (Côté et al. 2003, Organ 2007), comprise a large portion of coyote diet in both study areas. Thus, human land uses, both agricultural and road traffic, may create a hospitable environment for coyotes and individuals may not be limited by their ability to hunt and kill prey. In fact, a high human-caused coyote mortality rate in Otsego County may be spurning increases in coyote density (Knowlton et al. 1999) which are then sustained by abundant forage resources.

High coyote density resulting in high fawn predation may be impacting deer population size in Otsego County, and thus partially responsible for the relatively low density of deer in that site. Deer harvest records have remained mostly constant in the past 20 years while coyote harvest records indicate that coyote populations may have been increasing (Department of Environmental Conservation 2008). However the population level-effects of coyote predation on fawns may be masked by numerous other factors interacting with deer populations, compounded over decades. Harsh winters and unusually large amounts of snowfall may impact adult male harvest, (which is used as an index to deer population size; Organ 2007). Changes in the land-cover may alter densities of white-tailed deer such that increased edge habitat increases browse, increasing carrying capacity and deer density (Alverson et al. 1988, Côté et al. 2003). There has

been a decrease in agricultural land cultivated in the Northeast in the last century, and within my study areas (Zipperer et al. 1990) and it is likely that the amount of edge habitat on the landscape has also decreased (O'Neill et al. 1992, He and Hubbell 2003). Thus, changes in human land use and habitat modifications may partially explain the discrepancies in deer densities between areas.

The diversity of coyote diet, substantial carrion consumption, and selection for movements that minimize mortality risk and energetic cost, indicate that prey availability is not limiting coyote populations. In the absence of a top-down control, coyote populations may continue to increase while prey is not limiting. While coyote movement and space use may be limited by territoriality (which was not studied here), the availability of perceived low-risk habitat, and the magnitude and category of human land-use are not likely to limit coyote density.

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Institute for Wildlife Studies	2006-2007	Field Crew Leader
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