EVOLVING NICHE OF COYOTES IN THE ADIRONDACK MOUNTAINS OF NEW YORK:

LONG-TERM DIETARY TRENDS AND INTERSPECIFIC COMPETITION

by

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Abstract

S. A. Warsen.   Evolving Niche of Coyotes in the Adirondack Mountains of New York: Long-term Dietary Trends and Interspecific Competition, 90 pages, 4 tables, 8 figures, 2012.

Geographic expansion of the coyote's range over the last century has been due in large part to its adaptable and opportunistic foraging behavior. Arriving in the Adirondacks in the 1950s, coyotes today compete with and predate upon a wide array of species. To identify whether coyotes may be specializing on white-tailed deer, I compared seasonal diets in the central Adirondacks during 2009-11 to coyote diets reported in the 1950s-1980s. Use of deer and alternative prey appears to be driven not by changes in deer population size, but by changes in alternate prey populations. Estimates of total biomass consumed indicated beaver are the main source of biomass consumed in summer (51.4%), whereas deer continued to dominate the winter diet (81.0%). Niche partitioning among coyotes, bobcats, gray fox, and red fox was investigated using stable carbon and nitrogen isotope analysis and results indicate differential use of anthropogenic resources among species.

Key Words: Adirondacks, beaver, coyote, New York State, niche partitioning, prey switching, snowshoe hare, stable isotope analysis, white-tailed deer

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Prologue

At the time of European settlement of North America, the coyote (*Canis latrans*) was geographically restricted to the prairie ecosystems of the North American Great Plains, while the forests of the Northeastern United States were home to larger-bodied mammalian predators such wolves (*Canis lupus sensu lato*) and cougars (*Puma concolor*; Moore and Parker 1992). Following a series of human-mediated events that culminated in the early 20th century – namely, the extirpation of large carnivores coupled with large-scale forest clearing and agricultural development – coyotes underwent a dramatic range expansion and today occur in all 48 contiguous United States, Alaska, Canada, Mexico, and south to the Panama canal (Gompper 2002). Their success in colonizing new regions has been rivaled by few North American mammals in recent history (Fener et al. 2005).

The first record of coyotes in New York State dates back to 1925 and comes from the northern portion of the state in Franklin County, 12 miles south of the Canadian border (Severinghaus 1974). Based on first occurrence reports and documented sightings, it appears that coyotes likely colonized the state in two geographically distinct waves: first in the 1940s by traveling across Ontario, Canada and entering northern New York by crossing the St. Lawrence River, and that was followed by a second wave in the 1960s that traveled south of Lake Ontario and entered western New York via Pennsylvania (Fener et al. 2005). The Adirondack Mountains of northern New York were one of the last reaches of the state to be colonized by the northern wave of coyotes, with initial colonization records in the region dating back to the 1950s. Over the last few decades coyotes have become the most ubiquitous large carnivore in the region, and they are here to stay.

Adding to the intrigue surrounding coyotes in the Northeast is the fact those descended from the northerly colonization wave share DNA with eastern wolves, likely due to previous interbreeding as coyotes expanded eastward and northward across Ontario (Kays et al. 2010). Additional differences between northeastern coyotes and their western counterparts include a slightly larger body size (on the order of 10-15% larger; Gompper 2002), a greater tendency to hunt in extended family groups (Messier and Barrette 1982, Harrison 1992), and dietary differences (Thurber and Peterson 1991). The ecological role of coyotes in the Northeast, and speculation that they may perhaps fill the vacant niche once held by wolves in the region, remains of great interest to scientists, resource managers, and the general public alike. Two specific ways that coyotes may be impacting ecological communities in the Northeast are through their foraging habits and competition with native mammalian predators. The goal of this study was to examine the ecological niche of coyotes in the central Adirondacks, focusing specifically on those two aspects of coyote ecology: foraging ecology and potential competition with native predators.

Coyotes are opportunistic feeders, and their diet varies with geographic location depending on what prey species are abundant. In the southwestern United States, coyote diets focus primarily on lagomorphs and small rodents and seasonally available fruits, while snowshoe hare (*Lepus americanus*) are the preferred prey in Alaska and boreal Canada (Parker 1995, Prugh 2005). In the Northeast, ungulate prey such as white-tailed deer (*Odocoileus virginianus*) and, in some areas, caribou (*Rangifer tarandus*) and moose (*Alces alces*) make up a large portion of the coyote diet (Litvaitis and Harrison 1989, Crête and Desrosiers 1995, Samson and Crete 1997). Although coyotes are certainly capable of killing deer, especially fawns in summer and adults when deep snows increase their vulnerability to predation (Brundige 1989, Patterson 1998), it

appears that a great majority of the deer that coyotes consume is a result of scavenging (Hamilton 1974, Samson and Crete 1997, R. Holevinski, personal communication).

In the central Adirondacks, studies of coyote foraging ecology have occurred at 5-15 year intervals over the past 50 years (Hamilton 1974, Chambers 1987, Brundige 1993) and show that the diet of coyotes has become increasingly focused on and dominated by white-tailed deer. In Chapter One of this thesis, I compare contemporary coyote diets based on scats collected 2009-2011 to coyote diets reported in the 1950s-1980s and evaluate whether changes in coyote use of deer and alternative prey items has been driven by changes in deer population size over time. In contrast to these earlier studies, I also correct for known biases in diet analyses based on scats due to differential digestibility of prey items in order to more accurately reflect the relative importance of specific prey items in the contemporary coyote diet.

Given morphological and dietary similarities, coyotes are expected to compete most directly with bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*) in the central Adirondack region. In Chapter Two of this thesis, I test specific hypotheses about resource use and potential niche partitioning among this suite of carnivore species using carbon and nitrogen stable isotope analysis (δ^{13}C and δ^{15}N, respectively). This provided a cost-effective method of comparing diets among multiple species because relatively few samples were required (~10 samples/species; Fox-Dobbs et al. 2007) compared to scat-based analyses (~100 samples/species/season; Trites and Joy 2005), and these samples could be collected from the legal harvest of fur-bearing animals at little cost. Samples are also species ID positive, whereas scat-based studies may unintentionally include a non-target species, although this risk is generally considered acceptably low for carnivore studies.

Both chapters of this M.S. thesis are written for submission to the Journal of Wildlife Management and conform to that journal's style requirements. At the end of this thesis is an epilogue in which I synthesize the results of my two chapters, make recommendations for continued investigations capitalizing on this research, and summarize the management implications stemming from this work.

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RH: Warsen • Long-term Coyote Diet

Evolving dietary niche of coyotes in the Adirondack Mountains of New York State

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ABSTRACT

Geographic expansion of coyote (*Canis latrans*) range over the last century has been due in large

part to the coyote's adaptable and opportunistic foraging behavior. Despite well-documented

plasticity in coyote diets across North America, coyote diets in the northeastern United States

and eastern Canada have become increasingly focused on and dominated by white-tailed deer

(*Odocoileus virginianus*). To identify whether coyotes may be specializing on deer, I compared

seasonal diets in the central Adirondack Mountains during 2009-2011 to coyote diets reported in

the 1950s-1980s from the same region. I evaluated whether use of deer and alternative prey

items was driven by changes in deer population size over time. From the late 1970s through the

current study, white-tailed deer was the most frequent prey item in both seasons. However, a

sharp decline in deer use was documented in the present study with deer comprising 42-59% of

seasonal diets compared to the 63-94% use previously observed. Snowshoe hare (*Lepus*

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americanus), which dominated coyote diets in the 1950s, declined to only a trace item by winter 1986, and rebounded to the third most common prey item in the present study. Beaver (*Castor canadensis*) showed a steady increase in use from trace levels in the 1950s to becoming the second most common prey item in the present study. Estimates of total biomass consumed based on the digestibility of different prey items indicated beaver to be the main source of biomass in summer (51.4%), whereas deer continued to dominate the winter diet (81.0%). Importantly, temporal changes in coyote diet most directly tracked the recovering beaver population rather than changes in the deer population. This study confirms the coyote's generalist foraging behavior, and provides evidence that coyotes have not become specialists on deer in the Northeastern United States.

KEY WORDS Adirondack Park, beaver, *Canis latrans*, *Castor canadensis*, coyote, *Lepus americanus*, *Odocoileus americanus*, prey switching, snowshoe hare, white-tailed deer

INTRODUCTION

Originating in the Great Plains and western United States, the coyote (*Canis latrans*) has been steadily expanding its geographic range over the past century (Moore and Parker 1992). In the eastern United States, this range expansion has been facilitated by the extirpation of large carnivores, namely wolves (*Canis lycaon*) and cougars (*Felis concolor*), coupled with the conversion of forests into agricultural lands. Coyotes were first documented in northern New York State in the 1920s (Bromley 1956) and colonized the Adirondack region beginning in the late 1940s (Severinghaus 1947). In the relatively short time period following their colonization of the Adirondacks, coyotes have become the most widespread and abundant large predator in the region. This burgeoning population is likely to have important ecological implications for the Adirondack ecosystem.

In the central Adirondacks, studies of coyote foraging ecology have occurred at <15 year intervals over the past 50 years (Hamilton 1974, Chambers 1987, Brundige 1993) and indicate that the diet of coyotes has become increasingly focused on white-tailed deer (*Odocoileus virginianus*). Based on a percent of scats approach, deer comprised 39% of the winter diet of coyotes in 1956-61 (Hamilton 1974), increasing to 88% in 1975-80 (Chambers 1987), and remaining high at 94% in 1986-89 (Brundige 1993). Summer diets showed a similar trend with 14% of coyote scats containing deer in 1956-61 (Hamilton 1974), increasing to 89% in 1975-80 (Chambers 1987), and remaining moderately high at 64% in 1986-89 (Brundige 1993). Similarly to the central Adirondack region, deer have been documented as the most common component of coyote diets elsewhere in New York State (37-63% of scats; Boser 1999) along with Maine (9-63% of scats; Major and Sherburne 1987, Litvaitis and Harrison 1989, Dibello et al. 1990), Québec (20-80% of scat volume; Messier et al. 1986, Samson and Crete 1997), New Brunswick (25% of stomachs; Moore and Millar 1986 and 10-45% of scats; Parker 1986), and Nova Scotia (14-59% of volume in scats; Patterson 1995).

Rare, long-term studies of coyote diets with respect to changes in prey availability in northern regions have documented the prey-switching behavior expected of generalist predators. In particular, changes in the density of snowshoe hare (the primary prey species) drove changes in consumption of white-tailed deer (the secondary prey item) by coyotes in Nova Scotia (Patterson et al. 1998) and Alaska (Prugh 2005). In the Adirondacks, snowshoe hare (*Lepus americanus*) declined from occurring in 42-45% of scats in summer and winter in the 1950s, respectively, to comprising less than 12% of the seasonal diets in later studies. These temporal trends in coyote diet – increasing frequency of deer in the diet coupled with a decreasing frequency of secondary prey items – may indicate niche specialization over time, with coyotes

evolving to more efficiently hunt deer. Although deer dominate coyote diets in the Northeast, long-term comparisons of coyote diets to prey populations are necessary to make inference regarding prey specialization.

The objectives of this study were to quantify the contemporary coyote diet in the central Adirondack region, to compare contemporary and historic coyote diets in the region, and to determine whether the use of deer and other prey by coyotes closely track changes in the deer population. If coyotes have become deer specialists, I expected coyote use of deer to remain high today despite potential fluctuations in deer numbers. If, however, coyotes remain generalist predators, then their increasing use of deer should reflect either an increase in deer availability or a decrease in the availability of preferred prey, namely snowshoe hare.

STUDY AREA

This study focuses on the foraging ecology of coyotes in the central Adirondack region of New York State. The Adirondack Park is a 24,000 km^2 tract of largely forested land in northern New York State that is comprised of 51% privately-owned and 49% publicly-owned land. The main land cover types in the Adirondack Park are deciduous forest (61%), coniferous forest (15%), mixed deciduous-coniferous forest (11%), open water (6%), and wetlands (5%; Homer et al. 2004). This study took place at the Huntington Wildlife Forest (HWF), a 6,000-ha research forest operated by the State University of New York College of Environmental Science and Forestry, and the surrounding vicinity, an area encompassing approximately 600 km^2 between the towns of Long Lake, NY and Minerva, NY (Figure 1). Elevations in the study area range from 400 to 1,600 m. Precipitation averaged 101 cm per year and mean annual snowfall was 289 cm (HWF, unpublished data). Potential coyote prey species in the study area include white-tailed deer, snowshoe hare, beaver, red squirrel (*Tamiasciurus hudsonicus*), muskrat (*Ondatra*

zibethicus), porcupine (*Erethizon dorsatum*), moose (*Alces alces*), woodchuck (*Marmota monax*), deer mice (*Permyscus* spp.), jumping mice, (*Napaeozapus insignis*, *Zapus hudsonius*), voles (*Myodes gapperi*, *Microtus* spp.), Eastern chipmunk (*Tamias striatus*), flying squirrels (*Glaucomys* spp.), Eastern wild turkey (*Meleagris gallopavo*), ruffed grouse (*Bonasa umbellus*), and various songbirds and waterfowl. Seasonal plant food sources include raspberries and blackberries (*Rubus* spp.), cherries (*Prunus* spp.), apples (*Malus* spp.), and American beech nuts (*Fagus grandifolia*). Other mammalian predators in the area include black bear (*Ursus americanus*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), fisher (*Martes pennanti*), and American marten (*Martes americana*).

METHODS

Quantifying Coyote Diet

To allow for an accurate temporal comparison of coyote foraging ecology in the study area, my methods follow those of previous studies in the region (Hamilton 1974, Chambers 1987, Brundige 1993). Putative coyote scats, those having a diameter ≥ 2cm, were collected at regular time intervals (generally every 2 weeks) and also opportunistically from roads, hiking paths, and wildlife trails in the study area in winter (Dec – mid Apr) 2009-2011 and summer (Jun – Aug) 2010-2011. Only scats considered ≤ 1 month old, based on consistency and cohesiveness, were analyzed. Scats were placed in a paper bag labeled with date and location of collection and placed in a drying oven at 50°C for 48 hours to kill *Echinococcus* eggs, a tapeworm which can adversely affect humans (Veit et al. 1995). Sterile samples were placed in nylon bags, rinsed twice in a clothes washing machine on a warm delicate cycle to remove fecal material, and air-dried prior to analysis (Brundige 1993, Prugh 2005). Dried scats were separated by hand into component food items, and all food items present were recorded. Hairs were examined under a

binocular microscope and identified based on hair medulla pattern and cuticular scales, using reference hair collections and mammalian hair keys (Adorjan and Kolenosky 1969, Moore et al. 1974). Scale impressions were made for white-tailed deer hair from summer scats to differentiate adults from fawns, which can be done reliably until late August (Brundige 1993). Due to the high possibility for error in small mammal (i.e., Cricetid mammals) and songbird identification, these prey species were considered collectively as small mammals and birds (Patterson et al. 1998).

To enable an accurate comparison with previous studies conducted along the same collection routes, I present results as the percent of scats containing a particular food item (Hamilton 1974, Chambers 1987, Brundige 1993, Klare et al. 2011). Although the percent of scats approach is known to bias results in favor of larger-bodied prey items (Weaver 1993), this bias should be consistent across studies. Therefore, I limited my conclusions to the temporal comparisons within a prey species rather than comparing the relative importance of different prey items during a specific time period. Pearson's chi-squared test was used to test for differences among time periods within each prey species in both summer and winter, and differences were considered statistically significant at a Bonferroni-corrected significance level ($\alpha = 0.008$) in order to control the experimentwise error rate.

To provide additional insight into the relative importance of different prey items observed during this study period, I used a biomass correction method to report the estimated percent of total biomass consumed by coyotes for each prey item (Kelly 1991), which may change the relative ranking of specific prey items. Biomass corrections are based on each prey item's coefficient of digestibility (i.e., ratio of fresh weight of a given prey species to the dry weight of its remains in scats; Jędrzejewska and Jędrzejeswki 1998:183). To calculate the amount of

biomass consumed by coyotes for each prey species (B_i), dry prey remains in scats were separated by species and the mass of prey remains in each scat was multiplied by the respective coefficient of digestibility:

$$B_i = \sum_{j=1}^{n} M_{ij} R_i \qquad [1]$$

where M_{ij} is the dry mass (kg) of prey species i in scat j, and R_i is the coefficient of digestibility for prey species i. The coefficients of digestibility (Table 1) are based on the published average body size of prey species in the Adirondacks (Saunders 1989) and the controlled feeding trials of Kelly (1991) where captive coyotes were fed prey ranging in mass from 0.03 kg to 45 kg. The percent of biomass consumed for prey species i (P_i) was then calculated as:

$$P_i = 100 * B_i / B \qquad [2]$$

where B is the total amount of biomass consumed for all species. I computed P_i for each prey item for both winter and summer seasons.

Prey Population Trends

To compare historic trends in coyote diets to fluctuations in the population of white-tailed deer in the region, deer hunter harvest records were compiled from the New York State Department of Environmental Conservation (NYSDEC, unpublished data). Sage et al. (1983) showed that regional deer population levels and the fall buck harvest in the study area were positively correlated ($r^2 = 0.86$, $P < 0.05$), so I used the annual buck harvest as an index to deer population size. I calculated a five-year moving average of the estimated legal hunter buck harvest for NYSDEC wildlife management unit 5F, an area comprising the study area and the surrounding 2,000 km^2, for the period of 1955 to 2010.

Snowshoe hare population trends were tracked at the statewide and study area scales. The estimated statewide snowshoe hare hunter harvest and annual hare harvest per hunter (NYSDEC, unpublished data) were used as an index to track broad-scale trends in the snowshoe hare population for the period of 1958-2010. Trends in snowshoe hare in the study area were tracked using winter snow-tracking survey data from HWF for the period of 1987-2010. The methods follow those of Jensen et al. (2012) and, briefly, consist of 3-5 snow-tracking surveys conducted each winter where a trained observer identifies and counts wildlife tracks crossing the survey route. Results are standardized by survey effort and amount of time since the last snowfall.

Winter Severity

To better understand trends in the deer population, meteorological data from the weather station at HWF were used to develop a winter severity index (WSI) for each winter (1 Nov – 30 Apr) from 1954 to 2011. Following Underwood (1990), I tallied the cumulative number of days where the minimum temperature was $\leq$ -18°C (critical temperature days) and the number of days with a snow depth $\geq$ 38 cm or more (critical snow days). Critical snow days (CSD) were weighted twice as important as critical temperature days (CTD) because snow depth is the main driver of deer migration to wintering yards (Underwood 1990, Severinghaus 1947), resulting in the following index:

$$WSI = CTD + 2*CSD \qquad [3]$$

where CTD is the cumulative number of critical temperature days and CSD is the cumulative number of critical snow days (Severinghaus 1947, Underwood 1990).

RESULTS

Coyote diet

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I identified 14 prey items in 174 coyote scats from winter 2009-2011 and summer 2010-2011 (*n* = 74 and 100, respectively). White-tailed deer was the most prevalent food item in both seasons, occurring in 59% of winter scats and 49% of summer scats (Table 2). In summer scats, deer fawns occurred nearly three times as often as adult deer (31 versus 11% of scats, respectively). Beaver and snowshoe hare were the second and third most common mammalian prey species, respectively. Diet diversity was greater in summer than winter (14 vss 10 prey items), reflecting the seasonal availability of plant food sources. Seasonally important food items that showed a high occurrence (>10%) in summer scats included fruits (blackberries, cherries, and apples), beech nuts, and insects (Orthoptera and Coleoptera). In winter, birds (primarily wild turkey) occurred in 18% of scats. Interestingly, moose hair was found in one summer scat, the first time this has been recorded in New York State, though it is unclear if this was from scavenging or predation on neonates.

As anticipated, biomass corrections altered prey rankings compared to the percent of scats analysis. After correcting for differential digestibilities, beaver were the most utilized summer food source (51.4% of biomass consumed), followed by adult deer (22.5%), fawn deer (21.8%), and snowshoe hare (3.3%). In winter, when beavers spend much of their time within the confines of their lodges, white-tailed deer (81.0%) made up the majority of coyote biomass consumed, while beaver remained an important secondary prey item (17.8%).

Compared to historical records of coyote diet in the region, contemporary diets showed a decline in deer use coupled with an increase in use of alternate prey (Figure 2). Occurrence of deer in the diet declined to 42% of scats in summer from the previous highs of 62-94% and to 59% of scats in winter compared to the previous highs of 89-94%. Use of deer today remains higher than the 17-36% occurrence observed in the 1950s when coyotes were first colonizing the

region. Interestingly, the deer age-class that coyotes consume has inverted from the 1980s: fawns outnumber adult deer in the contemporary summer diet (31 and 11% of scats, respectively), whereas in the 1980s adult deer were more common than fawns (51 and 34% of scats, respectively). Red squirrel, an important prey item in the 1950s, has steadily declined in coyote diets with each successive study period   Snowshoe hare showed a resurgence in coyote diets, though not yet to the levels seen in the 1950s when it was the most common prey item. A steady and marked increase in use of beaver was observed, which occurred in ≤0.5% of scats in the 1950s and today is the second most common prey item.

Prey Population Indices

Regional buck harvest records indicate a sharp decline in deer population size in the late 1960s and early 1970s (Figure 3), coincident with severe winters during 1968-69, 1969-70, and 1970-71. The deer population rebounded to moderate levels between ~1980-1988 and has remained relatively stable since then. Statewide records of total snowshoe hare harvest and hare harvest per hunter indicate a general decreasing trend over the period of 1958-2010 (Figure 4). Although indices of snowshoe hare abundance in the central Adirondack region date back only to 1987, they show a lower population level since 1996, but with a recent peak overlapping this study period (Figure 5).

Coyote use of deer was not positively correlated with deer abundance. Over the last 60 years, the use of deer by coyotes was lowest when the deer population was at its highest, early in the colonization of the Adirondacks by coyotes (late 1950s). Coyote use of deer peaked coincident with the lowest levels in deer population size (late 1970s) and remained high as deer populations rebounded to moderate levels (late 1980s). In the current study, use of deer declined despite deer still occurring in moderate numbers and at levels equivalent to the late 1980s.

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DISCUSSION

This study provides evidence that coyotes have not become specialized on deer in the northeastern United States. The first line of evidence is that occurrence of deer in coyote diets has varied markedly over time, declining sharply in the current study from previously high consumption levels. Had coyotes become specialists on deer, I expected to see continued high levels of deer consumption unless deer populations had dropped below a threshold that made it unprofitable for coyotes to continue to pursue them (May 1981). This has not been the case because deer populations have been relatively stable over the past 30 years. A second and related line of evidence is that the levels of consumption of deer by coyotes did not correlate to observed changes in deer numbers. Consumption of deer by coyotes was lowest when deer populations were abundant, highest when deer populations were low to moderate, and dropped sharply in this study despite deer population size remaining moderately large. The last line of evidence, which I'll develop in the paragraph to follow, is that coyotes appear to be "switching" off deer as a potentially more preferred prey item becomes sufficiently abundant. However, this more preferred prey item is not snowshoe hare as was originally hypothesized.

Prey switching is a foraging behavior often demonstrated by generalist predators and involves a change in resource use based on the energetic costs of pursuing and handling prey (Murdoch 1969, Prugh 2005). It is primarily a function of prey abundance and profitability and can explain the trends of increasing use of beaver by coyotes in this study. As a highly sought-after furbearer, beaver were intensively trapped in North America throughout the 17th to 19th centuries and by the late 1800s were effectively extirpated from large areas of the United States (Jenkins and Busher 1979, Larson and Gunson, 1983). By 1903 only a single beaver colony persisted in New York State (Saunders 1989), but following regulation of trapping in the early

20th century and post-agricultural reforestation, beaver populations have slowly but steadily rebounded in the region (Müller-Schwarze and Sun 2003, Foster et al. 2002; Figure 6). When coyotes colonized the Adirondacks in the 1950s, beaver were still relatively scarce, and hunting beaver would not have been energetically advantageous when alternate prey species (i.e., snowshoe hare and deer) were more abundant. Since that initial study period, coyote consumption of beaver has steadily increased, reflecting recovering beaver populations. In contrast, regional snowshoe hare population levels appear to be trending slightly downward over the last 60 years (Hodges 2000), corresponding to the generally observed decline in use of snowshoe hare by coyotes. In the Huntington Wildlife Forest, decline in snowshoe hare abundance is likely due to a loss of optimal snowshoe hare habitat as the forested landscape has continued to advance in age (McGee et al. 2007, Hodson et al. 2011), but periodic increases in hare numbers (e.g., 2008-09) may contribute to reduced use of deer. Although snowshoe hare may have initially been the preferred prey item when coyotes first colonized the Adirondacks, beaver populations have likely reached a level at which searching for and preying upon beaver is now the most energetically efficient option. Indeed this trend has been observed elsewhere: as beaver populations have recovered, they have become a major prey item for coyotes in Quebec (Samson and Crete 1997), coyote-wolf (*C. latrans* x *C. lupus*) hybrids in Ontario (Sears et al. 2003), and wolves in Algonquin Provincial Park, Ontario (Voigt et al. 1976, Forbes and Theberge 1996) and Latvia (Andersone 1999).

The importance of beaver relative to deer and hare in coyote diets is difficult to quantify using the percent of scats method of quantifying diet. Although this method allows accurate temporal comparisons of the use of a specific prey item, potential biases arise when making comparisons among prey species of grossly different sizes or compositions. Prey of all body

sizes, from a grasshopper to a moose, are counted equally using the percent of scats approach. Furthermore, the differential digestibility of mammalian prey of differing sizes causes smaller-bodied prey to be over-represented and larger-bodied prey to be under-represented in the scats. Correcting for the percent biomass consumed compensates for this shortcoming and allows a more realistic analysis of relative prey importance (Kelly 1991, Klare et al. 2011). After correcting for differential prey digestibility in the current study, beaver were the largest source of biomass consumed by coyotes in summer (51.4%) and the second largest source of biomass consumed in winter (17.8%), while snowshoe hare were ≤ 3.3% of biomass consumed. Considered on a seasonal basis, beaver may currently be equally if not more important to coyotes than deer. In summer, as beavers forage on shore and juvenile beavers disperse long distances away from water (11-48 km; Müller-Schwarze and Sun 2003) they may be vulnerable to predation by coyotes. In winter, however, beaver spend the majority of their time in their lodge or under ice (Lancia et al. 1982), and their importance as a prey item may be seasonally replaced by deer, which have an increased vulnerability to predation in winter in more northern regions with deep snows and long winters (Messier and Barrette 1985, Brundige 1989, Patterson et al. 1998).

An alternative explanation to the growing availability of beaver as a driver of reduced use of deer is a reduced availability of deer in winter owing to an increasingly milder climate. Climate in the Adirondack region has exhibited a gradual warming trend over the period from Hamilton's (1974) study in the late 1950s until today (Beier et al. 2012). The winter severity index for the two winters corresponding to the contemporary diet study (WSI = 47-157 in 2009-10 and 2010-11, respectively) were below the average WSI recorded during 1955-2011 (166.3 ± 68.5; mean ± SD) and also fall below the WSI for the periods of Hamilton's (175.2 ± 91.6),

Chambers' (184.5 ± 78.3), and Brundige's (173.3 ±40.1) studies. A warming climate may effectively reduce the winter predation risk experienced by deer as prolonged deep snows that are known to impair their movement become less common. The majority of deer consumed by coyotes in winter are likely scavenged (Hamilton 1974, Samson and Crete 1997), and milder winters may also mean fewer scavenging opportunities. A warming climate may have the opposite effect on the winter predation risk experienced by beaver, as the period of time when lakes are covered with a protective layer of ice has become progressively shorter in duration (Beier et al. 2012). If climatic warming trends continue, beaver may become increasingly important to coyotes in winter.

Additional alternative explanations for the temporal patterns observed in this study, e.g., multiple observers and sample size discrepancies, bear consideration but are not a major concern. The effects of different observers in the processes of identifying prey remains in scats are considered minimal because mammal hair can quite easily be identified to the level of Order, so considering small rodents, birds, and insects in collective groups likely minimized species biases. Moreover, the major prey items (i.e., deer, beaver, snowshoe hare) were readily identifiable through hair medulla patterns. Identification of putative coyote scats among different observers in areas where red fox and bobcat also occur can be difficult. Misidentification of scats was minimized in this study by collecting only scats having a diameter ≥ 2cm, a conservative cutoff for identifying scats of eastern coyote (Gompper et al. 2006). The three previous studies in the study area indicated that coyote scats were identified based on size and appearance, though no further details are given. Sample sizes in this study ($n = 74$-100 in winter and summer, respectively) were smaller than those published for Hamilton (1974; $n = 458$-873 in winter and summer, respectively), Chambers (1986; $n = 366$-555 in summer and winter, respectively), and

Brundige (1989; $n = 143$-284 in summer and winter, respectively) because this study was conducted over 2 summers and 2 winters whereas previous studies included 3-6 summers and winters. The simulations of Trites and Joy (2005) indicated that a sample size of 94 scats for each treatment (e.g. season or study period) was necessary to reliably detect differences in diets containing 6 or more species, with the number of scats needed to detect differences in diet decreasing as the number of prey items in a diet increases. With a sample size of 74-100 scats I detected 14 prey species, meaning that the seasonal scats collected in the contemporary diet study were likely comparable to the larger sample sizes in previous studies. Furthermore, the risk of collecting too few scats is missing rarely consumed prey items. The objective of this study was to document use of major prey items, so a larger sample size would likely not alter any conclusions drawn herein.

MANAGEMENT IMPLICATIONS

Much of the interest in coyote management focuses on the potential regulatory influence of coyote predation on white-tailed deer abundance in the eastern United States. Coyotes are certainly capable of killing deer, especially when long winters and deep snows increase deer vulnerability to predation (Brundige 1989, Dibello et al. 1990, Decker et al. 1992, Patterson 1998). That eastern coyotes share some DNA with eastern wolves further fuels speculation about their potential ecological niche as a top predator in the region (Gompper 2002, Kays et al. 2010, Wheeldon et al. 2010). However coyotes likely scavenge the great majority of deer they consume (Hamilton 1974, Samson and Crete 1997), with the exception of fawns in summer, and coyote predation is likely to be compensatory to at least some degree. Although this study does not offer direct evidence regarding the potentially limiting or regulating effects coyotes may have on deer populations in the East, it does offer evidence that deer may not be the preferred

prey of coyotes in the region, meaning that we would not expect high levels of deer consumption by coyotes even if deer numbers declined. Deer obviously augment coyote diets and even dominated their diet in the Adirondacks when both beaver and snowshoe hare were scarce. However, the strong increasing trend in consumption of beaver since the 1950s corresponds most directly with the recovering beaver population, providing strong evidence that beaver are becoming a preferred prey of coyotes in this region. It follows that if beaver populations continue to increase, we may also observe increases in the number of coyotes in the region. Elevated numbers of coyotes, with spill-over predation on deer fawns, could be partly responsible for the failure of the regional deer herd to recover to the high numbers observed in the 1950s, although changes in habitat since that time leading to the relative lack of early successional habitats today may also explain trends in deer numbers (Jenkins and Keal 2004, McGee et al. 2007). Future research focused on coyote predation in the Adirondacks will help to gain a better understanding of the roles that winter severity (along with a changing climate) and differential prey availability have in driving coyote foraging ecology.

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Table 1. Average live mass and coefficient of digestibility for prey items in coyote scat.

Prey item	Mass (kg)[a]	Coefficient of digestibility
Moose	270	1462
White-tailed deer adult (summer)	80	532
White-tailed deer (winter)	56	392
Beaver	26	208
White-tailed deer fawn (summer)	12	110
Porcupine	6	61.8
Snowshoe hare	1.5	19.5
Muskrat	1.5	19.5
Unknown	1.5	19.5
Bird	0.75	11
Red squirrel	0.25	4.4
Small rodents	0.05	1.2
Insect	-	1.0
Plant	-	1.0

[a]Mass of prey items taken from Saunders (1989).

Table 2. Summary of prey remains found in coyote scats collected winter 2009-11 and summer 2010-11 in the central Adirondacks, New York State, USA.

| Food Item	Winter (*n* = 74)			Summer (*n* = 100)		
	Percent of scats	% Dry mass in scats	% Biomass consumed	Percent of scats	% Dry mass in scats	% Biomass consumed
Mammals						
White-tailed Deer	59	62.4	81.0	-	-	-
Adult	-	-	-	11	5.0	22.5
Fawn	-	-	-	31	23.6	21.8
Beaver	24	13.7	17.8	25	29.5	51.4
Snowshoe Hare	8	9.5	0.7	20	20.5	3.3
Red Squirrel	1	2.4	0.0	3	1.4	0.0
Small Mammals	5	2.8	0.0	5	1.9	0.0
Muskrat	1	2.1	0.2	1	0.4	0.0
Porcupine	0	0.0	0.0	1	0.1	0.0
Moose	0	0.0	0.0	1	0.2	0.7
Unknown mammal	3	0.2	0.0	2	0.6	0.1
Birds	18	3.9	0.2	5	0.6	0.0
Insects	4	0.3	0.0	18	1.3	0.0
Fruit	3	0.1	0.0	14	14.7	0.0
Beech Nut	9	2.5	0.0	2	0.1	0.0
Human Refuse	0	0.0	0.0	3	0.0	0.0
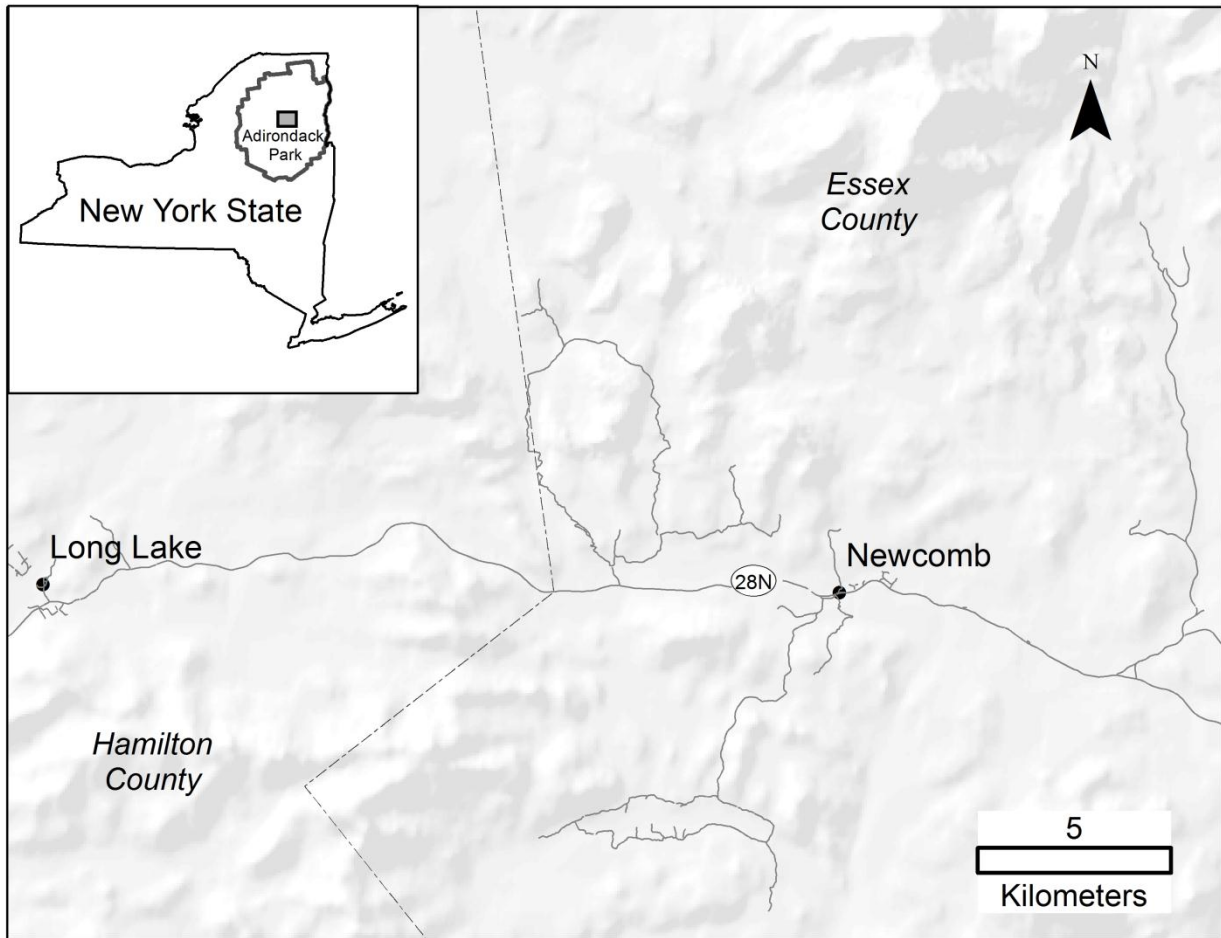
Figure 1. Map of the study area in the central Adirondacks of New York State, USA.
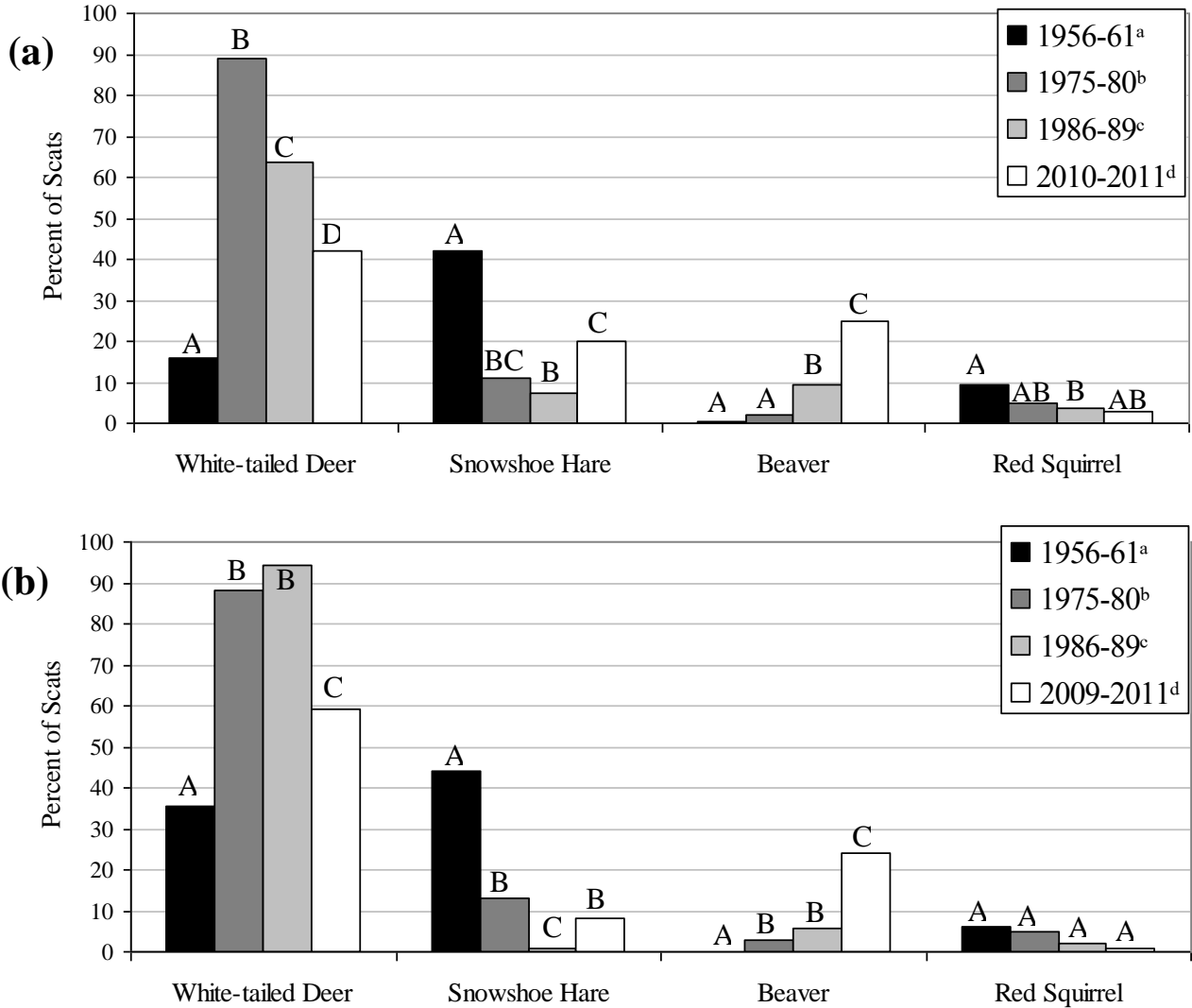
Figure 2. Frequency of prey items (percent of scats) in the summer (a) and winter (b) diet of coyotes (*Canis latrans*) over four time periods[a,b,c,d] in the central Adirondack region of New York State, USA. Differing letters among time periods indicate significant differences (p < 0.008) in the percent of scats containing a given prey item based on Pearson's chi-squared test.

[a] Hamilton (1974)

[b] Chambers (1987)

[c] Brundige (1993)

[d] This Study
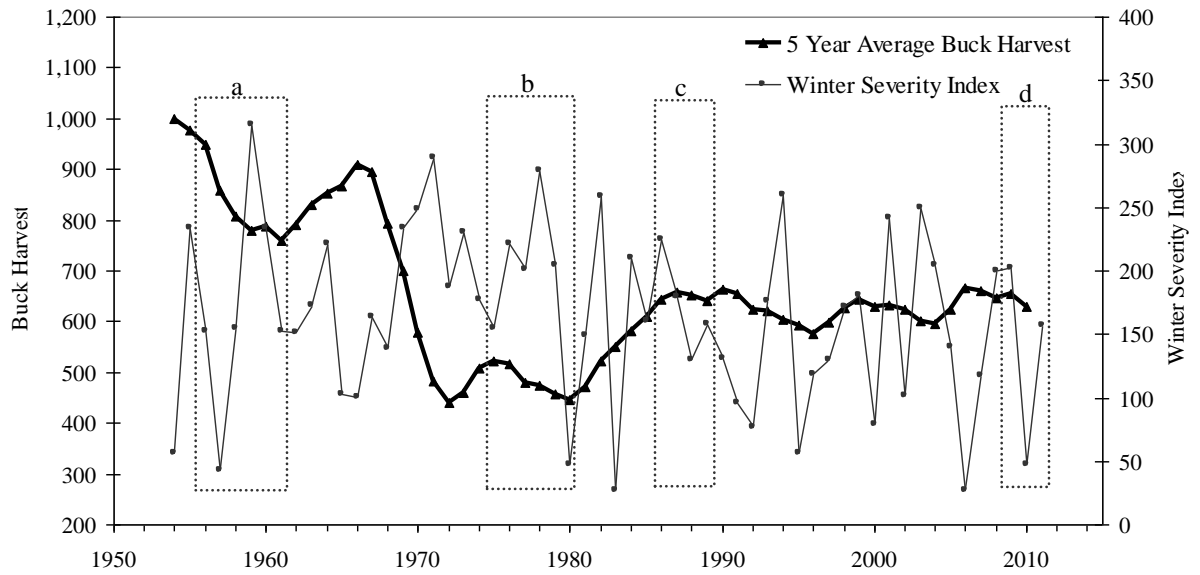
Figure 3. Five-year moving average of the regional white-tailed deer (*Odocoileus virginianus*) buck harvest and annual winter severity index in the central Adirondacks, NY, USA. Rectangles indicate periods[a,b,c,d] when coyote (*Canis latrans*) diet was studied in the region.

[a] Hamilton (1974) analyzed coyote diet in 1956-61.

[b] Chambers (1987) analyzed coyote diet in 1975-80.

[c] Brundige (1993) analyzed coyote diet in 1986-89.

[d] This study analyzes coyote diet in 2009-2011.
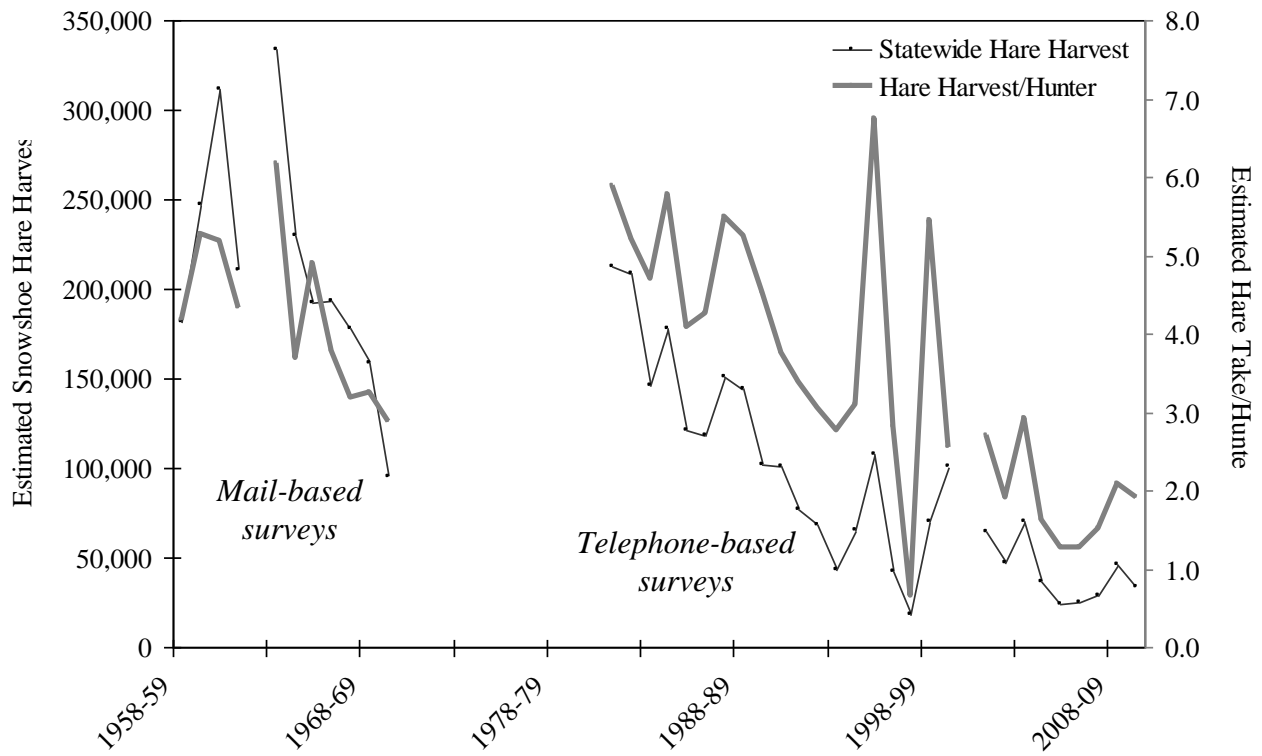
Figure 4. New York statewide estimated snowshoe hare harvest and hare harvest per hunter for the period of 1958-2010. Snowshoe hare were not included in hunter harvest surveys in 1970-1981. The hunter harvest survey was initially conducted via mail, but was changed to a telephone-based survey beginning with the 1983-84 season.
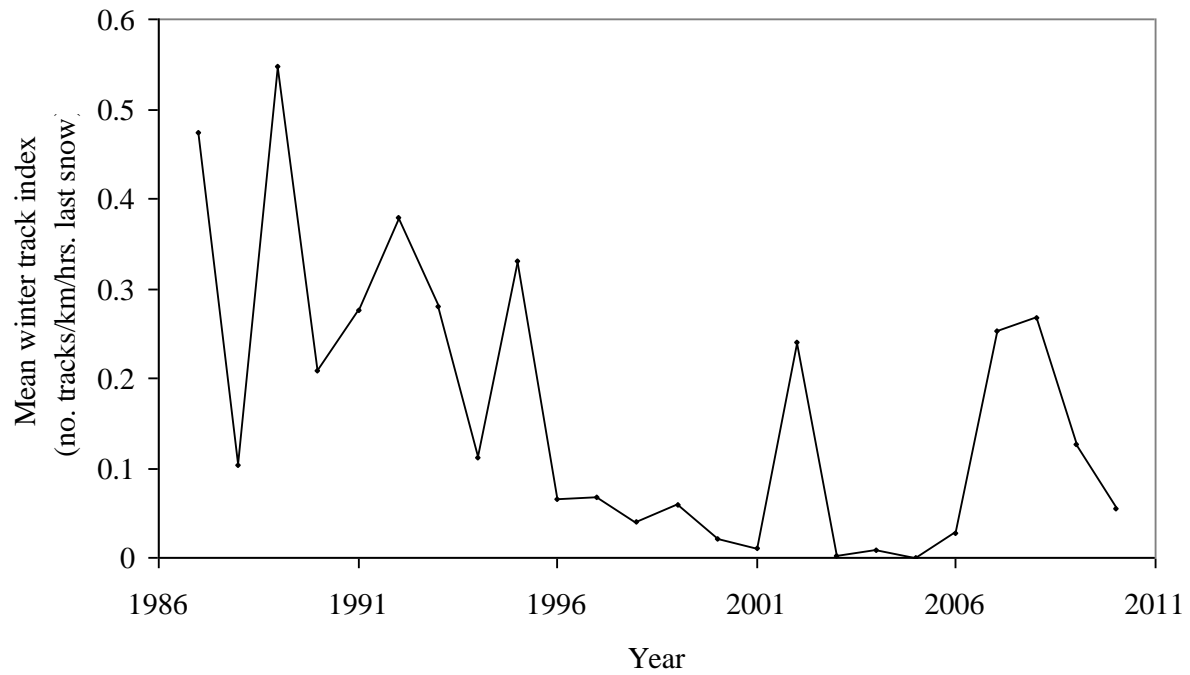
Figure 5. Mean winter track index[a] for snowshoe hare (*Lepus americanus*) at Huntington Wildlife Forest (HWF),

Newcomb, NY, USA 1987-2009. Track surveys were conducted by a trained observer 3-5 times each winter and are

standardized based on distance surveyed and time since last snowfall.

[a] See Jensen et al. (2012) for detailed HWF winter track count methodology.
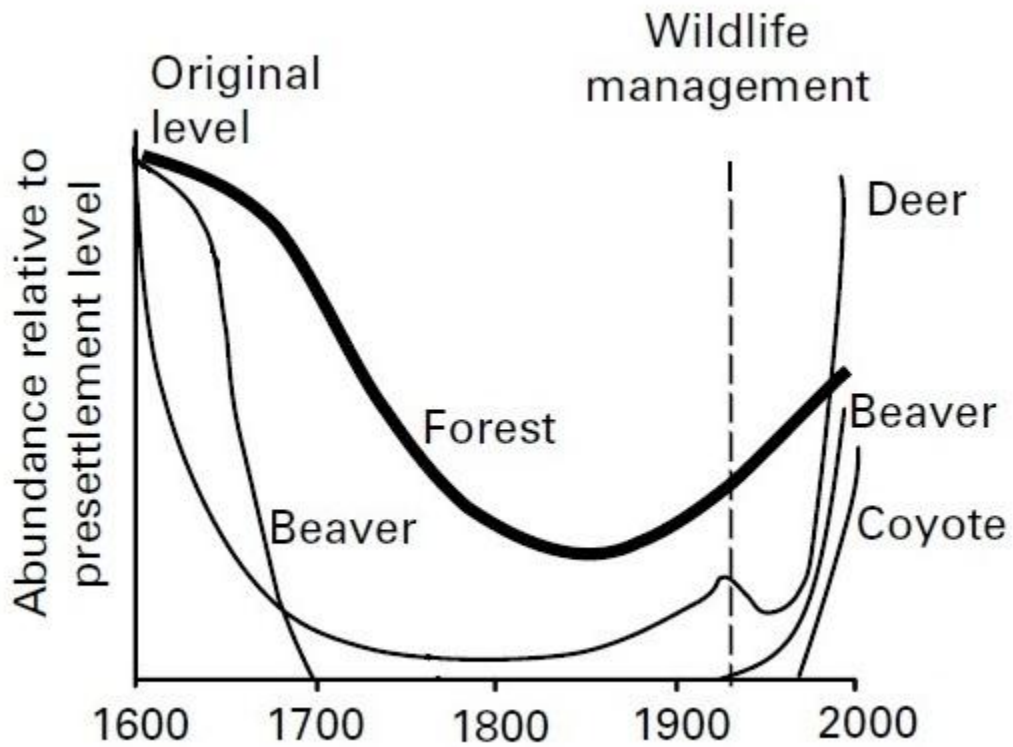
Figure 6. Estimated relative abundance of coyotes (*Canis latrans*) and two key prey species, white-tailed deer (*Odocoileus virginianus*) and beaver (*Castor canadensis*), in the northeastern United States over the last four centuries[a].

[a] Modified with permission from Foster et al. (2002).

Chapter 2

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RH: Warsen • Carnivore Stable Isotope Analysis

Stable Isotope Analysis as Evidence of Differential Resource Use Among Mammalian Carnivores in the Adirondack Park

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ABSTRACT

Stable isotope analysis is a powerful tool for exploring foraging strategies, but has been little

used in studies of terrestrial mammals. I used stable isotope analysis to explore alternative a

priori hypotheses regarding resource use among mammalian carnivores in the Adirondack Park,

New York State. Guard hair samples were collected from pelts of bobcat (*Lynx rufus*), coyote

(*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*). Stable

carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) were used to explore isotopic niche differentiation

among these four sympatric carnivores. Enrichment along the $\delta^{13}C$ axis was expected to reflect

use of human food sources of food (reflecting a corn subsidy), and by extension tolerance for

human-modified environments, whereas enrichment along the $\delta^{15}N$ axis was expected to reflect a

higher level of carnivory (i.e., amount of animal-based protein in the diet) – two mechanisms by

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which these species may achieve a dynamic coexistence. Although bobcats were the only obligate carnivore, all four species shared a similar $\delta^{15}N$ space. In contrast, bobcat had a lower and distinct $\delta^{13}C$ signature compared to foxes, consistent with the a priori expectation of bobcats being the species least tolerant of human activities. Isotope signatures for coyotes largely overlapped the other three species, bobcats the least, gray fox the most, indicating their potential competitive influence on this suite of native carnivores.

KEY WORDS Adirondacks, bobcat, coyote, gray fox, hair, New York State, niche partitioning, red fox, stable isotope analysis

INTRODUCTION

When Europeans first settled North America, the northeastern United States was home to wolves (*Canis lupus lycaon*) and cougars (*Puma concolor)*, while the smaller coyote (*Canis latrans*) occurred only in the Great Plains and western states (Parker 1995). A series of human-mediated events culminating at the turn of the 20th century – namely, the extirpation of large carnivores combined with large-scale forest clearing – allowed coyotes to dramatically expand their range across North America. The earliest records of coyotes in the northeastern United States occurred in 1925 in New York State (Bromley 1956). Over the past few decades coyotes have become the most ubiquitous mid-large bodied carnivore throughout the Northeast. Given that coyotes compete with and predate upon a wide array of species, they may profoundly affect the structure of ecological communities. Based on body size and dietary overlap, the native predators in the Northeast that coyotes are expected to compete with include red fox (*Vulpes vulpes*), gray fox (*Urocyon cineroargenteus*), and bobcat (*Lynx rufus*). Assuming coyotes to be a strong competitor, owing to their large body size and social structure, they may drive either changes in

the relative abundance of different species or strong niche differentiation among the native carnivores in the region.

The geographic range of coyotes overlaps that of bobcat, red fox, and gray fox throughout much of the United States, and comparative studies of species behavior and diet reveal two key patterns underlying potential niche differentiation among these species. First, these species differ in the degree to which they augment their diets with plant matter (Table 1). The inability of felids to produce certain essential amino acids (e.g. taurine) renders bobcats obligate carnivores (Scott 1968, Ballard et al. 2001, Vester et al. 2008, Pietsch et al. 2011). Bobcats therefore consume little plant matter. In contrast, gray foxes are facultative carnivores documented to supplement their diet with a high degree of plant matter, including persimmon (*Diospyros virginiana*), grapes (*Vitis* spp.), apples (*Malus* spp.), corn (*Zea mays*), juniper berries (*Juniperus* spp.), and prickly pear (*Opuntia* spp.; Small 1971, Pils and Klimstra 1975, Trapp and Hallberg 1978, Fritzell and Haroldson 1982, Walker 1991, Harrison 1997). Likewise, coyotes and red foxes consume plant matter to varying degrees, though to a lesser extent than gray foxes (Fritzell and Haroldson 1982, Chambers 1987, Feldhamer et al. 2003, Prugh 2005).

Second, these species differ in their tolerance for human-disturbances and human-modified environments (Table 2). Bobcats appear least tolerant of humans, avoiding roads (Major and Sherburne 1987) as well as urban and developed lands (Tigas et al. 2002, Thornton et al. 2004, Riley 2006, Ordenana et al. 2010), and also may be readily displaced by recreationists (George and Crooks 2006). In contrast, red fox and coyotes show rather high tolerance for humans, with higher population densities documented in urbanized areas than in adjacent rural habitats (Fedriani et al. 2001, Ordenana et al. 2010), and populations of both species have colonized and thrived in major metropolitan areas throughout North America (Gehrt et al. 2009,

Gehrt et al. 2010). Gray fox fall intermediate between red fox and bobcats, tolerating and

adapting to human influence to a degree, but avoiding high density subdivisions and showing a

preference for thickly vegetated habitat (Harrison 1997, Gehrt et al. 2010).   Importantly, use of

human-modified environments likely corresponds to access to anthropogenic food sources

(Fedriani et al. 2001, Newsome et al. 2010), which may subsidize natural food sources, allowing

for greater niche differentiation (Faeth et al. 2005).

An efficient way of exploring these two mechanisms of niche differentiation – levels of

carnivory and diet augmentation with anthropogenic food sources – is via stable isotope analysis.

The ratio of heavy to light nitrogen isotopes (reflected by δ^{15}N values) in living or keratinized

tissue changes in a predictable manner with trophic level. This is due mainly to the preferential

excretion of the lighter nitrogen isotope in waste products, yielding higher δ^{15}N values for

species occupying higher trophic levels (Minigawa and Wada 1984, Roth and Hobson 2000).

Furthermore, a direct relationship between increasing levels of animal protein in diet and

increasing δ^{15}N values in hair has been demonstrated in human populations (Yoshinga et al.

1996, O'Connel and Hedges 1999, Bol and Pflieger 2002). Bobcat, coyote, gray fox, and red fox

overlap in trophic position and diet, and therefore I do not expect statistically different positions

in δ^{15}N values. Instead, based on their observed levels of diet augmentation with plant matter I

expect the ranking of δ^{15}N values to be bobcats > coyote and red fox > gray fox, and following

the advice of Flaherty and Ben-David (2010), I focus on rankings rather than statistical tests.

The ratio of carbon isotopes (reflected by δ^{13}C values) changes only slightly between

trophic levels; however, differences do exist among species and largely reflect the source of

primary productivity in the food web (Schoeninger and DeNiro 1984). The presence of corn and

corn-derived materials in the diet of carnivores is a good indicator of foraging in anthropogenic

habitats due to the increasing abundance of corn and corn-syrup in processed foods intended for human consumption (Bol and Pflieger 2002, McCullagh et al. 2005, Jahren and Kraft 2008). The δ^{13}C values of corn materials are significantly enriched relative to the dietary material that comes from the native environment in my study area (Sage et al. 1999), a consequence of the different photosynthetic pathways used in corn (a C_4 plant) and the native vegetation (C_3 plants) in the Northeastern United States (Peterson and Fry 1987). Based on their tolerance for human-modified environments I expected the δ^{13}C ranking to be red fox > coyote and gray fox > bobcat. I tested these hypothesized rankings of stable isotope values in the Adirondack Park, New York, USA to investigate potential methods of niche partitioning among these four carnivores.

STUDY AREA

Mammalian guard hair samples were collected from bobcat, coyote, red fox, and gray fox pelts harvested by licensed trappers in the central Adirondack Park (Figure 1), a 23,700 km^2 tract of largely forested land in northern New York State. Pelts were sought in the central part of the park to avoid species access to agricultural fields that surround the park; however, some bobcat pelts came from peripheral areas. Main land cover types in the Adirondack Park are: deciduous forest (61%), coniferous forest (15%), mixed deciduous-coniferous forest (11%), open water (6%), and wetlands (5%; Homer et al. 2004). The park consists of large tracts of relatively undeveloped lands interspersed with pockets of human development. Average road density across the park is 0.35 km/km^2, and nearly one sixth of the park is roadless wilderness area. The estimated human population was 130,137 year-round residents in 2010, with the population more than doubling at the peak of the summer tourist season (Barge 2010).

METHODS

Stable isotope analysis was performed on mammalian guard hair, as stable isotope values of hair reflect the diet over a wide range of time (up to 9 months) relative to other types of tissue and it is the easiest and least expensive type of tissue to collect. Like most North American Carnivora, the four species studied here undergo a molt in the late spring or early summer months (Ling 1970, Newsome 2010). All samples came from individuals harvested in the 2010 trapping season. A sample of approximately 20 hairs was collected from 9-10 individuals of each species. Hair samples were cut as close to the skin as possible using a razor blade and, given the molt cycle and time of harvest (i.e., October – December 2009), likely reflect the individual's diet over the previous 5-7 months.

For stable carbon (δ^{13}C) and nitrogen (δ^{15}N) analyses, follicles were removed, hair samples were rinsed in a 2:1 dichloromethane:methanol solution to remove surface contaminants, then rinsed with distilled water, and air dried for 2 hours (Newsome 2010). Samples were homogenized with a mortar and pestle and sealed in tin boats for isotopic analysis (Teece and Fogel 2004). Stable carbon and nitrogen values were measured using a Costech ECS 4010 Elemental Analyzer coupled to a Thermo-Finnigan Delta XL Plus stable isotope ratio mass spectrometer via a Thermo-Finnigan Conflo III Interface at the Environmental Science Stable Isotope Laboratory at the State University of New York College of Environmental Science and Forestry in Syracuse, NY. Values are presented using the standard delta (δ) notation in parts per thousand (‰):

$$\delta^{13}C \text{ or } \delta^{15}N = [R_{SAMPLE} / R_{STANDARD} - 1]*1000,$$

where R_{SAMPLE} and $R_{STANDARD}$ correspond to the ratio of heavy to light isotopes in the sample and the international standard, respectively (Vienna PeeDee Belemnite [V-PDB] for carbon and

atmospheric nitrogen [N_2] for nitrogen). Accuracy and precision of stable isotope measurements were verified using standard reference materials including National Institute of Standards and Technology RM8573 ($\delta^{13}C$ = -26.4 ± 0.1‰, $\delta^{15}N$ = -4.5 ± 0.3‰ [n=38]) and RM8574 ($\delta^{13}C$ = +37.6 ± 0.2‰, $\delta^{15}N$ = +47.6 ± 0.3‰ [n=38]). Daily precision of the instrument was verified by repeated analyses of internal laboratory standards including acetanilide ($\delta^{13}C$ = -29.9 ± 0.2‰, $\delta^{15}N$ = -0.5 ± 0.3‰ [n=35]) and fish muscle tissue ($\delta^{13}C$ = -18.1 ± 0.2‰, $\delta^{15}N$ = +15.3 ± 0.3‰ [n=32]) during the sample runs.

The approximate location of harvest for each hair sample was recorded, and tests of geographic bias were conducted within each species for significant correlation between $\delta^{13}C$ or $\delta^{15}N$ values and elevation, latitude, and distance from the perimeter of the Adirondack Park (Vulla et al. 2009).

RESULTS

There was a high degree of overlap in stable carbon isotope values among individual red foxes, gray foxes, and coyotes (Figure 2A). The $\delta^{13}C$ values of bobcats, however, were conspicuously lower than the other three species, with no overlap observed between individual bobcats and gray or red foxes. When comparing mean isotope values among species, the predicted $\delta^{13}C$ rankings were observed: red fox had the highest mean ± 1 *SD* $\delta^{13}C$ values (-21.2 ± 1.0‰), gray fox and coyote had intermediate values (-21.8 ± 0.9‰ and -22.7 ± 1.2 ‰, respectively), and bobcat had the lowest values (-24.4 ± 0.5 ‰; Figure 2B). Bobcats also showed the least variation in $\delta^{13}C$ values among the four species.

The predicted rankings in $\delta^{15}N$ values, bobcat > coyote and red fox > gray fox, were not observed here. There was considerable overlap among the individual $\delta^{15}N$ values, as well as among mean species values (Figure 2B). The $\delta^{15}N$ values for red fox (6.8 ± 0.7‰) and coyote

(6.8 ± 0.7‰) were slightly higher than gray fox (6.6 ± 0.3 ‰), followed closely by bobcat (6.3 ±

1.1‰; Figure 2B). Gray fox $\delta^{15}N$ values were clustered tightly on the nitrogen scale, while

bobcats had the widest dispersion, registering both the highest and lowest individual $\delta^{15}N$ values

observed among all species.

Tests within species for geographic bias revealed no significant correlation between $\delta^{13}C$

or $\delta^{15}N$ values and elevation, latitude, or distance from the perimeter of the Adirondack Park (r^2

≤ 0.38, p ≥ 0.08).

DISCUSSION

Although stable isotope analysis has been used to compare individuals within a population, few

studies have demonstrated the utility of this technique for comparing resource use and niche

overlap among mammalian carnivores at the community level (but see Hobson et al. 2000, Lavin

et al. 2003, Urton and Hobson 2005). Hypothesized rankings of species in isotopic niche space

formed from a priori expectations and based on habitat use proved a useful way to explore

foraging strategies among species. I hypothesized that varying degrees of tolerance for human-

modified environments, corresponding to differential access to anthropogenic food sources that

are enriched in ^{13}C, would be reflected in the $\delta^{13}C$ values among these four species. Drawing

from radio-telemetry based studies of differential habitat use among these four species

(Blankenship 1995, Fedriani et al. 2000, Gosselink et al. 2003, Markovchick-Nicholls et al.

2008), the expectation of red fox > coyote and gray fox > bobcat in terms of $\delta^{13}C$ proved

accurate in the Adirondack Park, supporting the hypothesis that red fox, the most human-tolerant

of these four species, were the most likely to exploit anthropogenic food resources. Furthermore,

coyote and gray fox showed intermediate $\delta^{13}C$ values as predicted, and bobcat, the least human-

tolerant of these species, had the lowest $\delta^{13}C$ values. This order in $\delta^{13}C$ values among the four

species is likely due to varying incorporation of the C_4 signal into their respective diets by way of corn (and its derivative corn syrup in anthropogenic foods), contrasting the native flora of the Adirondack region which follows the C_3 photosynthetic pathway (Paruelo and Lauenroth 1996, Bol and Pflieger 2002, McCullagh et al. 2005, Jahren and Kraft 2008). Furthermore, this ordering of $\delta^{13}C$ values follow expectations: numerous dietary studies of red fox have found anthropogenic foods to be one of the most common items in their diet (Saunders et al. 1993, Lavin et al. 2003, Contesse et al. 2004). In this study site, anthropogenic foods are likely a supplemental, though not exclusive, source of food for red foxes. In contrast, a population of urban kit fox (*Vulpes macrotis*) in central California which extensively exploited anthropogenic food sources had hair $\delta^{13}C$ values of -17.4 ± 1.0‰, or 3.8‰ more positive than red fox hair $\delta^{13}C$ values in this study (Newsome et al. 2010). Bobcats, on the other hand, consume almost exclusively native prey, even when found in human-modified environments (Knick 1990, Riley 1999, Fedriani et al. 2000, Gehrt et al. 2010). Given that there is an enrichment of 1-2‰ in $\delta^{13}C$ values between a carnivore and its food, the mean $\delta^{13}C$ values of bobcat are consistent with a secondary consumer feeding almost exclusively on wild (i.e., non-anthropogenic) foods (Roth and Hobson 2000). A high degree of overlap is seen in coyote and gray fox $\delta^{13}C$ values. Niche partitioning between these two species may perhaps be driven not by differential resource use, but instead by differences in microhabitat use (e.g., gray foxes are able to climb trees while coyotes are not; Harrison 1997) or differences in temporal activity patterns (Atwood et al. 2011).

I hypothesized that the extent to which these four species supplement their diet with plant matter would be reflected in the ranking of $\delta^{15}N$ values, as has been demonstrated in humans with varying levels of animal protein in their diet (Yoshinga et al. 1996, O'Connel and Hedges 1999, Bol and Pflieger 2002). This was not the case as there was considerable overlap in $\delta^{15}N$

values of hair samples among the four species, with no significant differences among the mean signatures of the four species. Bobcat, the species I predicted would have the highest $\delta^{15}N$ values due to the high degree of carnivory and low plant consumption in its diet, did show the highest individual $\delta^{15}N$ value of all four species, though it also showed the lowest individual $\delta^{15}N$ value among all species. A possible explanation for the large range in $\delta^{15}N$ values of bobcat may be due to age or sex-related dietary differences, data which were unavailable for individuals in this study. McLean et al. (2005) found that male bobcats were more likely to consume meso-predators such as raccoon (*Prycyon lotor*) and Virgina opossum (*Didelphis virginiana*) which would likely result in $\delta^{15}N$ values higher than those of an individual bobcat feeding on strictly herbivorous species like white-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus* spp.), and snowshoe hare (*Lepus americanus*). An additional explanation for the similar $\delta^{15}N$ values across species may be due to how scat-based dietary studies (Table 1), on which I based my expectations, are quantified. The most simple and, therefore, most widely used method of quantifying diet in scat-based studies is to present the frequency of occurrence, expressed as the percentage of scats containing a particular food item. Critiques of this method are that it has minimal ecological significance and its results can be misleading (Klare et al. 2011). For example, the consumption of fruits and berries by canids tends to increase scat production, resulting in a greater apparent importance of fruits in the diet of those species (Neale and Sacks 2001). If this bias were present in the scat-based studies referenced (Table 1), predictions of $\delta^{15}N$ values in frugivorous species (e.g. gray fox) based on those biased studies would be lower than observed $\delta^{15}N$ values. Stable isotope analysis is robust against this bias, thereby providing a more accurate depiction of energy assimilated.

Although it is natural to assume that the variance in isotope values (i.e., isotopic niche) is a proxy for comparing ecological niches among species (Figure 2), one must use caution as the relation between isotopic and ecological niches is not necessarily straight-forward (Flaherty and Ben-David 2010), and isotopic niche can yield deceptive estimates of ecological niche width or breadth (Newsome et al. 2007). For example, the relatively small variance in $\delta^{15}N$ values of gray foxes does not mean they occupy a smaller ecological niche than the other three species. Rather, these results would indicate the opposite, as Bearhop et al. (2004) and Flaherty and Ben-David (2010) demonstrated that populations of dietary generalists will have narrower isotopic niche breadth compared to populations of dietary specialists because generalists sample broadly and thus average their diets. Furthermore, when comparing isotopic niches among species, one must also take into account the fact that isotopic niche is a property of not only foraging, but also habitat use (Newsome et al. 2007). I accounted for these two sources of isotope variability in my hypotheses: that varying tolerances for human-modified environments (i.e., differential habitat use) corresponds to differential access to anthropogenic food sources (Fedriani et al. 2001, Faeth et al. 2005, Newsome et al. 2010). Rather than attempting to calculate niche breadth and overlap based on stable isotope values, I followed the advice of Flaherty and Ben-David (2010) and investigated broad-scale patterns in the responses of individuals to the conditions they encounter in their environment. With that in mind, the observed $\delta^{13}C$ data support the hypothesis that red fox are the most likely and bobcat the least likely to exploit anthropogenic foods, though I have not found support for my hypothesis that the degree of carnivory in the diet of mammalian carnivores leads to predictable patterns in $\delta^{15}N$ values. The differential use of anthropogenic resources may be one factor preventing competitive exclusion and facilitating the dynamic co-existence of these four mammalian carnivores in the Adirondack Park.

MANAGEMENT IMPLICATIONS

Stable isotope analysis can be a valuable tool for examining foraging strategies and resource use (Flaherty and Ben-David 2010), especially when a hypothetico-deductive approach is taken and a priori hypotheses are confronted with stable isotope values. Due to the large difference in δ^{13}C values between native C_3 plants and anthropogenic corn-based diets (C_4 plants), stable isotope analysis of mammalian hair can function as a non-invasive and cost-effective means of monitoring wildlife baiting bans or proper disposal of human refuse.

Compared to traditional means of monitoring diet and resource use (e.g., scat-based survey or stomach content analysis), stable isotope analysis proves to be superior in several ways. Comparative scat-based surveys have an inherent uncertainty when multiple species in a study area produce scats of a similar appearance (e.g., coyotes and red foxes), while there is absolute certainty as to the species of origin when a hair sample is collected from a furbearer pelt. Stable isotope analysis also requires a much smaller time and labor commitment than traditional methods. These sample in this study were collected from two regional fur sales (~20 hours of labor) which was followed by minimal lab work (~20 hours) processing and analyzing the samples to eventually produce a summary of resource use over a period of approximately 6 months. In contrast, a scat-based study of diet over this same time period would require nearly weekly field work over the course of the 6 months (~240 hours) followed by extensive lab work processing scats and identifying prey remains (200+ hours). While a researcher must actively search for scats, at regional fur sales the samples come to the researcher. This disparity in time investments translates into a large difference in monetary costs between stable isotope analysis and traditional methods. The cost of collecting samples and running stable isotope analysis

(~$10/sample) is much lower than a scat-based survey (approximately $1,000 and $5,000; respectively).

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Table 1. Literature review of comparative studies of the diets of bobcats (B), coyotes (C), gray foxes (GF), and red foxes (RF) in USA. Varying degrees of carnivory exist among these four species: bobcats are obligate carnivores, whereas gray foxes are largely omnivorous and supplement their diet with a high degree of plant matter.

Species	Key Findings	Site	Study
GF,RF	Plant remains were more frequent and of a larger quantity in GF stomachs than RF stomachs.	IA	Scott (1955)
GF,RF	Mammals were most common RF food; plants were most common GF food	MD	Hockman and Chapman (1983)
B,C,RF	In summer, seeds and berries were of highest importance for RF, then C, and of little importance for B	ME	Major and Sherburne (1987)
B,C	B were strict carnivores; C consumed seeds and berries in summer and fall	ME	Litvaitis and Harrison (1989)
C,RF	Vegetation was slightly more common in RF diet than C diet	YT	Theberge and Wedeles (1989)
B,C,RF	Fruit was common in summer RF and C diet, but absent from B diet	ME	Dibello et al. (1990)
C,GF,RF	GF consumed greater proportion of fruit than RF or C	IL	Cypher (1993)
B,C,GF	B were solely carnivorous, while C and GF also consumed fruit	CA	Fedriani et al. (2000)
B,C,GF	Fruit was most prevalent in diet of GF, then C, and absent in B diet	CA	Neale and Sacks (2001)
B,C	C ate more fruit and seeds than B	AZ	McKinney and Smith (2007)

Table 2. Literature review of comparative studies of the responses of bobcats (B), coyotes (C), gray fox (GF), and red fox (RF) to human activities. Red fox are the most tolerant of human activity and bobcats are the least tolerant.

Species	Key Findings	Site	Study
B,C,RF	RF were most likely to travel on roads, followed by C, and B were least likely.	ME	Major and Sherburne (1987)
C,RF	Abandoned farmsteads were primary RF den sites	IL	Gosselink (1999)
B,C,GF	Occupancy surveys were conducted in a variety of habitats and C were only species detected in developed areas	CA	Fedriani et al. (2000)
C	C densities were higher in areas with anthropogenic foods	CA	Fedriani et al. (2001)
B,C	Greater proportion of C radio-locations were in developed areas than were those for B	CA	Tigas et al. (2002)
B,C,GF	C and GF were detected in urban habitat fragments more than B	CA	Crooks (2002)
C,RF	RF selected human-associated habitats and urban areas, which C generally avoided	IL	Gosselink et al. (2003)
C,RF	Sympatric RF and C; RF were found in urban habitat while C were absent	IL	Lavin et al. (2003)
B,C	Home range of B had lower proportion of human-modified habitat than that of C	CA	Riley et al. (2003)
B,C	B avoided developed sites while C used them proportional to their availability	FL	Thornton et al. (2004)
B,C	B showed greater spatial and temporal displacement in response to human recreation than did C	CA	George and Crooks (2006)
B,GF	Sympatric B and GF; GF used urban areas while B did not	CA	Riley (2006)
B,C,GF	C relative abundance increased with proximity to and intensity of urbanization; B and GF exhibited the opposite effect	CA	Ordenana et al. (2010)
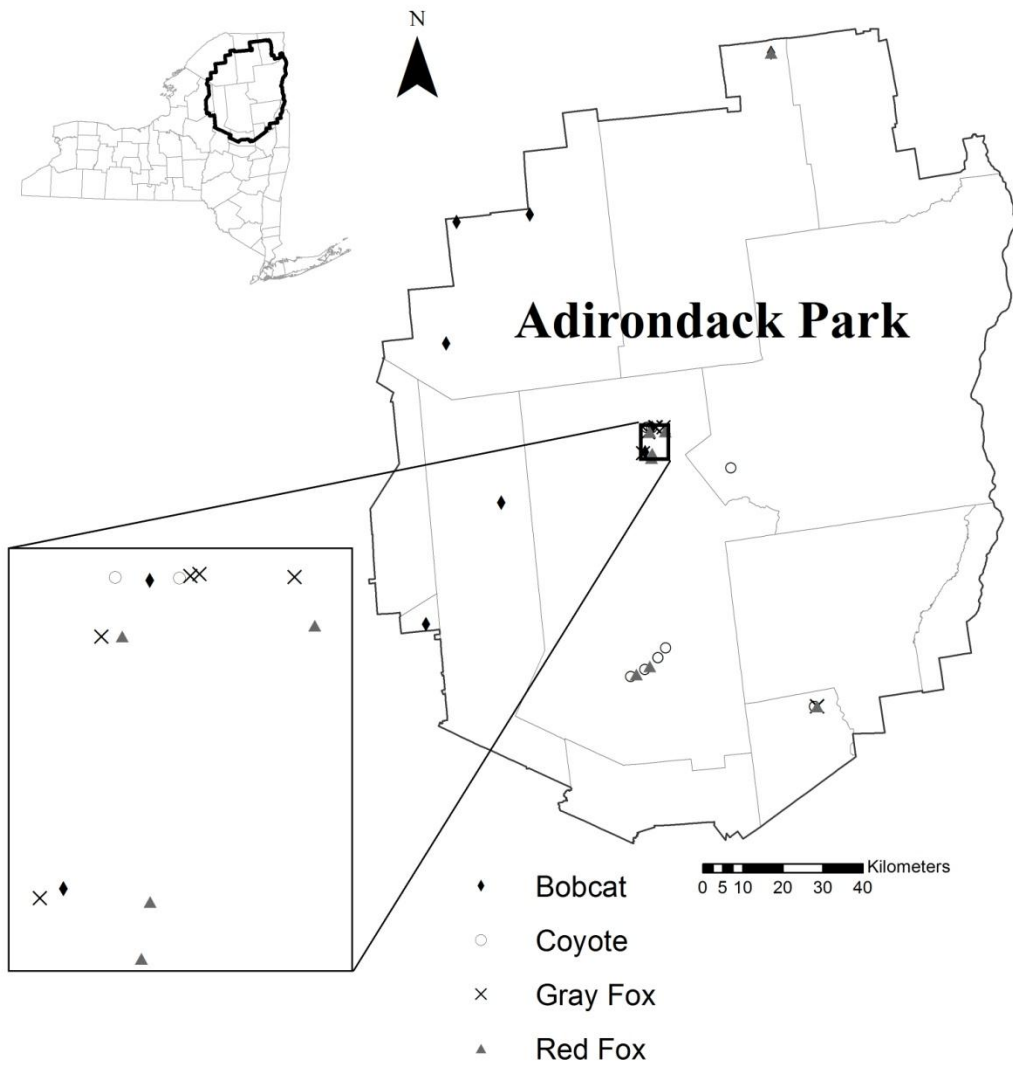
Figure 1. Map of New York State's Adirondack Park with locations where carnivore hair samples were collected in winter 2010-11.
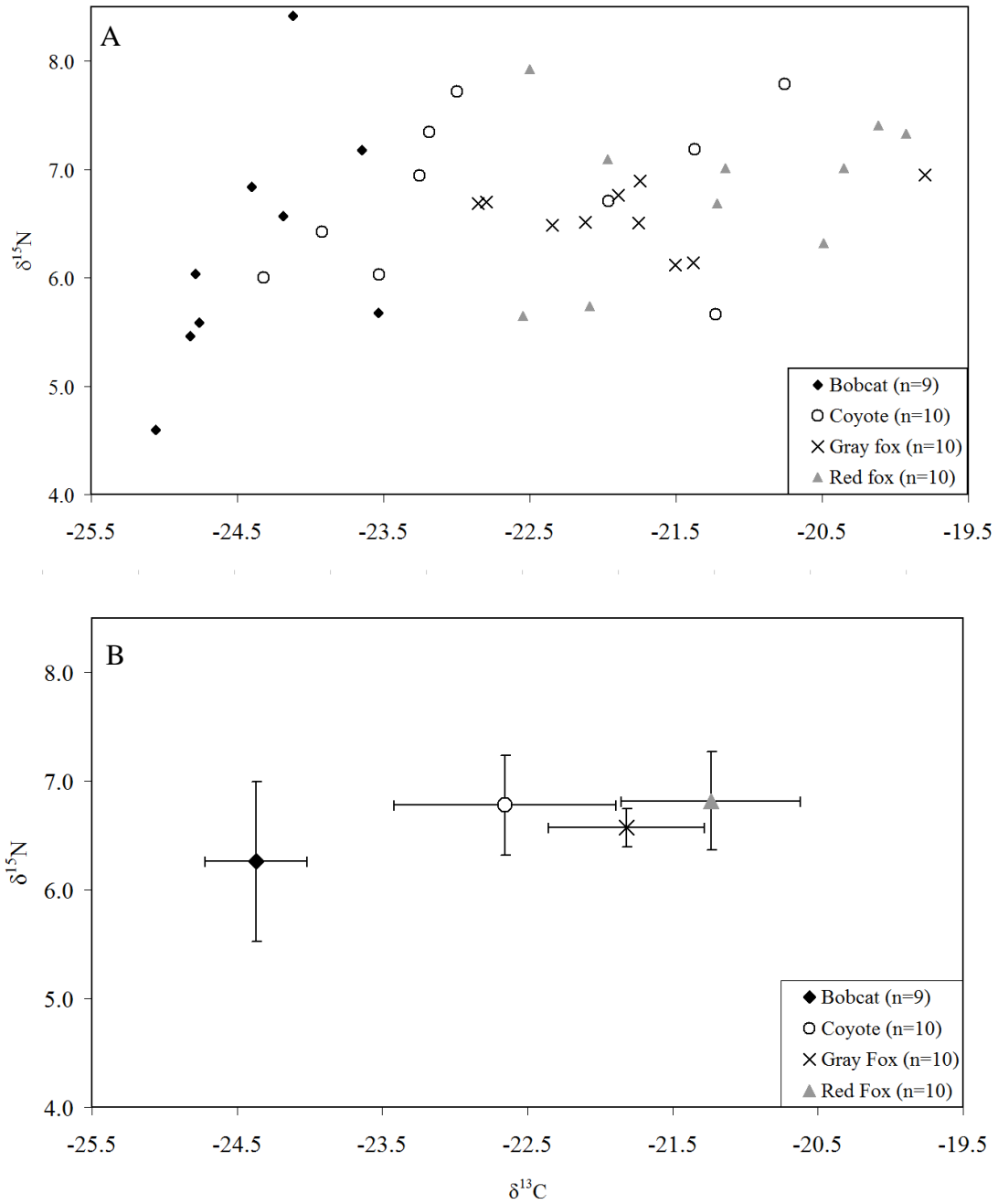
Figure 2. Individual (A) and mean (B) bobcat, coyote, gray fox, and red fox hair carbon and nitrogen stable isotope values (δ¹³C and δ¹⁵N, respectively) from samples collected in the Adirondack region of New York State. Values are expressed in permil (‰) and error bars represent 95% confidence intervals of the means.

Epilogue

Speculation as to whether coyotes (*Canis latrans*), a relatively new species in the Northeast, may perhaps fill the ecological niche of top predator once held by wolves (*Canis lupus senso lato*) is fueled by their partially-shared DNA as well as morphological and behavioral differences between northeastern coyotes and their western counterparts (Thurber and Peterson 1991, Parker 1995). One of the major gaps in our knowledge of coyote ecology and a recommended priority for research on northeastern coyotes is their role in structuring communities (Gompper 2002). This thesis begins to shed light on potential mechanisms by which coyotes may impact both prey species and potential competitors in the central Adirondacks of New York State.

In Chapter One, by quantifying contemporary coyote diet and comparing it to previous studies of coyote foraging ecology in the region (Hamilton 1974, Chambers 1987, Brundige 1989), we see that the previously observed trend of coyote diets becoming increasingly focused on and dominated by white-tailed deer (*Odocoileus virginianus*) has not continued. The sharp decline in deer use that I have documented occurs at a time when the regional deer population has stayed relatively constant since the previous study (Brundige 1989). Temporal changes in coyote diet most directly track the recovering beaver (*Castor canadensis*) population rather than changes in the deer or hare population. Furthermore, this study adds to our knowledge of Adirondack coyotes by incorporating information on the digestibility of different prey items to estimate total biomass consumed (Kelly 1991, Jędrzejewska and Jędrzejeswki 1998). These estimates indicate that beaver has become the main source of biomass consumed by coyotes in summer, whereas deer continue to dominate the winter diet. The generalist foraging behavior of the coyote is confirmed by this study, but, importantly, if an ongoing increase in the regional

beaver population is latently followed by an increase in the coyote population, then occasional coyote predation on a deer herd already exposed to frequent severe winters could eventually result in additive mortality and potentially limit deer numbers in the region. Future research on coyote predation in the Adirondacks will help to gain a more thorough understanding of how coyotes may structure prey species communities and the degree to which their predation is additive or compensatory.

Chapter Two, the use of stable carbon and nitrogen isotope analysis (δ^{13}C and δ^{15}N, respectively), presented a potential mechanism by which four sympatric mammalian carnivores – bobcats (*Lynx rufus*), coyotes, red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) – may be partitioning their ecological niches through differential resource use in the Adirondacks. Based on the ordering of δ^{13}C values, it appears that coyotes may be driving bobcats and red foxes to two different extremes of use of anthropogenic habitats and resources, with red foxes focusing most strongly on anthropogenic resources and bobcats, conversely, focusing on natural resources. As coyotes and gray foxes overlap in δ^{13}C space, their co-occurrence may instead be due to differences in microhabitat use and the ability of gray foxes to climb trees (Fedriani et al. 2000). Hair δ^{15}N values were not reflective of differences in the extent of carnivory among these four species. Previous work demonstrating the relationship between increasing levels of carnivory and δ^{15}N values has primarily been conducted on a single species (i.e., humans; Yoshinga et al. 1996, O'Connel and Hedges 1999, Bol and Pflieger 2002), and minor physiological differences among these species in how isotopes accumulate within and are excreted from the body (i.e., fractionation) may have masked any slight differences related to varying levels of intake of animal protein (Sponheimer et al. 2003).

Although minor differences in the degree of carnivory among species is difficult to detect by using δ^{15}N values in hair, this method does, however, allow comparison of trophic level among mammalian carnivores. In addition to the four mammalian carnivore species mentioned earlier, and following the methods outlined in Chapter 2, hair samples were collected from legally harvested pelts of all mammalian carnivores known to occur in the central Adirondacks: American marten (*Martes americana*), black bear (*Ursus americanus*), fisher (*Martes pennanti*), mink (*Neovison vison*), raccoon (*Procyon lotor*), river otter (*Lontra canadensis*), and weasel (*Mustela* spp.). Stable carbon and nitrogen stable isotope analysis was performed on hair samples and differences in trophic level appear to be accurately represented by δ^{15}N values (Figure 1). Black bears, whose seasonal diet may be comprised of up to 98% plant material (Brown 1993, Hellgren 1993, Rode et al. 2001), show the lowest δ^{15}N values (5.2 ± 1.2‰; mean ± SD) and are comparable to those reported for the hair of herbivores such as white-tailed deer (δ^{15}N = 3.8 – 5.9‰), goats (*Capra hircus*; δ^{15}N = 4.5 – 5.5‰), and horses (*Equus caballus*; δ^{15}N = 4.2 – 5.0; Darr and Hewitt 2008, Sponheimer et al. 2003). The opposite effect is seen in river otter and mink, which both forage extensively on aquatic prey species (e.g., fish, frogs, crayfish). Aquatic food chains tend to be longer than terrestrial food chains (Chase 2000, Post 2002), thus placing carnivores that forage on aquatic resources at a higher trophic level, and this is observed in the elevated δ^{15}N values of river otter and, to a lesser extent, mink.

Future research, perhaps involving museum specimens of these species, would help to better understand the degree to which the arrival of coyotes in the Adirondacks has driven this partitioning of resource use and how much of it occurred before coyotes colonized the region. In addition, the diet of beavers, which forage extensively on tree bark (Saunders 1989) may make them isotopically distinct from other herbivores in the region. If this is the case, stable isotope

analysis could be used to determine if the burgeoning Adirondack beaver population is now a major source of biomass consumed not only by coyotes, but also the other mammalian carnivores in the region.

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Papuans. American Journal of Physical Anthropology 100:23-24.
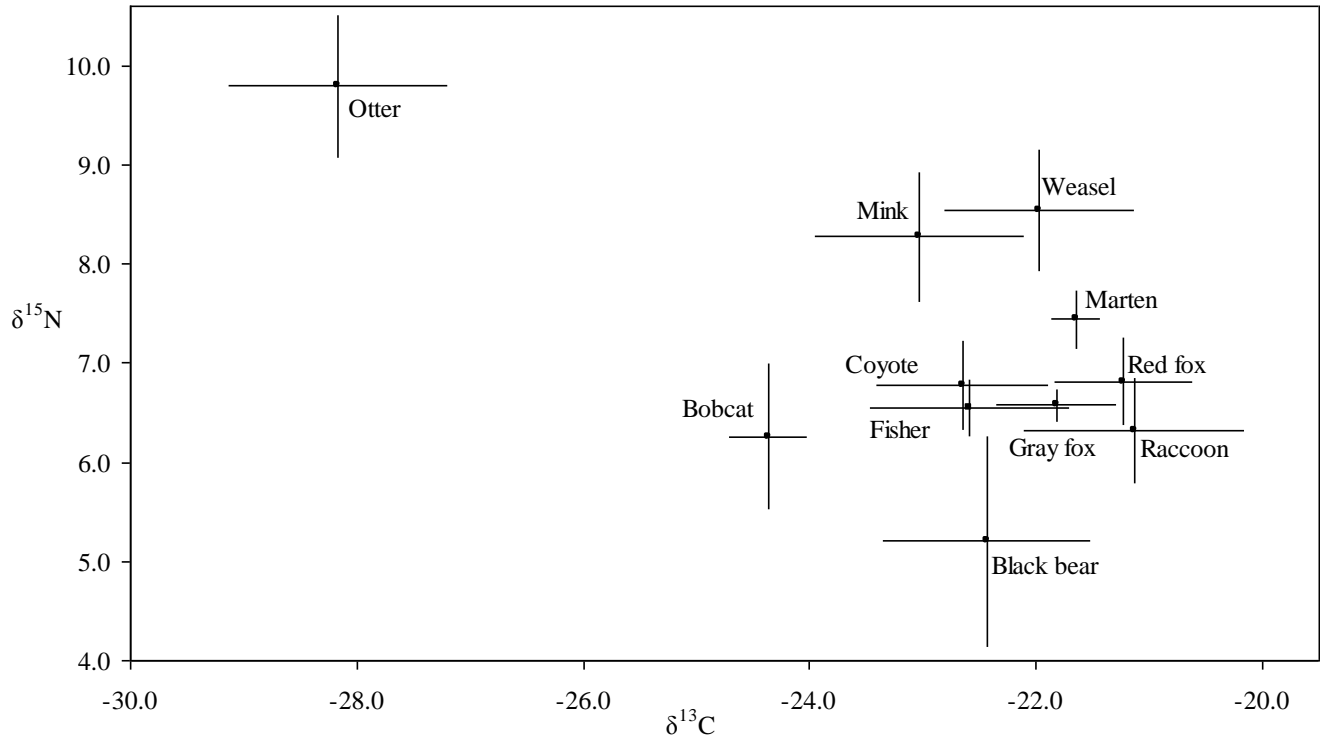
Figure 1. Mean carbon and nitrogen stable isotope values ($\delta^{13}C$ and $\delta^{15}N$, respectively) of hair samples collected from pelts of mammalian carnivores in the Adirondack region of New York State in winter 2010-11. Values are expressed in permil (‰) and error bars indicate 95% confidence intervals of the means.

Appendix A: Prey remains found in 100 summer coyote scats collected in the central Adirondacks 2010-2011.

Scat #	Item	Contents	Volume (%)	Mass (g)	Notes
1	a	fruit	100	10.7	rubus
2	a	beaver	80	11.58	
2	b	fruit	20	12.48	prunus
3	a	deer	100	13.1	fawn
4	a	deer	75	2	fawn
4	b	beaver	25	0.6	
5	a	deer	50	6.1	adult
5	b	beaver	50	6	
6	a	red squirrel	100	5.75	
7	a	deer	100	5.33	fawn
8	a	beaver	30	0.92	
8	b	fruit	30	1.85	rubus
8	c	fruit	35	1.55	apple
8	d	deer	5	0.39	fawn
9	a	fruit	70	0.95	apple
9	b	insect	30	4.75	
10	a	fruit	100	9.95	apple
11	a	beaver	90	5.55	
11	b	deer	10	1.9	fawn
12	a	beaver	65	12.2	
12	b	fawn	30	10.9	
12	c	insect	5	0.08	
13	a	beaver	100	18	
14	a	fruit	90	3.88	apple
14	b	insect	5	0.08	
14	c	beaver	5	1.1	
15	a	beaver	100	18.74	
16	a	snowshoe hare	70	4.53	
16	b	fruit	30	4.78	apple
24	a	deer	100	7.7	adult
25	a	fruit	95	6.48	rubus
25	b	insect	5	0.08	
26	a	fruit	100	22.05	prunus
27	a	fruit	90	11.28	prunus
27	b	fruit	5	0.28	rubus
27	c	deer	5	0.4	fawn

Scat #	Item	Contents	Volume (%)	Mass (g)	Notes
28	a	insect	60	0.1	
28	b	deer	40	0.05	fawn
100	a	deer	100	1.63	adult
103	a	beaver	100	8.48	
105	b	snowshoe hare	30	4.38	
106	a	beaver	100	6.58	
107	a	beaver	100	2.23	
109	a	beaver	100	13.39	
110	a	insect	100	0.98	
111	a	deer	100	6.96	fawn
112	a	muskrat	80	2.65	
112	b	bird	10	1.45	
112	c	insect	10	0.35	
113	a	deer	100	4.1	fawn
114	a	unknown	100	2.38	
115	a	deer	100	7.18	fawn
116	a	deer	70	4.45	fawn
116	b	red squirrel	30	1.69	
117	a	moose	60	1.05	
117	b	paper towel	40	1.28	
118	a	deer	100	9.2	fawn
119	a	deer	60	9.1	fawn
119	b	beaver	40	10.4	
119	c	insect	Trace	0.08	
120	a	beaver	100	3.66	
121	a	snowshoe hare	100	0.56	
122	a	snowshoe hare	100	5.21	
123	a	snowshoe hare	50	3.76	
123	b	deer	50	3.7	fawn
124	a	snowshoe hare	100	5.13	
125	a	deer	100	1.85	adult
126	a	deer	100	3.68	fawn
127	a	deer	100	15.23	fawn
128	a	deer	100	9.33	fawn
129	a	snowshoe hare	100	1.66	
130	a	deer	100	1.16	fawn
131	a	snowshoe hare	100	1.48	
132	a	beaver	100	29.51	
133	a	snowshoe hare	100	9.9	

Scat #	Item	Contents	Volume (%)	Mass (g)	Notes
134	a	deer	100	3.36	adult
135	a	small mammal	25	0.34	
135	c	fruit	75	3.18	rubus
136	a	beaver	95	0.28	
136	b	insect	5	0.02	
137	a	snowshoe hare	100	4.04	
138	a	snowshoe hare	100	3.46	
139	a	small mammal	100	0.58	
140	a	unknown	100	1.58	
141	a	deer	100	2.23	fawn
142	a	snowshoe hare	100	3.36	
143	a	snowshoe hare	60	2.18	
143	b	deer	40	1.81	adult
144	a	deer	100	3.25	fawn
145	a	deer	100	5.08	fawn
146	a	deer	100	1.55	adult
146	b	insect	Trace	0.05	
147	a	beaver	100	5.7	
148	a	small mammal	75	1.48	
148	b	insect	25	0.48	
148	c	bird	Trace	0.03	
149	a	Fruit	90	0.55	rubus
149	b	deer	10	0.2	fawn
150	a	deer	100	7.03	fawn
150	b	bird	Trace	0.08	
150	c	insect	Trace	0.08	
151	a	deer	100	2.44	adult
152	a	bird	70	2.44	
152	b	plastic	10	0.08	
152	c	beech	20	0.18	
153	a	insect	100	0.08	
154	a	insect	100	0.18	
155	a	insect	100	0.28	
156	a	insect	100	0.08	
157	a	beech	100	0.45	
158	a	insect	100	0.21	
159	a	deer	45	1.35	adult
159	b	bird	5	0.04	
159	c	snowshoe hare	45	1.02	

Scat #	Item	Contents	Volume (%)	Mass (g)	Notes
160	a	deer	100	5.76	fawn
161	a	deer	70	10.1	fawn
161	b	beaver	30	6.91	
162	a	deer	100	5.74	fawn
163	a	deer	100	1.26	fawn
164	a	fruit	100	5.65	rubus
165	a	beaver	90	6.24	
165	b	porcupine	10	0.44	
166	a	red squirrel	100	1.36	
167	a	deer	50	2.94	adult
167	b	snowshoe hare	50	2.9	
168	a	small mammal	75	4.81	
168	b	fruit	25	1.39	rubus
169	a	snowshoe hare	100	29.71	
170	a	deer	100	9.63	fawn
171	a	deer	100	1.86	fawn
172	a	beaver	100	3.06	
173	a	snowshoe hare	100	12.39	
174	a	snowshoe hare	100	15.01	
175	a	fruit	80	2.48	rubus
175	b	insect	10	0.58	
175	c	deer	10	0.43	fawn
176	a	snowshoe hare	80	10.25	
176	b	beaver	20	4.08	
177	a	beaver	100	9.06	
178	a	deer	100	1.66	adult
179	a	beaver	100	4.51	
180	a	deer	75	1.93	fawn
180	b	beaver	25	0.53	
181	a	snowshoe hare	100	10.73	
182	a	small mammal	100	4.83	

Appendix B: Prey remains found in 74 winter coyote scats collected in the central Adirondacks 2009-11.

Scat #	Bag	Contents	Volume (%)	Mass (g)	Notes
17	a	deer	100	0.65	
31	a	beaver	50	0.4	
31	b	plant matter	50	0.15	
32	a	unknown	100	0.19	
33	a	beech	100	0.29	
34	a	small mammal	75	2.38	
34	b	plant matter	25	0.18	
35	a	beech	95	1.65	
35	b	bird	5	0.1	
36	a	beech	90	1.35	
36	b	deer	5	0.3	
36	c	bird	5	0.1	
37	a	beech	90	0.48	
37	b	deer	10	0.13	
38	a	deer	95	1.28	
38	b	bird	5	0.08	
39	a	bird	80	0.85	
39	b	deer	20	0.3	
40	a	beech	75	1.08	
40	b	deer	25	0.71	
41	a	deer	100	7.75	
42	a	snowshoe hare	100	10.18	
43	a	snowshoe hare	50	3.03	
43	b	beaver	50	3.53	
44	a	beaver	100	8.23	
45	a	deer	100	5.44	
46	a	bird	100	4.85	turkey
47	a	red squirrel	100	6.12	
48	a	deer	100	1.77	
49	a	muskrat	70	5.35	
49	b	snowshoe hare	30	2.42	
50	a	deer	100	2.16	
51	a	deer	100	2.5	
52	a	small mammal	100	1.26	
52	b	insect	Trace	0.18	
53	a	deer	100	3.35	
54	a	deer	100	8.18	

Scat #	Bag	Contents	Volume (%)	Mass (g)	Notes
54	d	plant matter	10	0.18	
55	a	plant matter	100	0.18	
56	a	deer	80	0.34	
56	c	fruit	20	0.05	apple
57	a	beaver	100	3.68	
58	a	snowshoe hare	100	1.14	
59	a	deer	100	2.13	
60	a	beaver	100	6.18	
61	a	small mammal	100	2.68	
62	a	deer	100	2.26	
63	a	beech	100	0.95	
64	a	beaver	100	3.69	
65	a	deer	100	7.25	
66	a	beaver	100	2.39	
67	a	deer	80	1.88	
67	b	beaver	15	0.49	
67	c	bird	5	0.08	
68	a	deer	100	13.48	
69	a	beaver	100	1.94	
70	a	snowshoe hare	70	0.77	
70	b	insect	20	0.11	
70	c	bird	10	0.13	
71	a	deer	100	0.06	
72	a	deer	30	0.18	
72	b	beaver	40	0.93	
72	c	bird	30	0.28	
73	a	deer	100	1.64	
74	a	insect	50	0.48	
74	b	bird	30	0.28	
74	c	beaver	20	0.49	
75	a	beaver	100	8.43	
76	a	deer	100	7.9	
77	a	deer	60	1	
77	b	beaver	40	1.13	
78	a	deer	100	1.05	
79	a	deer	75	8.03	
79	b	beaver	25	4.16	
80	a	deer	100	0.2	
81	a	deer	100	1.4	
82	a	deer	100	0.46	

Scat #	Bag	Contents	Volume (%)	Mass (g)	Notes
83	a	bird	100	0.6	
84	a	deer	90	1.23	
84	b	insulation	10	0.68	
85	a	unknown	100	0.38	
86	a	beaver	100	5.88	
87	a	deer	100	5.4	
88	a	deer	100	5.33	
89	a	deer	100	0.56	
90	a	deer	100	2.46	
91	a	small mammal	100	0.8	
92	a	deer	70	0.29	
92	b	beaver	30	0.24	
93	a	deer	100	1.66	
94	a	bird	100	2.34	
95	a	deer	100	1.86	
96	a	deer	50	0.18	
96	b	beaver	50	0.29	
97	a	deer	100	6.53	
97	b	bird	Trace	0.09	
98	a	deer	100	2.16	
99	b	beech	100	0.38	
101	a	deer	95	4.14	
101	b	fruit	5	0.19	apple
102	a	deer	100	0.68	
104	a	snowshoe hare	100	6.53	
105	a	deer	70	12.35	
108	a	deer	80	6.55	
108	b	beaver	20	3.93	
108	c	bird	Trace	0.14	turkey

Appendix C: Carbon and nitrogen stable isotope values (δ^{13}C and δ^{15}N, respectively) of guard hair samples collected from mammalian carnivores in the Adirondack Park in winter 2010-11.

Sample #	Species	δ^{13}C	δ^{15}N
245	bear	-22.0	4.9
285	bear	-23.2	4.0
356	bear	-20.3	4.0
357	bear	-23.0	4.9
358	bear	-23.1	6.6
359	bear	-23.1	6.8
16	bobcat	-23.5	5.7
17	bobcat	-25.1	4.6
253	bobcat	-24.2	6.6
262	bobcat	-24.8	6.0
271	bobcat	-24.8	5.6
272	bobcat	-24.8	5.5
349	bobcat	-24.4	6.8
351	bobcat	-23.6	7.2
352	bobcat	-24.1	8.4
161	coyote	-22.0	6.7
163	coyote	-23.2	7.3
184	coyote	-21.2	5.7
263	coyote	-24.3	6.0
264	coyote	-23.5	6.0
268	coyote	-23.9	6.4
269	coyote	-23.0	7.7
286	coyote	-21.4	7.2
287	coyote	-20.8	7.8
288	coyote	-23.3	6.9
215	fisher	-22.0	6.6
292	fisher	-23.8	6.0
293	fisher	-22.0	6.7
321	fisher	-23.5	6.7
322	fisher	-19.4	7.4
323	fisher	-23.1	5.9
325	fisher	-22.8	6.4
326	fisher	-23.1	6.5
327	fisher	-23.6	6.7
167	gray fox	-22.3	6.5
168	gray fox	-21.8	6.5

Sample #	Species	$\delta^{13}C$	$\delta^{15}N$
169	gray fox	-22.9	6.7
170	gray fox	-21.7	6.9
171	gray fox	-22.8	6.7
299	gray fox	-21.4	6.1
300	gray fox	-21.5	6.1
301	gray fox	-21.9	6.8
302	gray fox	-22.1	6.5
303	gray fox	-19.8	6.9
216	marten	-22.3	7.5
217	marten	-21.8	7.9
218	marten	-21.2	7.6
220	marten	-21.2	7.6
275	marten	-21.6	6.5
276	marten	-21.8	8.1
277	marten	-21.5	8.0
289	marten	-21.6	6.9
290	marten	-21.6	7.2
291	marten	-22.0	7.1
221	mink	-23.8	7.9
222	mink	-23.1	7.6
223	mink	-23.5	7.4
224	mink	-24.3	8.3
225	mink	-23.8	7.5
274	mink	-20.1	11.1
328	mink	-22.4	8.4
329	mink	-21.3	8.2
330	mink	-22.6	8.5
360	mink	-25.4	7.8
185	otter	-31.2	10.7
186	otter	-26.9	10.7
187	otter	-27.1	9.6
231	otter	-26.7	8.8
232	otter	-28.7	8.0
233	otter	-29.6	9.6
234	otter	-29.2	8.7
240	otter	-28.3	10.7
273	otter	-26.0	11.9
252	otter	-28.0	9.1
172	raccoon	-23.1	6.9
241	raccoon	-18.0	6.4

Sample #	Species	$\delta^{13}C$	$\delta^{15}N$
242	raccoon	-20.4	5.1
243	raccoon	-21.0	5.0
244	raccoon	-19.3	6.2
278	raccoon	-21.8	6.9
279	raccoon	-21.8	7.2
318	raccoon	-20.9	6.4
319	raccoon	-22.6	5.6
320	raccoon	-22.4	7.5
165	red fox	-22.1	5.7
265	red fox	-20.4	7.0
266	red fox	-20.5	6.3
267	red fox	-21.2	7.0
283	red fox	-22.0	7.1
284	red fox	-22.5	5.6
295	red fox	-20.1	7.4
296	red fox	-21.2	6.7
297	red fox	-22.5	7.9
247	red fox	-19.9	7.3
361	weasel	-21.1	8.5
362	weasel	-21.4	7.9
363	weasel	-23.5	9.6
364	weasel	-21.7	7.6
365	weasel	-21.2	7.2
260	weasel	-22.0	8.0
261	weasel	-20.5	8.6
281	weasel	-21.8	9.4
282	weasel	-24.6	10.0

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