

Diet and Feeding Ecology of Coyotes, Black Bears, and Bobcats in Western Virginia and Preliminary Assessment of Coyote Parasites

David M. Montague

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Marcella J. Kelly
Mike Fies
James Parkhurst
Kathleen Alexander
Anne Zajac

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ABSTRACT

Although deer abundance is high throughout most areas of Virginia, parts of western Virginia, especially on public lands, have comparatively low density deer populations. Concerns voiced by sportsmen regarding declining deer numbers in this region prompted interest in research to investigate the role of predation on deer populations. The coyote (*Canis latrans*) is a relative newcomer to Virginia, and relatively little is known about the role coyotes play in Virginia ecosystem dynamics, including their interactions with other sympatric predators. Research studies in other areas suggest that predation from coyotes, bobcats (*Lynx rufus*), and black bears (*Ursus americanus*) may be a significant source of deer (*Odocoileus virginianus*) mortality, especially for fawns, and the cumulative effects of predation from these sources may also increase the potential for additive mortality in deer populations. An important consideration when comparing feeding strategies of carnivores is the relative availability of food items across the landscape. I estimated the relative seasonal availability of several potential food items in a mosaic landscape that included some areas of prescribed burning and variable timber harvest in the mountains of western Virginia between June 2011 and May 2013. I focused on 4 broad categories of food items: white-tailed deer, mid-sized mammals (raccoons, *Procyon lotor*, opossums, *Didelphis virginiana*, cottontails, *Sylvilagus* spp., and squirrels, *Sciurus* spp.), small mammals, and soft mast. I used distance sampling to estimate deer density, camera trapping techniques to estimate mid-sized mammal trapping rates and occupancy, mark-recapture

techniques to estimate small mammal abundance, and vegetation sampling to estimate % cover, which I used as measures of food availability for predation. To estimate carnivore diet, I analyzed scats of coyotes ($n = 334$), bobcats ($n = 258$), and black bears ($n = 107$) collected monthly from June 2011 and May 2013. Additionally, I compared estimates of % occurrence to estimates of seasonal availability of deer, mid-sized mammals, small mammals, and soft mast by ranking availability of food items from 0 (unavailable) to 4 (highly available) from my monthly and seasonal food item abundance and density estimates. I then ranked % occurrence in scat on a 0 - 4 scale and compared diet rankings to food item availability where changes in rank indicate differences from the generalist diet.

Deer densities were substantially higher in Bath County ($4.75 - 16.06$ deer/km²) than in Rockingham County ($0.17 - 3.55$ deer/km²). I estimated availability of other food items only in Bath County. For mid-sized mammals, I estimated low activity as shown by constant, but low, trapping rates ($\# \text{photo events} / \text{trap nights} * 100$) of opossums, and relatively higher, constant trapping rates of cottontails. Raccoon and squirrel trapping rates were highly variable across seasons and raccoon occupancy (proportion of sites occupied) was higher in summer and fall ($0.51 - 0.59$) whereas squirrel occupancy was highest in October-November ($0.51 - 0.53$). Cottontail and opossum occupancies were higher in burned areas ($0.40 - 0.57$, $0.24 - 0.46$, respectively), whereas raccoon and gray squirrel occupancies were higher in unburned areas ($0.23 - 0.78$, $0.12 - 0.58$, respectively). Using program MARK I estimated high abundance and density of *Peromyscus* spp. in all seasons relative to other small mammal species. Densities of meadow voles and jumping mice were high seasonally in open field habitat. Densities of eastern chipmunks, red-backed voles, and *Peromyscus* spp. were significantly higher in burned areas relative to unburned sites. Among soft mast species, blueberries comprised the largest %

occurrence. I expect a generalist predator to consume deer at a constant rate and have lower % deer occurrence in Rockingham County where deer densities are much lower. I expect seasonally constant, but low, occurrence of opossum and relatively higher, but similarly constant, occurrence of cottontail. I expect raccoon occurrence to be relatively high in summer and fall, and lower in winter. Squirrel occurrence should peak in October and November, followed by a steady decline until June. Based on availability, *Peromyscus* spp. should be the most commonly occurring small mammal in the diet of a generalist predator, rivaled by meadow voles (*Clethrionomys gapperi*) in fall and perhaps summer. I expect chipmunks (*Tamias striatus*) and red-backed voles to occur at constant but low rates in predator diets. I predict that various species of soft mast may occur during their respective fruiting seasons.

Deer were the most frequently occurring food item of coyotes in all months in both counties, with % biomass consumed highest in June (Bath: 60.0 - 90.9 %; Rockingham: 55.6 - 92.3%). Deer occurrence in bobcat scat peaked in June (77.54 %). In black bear scat, deer occurrence was highest in February and March (100 %), however sample sizes in these months were extremely low (n = 2, 3 respectively). All 3 predators consumed deer more than expected in June and July. In most months, coyotes consumed deer and soft mast more often than expected (1 rank higher) and they consumed deer much higher (2-3 ranks higher) than expected in January and February. While deer was a major food item in the diets of all 3 predators, it is unclear whether this observed result was caused by predation or scavenging. It is unlikely that coyotes, bears, or bobcats are preying on adult deer with high frequency. I did not estimate the availability of deer carcasses for scavenging in this study. If deer carcasses are highly available in the study area, this may explain the high occurrence of deer in carnivore scat and the lack of seasonality in coyote samples.

Mice (*Peromyscus* spp.) were consumed by predators less than expected based on availability, whereas squirrels and chipmunks were consumed by bobcats more than expected. Meadow and red-backed voles were consumed more than expected by both bobcats and coyotes. Mid-sized mammals occurred with expected frequency or lower in predator scats. Coyotes had the lowest diversity and variation in diet, whereas bobcat and bear diets were more diverse including seasonal use of many species. Coyotes exhibited more selectivity (based on changes, and magnitude of changes, in rankings for food item occurrence versus availability) and appear more specialized on deer in all months than bobcats.

I analyzed 203 randomly-selected coyote fecal samples using a modified Wisconsin fecal flotation technique. I identified 13 parasite taxa, 9 of which occurred with adequate frequency to permit statistical analysis. No landscape patterns or statistically significant seasonal differences were found in prevalence of parasite taxa, and only *A. caninum* and *Eimeria* spp. were significantly higher, and *Cystoisospora* spp. was somewhat significantly higher, in Bath versus Rockingham Counties. By comparing my data on spatio-temporal patterns of food availability to patterns in the scats of predators, we have better understanding of predator foraging strategies and can identify opportunities for targeted management to balance predator-prey dynamics with human needs and values. More research is needed on the interactions of sympatric predators in specific areas to gain further inferences regarding population-level impacts of predation on deer in western Virginia.

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Jacob Barbee	Nelson Lafon
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Kurtis Blosser	Michael Lopez
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Samantha Bunn	Casey Maynard
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Table of Contents

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	vi
TABLE OF CONTENTS.....	viii
LIST OF FIGURES	x
LIST OF TABLES.....	xiii
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW	
Introduction and Justification	1
Food Availability	5
Diet of Coyotes	8
Diet of Bobcats	12
Diet of Black Bears.....	15
Cumulative Effects on Deer Populations.....	16
Scat Study Techniques.....	17
Coyote Parasites.....	21
Expected Outcomes and Management Implications.....	24
Study Area	25
Literature Cited.....	26
Tables and Figures	39
CHAPTER 2: FOOD AVAILABILITY FOR CARNIVORES IN THE APPALACHIAN MOUNTAINS OF VIRGINIA	
Abstract.....	41
Introduction.....	43
Methods.....	44
Results.....	51
Discussion.....	56
Acknowledgements.....	63
Literature Cited.....	63
Tables and Figures	70

CHAPTER 3: SEASONAL DIETS OF COYOTES, BLACK BEARS, AND BOBCATS IN WESTERN VIRGINIA

Abstract85
Introduction.....86
Methods.....88
Results.....93
Discussion100
Acknowledgements.....109
Literature Cited110
Tables and Figures120

CHAPTER 4: INTERNAL PARASITES OF COYOTES IN VIRGINIA

Abstract137
Introduction.....138
Methods.....140
Results.....142
Discussion144
Acknowledgements.....147
Literature Cited148
Tables and Figures151

CHAPTER 5: CONCLUSIONS162

LIST OF FIGURES

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

- Figure 1: Deer hunter harvest indices (harvested bucks/mi²) from 1994 to 2013 for Bath County (public and private lands combined) and Rockingham County (public land only), Virginia, as tabulated by Virginia Department of Game and Inland Fisheries.39
- Figure 2: Map of the study areas for predator research in Virginia highlighting (L to R) Bath and Rockingham Counties. Orange boxes denote the general region of each county studied.40

CHAPTER 2: PREY AVAILABILITY FOR CARNIVORES IN THE APPALACHIAN MOUNTAINS OF VIRGINIA

- Figure 1: Thermal images of deer as seen through forward-looking infrared (FLIR) imagery....81
- Figure 2: Seasonal deer density estimates with 95% confidence intervals for Bath and Rockingham Counties as determined by distance estimation in Program DISTANCE.81
- Figure 3: Seasonal activity by habitat type of 4 mid-sized mammal species in Bath County, Virginia as determined by trapping rates and 95% confidence intervals of trail cameras (n = 48) between June 2011 and May 2013. * denotes significance between habitat types; + denotes near-significance ($\alpha = 0.05$).82
- Figure 4: Monthly availability (occupancy) and 95% confidence intervals of 4 mid-sized prey species modeled in Program Presence with monthly data pooled from 2011, 2012, and 2013.83
- Figure 5: Estimates of seasonal population density and 95% confidence intervals of small mammal species trapped in Bath County in A) burned/unburned habitats and B) fields.84

CHAPTER 3: SEASONAL DIETS OF COYOTES, BLACK BEARS, AND BOBCATS IN WESTERN VIRGINIA

- Figure 1: Locations of transects in (a) Bath and (b) Rockingham Counties, Virginia where carnivore scats were collected from June 2011 to May 2013. Note the hard edge between public and private lands in Rockingham County.127
- Figure 2: Monthly % occurrence and 95% confidence intervals of common prey items found in **coyote** scats (n = 334) in a) Bath County (n = 206) and b) Rockingham County (n = 128) from June 2011 to May 2013 (years combined). Deer occurrence is not shown (Fig. 3). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.128

- Figure 3: Monthly % occurrence of white-tailed deer with 95% confidence intervals found in **coyote** scats (n = 334) in Bath County (n = 206) and Rockingham County (n = 128) from June 2011 to May 2013 (years combined).....129
- Figure 4: Estimated monthly % biomass consumed with 95% confidence intervals from **coyote** scats (n = 334) in a) Bath County and b) Rockingham County collected from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.130
- Figure 5: Monthly % occurrence and 95% confidence intervals of common prey items found in **bobcat** scats (n = 258) in a) Bath County (n = 134) and b) Rockingham County (n = 118) from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.131
- Figure 6: Estimated monthly % biomass consumed with 95% confidence intervals from **bobcat** scats (n = 258) in Bath County (a) and Rockingham County (b) collected from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher occurrence.132
- Figure 7: Seasonal % occurrence and 95% confidence intervals of broad diet categories found in **black bear** scats (n = 107) in western Virginia from June 2011 to May 2013 (years combined). Seasons include winter (Dec - Feb), spring (March - May), summer (June - Aug), and fall (Sept. - Oct.) Seasons not connected by same letters are significantly different.....133
- Figure 8: Estimated seasonal % biomass consumed with 95% confidence intervals from black bear scats (n = 107) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years combined). There were no significant differences between seasons.134
- Figure 9: Monthly % occurrences of white-tailed deer with 95% confidence intervals found in scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years and sites combined).135
- Figure 10: Monthly % biomass consumed of white-tailed deer with 95% confidence intervals found in scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107) in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years and sites combined). 136
- CHAPTER 4: INTESTINAL PARASITES OF COYOTES IN WESTERN VIRGINIA
- Figure 1: Mode and timeline of coyote range expansion in the eastern United States (Parker 1995).154

Figure 2: Map of the study area highlighting (L to R) Bath and Rockingham Counties. Orange boxes denote the general region of each county studied.....155

Figure 3: Locations of coyote feces (n = 215) containing 9 different parasite species in Bath (left panel) and Rockingham (right panel) Counties, Virginia relative to survey transects.156

Figure 4: Prevalence and 95% confidence intervals of fecal parasites of coyotes (n = 215) in Bath and Rockingham Counties, VA, collected from June 2011 to May 2013 (years and months combined). * denotes significance. + denotes near significance.159

Figure 5: Bi-monthly prevalence and 95% confidence intervals of common fecal parasites of coyotes (n = 215) in Bath and Rockingham Counties, VA from June 2011 to May 2013 (years and counties combined).....160

Figure 6: Seasonal proportion and 95% confidence intervals of coyote fecal samples (n = 215) from June 2011 to May 2013 in which no parasites were detected.161

LIST OF TABLES

CHAPTER 2: FOOD AVAILABILITY FOR CARNIVORES IN THE APPALACHIAN MOUNTAINS OF VIRGINIA

Table 1: Some of the models of deer density (D) in Bath and Rockingham Counties, Virginia tested in Program DISTANCE. Models with delta Akaike Information Criteria (AIC) > 8 are not shown. For Rockingham County, January and April 2012 and January 2013 are not displayed because there were insufficient detections for extensive modeling in these months.	70
Table 2: Some of the models of mid-sized mammal occupancy tested in Program PRESENCE by species. Models are ranked according to Akaike Information Criteria. Models with delta AIC > 8 are not shown.	72
Table 3: Models Some of the models of small mammal abundance in Bath County, Virginia tested in Program MARK ranked by Akaike Information Criteria corrected for small sample sizes (AICc). Models with delta AICc > 8 are not shown. t indicates time effect; “.” Indicates constant or null effect; hab indicates differences by habitat type; where s = survival, i = immigration, e = emigration, p = capture probability, and c = recapture probability.	73
Table 4: Seasonal deer densities in Bath and Rockingham Counties, Virginia with top models for each season as determined by Akaike Information Criteria corrected for small sample sizes (AICc).	74
Table 5: Wildlife captured by 48 remote camera traps deployed in Bath County, Virginia from June 2011 to May 2013.	75
Table 6: Significant and nearly significant differences in trapping rates among 48 cameras deployed in 3 habitat types in Bath County, Virginia based on Kruskal-Wallis ranked sums tests with Dunn’s multiple comparisons. Asterisks denote significance ($\alpha = 0.05$).	76
Table 7: Species captured in Sherman live traps in 11 grids in 3 habitat types during 19,322 trap nights in Bath County, Virginia from July 2011 to May 2013.	77
Table 8: Estimates of seasonal mean maximum distance moved (MMDM) and population density of small mammal species trapped in Bath County, Virginia from July 2011 to May 2013.	78
Table 9: Expected monthly seasonal diet of a generalist predator based on estimates of food availability in Bath and Rockingham Counties, Virginia. * denotes higher occurrence potentially due to fawning season; + denotes higher occurrence potentially due to hunting season. NA is not available.	80

CHAPTER 3: SEASONAL DIETS OF COYOTES, BLACK BEARS, AND BOBCATS IN
WESTERN VIRGINIA

- Table 1: Site comparisons of monthly % occurrence of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Wilcoxon Tests ($\alpha = 0.95$). Only months in which % occurrence varied significantly between sites are shown.120
- Table 2: Site comparisons of monthly % biomass consumed of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Wilcoxon Tests ($\alpha = 0.95$). Only months in which % biomass consumed varied significantly between sites are shown.121
- Table 3: Monthly comparisons of % biomass consumed of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Kruskal-Wallis Tests with Dunn’s multiple comparisons ($\alpha = 0.95$). Only months in which % biomass consumed varied significantly are shown.122
- Table 4: Seasonal and site comparisons of % occurrence and % biomass consumed of white-tailed deer in scats of coyotes, bobcats, and bears collected in Bath and Rockingham Counties, Virginia during the limited mobility period (LMP) and social mobility period (SMP) using Wilcoxon Tests ($\alpha = 0.95$), with sample sizes denoted (n). Only significant interactions are shown.123
- Table 5: Monthly comparisons of % occurrence of food items in bobcat scats, with sample sizes (n), collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 and compared using Kruskal-Wallis Tests with Dunn’s multiple comparisons ($\alpha = 0.95$). Only months in which % occurrence varied significantly are shown.124
- Table 6: Seasonal comparisons of % occurrence of food items in black bear scats, with sample sizes (n), collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 and compared using Kruskal-Wallis Tests with Dunn’s multiple comparisons ($\alpha = 0.95$). Seasons include winter (Dec - Feb), spring (March - May), summer (June - Aug), and fall (Sept. - Oct.) Only seasons in which % occurrence varied significantly are shown.125
- Table 7: Expected monthly seasonal diet of a generalist predator based on estimates of food availability in western Virginia (Chapter 2) compared to findings from diet analysis of scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107). Rankings are: 0 = none, 1 = low, 2 = moderate, 3 = high, 4 = very high. The first rank in each column is the expectation based on availability, the 2nd rank represents that found in coyote diet, denoted suffix “C”, and the 3rd rank represents that found in the bobcat diet, denoted with suffix “B”. The ranks within squares denote predator being more selective than availability with green for coyotes and orange for bobcats. The darker the color the bigger difference in selectivity (i.e. larger rank change from availability). “BA” indicates Bath County; “RO” indicates Rockingham County.126

CHAPTER 4: INTESTINAL PARASITES OF COYOTES IN WESTERN VIRGINIA

Table 1: Parasite species detected in fecal surveys of coyotes (n = 215) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013. x = presence; + = high prevalence; - = low prevalence.	151
Table 2: Prevalence of common parasites of coyotes (n = 215) collected in Bath and Rockingham Counties, VA from June 2011 to May 2013 and results of t-tests comparing prevalence between counties ($\alpha = 0.05$).....	152
Table 3: Bi-monthly prevalences of common parasites of coyotes (n = 215) collected in Bath and Rockingham Counties, VA from June 2011 to May 2013 (years combined), with results of a one-way analysis of variance ($\alpha = 0.05$).	153

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION AND JUSTIFICATION

Although deer abundance is high throughout most areas of Virginia, parts of western Virginia have comparatively low density deer populations, as inferred from trends in harvest data (VDGIF unpublished data, Fig. 1). Possible reasons for declining deer harvests in this region include decreases in the number of deer hunters, reductions in habitat quality, or increased mortality due to predation (Knox 2011). Concerns from deer hunters prompted interest in research to investigate the role of predation as a possible mechanism causing deer declines in western Virginia.

In the mid-20th century, deer hunters flocked to the counties west of the Shenandoah during deer season, setting up temporary camps and spending a week or more hunting the large tracts of public land in these areas. However, in recent decades, relatively few deer hunters have traveled to these counties, and those that do report seeing fewer deer and poor quality deer hunting on public lands (N. Lafon, VDGIF, personal comm.). To some degree, the reduction in hunting tourism corresponds with the decline in the overall number of hunters. Based on license sales, the number of hunters in Virginia has declined by 38% since 1980 (VDGIF 2010). Also, the decline in hunting-based tourism in these areas could be attributed to the increased availability of alternative deer hunting opportunities in other parts of the state (M. Knox, personal comm.). When hunting tourism was high in Bath and Rockingham Counties, deer populations in many other parts of the state, such as Southwest Virginia, were very small, which is no longer the case.

Alternatively, reductions in hunting tourism could be due to lower deer densities and overall poorer quality of deer habitat on public lands in Bath, Rockingham, and other western counties,

when compared to conditions 30+ years ago (VDGIF unpublished data, Fig. 1). During this time, reduced timber harvest on public lands, particularly national forest, has resulted in a dominant habitat type that is of poor quality for deer: even-aged intermediate and mature hardwood forests with very little disturbance, fewer stands of young forest, and less edge habitat (M. Knox, VDGIF, personal comm.). The positive association between robust white-tailed deer populations and young, disturbed forests and edges is well-established (Roseberry and Woolf 1998; Vreeland et al. 2004; Williamson and Hirth 1985). As forests age and habitat structure becomes increasingly homogeneous, carrying capacity for deer declines (Sinclair 1997).

Other hypothesized reasons for declines in deer density include the increase in predators, specifically coyotes (*Canis latrans*), and the effects of multiple sources of predation on a prey population that is already stressed by marginal habitat quality. Although deer in Virginia evolved in the presence of other canid predators, coyotes are relative newcomers, having first appeared in the state in the 1950s and becoming an established fixture of the landscape only since the late 1970s or early 1980s (VDGIF 2011). Traditionally considered a desert and grassland species of western and mid-western North America, coyotes have expanded their range rapidly in the past century to include all of the contiguous United States, most of southern Canada, parts of Alaska, Mexico, and Central America. This range expansion likely was facilitated, at least in part, by widespread habitat alteration related to European colonization and settlement and, in the eastern United States, by the extirpation of large predators like wolves (*Canis lupus*, *C. lycaeon*, *C. rufus*) and mountain lions (*Puma concolor*) (Parker 1995).

Although coyotes now are well established in every county in Virginia, relatively little is known about the role coyotes play in Virginia ecosystem dynamics. As relatively large predators, coyotes have the potential to exert a top-down influence on an ecosystem by suppressing prey

populations and influencing the behavior of other wildlife (Stout 1982; Rogers and Caro 1998; Lingle 2002). Numerous studies in the western US and the Northeast have emphasized the adaptability of the coyote. Some research suggests the coyote is a generalist predator, targeting whatever food item is most abundant and readily available (Bowyer et al. 1983; Huebschman et al. 1997; Morey et al. 2007; Schrecengost et al. 2008). Other studies have shown a surprising degree of specialization in coyotes' diet, including a tendency to alternate between preferred foods while virtually ignoring other available foods considered to be staples of coyote diets in other parts of their range (Patterson et al. 1998; Stoddart et al. 2001). Very few large-scale studies of coyote ecology have occurred in the Mid-Atlantic and Central Appalachian regions, and, to date, no large-scale studies have been conducted in Virginia.

Only 2 studies of coyote diet have occurred in Virginia in recent years. The first was an undergraduate research project (Gammons 2004) that provided a limited snapshot of coyote diet based on 17 scats collected in Campbell and Bath Counties during a single fall season. In the second, Robinson (2005), described coyote diet at Marine Corps Base Quantico using 94 scat samples; food items were grouped into broad categories of fur, vegetation, and insects. Neither of these studies provides an adequate description of the diet and feeding ecology of coyotes in Virginia.

As coyote populations have expanded in Virginia, the potential for conflict with human interests has also grown (Pederson 2005). Throughout their range, coyotes are known to prey upon domestic livestock and pets, and there are documented cases of both in Virginia (Sacks and Neale 2002; Houben 2004; Jones 2004). Additionally, coyotes prey upon valued game species like white-tailed deer, raising concerns among hunters and wildlife viewers (M. Fies, Virginia Department of Game and Inland Fisheries, personal communication). The extent to which

coyotes in Virginia are preying upon livestock, the effects of coyote predation on other wildlife populations, and the relative importance of available food items to coyotes all are poorly understood.

Equally unknown is the relationship between coyotes, black bears (*Ursus americanus*), and bobcats (*Lynx rufus*), the other extant predators of large game in Virginia. Anecdotal evidence suggests that black bears may be a significant source of mortality for white-tailed deer fawns (C. Croy, U.S. Forest Service, personal communication), and bobcats are known to eat deer in nearby parts of their range (Story et al. 1982, McLean et al. 2005). Because coyote predation is suspected to be a major source of fawn mortality in some areas (Stout 1982; Long et al. 1998), the cumulative effect of predation from these sources may increase the potential for additive mortality in deer populations.

Understanding the diet and feeding ecology of coyotes, bears, and bobcats in Virginia is a crucial first step toward understanding the impacts of the coyote's arrival on predator and prey communities in Virginia's ecosystem at large. My goal in this study was to determine seasonal dietary patterns of coyotes, black bears, and bobcats in western Virginia and assess the potential for cumulative mortality in white-tailed deer.

Predators often act as a mechanism of transmission of parasites in wildlife communities through the ingestion of prey that are intermediate or alternate hosts for indirectly or directly transmitted parasites (Schweiger et al. 2007).

Understanding the diet and feeding ecology of coyotes, bears, and bobcats, and the parasites infecting coyotes in Virginia, are crucial steps toward understanding the role of these predators in the ecosystem at large. This study has 3 main objectives:

- 1.) Estimate seasonal abundance and density of multiple food items in western Virginia to determine, and rank, food availability across the landscape.
- 2.) Determine seasonal diet patterns of coyotes, bobcats, and black bears and compare food availability to % food item occurrence in predator diets.
- 3.) Determine the seasonal prevalence of intestinal parasites of coyotes in western Virginia to provide a descriptive baseline on coyote parasite ecology.

Food Availability

An important consideration when comparing feeding strategies of carnivores is the relative availability of food items across the landscape. I define food availability as a combination of a food item's density and its vulnerability to predation or consumption. A potential food item with high population density and high vulnerability would be highly available to predators and should occur in the diet of a generalist predator with high frequency. In contrast, a potential food item that is absent or has extremely low population density on the landscape, or a high density species that has low vulnerability to a given predator, would have low availability and would occur infrequently in a predator's diet. I estimated the relative availability of several potential food items of 3 sympatric predators – coyotes, black bears, and bobcats – in a mosaic landscape in western Virginia. I estimated food availability seasonally and compared it to seasonal predator diet (Chapter 2) to determine whether carnivore diets fluctuate in tandem with changes in food availability. I focused on 4 broad categories of foods: small mammals, mid-sized mammals,

deer, and soft mast. I used mark-recapture techniques, distance estimation, camera trapping, and vegetation sampling to estimate density, occupancy, and % cover which I used as indices of availability for predation.

Food density is of particular interest in the context of different habitat treatments. Many central Appalachian ecosystems naturally are adapted to, or dependent upon, periodic fire. In the areas of Virginia where I collected my data, prescribed fire has become an increasingly common tool for habitat management that is used primarily by the U.S. Forest Service, The Nature Conservancy, Virginia Department of Game and Inland Fisheries (VDGIF), and Virginia Department of Conservation and Recreation (C. Croy, U.S. Forest Service, personal communication). For this reason, my estimates of food availability focused on burned and unburned treatments in forested habitats. In addition, I sampled mid-sized food items in areas of recent timber harvest, and I trapped small mammals in open fields during the second year of the study to target specific food items that were not occurring in forested sites.

Concerns over the effects of potentially high predation on white-tailed deer by coyotes and other predators were among the primary reasons for conducting this research. My study areas in Bath and Rockingham Counties were identified by the Virginia Department of Game and Inland Fisheries (VDGIF) as priorities for predator research based, in part, on the perception of lower population density of white-tailed deer there relative to other parts of the state. This perception comes from deer hunters' reports of fewer deer sightings per unit effort, a marked decline in the number of deer harvested, and observations of wildlife professionals in the field who also report fewer deer sightings (M. Fies, VDGIF, personal communication).

Current estimates of deer population abundance and density in this area are derived using hunter harvest data as an index of change in population abundance (VDGIF 2011). This is a common technique used to monitor hunted deer population trends with minimal expense or sampling effort; however, such data have limited utility for estimating actual deer population density because hunter harvest fluctuations can result from numerous variables unrelated to actual deer abundance, including changes in hunter effort or success rate (Roseberry and Woolf 1991).

Previous studies of deer populations in Virginia estimated populations through DISTANCE estimation of 9.4 – 30.1 deer/km² (Lovely et al. 2013), 5 – 47 deer/km² (McShea et al. 2008), and 5.8 – 33.4 deer/km² (McShea et al. 2012). However, these studies occurred in areas where better habitat structure and regulations limiting deer harvest in suburban areas are expected to result in much higher deer densities. Based on VDGIF deer harvest data, deer population abundance in Bath and Rockingham Counties was anticipated to be lower than the areas studied by McShea et al. (2008) and Lovely et al. (2013) (N. Lafon, VDGIF, personal communication). Therefore, I used similar DISTANCE estimation techniques to compare deer densities in Bath and Rockingham to each other and to other parts of the state.

In addition to white-tailed deer density estimation, I used remote camera traps to estimate trapping rate, as an index of potential prey activity, and site occupancy, as a measure of availability, of 4 medium sized potential prey species: raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), cottontails (*Sylvilagus* spp.), and squirrels (*Sciurus* spp.).

I targeted areas with and without recent timber harvest to examine impacts of such disturbance on medium-sized prey species. Published camera trapping studies in Virginia have focused on carnivores or deer, (McShea and Rappole 1992; Kelly and Holub 2008; Curtis et al. 2009), but

authors have noted that numerous other species were returned in remote camera images. These data are often little-used, yet may provide useful information on prey population presence and activity in the target area.

I used Sherman live traps in a mark recapture design to estimate abundance and density of small mammals. While trapping in Highland County, which is located between my two study sites, McShea et al. (2003) reported highest trapping rates for white-footed mice (*Peromyscus leucopus*) and deer mice (*Peromyscus maniculatus*), followed by eastern chipmunks (*Tamias striatus*), red-backed voles (*Clethrionomys gapperi*), and short-tailed shrews (*Blarina brevicauda*). Species abundance and richness were associated with mesic forests. In West Virginia, Kaminski et al. (2007) observed relative abundances of small mammals similar to McShea et al. (2003) and noted higher abundance of *Clethrionomys gapperi* in disturbed (timber harvested) areas. These results contrast with Healy and Brooks (1988) who found no significant difference in small mammal trapping rates or abundances in even-aged stands of varying ages in West Virginia. However, Healy and Brooks (1988) recorded high capture rates for the same 5 species noted by McShea et al. (2003) and Kaminski et al. (2007) in addition to *Napeozapus insignis* and *Microtus chrotorrhinus*.

Diet of Coyotes

Studies of coyote diet from various parts of the species' range indicate a high degree of variability in diet and feeding behavior (Lee and Kennedy 1986; Andelt et al. 1987; Stratman and Pelton 1997; Schrecengost et al. 2008). What is true for coyotes in one area may be very different for coyotes in other areas. This adaptability may be a primary reason for the coyote's success.

Although small mammals, lagomorphs, other mid-sized mammals, ungulates, soft-mast, birds and birds' eggs, insects, and reptiles are all common food items for coyotes, the relative importance of these items varies regionally and seasonally. Small mammals consistently comprise a major portion of coyotes' diet throughout their range (Korschgen 1957; Wooding et al. 1984; Lee and Kennedy 1986; Crosset and Elliott 1991; Hidalgo-Mihart et al. 2001). In a nearby region of West Virginia, Albers (2012) did not find raccoon or opossum among the mid-sized mammals found in coyote stomachs and scats. In Ohio, Cepek (2004) found raccoon in 18 % of coyote scats but no evidence of opossums. Crossett and Elliot (1991) found opossums in 2 % of coyote stomachs from Kentucky, and Lee and Kennedy (1986) reported opossums in just 0.05 % of coyote stomachs from eastern Tennessee. Estimates for % occurrence of squirrels in coyote diets include 13.9 % (Albers 2012), 1.0 % (Crossett and Elliot (1991), and 4.7 % (Schrecengost 2011). In areas where coyotes live in close proximity to humans, domestic livestock, pets, garbage, and agricultural crops are also utilized to varying degrees (Jones and Woolf 1983; Sacks and Neale 2002; Morey et al. 2007; Lukasik 2009).

Many studies have emphasized the plasticity of the coyote's diet and have shown coyotes to be opportunistic feeders. Windberg and Mitchell (1990) noted that high occurrence of cotton rats (*Sigmodon spp.*) in the scats of coyotes in south Texas was related to population eruptions of cotton rats; reliance on minor prey items like white-tailed deer and small rodents was inversely proportional to abundance of major prey items like woodrats (*Neotoma spp.*) and lagomorphs. In Idaho, Stoddart et al. (2001), found that depredations on domestic sheep corresponded with periods of low jackrabbit abundance. Korschgen (1957) noted a strong correlation between abundance of rabbits and their occurrence in coyote scats in Missouri.

Relative proportions of food items in coyote diet also vary seasonally. This seasonality may reflect differences in abundance throughout the year. For example, occurrence of soft mast in coyote diet typically peaks when fruits ripen in the late-spring and early-fall (Bond 1939; Wooding et al. 1984; Toweill and Anthony 1988; Hoerath and Causey 1991; Chamberlain and Leopold 1999; Robinson 2005), while insect use generally is highest in summer (Bowyer et al. 1983; Hoerath and Causey 1991; Henke 2002; Lemons et al. 2010).

Seasonal differences in importance of food items may reflect variation in vulnerability, especially among large prey species. Predation on deer is most common in early summer when young fawns are vulnerable (Andelt et al. 1987; Huebschman 1997; Patterson et al. 1998; Henke 2002; Schrecengost 2008). Similarly, the rate of predation on livestock like cattle, sheep, and pigs typically is most common during calving (Andelt et al. 1987), lambing (Stoddart et al. 2001), or farrowing (Jones and Woolf 1983). Predation on adult deer is most common in mid- to late-winter in areas of heavy snowfall (Wooding et al. 1984; Huegle and Rongstad 1985; Patterson et al. 1998), when deer condition is lowest and snow depth enables coyotes to more easily run down large adult deer (Crete and Lariviere 2003). Predation of adult deer is more common in northern latitudes, indicative of increased vulnerability related to winter weather severity (Gese et al. 1988) and possibly related to lower availability of alternative prey species.

In contrast, Wagner and Hill (1994) reported that wild turkeys (*Meleagris gallopavo*) occurred in $\leq 4\%$ of coyote scats from sites in Florida, Alabama, Mississippi, and Arkansas, with a non-significant increase in turkey occurrence in scats during the turkeys' reproductive season, a time of assumed vulnerability.

The low predation rate of coyotes on wild turkeys found by Wagner and Hill (1994) was supported by Houchin (2005) who found that wild turkey comprised $\leq 1\%$ of all food items consumed by coyotes in the Texas panhandle and southwest Kansas. A large body of literature shows that wild bird species represent a very small component of coyote diet. This trend is consistent throughout the coyote's range, including Texas (Andelt et al. 1987), California (Bowyer et al. 1983), tropical Mexico (Hidalgo-Mihart et al. 2001), Alberta (Lukasik 2009), Alaska (Prugh et al. 2008), Florida (Stratman and Pelton 1997), and Nova Scotia (Patterson et al. 1998). Exceptions include 2 studies from Nebraska (Fichter et al. 1955; Huebschman et al. 1997) that found high predation rates associated with migrating snow geese (*Chen caerulescens*) and high ring-necked pheasant (*Phasianus colchicus*) abundance, and a study from southern California (Bond 1939) that reported high occurrence of ducks (Anatidae) in scats during a period of disease outbreak.

Despite strong evidence that coyotes behave as generalist or opportunist predators, some studies have found a surprising degree of specialization in coyote diet, particularly related to preferential predation on white-tailed deer. Bartel and Knowlton (2005) identified black-tailed jackrabbits (*Lepus californicus*) as a preferred prey for coyotes, and as jackrabbit abundance declined, predation by coyotes on small rodents increased. However, among these small rodents, voles were fed upon selectively, regardless of the relative abundance of other rodent species. Patterson et al. (1998) found that coyotes in Nova Scotia switched from using white-tailed deer to snowshoe hare (*Lepus americanus*) as hare density increased, but the functional response was not proportional to the change in density of the 2 species. At low deer density, coyotes continued to prey heavily on deer despite higher availability of hares. In northwestern Florida, the frequency of deer remains in scats did not differ between areas of high and low deer density (Stratman and

Pelton 1997). Similarly, Schrecengost et al. (2008) found that deer fawns were the most common mammalian food item in coyote scats during May and June in South Carolina, despite low deer density in their study area. MacCracken and Hansen (1987) found that coyotes in Idaho preyed on the most calorically profitable prey items available, with less profitable foods consumed only as abundance of more profitable foods decreased; these less profitable foods were added to the diet in order from most to least profitable alternatives, suggesting that coyotes followed a classic optimal foraging model. Prugh et al. (2008) also found evidence of optimal foraging behavior in Alaskan coyotes, where dietary niche widths widened in response to decreasing primary prey (snowshoe hare) abundance.

Diet of Bobcats

As with coyotes, bobcat diets vary widely among regions and trends observed elsewhere may not apply to diets of bobcats in Virginia. Numerous studies have noted a high rate of occurrence of lagomorphs in bobcat diet (Beasom and Moore 1977, Brockmeyer and Clark 2007, Chamberlain and Leopold 1999, Neale and Sacks 2001). In a recent literature review, Blankenship (2001) reported that lagomorphs were the most common prey of bobcats in all regions. In an analysis of 85 bobcat stomachs, Mclean et al. (2005) found that rabbits occurred significantly more often in stomachs of females compared to males, concluding that male bobcats relied on larger prey such as deer. This sexual niche partitioning was also found by Tumilson and McDaniel (1990), whose dissection of 148 bobcat stomachs from eastern Arkansas also showed rabbits to be an important prey item to bobcats overall, but more so for female bobcats.

Many studies have found high occurrence of rodents and other small mammals in bobcat diet. In a study in northeastern Alabama, VanGlider (2008) found that small mammals collectively

represented the most commonly occurring prey group (63.9 %) in both scats and stomachs of bobcats. In southern Florida, Thornton et al. (2004) found small rodents in 70.9 % of bobcat scats. Mice and rats typically comprise the largest proportion of small mammals in bobcat diet, particularly in the southeastern US where cotton rats, cotton mice, harvest mice, and rice rats occur frequently (Beasom and Moore 1977, Chamberlain and Leopold 1999, Godbols et al. 2003, Thornton et al. 2004). However, *Peromyscus* spp. tends to be eaten less frequently, as noted by McLean et al. (2005) (18 %), Tumilson and McDaniel (1990) (2.33 %), and Story et al. (1982) (1.1 %). Estimates of % occurrence of squirrels in bobcat scats include 5.7 % (Story et al. 1982), 4.0 % (McLean et al. 2005), and 15 % (Brockmeyer and Clark 2007).

Percent occurrences of deer in bobcat diets from southern and Mid-Atlantic states range from 6.3% in southern Florida (Thornton et al. 2004) to 35.7% in Mississippi (Chamberlain and Leopold). Blankenship (2001) noted that deer are an important component of bobcat diets in the Northeast and Northwest, but that little deer occurs in bobcat diets in southern regions.

Chamberlain and Leopold (1999) found that, while deer occurrence was high in bobcat scat, it was still less than deer occurrence in scats of sympatric coyotes. This relationship between deer in the diets of coyotes and bobcats was echoed in VanGlider (2008), who found lower occurrence of deer in bobcat scats and peak occurrence of deer during fawning and hunting seasons.

I found only one report of soft mast in bobcat diet, with manzanita (*Arctostaphylos* sp.) occurring in 2.4 % of bobcat scats from California (Neale and Sacks 2001). Birds occurred infrequently in bobcat diets in most studies. Beasom and Moore (1977) reported averages of 5 % occurrence of quail and 0.5 % occurrence of wild turkey in Texas bobcats. Brockmeyer and Clark (2007) found birds in only 2 % of the 100 bobcat stomachs from Iowa that they analyzed. Other

estimates included 20.9 % in Arkansas (Tumlison and McDaniel 1990), 35.8 % in Alabama (VanGlider 2008), 12.5 % in Florida (Thornton et al. 2004), 13.1 % in Tennessee (Story et al. 1982), 11.1 % in California (Neale and Sacks 2001), and 31 % in Pennsylvania (McLean et al. 2005). Most birds documented were passerines, waterfowl, or unidentified birds. In studies where % occurrence of birds was fairly high, the authors noted that estimated weight or biomass of birds was very low. In a literature review of 54 studies of bobcat diet, Tewes et al. (2002) found that 9 studies that documented quail in bobcat diet, and quail comprised > 3% of diet in only 2 studies. Tewes et al. (2002) concluded that bobcats are minor predators of quail and other birds.

Meso-mammals occurred in many studies with low frequency. Of interest to my study area are instances of opossum and raccoon in bobcat diet. Tumlison and McDaniel (1990) found opossums in 1.96% of stomachs of male bobcats, and both opossums and raccoons in 1.54% of juvenile bobcats. Mclean et al. (2005) found opossums in 2.7% of bobcat stomachs and raccoons in 1.4%. Chamberlain and Leopold (1999) and Godbols et al. (2003) also reported raccoons and opossums in low % occurrences (< 2%) in bobcat diets. Multiple studies have found little or no seasonal variation in bobcat diet (Godbols et al. 2003, VanGlider 2008). Beasom and Moore (1977) observed an increase in % occurrence of cotton rats and a decrease in dietary diversity and % occurrence of all other food items when cotton rat abundance increased sharply in their study area. Cotton rats were consumed in proportion to their availability, whereas all other species were eaten less than expected. Chamberlain and Leopold (1999) found that bobcats consumed mice proportional to their availability.

Diet of Black Bears

Black bears have a very diverse, omnivorous diet that can include vegetation, hard and soft mast, insects and larvae, carrion, fish, and small- and medium-sized mammals. Unlike that of the coyote and bobcat, the feeding ecology of the black bear has been studied thoroughly in Virginia and throughout the central Appalachian region. Cottam et al. (1939) dissected the stomachs of 25 black bears killed by hunters in the George Washington National Forest in western Virginia. They reported that, of the total food found in these bear stomachs, 51.99% consisted of acorns, 17.44% blueberries, 6.57% tupelo, and 5.14% grape. Chokeberry (*Aronia melanocarpa*), cottontail rabbit (*Sylvilagus floridanus*), greenbriar (*Smilax spp.*), and lobelia (*Lobelia spp.*) comprised minor dietary components. Hellgren et al. (1989) characterized the seasonal diet of bears in the Great Dismal Swamp in southeastern Virginia into 4 distinct periods: herbaceous material in spring, soft mast and corn in summer, hard mast in early fall, and fruits of evergreens and vines in late fall and winter. Animal foods comprised only 3% of the annual diet of Dismal Swamp bears. In Great Smoky Mountains National Park, North Carolina, Beeman and Pelton (1977) found that herbaceous material, acorns, and soft mast accounted for $\geq 80\%$ of black bear diet by volume compared to only 11% from animal sources, mostly Coleoptera and Hymenoptera. Subsequent research by Eagle and Pelton (1980) supported these relative proportions of plant to animal diet items (80% and 12%, respectively.) This reliance on mast production is not surprising considering that, at the nearby Pisgah Bear Sanctuary, Powell and Seaman (1989) found that southern Appalachian bear habitat produces an average of 52 kilograms of berries per hectare and ≥ 58 kilograms of acorns per hectare. Furthermore, Rogers (1976) linked mast and berry crop failures to declines in survival, growth, and reproductive rate of Minnesota black bears.

Recent anecdotal evidence suggests that black bear predation on white-tailed deer fawns potentially may be high in Virginia and has raised concern about the effect of bear predation on deer populations in areas with already low deer density. Zager and Beecham (2006) concluded that such predation is frequently additive at low prey density, resulting in a potential limiting effect on ungulate populations. The significance of black bears as predators of white-tailed deer has only recently been recognized (Zager and Beecham 2006). Though reports of black bear predation on adult deer are not unheard of, neonatal fawns are especially vulnerable. Mathews and Porter (1988) attributed 3 of 5 predation-related mortalities among 17 radio-transmitted neonatal white-tailed deer in New York to black bears. Similarly, Kunkel and Mech (1994) found that black bears accounted for 49% of mortality among white-tailed deer neonates in Minnesota, and Barber et al. (2005) found that bears (black and grizzly [*Ursus arctos*] combined) were responsible for 55-60% of all mortality of elk (*Cervus elaphus*) calves in Yellowstone National Park, compared to 15% each for gray wolves and coyotes. On the Olympic Peninsula of Washington, black bears accounted for 3 of 72 (4.2%) known predation events of black-tailed deer (*Odocoileus hemionus columbianus*) (McCoy and Murphie 2011). In Pennsylvania, white-tailed deer comprised 43% of the fall diet of black bears, but this was attributed primarily to carrion (Bennet et al. 1943).

Cumulative Effects on Deer Populations

Because coyotes, bears, and bobcats all prey on white-tailed deer fawns, there is a potential for direct, interspecific competition among these 3 predators for this seasonally-available food resource. Although competitive interaction between sympatric gray wolves and black bears is well-documented in areas of western and northern North America (Rogers and Mech 1981; Kunkel and Mech 1994), and many studies have compared the dietary overlap of coyotes and

bobcats (Chamberlain and Leopold 1999, Neale and Sacks 2001, Thornton et al. 2004, VanGlider 2008), the potential relationship among these 3 predators has received little attention or research, despite the now commonly acknowledged roles they play as predators of deer neonates. Not only is there a potential for resource competition among black bears, bobcats and coyotes, but the cumulative effects of all three sources of predation on white-tailed deer populations could result in additive mortality, and a resulting decrease in population density, of white-tailed deer that is less likely in the presence of a single predatory species.

Scat Study Techniques

Common techniques for estimating predator diet and feeding ecology include direct observation of feeding behavior (Huegel and Rongstad 1985; Tremblay et al. 1998), examination of the stomach contents of dead specimens (e.g., Bond 1939), and examination of the scat of animals presumed to still be alive in the population (Schrecengost et al. 2008; Grigione et al. 2011). I focused on scat analysis, which presents unique opportunities, but also requires meeting certain assumptions and considerations. Assumptions to consider include: 1) proportions of food items consumed are relative to the proportions detected in scats; 2) species of origin of each scat is accurately identified; and 3) food items in scats have an equal probability of detection, when present.

Traditional diet analyses based on scat collection have relied primarily on morphological characteristics to distinguish coyote scats from other species. Segment diameter, segment length, weight, color, odor, and associated tracks are all common metrics used to identify carnivore scats. For coyote scat identification in areas where other canids are present, maximum scat diameter typically is used to distinguish coyote scats, with scats larger or smaller than a specified

threshold diameter discarded as being uncertain in origin. For example, Cepek (2004) discarded scats ≤ 17 mm in diameter to avoid unintentional inclusion of fox scats, whereas, in Idaho, Elliott and Guetig (1990) discarded scats ≤ 20 mm in diameter. Hoerath and Causey (1991) included only scats between 18 and 24 mm in diameter to exclude fox and domestic dog from their Mississippi study. While studying sympatric gray wolves (*Canis lupus*) and coyotes in northwestern Montana, Arjo et al. (2002) attributed scats ≤ 25 mm in diameter to coyotes, whereas scats ≥ 30 mm in diameter were considered to be from wolves; scats between 25 and 30 mm in diameter were discarded unless tracks or other evidence were available to aid in identification.

Two major problems arise from using these techniques. First, there is considerable disagreement about what threshold diameters should be used when discarding or including scats. Even in the studies cited here, minimum diameters for distinguishing coyote from fox scats differ. A brief comparison of morphometric descriptions of coyote scats from common field identification guides shows disagreement among authors. Stokes (1986) states that scats “3/4 inch or more in diameter are *probably* coyote or one of its hybrids; scats 7/16 inch in diameter are *probably* fox” (emphasis from the original). Murie and Elbroch (1982) simply note that coyote scats vary in size and typically are intermediate between red fox and gray wolf. Knopf (1996) eschews the issue of scat diameter altogether and simply describes coyote scat as “typically canine” and “full of hair.” Obviously, attempting to determine coyote diet based on scats identified by the diet items they contain could introduce significant sampling bias to a study. With such vague descriptions from leading field reference materials, establishing any reliable criteria for conclusive scat identification is nearly impossible.

The second problem with discarding scats of uncertain origins based on diameter is the potential for sample bias. Scat diameter, segment length, color, and odor all vary with diet. By discarding scats that do not fit the rigid criteria of “acceptable” appearance, key diet items may be inadvertently excluded from the sample. For example, if consuming a particular food item results in a runny stool, small segment diameter, or unusual color, scats associated with that food item may not be included in analysis. The resultant data would be biased, disproportionately emphasizing the abundance of detected food items while failing to account for other potentially common or important food items.

An alternative means of identifying scats is through mitochondrial DNA analysis. DNA can be extracted from epithelial cells left on the exterior of scat and used to identify not only the species that deposited the scat, but also the individual and the relatedness of individuals (Dalen et al. 2004) among numerous scats. Robinson (2005) compared field identification of scats with results from genetic analysis. Robinson sought to describe the diet of coyotes, however, genetic analysis revealed that a large proportion of presumed coyote scat ($\geq 50\%$ in some seasons) actually was deposited by gray foxes (*Urocyon cinereoargenteus*) or red foxes (*Vulpes vulpes*). She failed to find any correlation between scat diameter and canid species, noting that it was impossible to consistently distinguish among the scats of the 3 canid species based on diameter alone, especially for scats 1.5 – 2.0 cm in diameter. Robinson concluded that the only scat size-class that could be attributed to coyote with near certainty (in her study area) was for scats ≥ 2.5 cm in diameter. Obviously, eliminating all scats ≤ 2.5 cm in diameter would lead to major sampling bias in any study. For example, such a criterion for identification would have eliminated all coyote scats from Hoerath and Causey’s (1991) Mississippi study as well as all scats confidently identified as being from coyotes in Arjo et al.’s (2002) Montana study.

Using DNA from scat to identify individuals for genetic capture-mark-recapture (CMR) estimation of population abundance and density is an increasingly common tool of wildlife professionals, but such techniques can also be used to identify dietary patterns for individuals. Prugh et al. (2008) successfully used this method to assess diets of 42 individual coyotes in Alaska and found it worked best when ≥ 10 scats were available to construct an individual diet “history.” Comparisons of individual diet to “population” diet trends determined by scat analysis could be used to determine the effectiveness of population-level diet studies to predict individual coyote behavior and feeding habits and could be a way to calibrate population-level studies.

Detection probability of scat may differ among observers and among months or seasons. For example, in the event of deep winter snowfall, detection of scat may be increased if tracks in the snow help observers recognize carnivore activity along a transect and locate scat deposits.

Alternatively, deep snow may decrease scat detection if scats are deposited prior to snowfall or if high winds cause snow to drift over tracks and scats. Another consideration is spatial or temporal variation in carnivore activity along transects that could result in higher or lower rates of scat deposition, leading to variation in scat detection at each transect. As a result of this variation in detection, it is possible that carnivores at certain transects may be more strongly represented during certain times of the year than others.

Scat deposition rate also changes with diet. For example, highly digestible foods (e.g., soft-mast) can result in high deposition rates compared to foods that contain large proportions of animal matter. Similarly, Monroy-Vilchis and Frieven (2006) found that scat expulsion rate (i.e., number of scats per gram of ingested biomass) for coyotes increases significantly with prey size, resulting in more scats when coyotes consume large prey items than when an equal biomass of small prey items is consumed. Hence, variation in the relative proportion of large to small prey

items among months or sites could result in different rates of scat deposition and artificially inflate the proportion of highly digestible food items relative to less digestible food items detected in scats.

An assumption of diet analysis from scat is that scats do not move from the site of deposition. The potential for coprophagy (consumption of feces) has been suggested as a source of bias in diet analyses (Livingston et al. 2005). A study from Fort Riley, KS, found that as many as 50% of artificially placed coyote scats were removed, and opossums were associated most commonly with scat removal (Livingston et al. 2005). It is unclear whether the composition of scat affects removal rate.

There are several common methods for quantifying carnivore diet composition based on scat analysis. The terminology used in diet analyses varies from study to study, often confounding attempts to compare results among studies. Frequency of occurrence, % of scats, % occurrence, and % abundance are all common terms. "Percent of scats" frequently is defined as the "percent of a sample of scats in which a food items occurs," whereas "% of occurrences" is often defined as the "number of times a prey species occurs as a % of total number of occurrences for all prey species" (Wagner and Hill 1994; pg. 176).

Coyote Parasites

Predators like coyotes often act as a mechanism of transmission of parasites in wildlife communities through the ingestion of prey that are intermediate or alternate hosts for indirectly or directly transmitted parasites (Schweiger et al. 2007). In wild coyotes, parasites typically are studied by necropsy or scat analysis, which relies on identification of parasite eggs that are shed in feces (Gompper et al. 2003; Trout et al. 2006; Miller et al. 2009).

Parasite prevalence, parasite species richness, and infection intensity within a host or population can be affected by many physiological and environmental factors. Host body mass, geographic range size, and population density all correlate positively with species richness of non-vector borne parasites in carnivores (Lindenfors et al. 2007). It has been suggested that high testosterone levels may increase susceptibility to parasites (Folstad and Karter 1992; Roberts et al. 2004), whereas home range size (Bordes et al. 2009) and distance from the equator (Lindenfors et al. 2007) both correspond negatively to parasite species richness.

The spread of coyotes into Virginia in the latter half of the 20th century is hypothesized to have occurred along 2 fronts: one moving south from New England and the Ohio River Valley and the other moving north along the eastern edge of the Southern Appalachians (Parker 1995). It is reasonable to assume that the parasite communities of coyotes in Virginia are a combination of the parasite diversity of coyote populations in states in both regions. In 1978, Franson et al. found *Ancylostoma caninum*, *Taenia* sp., *Trichuris vulpis*, *Toxascaris leonina*, *Physaloptera* sp., and coccidia in Iowa coyotes. They demonstrated a high prevalence of *Taenia* sp. and low prevalence of *T. vulpis*, with prevalence of *A. caninum* inversely related to age. More recently, Gompper et al. (2003) found a relatively high diversity of parasites in New York coyotes. In addition to the parasites observed by Franson et al., they found 3 species of capillarids, *Toxocara canis*, *Uncinaria stenocephala*, *Spirurida*, *Sarcocystis* sp., and 3 species of *Isospora*. *A. caninum*, which was highly prevalent in coyotes sampled by Franson et al. in Iowa, was not observed in the New York coyotes sampled by Gompper et al. On the southern front, a parasite fauna similar to that found in Iowa was observed in Georgia, including *A. caninum*, *Physaloptera* sp., *Taenia* sp., and *Sarcocystis* sp. (Holtzman et al. 1992). Miller et al. (2009) observed very low species richness in fecal samples of coyotes in South Carolina. *Ancylostoma* spp. was

observed in >50% of samples, and *Trichuris* spp. and *Isospora* spp. were the only other fecal parasites found, both with extremely low prevalence. These studies from coyote populations both north and south of Virginia all indicate a relatively consistent parasite fauna with typically high prevalence of hookworms (*Ancylostoma* spp. or *Uncinaria* spp.), taeniids, *Isospora* spp., *Physaloptera* spp., and *Sarcocystis* spp. Capillarids, *Trichuris* spp., and ascarids (*T. canis* and *T. leonina*) also occurred in multiple nearby states. Prevalence of these parasites varied widely among studies, but parasite fauna composition was relatively consistent.

Although many common parasites of coyotes can infect domestic dogs, empirical evidence linking parasite prevalence in coyotes to incidence in dogs is lacking. Perceived risk of disease transmission from coyotes to domestic dogs can be high (Watts 2009) and increasing interaction between coyotes and dogs along the urban interface (Pederson 2005) suggests that the potential for pathogen transmission may be an emerging concern.

Macroparasite dynamics between domestic dogs and coyotes are poorly studied. Manning (2007) found a higher prevalence of helminths in coyotes in urban habitats compared to a protected wildland area (i.e., an area which is protected from human alteration by law) and attributed this difference to transmission from domestic dogs to coyotes. The prevalence of *Ancylostoma caninum*, a parasite that has been suggested as a population regulator of coyotes by increasing neonatal mortality (Pence et al. 1988) and a common parasite of domestic dogs, is increasing among coyotes living in human-altered landscapes.

The parasites of coyotes in Virginia, and the role of coyotes in the disease ecology and transmission dynamics of parasites in Virginia, have not been studied previously. I examined coyote feces from the western part of the state to determine the prevalence of parasites in coyote

populations. In addition, I sought to identify spatial and temporal patterns of parasite occurrence in coyote feces.

Expected Outcomes and Management Implications

This research provides baseline information on the diets of coyotes, bobcats, and black bears in the western mountains of Virginia. Diet data from scats allow for estimates of the relative seasonal use of available food items in central Appalachian ecosystems. Although actual predation rates cannot be determined by this method, identifying key food resources used by these predators can provide direction for future research to focus on specific impacts of coyotes, bobcats, and black bears on prey species of interest like white-tailed deer. Comparing predators' use of food items to the availability of food items in the landscape will provide insight into foraging strategies used by predators, a key aspect of predator behavior. For example, if predators select foods preferentially, regardless of the densities (i.e., are more specialist in behavior), that may be more cause for concern in managing white-tailed deer populations. In addition, understanding the effects of habitat treatments, particularly fire restoration and timber harvest, on predators and their prey base can aid managers in planning future management of this region. Density and habitat use estimates of prey species can further inform management strategies for a variety of species, particularly in the George Washington National Forest. Determining the prevalence of parasites of coyotes in Virginia would be a necessary first step in understanding the potential for parasite transmission from coyotes to humans, pets, and livestock. The results of this research alone are not adequate to prevent threats from parasites to human health and economic concerns, but may provide direction for future research that can address these issues. Ultimately, this study will provide greater knowledge of predator habits

and behavior in Virginia and will open avenues for new research that can focus on specific concerns related to predator-ecosystem interactions and human-predator conflicts.

STUDY AREA

The study area is located in the western portions of Bath and Rockingham Counties (Fig. 2). Land ownership in the study area includes state, federal, and private holdings. The George Washington National Forest constitutes the largest public landholder in the region. National forest land is limited primarily to higher elevations along ridgetops creating long, linear patches of public land interspersed with private land in the valley bottoms. Large portions of the national forest consist of contiguous, even-aged forests ≥ 70 years old, periodically broken up by small “wildlife clearings” dominated by cool-season grasses and planted clover (*Trifolium spp.*) or through modified shelterwood timber harvests and fire restoration areas (C. Croy, USFS, personal communication). State lands include the T.M. Gathright Wildlife Management Area, managed by VDGIF, and Douthat State Park, managed by the Virginia Department of Conservation and Recreation (DCR).

Private protected areas include The Warm Springs Mountain Preserve, managed by The Nature Conservancy (TNC) in western Bath County. The preserve covers $\sim 37 \text{ km}^2$ and adjoins both the national forest and Douthat State Park, creating an area of roughly 77,000 acres (311 km^2) of largely unfragmented forest (TNC 2011). Ongoing management of TNC land focuses on using prescribed burns to restore the historic fire regimen to the Allegheny Highlands ecosystem.

Private land in the area is concentrated at lower elevations along roadways in the valleys. Bath County has the second-lowest human population of all Virginia counties ($\sim 4,300$ residents; U.S.

Census Bureau 2010); Rockingham County has a population of 76,000, primarily in the vicinity of the City of Harrisonburg located east of the study site. Agriculture in the area includes poultry and sheep farming, the latter occurring mostly in the northwestern corner of Rockingham County. Cattle and dairy farming also occur, along with agricultural crops like corn and alfalfa.

In Bath County, the landscape forms a mosaic of forested mountain land under predominately public ownership (federal or state) heavily interspersed with privately-owned open land used primarily for pasture and silage production. By comparison, forested habitat in the Rockingham study site is nearly contiguous with very few private inholdings and little open land. However, at the eastern edge of the Rockingham study site, the forest ends abruptly and transitions into an agricultural area with high livestock concentrations (mostly dairy cattle and poultry) and very little forest or other natural ecosystems. The contrasting landscape compositions of the 2 study sites could result in different foraging behaviors of coyotes, bears, and bobcats, and different parasite assemblages in coyotes due to differing parasite prevalence.

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TABLES AND FIGURES

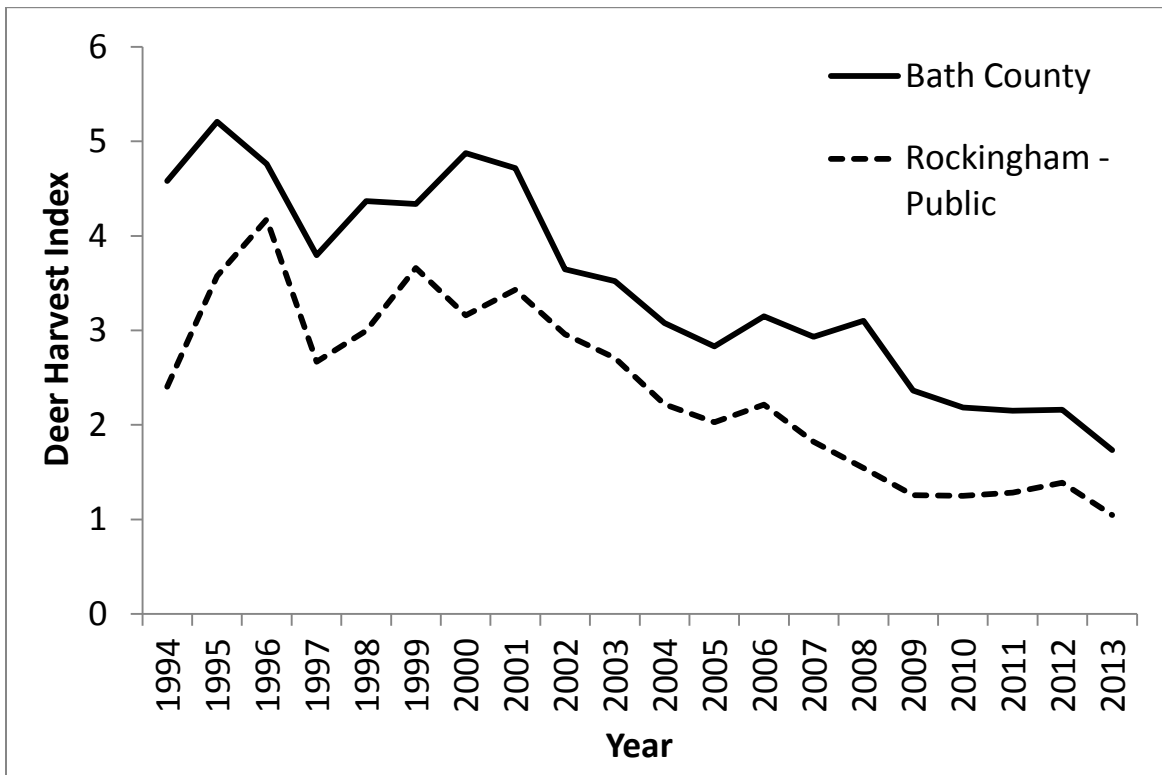


Figure 1: Deer hunter harvest indices (harvested bucks/mi²) from 1994 to 2013 for Bath County (public and private lands combined) and Rockingham County (public land only), Virginia, as tabulated by Virginia Department of Game and Inland Fisheries.

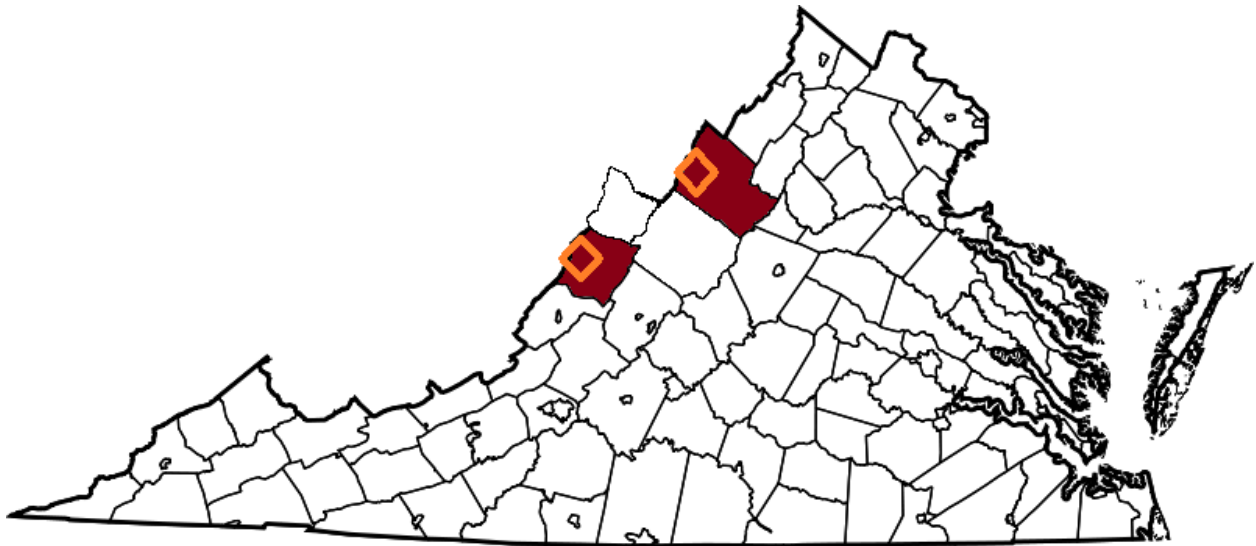


Figure 2: Map of the study areas for predator research in Virginia highlighting (L to R) Bath and Rockingham Counties. Orange boxes denote the general region of each county studied.

CHAPTER 2: FOOD AVAILABILITY FOR CARNIVORES IN THE APPALACHIAN MOUNTAINS OF VIRGINIA

ABSTRACT

An important consideration when comparing feeding strategies of carnivores is the relative availability of food items across the landscape. I estimated availability of multiple potential food items of 3 sympatric predators – coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*) – in a mosaic landscape that included areas of prescribed burning and variable timber harvest in the mountains of western Virginia. I focused on 4 broad categories of food items: white-tailed deer, mid-sized mammals (raccoons, *Procyon lotor*, opossums, *Didelphis virginiana*, cottontails, *Sylvilagus* spp., and squirrels, *Sciurus* spp.), small mammals, and soft mast. I used distance sampling to estimate deer density, camera trapping techniques to estimate mid-sized mammal trapping rates and occupancy, mark-recapture techniques to estimate small mammal abundance, and vegetation sampling to estimate % cover, to determine potential food availability. Using Program DISTANCE, I determined deer densities were higher in Bath County (4.75– 16.06 deer/km²) than in Rockingham County (0.17– 3.55 deer/km²). These estimates are lower than deer densities in other parts of Virginia. For mid-sized mammals, I estimated low availability as shown by constant but low trapping rates (# photo events/trap nights*100) of opossums, and relatively higher, constant availability of cottontails. Raccoon and gray squirrel trapping rates were highly variable among seasons; raccoon occupancy (proportion of sites occupied) was higher in summer (2011: 0.55 – 0.57; 2012: 0.51 – 0.55) and fall (2011: 0.53; 2012: 0.52 – 0.59) whereas gray squirrel occupancy was higher in June (2011: 0.55; 2012: 0.44), October (2011: 0.51; 2012: 0.46), and November (2011: 0.48; 2012: 0.53). Cottontail and

opossum occupancies were higher in burned areas (0.40 – 0.57, 0.24 – 0.46, respectively), whereas raccoon and gray squirrel occupancies were higher in unburned areas (0.23 – 0.78, 0.12 – 0.58, respectively). I estimated high abundance and density of *Peromyscus* spp. in all seasons relative to other small mammal species, with the top model in Program MARK incorporating seasonal variation. Densities of meadow voles (*Microtus pennsylvanicus*) and meadow jumping mice (*Zapus hudsonicus*) were high seasonally in open field habitat. Densities of eastern chipmunks (*Tamias striatus*), red-backed voles (*Clethrionomys gapperi*), and *Peromyscus* spp. were significantly higher in burned areas relative to unburned sites. Among soft mast species, blueberries comprised the largest % of occurrence. Managers seeking to reduce impacts of predation on species of special management interest, such as deer, should manage for a high diversity of food alternatives. This can be achieved in the mountains of western Virginia by using prescribed fire or timber harvest to increase acreage of young forest types. Based on my findings, I expect that a generalist predator would consume deer at a constant rate and have lower % deer occurrence in Rockingham County where deer densities are much lower. I expect seasonally-constant, but low, occurrence of opossum and relatively higher, but similarly constant, occurrence of cottontail. I expect raccoon occurrence to be relatively high in summer and fall, and lower in winter. Squirrel occurrence should peak in October and November, followed by a steady decline until June. *Peromyscus* spp. should be the most commonly occurring small mammal in the diets of generalist predators, rivaled by meadow voles in fall and perhaps summer. I expect chipmunks and red-backed voles to occur at constant, but low, rates in predator diets. I predict that various species of soft mast may occur during their respective fruiting seasons. By comparing spatio-temporal patterns of food availability to patterns in the

diets of predators, I hope to better understand foraging strategies used by predators and identify opportunities for targeted management to balance predator-prey dynamics with human values.

KEY WORDS: camera trapping, distance estimation, food availability, *Odocoileus virginianus*, small mammals, soft mast, Virginia, white-tailed deer

INTRODUCTION

An important consideration when comparing feeding strategies of carnivores is the relative availability of food across the landscape. I define food availability as a combination of a food species' presence, population density, and vulnerability to predation. A potential food species that occurs in high population density with high vulnerability would be highly available to predators and should occur frequently in the diet of a generalist predator. In contrast, a potential food species that is absent or has extremely low population density on the landscape, or a high density species that has low vulnerability to a given predator, would have low availability and would occur infrequently in a generalist predator's diet. I estimated the availability of several potential food species of 3 sympatric predators – coyotes, black bears, and bobcats – in a mosaic landscape in Bath and Rockingham Counties in western Virginia. I estimated food availability seasonally to compare it to seasonal predator diet (Chapter 3) to determine whether carnivore diet fluctuates in tandem with changes in food availability. I would expect generalist predator's diets (e.g., coyote and black bear) to track seasonal food availability, whereas bobcats, a more specialized carnivore, may not (Beasom and Moore 1977, Bowyer et al. 1983, Roof 1997).

I focused on 4 broad categories of food items: large prey (white-tailed deer), mid-sized mammals (raccoons, opossums, cottontails, and squirrels), small mammals, and soft mast. I used distance

estimation, camera trapping, mark-recapture techniques, and vegetation sampling to estimate density, occupancy, activity, and % cover which I used as indicators of availability for predation.

METHODS

White-tailed Deer

I sampled deer populations in January, April, and October 2012 and January and April 2013 in both Bath and Rockingham Counties. During the first 2 sessions, I sampled deer for 4 nights per county in each session. However, due to low sample sizes, I increased sampling effort in the next 3 sessions to include as many nights of sampling as needed to reach a target number of detections. In Bath County, where forested mountain land under state and federal management is highly interspersed with privately-owned, open pasture land and edge habitat, I targeted 40 detections in each of these land ownership types to avoid over-representing either type (40 public and 40 private; total of 80 detections). In the Rockingham County site, publicly-owned, forested mountain land is nearly contiguous, so I targeted a total of 40 detections.

I considered all roads within each study area as transects, and I scheduled visits to transects randomly or based on accessibility. When necessary, I repeated sampling at transects only after all available transects had been visited once. I sampled Bath County until I achieved the target number of detections, after which I immediately proceeded to sample Rockingham County.

During sampling, I traveled transects placed along dirt roads and state-maintained paved roads at night by 4x4 vehicles traveling at speeds ≤ 5 miles per hour. Two observers standing in the bed of the pickup truck used handheld Forward-Looking Infrared (FLIR) units to detect deer from the vehicle at night. Because FLIR detects body heat, deer appear as bright, white deer-shaped

objects against a black background, even when sparse vegetation would obscure the outline of the deer seen with the naked eye (Fig. 1). When a deer was detected, I recorded: the vehicle's location on the transect with a handheld GPS unit, the vehicle's distance from the transect starting point using the vehicle odometer, and the number of deer in the detected group. I used a handheld spotlight, laser rangefinder, and a large protractor mounted on the roof of the truck to obtain the sighting angle to the deer to convert measurements to perpendicular distance measurements from the transect to the deer. I recorded the time, weather conditions, and air temperature at each detection location, as well as the habitat type in which the deer were standing (woods, pasture, crop field, edge, riparian).

Data were analyzed in program DISTANCE (Thomas et al. 2009) using the multiple covariates distance sampling (MCDS) platform (Table 1). I used average windspeed (mph), minimum daily temperature ($^{\circ}\text{C}$), habitat type (woods, pasture, crop field, edge, riparian), and lunar phase (full, waning gibbous, waning crescent, new, waxing crescent, waxing gibbous) as covariates of detection. Windspeed, temperature, and lunar phase were based on archived NOAA weather data collected at stations located within the study sites. I used a 5% right truncation of the data according to conventions for analyzing ground-based linear survey data (Buckland et al. 2001). I added covariates in DISTANCE using forward stepwise model-building techniques, and I used various combinations of key functions, adjustment terms, and bin sizes to achieve model fit. Models were ranked in DISTANCE by Akaike's Information Criterion corrected for small sample size (AICc) and competing models were denoted as those within 2 delta-AICs of the top model.

Mid-sized Prey

Mid-sized prey included species that may form a significant component of coyote, bobcat, or black bear diet but cannot be caught in Sherman traps. These species include eastern cottontail (*Sylvilagus floridanus*), Appalachian cottontail (*S. obscurus*), eastern gray squirrel (*Sciurus carolinensis*), eastern fox squirrel (*Sciurus niger*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*). I estimated trapping rates and occupancy of these species from remote camera surveys in Bath County only.

In June 2011, I placed 32 remotely-triggered camera traps (Moultrie Gamespy D50, Moultrie Feeders, Alabaster, Alabama) in and around burned and unburned sites (16 burned, 16 unburned). The cameras were placed along game trails, roads, and fire trails with signs of target species' activity (i.e., tracks, scat, nests or burrows). I attempted roughly even distribution of cameras throughout the study area; however, I was restricted by the availability of adequate fire-restored sites. In June 2012, I placed 16 additional cameras in timber harvested areas ("logged"), focusing on areas logged within the past 10 years that had sustained >60 % canopy loss. I checked the cameras monthly until June 2013 to change batteries and download digital images, as needed.

Because I was unable to identify individuals of the target species from photographs, density estimation through mark-recapture and similar techniques was not possible. As a result, I analyzed the camera data through comparing trapping rates and through detection/non-detection within an occupancy modeling framework in Program PRESENCE.

Trapping Rate Analysis.—I calculated trapping rate as the number of independent capture events divided by the number of trap nights, where a trap night was 1 trap for 1 night.

Independent capture events are defined as photographs of distinctly different individuals of a particular species that occur within a 30-minute time interval regardless of the number of photos (Kelly et al. 2012). I calculated trapping rates for each species in each habitat type (averaged across all 16 cameras from each of the 3 habitat types) and compared trapping rates in each of the 3 habitats in each month for each species using Kruskal-Wallis ranked sums tests for nonparametric data with Dunn's multiple comparisons in SAS JMP (e.g., comparison among burned, unburned, and logged trapping rates for raccoon in January, February, ... etc.). In addition to monthly comparisons among habitat types, I compared monthly trapping rate *within* habitat types for each species (e.g. comparison of raccoon trapping rate among months in burned areas only, etc.) using Kruskal-Wallis and Dunn's tests. I interpret the results of trapping rates as relative activity of each species and potentially relative habitat use or vulnerability to predation since the more active a species, the more visible and potentially vulnerable.

Occupancy Analysis.—I analyzed camera data using the multi-season analysis platform in Program PRESENCE (Hines 2006) (Table 2). For covariates, I used % canopy cover, % softwood cover, % mast-bearing tree cover, mean canopy height, elevation, aspect, slope, habitat type, and trail width at the camera station. I normalized covariate data using a z-scale in PRESENCE. I included site covariates on occupancy using forward stepwise model-building procedure. In the multi-season model I constrained detection rate to be constant based on the assumption that camera functionality and visibility of wildlife at the camera sites did not change among months. I interpreted the results of these analyses as prey availability of each species and related this to the prevalence of these species in coyote scat found at burned, unburned, and logged sites (Chapter 3). I could not conclusively distinguish Appalachian and eastern cottontails, so both species were lumped and analyzed by genus (*Sylvilagus* sp.). Similarly, I

was unable to reliably distinguish remains of eastern gray squirrel and eastern fox squirrel in scats, so both species were lumped and analyzed by genus (*Sciurus* sp.) in trail camera analyses.

Small Mammals

I estimated small mammal density in Bath County using mark-recapture techniques. I trapped small mammals in July and November 2011; March, May, July, and November 2012; and March and May 2013. Each trapping session consisted of 5 nights of trapping. During the initial 5 trapping sessions from July 2011 through July 2012, I placed 8 trapping grids throughout the study area. I focused on areas disturbed by fire within the past 5 years (“burned”), and adjacent reference areas not burned during that time period (“unburned”). In selecting burned areas, I focused on burns that overlapped my camera trapping sites. Beginning in November 2012, I placed 3 additional trapping grids in open fields to target microtine voles, which preliminary analyses indicated were a frequent component of coyote diet. To encapsulate some of the variation in field habitats found in Bath County, I placed the 3 field grids in 3 different types of field habitat: a warm season grass field dominated by switchgrass (*Panicum virgatum*), a cool season grass field dominated by fescue and moderately infiltrated by Japanese barberry (*Berberis thunbergii*) and short autumn olive (*Eleagnathus umbellatum*), and a mixed warm season and cool season grass field infiltrated by a variety of woody shrubs and forbs. At all 11 trapping grids, I attempted to avoid edge effects by placing the grid ≥ 50 meters from the boundaries of fields, burned areas, and timber harvest areas. All grids were 8 by 8 with 10 meters between sites for a total of 64 traps in each grid. At each trap site, I placed a single Sherman live trap (8 x 9 x 23 cm, H.B. Sherman Traps, Inc., Tallahassee, Florida). I checked the traps every morning, left traps open during the day to capture diurnal species (e.g., *Tamias striatus*), and checked them again in the evening. Following a capture during morning trap checks, I placed loose sunflower

seeds in the trap during the day to avoid the loss of prepared bait bags to chipmunks. After evening trap checks, I added a new bait bag consisting of sunflower seeds and 3 cotton balls to each trap to improve survival rates of nocturnal captures.

All animals captured were identified to species except for mice of the genus *Peromyscus* which are difficult to distinguish by morphology and function similarly in the ecosystem, and therefore were identified only to genus. After identification, each animal was weighed, measured for head-and-body length and tail length, sexed, marked with unique ear tags (or hair clipping, in the case of Soricidae), and released at the point of capture.

During July 2011 and 2012, I measured microhabitat characteristics at all burned and unburned grids. I took the same measurements at the field grids in late October 2012. I collected microhabitat measurements in circular plots with 2 meter radii at every trap site. Groundcover %ages of leaf litter, grass, forbs, woody plants, moss, ferns, coarse woody debris, rock, and bare ground within each plot were estimated visually according to the Daubenmire scale method (Daubenmire 1959). I also measured leaf litter depth, woody stem counts, and diameter of coarse woody debris. Canopy cover was estimated to the nearest 10%. In field grids, grass height was measured also. I repeated the measurement of grass height at the field grids during every trapping session, since grass height was highly dependent on season. Also, I repeated all microhabitat measurements at one field grid (HV1) in May 2013 due to a prescribed fire treatment less than one month prior to trapping, which significantly altered microhabitat structure.

I modeled small mammal data in Program MARK (White and Burnham 1999) using Huggins' closed captures models for robust designs to estimate population abundance, survival,

immigration, and emigration (Table 3). I modeled data from burned and unburned grids together, stratified by habitat type, with sex as a covariate. Because the number of trapping sessions for field grids differed from burned and unburned grids, I modeled the field grids separately using sex as a covariate. I tested for time and behavior effects in the data. I used mean maximum distance moved (MMDM) (Wilson and Anderson 1985) and the delta method (Nichols and Karanth 2002) to calculate effective area sampled and determine population density and variance.

Soft Mast Plants

Soft mast sampling methods were adapted from Reynolds-Hogland et al. (2006) and Daubenmire (1959). Soft mast-producing species and taxa of interest included: cherries (*Prunus* spp.), blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.), blackberries/raspberries/wineberries (*Rubus* spp.), black gum (*Nyssa sylvatica*), grapes (*Vitis* spp.), black haw (*Viburnum* spp.), apples (*Malus* spp.), sumac (*Rhus* spp.), persimmon (*Diospyros virginianus*), and sassafras (*Sassafras* spp.).

I used the summer of 2011 as a pilot season to test field methods for soft mast data collection. Based on results from this pilot study, I redesigned my sampling protocols for summer 2012 which reduced my usable soft mast data to only one season. I used a simple random sample of 43 transects to estimate the relative % cover of mast producing plants in Bath County. Random starting points were generated in Esri ArcGIS 10.1. I used a random number generator in Microsoft Excel to select compass headings between 0 and 359 which were paired with each random starting point. At each random starting point, I used a 100 meter measuring tape to measure a 300 meter transect in the direction of the random compass heading. I estimated %

cover of soft mast plant species in 2 meter radius plots located every 50 meters along the transect (7 plots per transect; total of 301 plots). Within each plot, I estimated % cover of target soft mast species using the Daubenmire method (Daubenmire 1959). All data were collected by a single team of 3 field technicians to reduce observer bias. I collected data during a 6-week period in July – August 2012, during which time I estimated % cover of soft mast plants did not change significantly due to plant growth or disturbance. Due to time constraints, I was unable to visit sites more than once in the growing season.

From ArcGIS, I extracted slope, aspect, and elevation of each of the 301 plots using 30 meter digital elevation models from the USGS National Elevation Dataset. I extracted soils data from the STATSGO soil dataset. I analyzed % cover data from the Daubenmire plots using minimum least squares forward stepwise model building in SAS JMP Pro 10.

RESULTS

White-tailed Deer

I sampled deer during a total of 5 sessions in 2012 and 2013. In all 5 sessions, I detected an adequate number of deer clusters to produce global estimates of deer density in Bath County (Table 2). In the Rockingham County study site, I had too few detections in January 2012, April 2012, and January 2013 to obtain reliable density estimates. Reliable estimates were obtained for Rockingham County in October 2012 and April 2013; however, the spatial distribution of detections in October 2012 was limited to roughly one quarter of the study area, possibly resulting in an overestimate of population abundance when extrapolated to the entire study site.

Based on the overlap in the 95% confidence intervals, deer density did not vary among seasons within each site, and density estimates in Bath County were 4.3 – 91.3 times higher than Rockingham County in all seasons (Fig. 2). Among seasons in which covariates improved density models, average windspeed and minimum temperature were the most commonly significant covariates. Detection was negatively related to average windspeed and positively related to minimum temperature. Habitat type and lunar phase each improved estimates in 1 of the 10 top models.

In all seasons, the half-normal cosine detection function was highest ranked by AIC. In Bath County in April 2012, the half-normal cosine model with habitat type as a covariate was highest ranked by AIC, but models incorporating habitat+temperature+lunar phase and habitat+windspeed+lunar phase were competing. In Bath County in January 2013, the half-normal cosine model with average windspeed as a covariate was the top model, but the model incorporating both windspeed and minimum temperature was slightly competing ($\Delta AIC = 1.952$). In Rockingham County in October 2012, the half-normal cosine model without covariates was top-ranked, although the single covariate models using habitat type ($\Delta AIC = 0.347$), minimum temperature ($\Delta AIC = 1.699$), and average windspeed ($\Delta AIC = 1.928$) were competing.

Mid-sized Prey

Trapping rates.—Using 48 Moultrie GameSpy trail cameras, I collected 221,359 images between June 2011 and June 2013 (Table 5). This included photographs of 12,831 animals of 24 species, not including passerine birds, small mammals, and invertebrates. For the target species (raccoons, cottontails, opossums, and squirrels), I compared trapping rate by month to assess

relative activity or habitat use among burned, unburned, and logged camera stations (Fig. 3). I analyzed data from each month separately using a Kruskal-Wallis test to compare trapping rates (# “captures”/ 100 trap nights) among the 3 habitat types (4 species * 12 months = 48 separate analyses). In most months, trapping rates for opossums and cottontails were highest in burned areas, whereas trapping rates for squirrels and raccoons were highest in unburned sites (Table 6). In burned areas, the trapping rates for squirrels and raccoons also were higher relative to logged areas, but the difference was not statistically significant based on Kruskal-Wallis tests. Trapping rates were lowest in logged areas for all 4 species in most months. Trapping rates for squirrels, opossums, and cottontails peaked in September and October in both years, whereas the trapping rate for raccoons was highest in October and November in both years.

Other, non-target species photographed in high numbers included, black bears, bobcats, coyotes, gray foxes (*Urocyon cinereoargenteus*), striped skunks (*Mephitis mephitis*), and white-tailed deer (Table 5). Spotted skunks (*Spilogale putorius*), a locally uncommon species, were photographed on 3 separate occasions during the study. However, I did not statistically analyze trapping rate data for non-target species.

Occupancy.—The best model for cottontails incorporated the site aspect as a covariate of occupancy, with easterly aspects associated with higher cottontail occupancy relative to westerly aspects (Fig. 4; Table 2). Cottontails had relatively high, constant availability throughout the study. Raccoon occupancy varied seasonally, and was positively related to width of the trail and total % canopy cover, and negatively related to % cover of mast-producing trees (oaks, walnuts, and hickories). In both years of the study, raccoon occupancy was much higher in June-November compared to December-May. The best model for opossums used total % cover of tree canopy as a covariate of occupancy, with lower % tree cover resulting in higher occupancy. Like

cottontails, availability of opossums was also nearly constant, but lower relative to cottontails, raccoons, and squirrels in most seasons. Squirrel occupancy was negatively related to total % cover of tree canopy. Competing models for squirrels included positive relationships with tree height, slope, and unburned habitats. Squirrel occupancy varied seasonally with highest availability in October, decreasing steadily until May, then increasing through the summer until another peak in October.

Small Mammals

In 8 sessions, I trapped small mammals for a total of 19,322 trap nights (trap night = 1 trap set for 1 night). In all, I logged 4,502 captures of 1,463 individual small mammals from 11 species (Table 7). In the original 8 trapping grids, mice of the genus *Peromyscus* were the most commonly captured species, comprising 82% of total captures (n = 3,692). Eastern chipmunks (13%; n = 585) were the next most frequently captured species, followed by red-backed voles (2%; n = 90), and short-tailed shrews (2%; n = 88). Infrequently, I captured meadow jumping mice, southern flying squirrels (*Glaucomys volans*), meadow voles (*Microtus pennsylvanicus*), smoky shrews (*Sorex fumeus*), pygmy shrews (*Sorex hoyi*), and red squirrels (*Tamiasciurus hudsonicus*).

In the 3 field grids added in November 2012 specifically to target meadow voles, I captured meadow voles most commonly (78 % of captures; n = 256), followed by short-tailed shrews (15%; n = 51), and meadow jumping mice (7%; n = 23). I captured *Peromyscus* sp. infrequently, and I captured a single least weasel (*Mustela nivalis*) in November 2012.

In robust design models in Program MARK, survival, immigration, and emigration are modeled in addition to capture and recapture probabilities to better inform estimates of abundance. These

parameters have little relevance to prey availability, except in their effects on estimates of abundance. In all top models for all species, I constrained immigration and emigration to be constant within and among seasons, grids, and habitat types (null model). My models of abundance performed better when I allowed survival rate to vary by habitat type among all species modeled in burned/unburned forested habitats (*Peromyscus* spp., chipmunks, red-backed voles), but I kept survival rate constant within habitat types. For both species modeled in fields (meadow vole, meadow jumping mouse), I varied survival rates between each session (time model) but did not vary them by habitat type since only one habitat type was tested.

For red-backed voles and meadow voles, capture rates were the same as recapture rates (i.e. no trap response or behavioral effect of trapping) and varied over time within each trapping session (Table 8). By contrast, capture rates of *Peromyscus* spp. and meadow jumping mice varied over time and differed from recapture rates (behavior model), showing evidence of “trap happiness” for *Peromyscus* spp. and “trap shyness” for meadow jumping mice. However, for all 4 species, capture rates did not vary among trapping grids or trapping sessions.

For chipmunks, I detected no behavior effect, but capture rates varied over time within and among seasons and among grids, regardless of habitat type.

In burned areas, *Peromyscus* spp. population density peaked in November of 2011 and 2012 and was lowest in May and July sessions (Table 8, Fig. 5). *Peromyscus* spp. population density followed a similar pattern in unburned areas. Chipmunk density was higher in burned areas than in unburned areas in all months and showed very little seasonal variation in either habitat type. Red-backed vole density was higher in burned areas in most months and did not vary significantly by season, based on the lack of a seasonal effect in the top model. In fields,

meadow vole density declined steadily during the 3 trapping sessions in which the species was captured, whereas meadow jumping mice were only captured in May 2013.

Soft Mast

I recorded 15 species of soft mast producing plant species in 301, 2-meter plots. Of these, only 3 genera (*Gaylussacia*, *Vaccinium*, *Rubus*) had sufficient coverage to allow for statistical modeling in SAS JMP. The top model for *Gaylussacia* (huckleberries) included landcover type and soil type as covariates of % cover, with highest % cover in evergreen forests with inceptisols (new, unstratified soils) and lowest % cover in fields and other open areas with rich, clay soils. The best model for *Vaccinium* spp. (blueberries), incorporated soil type and landform (ridge side, valley, ridge top). *Vaccinium* spp. coverage was highest on ridge sides with inceptisols. *Rubus* spp. (blackberries) varied significantly by landcover type and landform type, with highest % cover occurring in mixed forest and edge habitats in valleys and lowest % cover in evergreen forests along the sides of ridges. % cover of *Vaccinium* spp. was higher in burned areas, whereas % cover of *Gaylussacia* spp. and *Rubus* spp. did not vary between burned and unburned sites. *Vaccinium* spp. had the highest mean coverage within plots (21.46 % \pm SE 2.71 %), whereas *Rubus* spp. had the lowest mean coverage (6.12 % \pm SE 2.56 %).

DISCUSSION

White-tailed Deer

The positive relationship between deer and young forests created by fire or timber harvest, edge habitats, and open agricultural landscapes is well documented (Beier and McCullough 1990, Roseberry and Woolf 1998, Vreeland et al. 2004). Given this established habitat association, I

was not surprised to find that the Bath County study site, with a higher proportion of these habitats, has a significantly higher deer density. In the 2 sessions in which detection rates were high enough to estimate density in the Rockingham County study site, deer were most commonly observed in the few areas that were close to fields, timber harvests, and agricultural edges. Since detection was negatively related to average windspeed and positively related to minimum temperature, my inability to achieve an adequate number of detections in mid-winter probably was due to abiotic factors. It is possible that cold, windy weather reduced deer movements and the detectability of deer during distance sampling. My inability to achieve adequate detections for density estimation in Rockingham County in April 2012 was likely due to inadequate sampling effort in that session, since only 4 nights of sampling resulted in detection of 14 groups of deer. The expenditure of additional sampling effort in future months enabled me to achieve an adequate number of detections.

Estimates of deer density in Bath County (53.17 deer/km^2 - 215.77 deer/km^2) are consistent with estimates inferred from deer harvest data collected by VDGIF in parts of Virginia with similar habitat composition. The lack of seasonal differences in population density may be due to the relatively short duration of the study. Comparisons of deer density among years may reveal significant differences over longer time periods. Although I did not observe significant differences in deer density seasonally, based on 95% confidence interval overlap, the inability to detect adequate numbers of deer in January 2012 and January 2013 may mimic the difficulties faced by predators during that season, if we assume coyotes, bobcats, and bears are consuming adult deer. This difficulty could result in lower availability of deer in winter months.

Mid-sized mammals

Raccoon and gray squirrel trapping rates were significantly higher in unburned habitats in some months. This may be due to the availability of large diameter trees with cavities for denning and escape cover. In the case of gray squirrels, this also may be a result of the availability of acorns and other hard mast in undisturbed forests with mature hardwood canopy. Cottontails were photographed more often in burned and logged habitats where canopy loss resulted in more herbaceous vegetation at ground level. In areas where fire intensity was not sufficient to result in canopy loss, cottontail trapping rates were not discernibly different from those in unburned habitats. Opossum trapping rate was highest in burned areas, but the difference relative to unburned areas was significant in only one month (July 2011: $p = 0.0733$). Given the diversity of opossum diet and habitat requirements, it is not surprising that they seem to distribute evenly across the landscape, regardless of habitat type.

Raccoons and cottontails were the most available of the 4 prey species in nearly every month; however, these species were associated with burned and logged areas, as previously noted. Raccoon availability (occupancy) varied among seasons. Periods of high raccoon availability from June to October in both years correspond with high levels of warm season activity relative to periods of winter dormancy previously noted for this species (Prange et al. 2004). Squirrel availability experienced large seasonal fluctuations in both years of the study. Annual peaks in availability of squirrels in June correspond with the dispersal of young, and peaks in October are most likely due to the availability of hard mast (acorns, hickories, walnuts, etc.) and the flurry of activity associated with caching behavior in preparation for winter.

Small Mammals

All 3 species modeled in forested habitat showed higher densities in burned areas in most seasons. This contrasts with the results of Kirkland et al. (1996), who found no significant difference in small mammal densities in burned versus unburned habitat in southern Pennsylvania. Similarly, Ford et al. (1999) found no significant difference in the density of the small mammal species captured between burned and control sites in western North Carolina. Krefting and Ahlgren (1974) observed an increase in deer mice (*Peromyscus maniculatus*) immediately following fire in Minnesota. In subsequent years, deer mice captures decreased steadily while red-backed vole captures increased at >7 years post burn. In my study sites, fire resulted in decreased canopy cover and leaf litter depth and increased understory density and coarse woody debris, all of which creates habitat favored by many small mammal species (Kaminski et al. 2007). The higher density of red-backed voles observed in unburned habitats in November 2011 was due to a high capture rate at 1 of the 4 unburned grids in which the landscape was dominated by rocks and ledges. These results are similar to Kaminski et al. (2007) who noted a positive relationship between red-backed voles and % groundcover dominated by rocks.

The seasonal variation I observed in *Peromyscus* spp. is consistent with well-established population cycles in mice of this genus that coincide with oak mast cycles (Elias et al. 2004). The downward trend in the meadow vole population, however, may have been due to a late spring in 2013 which caused the dormant period for voles to extend into May. In addition, the field in which the highest number of meadow voles was trapped was burned 2 weeks prior to the

May 2013 trapping session. Vole mortality was observed by fire crews during the prescribed burn (S. Tanguay, USFS, personal communication), and the altered vegetation structure of the microhabitat may have reduced vole activity or food availability. The appearance of meadow jumping mice in the final trapping session (May 2013) may be the result of mice entering hibernation prior to the November 2012 trapping session and leaving hibernation as day length increased prior to May 2013, regardless of unusually cool temperatures (Muchlinski 1980).

For all species, capture and recapture rates increased over time within each session. This may be the result of an acclimation period in which small mammals require time to find new traps and associate them with a food source. Some studies have used pre-baiting of trap sites prior to setting traps as a method to prevent this initial acclimation period (Babinska and Bock 1969). Similarly, after animals were captured in traps, I spread loose sunflower seeds in the trap to attract chipmunks during the day to avoid using more prepared bait bags than were necessary. Although this is a common technique when trapping both nocturnal and diurnal species using the same traps, this in conjunction with later re-baiting using bait bags may have inadvertently acted as a greater attractant than bait bags alone.

The variation in survival rates between burned and unburned habitats for all species may be attributable to differences in resource availability. Survival of red-backed voles and *Peromyscus* spp. was higher in unburned areas, whereas survival of chipmunks was higher in burned areas.

In field grids, meadow vole survival decreased over time.

Soft Mast

I estimated % coverage of 3 soft mast species known to occur in coyote, bear, and/or bobcat diets throughout their range. Because I had data from only 1 season, and sites could be visited only

once per season, I was unable to estimate fruit production per plant during the course of the season, and my data provide only a snapshot of potential production. Because some soft mast species exist as non-fruiting forest understory plants, % cover of vegetation does not necessarily correlate with relative fruit production among species. This, coupled with the fact that my data does not capture seasonal variation in fruit availability as a result of plant phenology and production rates, limits the utility of these data when comparing to rate and timing of soft mast occurrence in predator diets. To infer fruit availability from these data requires large assumptions about the relationship between vegetation coverage and fruit production per plant, which I am unable to test using my data. I include the data here as a rough baseline of the variety and relative distribution of soft mast plants available to predators in Bath County and similar landscapes.

Inference to Predator Diet and Implications for Management

My estimates of food species availability in Bath and Rockingham Counties indicate a food base that is highly variable on a seasonal and annual timescale. A generalist predator is defined as one that consumes food opportunistically in proportion to availability. Based on my estimates, I would expect a generalist predator in western Virginia to have a diverse diet that is highly seasonal (Table 9). Presuming adult deer are susceptible to predation, or that deer carcasses are available for scavenging in proportion to deer availability, I would expect scats of predators in Bath County to contain more adult deer than scats of predators in Rockingham County based on availability, with adult deer consumed in relatively constant amounts throughout the year in both counties. I did not collect data on deer fawn availability. Since fawns represent a highly seasonal food item that are much more vulnerable to predation than adult deer, occurrence of fawns in predator scats in addition to adult deer might produce a seasonal spike in overall deer

occurrence in predator scat. Furthermore, my methods for deer density estimation provide data only on availability of live deer. Since deer carcasses obviously are easier to “predate” than live deer, differences in the seasonal availability of carcasses (e.g., due to hunting seasons, rut-related high rates of vehicle collisions, or late winter kill) may result in seasonally higher rates of deer occurrence in predator scat.

I would expect evidence of seasonally-constant, but low, rates of opossum in generalist predator scats, and relatively higher, but similarly constant, occurrence of cottontail. I would expect raccoon occurrence to be relatively high in summer and fall and lower in winter. Squirrel occurrence in predator scat should peak in October and November, followed by a steady decline until June.

If all habitat types are foraged equally, *Peromyscus* spp. should be the most commonly occurring small mammal in the scats of generalist predators, rivaled by meadow voles in fall and perhaps summer. I would expect chipmunks and red-backed voles to occur at constant, but low, rates in predator scats, unless predators expend a disproportionate amount of effort foraging in burned habitats, in which case chipmunks may occur at higher rates.

I predict that various species of soft mast may occur in predator scats during their respective fruiting seasons. If total biomass of fruit corresponds with relative % cover of soft mast plants, I expect that *Vaccinium* spp. will occur most often in a generalist’s scat when fruiting season overlaps with other soft mast producing species.

I suggest that managers who seek to reduce impacts of predation on species of special management interest, such as deer, should manage for a high diversity of food alternatives.

Based on my results, this can be achieved in the mountains of western Virginia by using

prescribed fire or timber harvest to increase acreage of young forest types that provide habitat for cottontail, opossum, and small mammals, and may increase deer populations as well. By comparing spatio-temporal patterns of food availability to patterns in the diets of predators, better understanding of foraging strategies and identification of opportunities for targeted management will help balance predator-prey dynamics with human needs and values.

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TABLES AND FIGURES

Table 1: Some of the models of deer density (D) in Bath and Rockingham Counties, Virginia tested in Program DISTANCE. Models with delta Akaike Information Criteria (AIC) > 8 are not shown. For Rockingham County, January and April 2012 and January 2013 are not displayed because there were insufficient detections for extensive modeling in these months.

Session	County	Model	# of Parameters	Delta AIC	AIC	ESW/EDR	D	D LCL	D UCL	D CV
January 2012	Bath	HN_Cos_Wind+Moon+Temp	4	0.000	8.000	75.930	21.874	0.047	10188.880	100.000
		HN_Cos_Hab	3	0.000	186.002	72.562	13.740	7.369	25.619	0.311
April 2012	Bath	HN_Cos_Hab+Temp+Moon	5	0.330	186.332	67.890	15.024	7.999	28.221	0.316
		HN_Cos_Hab+Wind+Moon	5	0.730	186.732	69.653	14.483	7.730	27.137	0.314
		HN_Cos_Hab+Temp+Wind	5	0.980	186.982	70.236	14.104	7.532	26.411	0.314
		HN_Cos_Hab+Temp	4	1.126	187.128	72.229	13.534	7.256	25.244	0.311
		HN_Cos_Wind+hab	4	1.653	187.655	72.565	13.537	7.258	25.246	0.311
		HN_Cos_Hab+Moon	4	1.975	187.977	72.444	13.836	7.414	25.821	0.312
		HN_Cos_Hab+Temp+Wind+Moon	6	2.403	188.405	69.375	14.441	7.697	27.095	0.315
		HN_Cos_Wind+Moon	3	4.434	190.436	75.900	12.120	6.515	22.549	0.310
		HN_Cos_Temp	2	7.109	193.111	79.555	11.149	6.016	20.661	0.307
October 2012	Bath	HN_Cos_Wind+Moon+Temp	5	0.000	179.836	43.953	12.090	6.593	22.171	0.305
		HN_Cos_Wind+Moon	4	4.318	184.154	46.648	10.742	5.894	19.578	0.301
		HN_Cos_Wind	2	5.611	185.448	49.352	9.709	5.358	17.591	0.298
		HN_Cos_Wind+Temp	3	5.794	185.630	48.238	9.859	5.436	17.882	0.298
	Rockingham	HN_Cos	1	0.000	84.486	58.971	2.707	1.502	4.880	0.301
		HN_Cos_Hab	3	0.347	84.833	57.101	3.161	1.774	5.633	0.294
		HN_Cos_Temp	2	1.699	86.185	58.731	2.658	1.498	4.717	0.292
		HN_Cos_Wind	2	1.928	86.414	58.912	2.720	1.534	4.822	0.291

		HN_Cos_Wind+hab	4	2.258	86.744	57.048	3.161	1.747	5.717	0.303
		HN_Cos_Wind+Temp	3	3.647	88.133	58.663	2.673	1.504	4.750	0.292
		HN_Cos_Moon	6	7.013	91.499	56.191	3.093	1.711	5.590	0.302
January 2013	Bath	HN_Cos_Wind	2	0.000	243.051	98.340	4.749	2.871	7.856	0.257
		HN_Cos_Wind+Temp	3	1.952	245.003	98.396	4.833	2.911	8.023	0.259
		HN_Cos_Wind+Moon	5	5.134	248.185	95.202	5.049	1.166	21.858	0.851
		HN_Cos_Wind+Moon+Temp	6	6.904	249.955	89.066	5.558	0.013	2327.475	100.000
		HN_Cos_Temp	2	7.677	250.728	100.685	5.400	3.181	9.165	0.272
	Bath	HN_Cos_Wind+Moon	3	0.000	6.000	86.749	12.927	6.590	25.355	0.339
		HN_Cos_Wind+Moon+Hab	5	4.000	10.000	86.749	12.927	6.590	25.355	0.339
April 2013	Rockingham	HN_Cos_Hab	3	0.000	6.000	38.238	4.126	1.837	9.267	0.420
		HN_Cos_Wind+Hab	4	2.000	8.000	37.354	4.313	1.794	10.370	0.458
		HN_Cos_Hab+Temp	4	2.000	8.000	36.369	4.463	1.627	12.239	0.533
		HN_Cos_Hab+Temp+Wind	5	4.000	10.000	34.515	4.960	1.705	14.434	0.567
		HN_Cos_Hab+Moon	6	6.000	12.000	34.921	4.855	2.063	11.424	0.445
		HN_Cos_Wind+Moon+Temp	6	6.000	12.000	40.009	4.929	0.009	2625.899	100.000
		HN_Cos_Wind+Moon+Hab	7	8.000	14.000	28.647	6.496	2.054	20.547	0.614

HN = half normal key function; Cos = cosine adjustment term; Hab = habitat type; Wind = average windspeed; Temp = minimum temperature; Moon =

lunar phase

Table 2: Some of the models of mid-sized mammal occupancy tested in Program PRESENCE by species. Models are ranked according to Akaike Information Criteria. Models with delta AIC > 8 are not shown.

Species	Model	AIC	Delta AIC	AIC wgt	Model Likelihood	# of Parameters
Raccoon	psi(mo_width+%mast+%cover),gamma(),p()	2312.85	0	0.9321	1	31
	psi(mo_width+%mast+%cover+%soft),gamma(),p()	2319.69	6.84	0.0305	0.0327	32
	psi(mo_width+%mast+%cover+slope),gamma(),p()	2319.75	6.9	0.0296	0.0317	32
Cottontail	psi(mo_%softwood+elev),gamma(),p()	1118.06	0	0.3451	1	30
	psi(mo_aspect),gamma(),p()	1118.35	0.29	0.2985	0.865	29
	psi(mo_%softwood),gamma(),p()	1119.69	1.63	0.1527	0.4426	29
	psi(mo_elev),gamma(),p()	1120.75	2.69	0.0899	0.2605	29
	psi(mo_aspect+%soft),gamma(),p()	1121.91	3.85	0.0503	0.1459	30
	psi(mo_aspect+elev),gamma(),p()	1122.97	4.91	0.0296	0.0859	30
	psi(mo_%softwood+elev+aspect),gamma(),p()	1123.57	5.51	0.0219	0.0636	31
	psi(mo_slope),gamma(),p()	1125.34	7.28	0.0091	0.0263	29
Opossum	psi(mo_%cover),gamma(),p()	868.34	0	0.79	1	29
	psi(mo_hab+%cover),gamma(),p()	870.99	2.65	0.21	0.2658	30
Squirrel	psi(mo_%cover),gamma(),p()	2929.09	0	0.257	1	29
	psi(mo_height),gamma(),p()	2929.29	0.2	0.2325	0.9048	29
	psi(mo_hab),gamma(),p()	2929.43	0.34	0.2168	0.8437	29
	psi(mo_slope),gamma(),p()	2929.49	0.4	0.2104	0.8187	29
	psi(),gamma(),p()	2932.59	3.5	0.0447	0.1738	28
	psi(mo_%cover+height),gamma(),p()	2933.5	4.41	0.0283	0.1103	30
	psi(mo_%cover+aspect),gamma(),p()	2936.21	7.12	0.0073	0.0284	30

Psi = occupancy probability; gamma = colonization rate; p = detection rate; mo = varies by month; width = width of trail in front of camera; %cover = % canopy cover; %mast = % cover of hard mast-bearing species; %softwood = % of softwood cover; elev = elevation; height = mean canopy height; hab = habitat type; () = constant (null model).

Table 3: Some of the models of small mammal abundance in Bath County, Virginia tested in Program MARK ranked by Akaike Information Criteria corrected for small sample sizes (AICc). Models with delta AICc > 8 are not shown. t indicates time effect; “.” Indicates constant or null effect; hab indicates differences by habitat type; where s = survival, i = immigration, e = emigration, p = capture probability, and c = recapture probability.

Species	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	# of Parameters	Deviance
<i>Peromyscus spp.</i>	{s(hab)i(.)e(.)p(t)c(t)}	11073.4	0	1	1	13	11047.282
Chipmunk	{s(hab)i(.)e(.)p(all_t)=c(all_t)}	2040.004	0	0.99991	1	44	1942.9001
Red-backed Vole	{s(hab)i(.)e(.)p(t)=c(t)}	309.0378	0	0.33476	1	8	290.9201
	{s(hab)i(.)e(.)p(.)c(.)}	309.3685	0.3307	0.28374	0.8476	4	300.813
	{s(hab)i(.)e(.)p(.)=c(.)}	309.812	0.7742	0.22731	0.679	4	301.2565
	{s(hab)i(hab)e(hab)p(hab)=c(hab)}	312.0157	2.9779	0.07552	0.2256	5	301.1706
	{s(hab)i(hab)e(hab)p(hab)c(hab)}	313.5628	4.525	0.03484	0.1041	6	300.3628
	{s(.)i(.)e(.)p(.)=c(.)}	315.062	6.0242	0.01647	0.0492	3	308.7332
	{s(hab)i(.)e(.)p(t)c(t)}	316.5397	7.5019	0.00787	0.0235	12	287.6647
	{s(.)i(.)e(.)p(.)c(.)}	316.6694	7.6316	0.00737	0.022	4	308.1139
	{s(.)i(.)e(.)p(hab)=c(hab)}	316.9252	7.8874	0.00649	0.0194	4	308.3697
Meadow Vole	{s(t)i(.)e(.)p(t)=c(t)}	898.707	0	0.52246	1	7	891.291
	{s(t)i(.)e(.)p(t)c(t)}	899.6217	0.9147	0.3307	0.633	11	883.479
	{s(t)i(.)e(.)p(.)c(.)}	902.7474	4.0404	0.06929	0.1326	4	901.6673
	{s(.)i(.)e(.)p(.)c(.)}	903.553	4.846	0.04632	0.0887	4	902.473
	{s(t)i(.)e(.)p(all_t)c(all_t)}	904.9782	6.2712	0.02271	0.0435	25	855.5152
Jumping Mouse	{s(t)i(.)e(.)p(t)c(t)}	73.8858	0	0.41842	1	4	94.1647
	{s(t)i(.)e(.)p(all_t)c(all_t)}	73.8858	0	0.41842	1	4	94.1647
	{s(t)i(.)e(.)p(t)=c(t)}	75.8044	1.9186	0.16032	0.3832	4	96.0834

Table 4: Seasonal deer densities in Bath and Rockingham Counties, Virginia with top models for each season as determined by Akaike Information Criteria corrected for small sample sizes (AICc).

Session	County	Total Distance Sampled (km)	# of Groups Detected	Top Model	Density (per km²)	Lower Confidence Limit	Upper Confidence Limit
Jan-12	Bath	53.17	43	HN_Cos_Temp	15.52	6.07	39.68
Jan-12	Rock.	56.6	2	HN_Cos	0.17	0.00	0.69
Apr-12	Bath	74.56	91	HN_Cos_Hab	13.74	7.37	25.62
Apr-12	Rock.	64.82	14	HN_Cos	1.96	0.76	5.05
Oct-12	Bath	154.99	96	HN_Cos_Wind+Moon+Temp	12.09	6.59	22.17
Oct-12	Rock.	183.98	50	HN_Cos	2.71	1.50	4.88
Jan-13	Bath	215.77	105	HN_Cos_Wind	4.75	2.87	7.86
Jan-13	Rock.	158.16	6	HN_Cos	1.10	0.21	5.77
Apr-13	Bath	83.7	95	HN_Cos_Wind	16.06	8.15	31.66
Apr-13	Rock.	152.13	30	HN_Cos_Temp	3.55	1.96	6.44
Σ		1197.88	532				

HN = half normal key function; Cos = cosine adjustment term; Wind = average windspeed; Temp = minimum temperature;

Moon = lunar phase

Table 5: Wildlife captured by 48 remote camera traps deployed in Bath County, Virginia from June 2011 to May 2013.

Species	Common Name	# of Photo Events	# of Photos
Carnivores			
<i>Ursus americanus</i>	Black Bear	985	3056
<i>Lynx rufus</i>	Bobcat	461	814
<i>Canis Latrans</i>	Coyote	293	467
<i>Urocyon cineroargenteus</i>	Gray Fox	64	85
<i>Mustela frenata</i>	Long-tailed Weasel	1	1
<i>Didelphis virginianus</i>	Opossum	128	173
<i>Procyon lotor</i>	Raccoon	607	1059
<i>Vulpes vulpes</i>	Red Fox	23	32
<i>Spilogale putorius</i>	Spotted Skunk	3	4
<i>Mephitis mephitis</i>	Striped Skunk	37	55
Herbivores			
<i>Sylvilagus spp.</i>	Cottontail	234	874
	Eastern Fox		
<i>Sciurus niger</i>	Squirrel	18	56
	Eastern Gray		
<i>Sciurus carolinensis</i>	Squirrel	1885	6019
<i>Odocoileus virginianus</i>	White-tailed Deer	4418	15122
<i>Marmota monax</i>	Woodchuck	3	15
Other			
	Other birds	334	797
	Reptiles	3	9
<i>Bonasa umbellus</i>	Ruffed Grouse	34	84
<i>Meleagris gallopavo</i>	Wild Turkey	267	608
Total		9798	29330

Table 6: Significant and nearly significant differences in trapping rates among 48 cameras deployed in 3 habitat types in Bath County, Virginia based on Kruskal-Wallis ranked sums tests with Dunn's multiple comparisons. Asterisks denote significance ($\alpha = 0.05$).

Species	Month	Year	p - values		
			Unburned - Logged	Unburned - Burned	Logged - Burned
Cottontail*	Sept	2011		0.0386	
Cottontail	April	2012		0.0800	
Cottontail	March	2012		0.0800	
Squirrel*	May	2012	0.0537		0.0155
Squirrel*	July	2012			0.0296
Squirrel*	Sept	2012	0.0101		0.0083
Squirrel	Oct	2012	0.0720		0.0898
Opossum	July	2011		0.0733	
Opossum	Aug	2012			0.0650
Opossum*	Sept	2012			0.0414
Raccoon	Dec	2011		0.0798	
Raccoon	Jan	2012		0.0798	
Raccoon	Feb	2012		0.0765	
Raccoon*	May	2012			0.0441
Raccoon	June	2012			0.0994
Raccoon*	Aug	2012	0.0211		
Raccoon*	Sept	2012	0.0550		

Table 7: Species captured in Sherman live traps in 11 grids in 3 habitat types during 19,322 trap nights in Bath County, Virginia from July 2011 to May 2013.

Species	Grid	# of Captures and Recaptures	%age of Total Captures
<i>Peromyscus spp.</i>	Burned	1853	52.26
	Unburned	1555	45.53
	Field	7	2.05
Meadow Vole	Burned	6	2.27
	Unburned	2	0.76
	Field	256	96.97
Eastern Chipmunk	Burned	461	82.77
	Unburned	96	20.82
	Field	0	0
Red-backed Vole	Burned	55	61.11
	Unburned	35	38.89
	Field	0	0
Short-tailed Shrew	Burned	26	20.16
	Unburned	52	40.31
	Field	51	39.54
Meadow Jumping Mice	Burned	1	4.00
	Unburned	1	4.00
	Field	23	92.00
Southern Flying Squirrels	Burned	4	26.67
	Unburned	11	73.33
	Field	0	0
Smokey Shrews	Burned	3	75.00
	Unburned	1	25.00
	Field	0	0
Pygmy Shrews	Burned	0	0
	Unburned	1	100.00
	Field	0	0
Red Squirrels	Burned	0	0
	Unburned	1	100.00
	Field	0	0
Least Weasel	Burned	0	0
	Unburned	0	0
	Field	1	100.00
Total		4502	

Table 8: Estimates of seasonal mean maximum distance moved (MMDM) and population density of small mammal species trapped in Bath County, Virginia from July 2011 to May 2013.

Species	Habitat	Session	MMDM (m)	Density (ha)	Lower Confidence	Upper Confidence
<i>Peromyscus spp.</i>	Burned	July 2011	21.04	33.18	33.18	33.23
		November 2011	24.29	48.37	48.37	48.44
		March 2012	25.48	30.17	30.17	30.21
		May 2012	25.65	18.31	18.31	18.34
		July 2012	33.12	18.34	18.34	18.37
		November 2012	10.87	42.05	42.05	42.12
		March 2013	15.47	23.62	23.62	23.65
		May 2013	24.00	9.90	9.90	9.92
	Unburned	July 2011	21.10	38.86	38.86	38.92
		November 2011	21.96	33.70	33.70	33.76
		March 2012	22.16	22.96	22.96	23.00
		May 2012	30.10	19.96	19.96	19.99
		July 2012	28.34	20.16	20.16	20.20
		November 2012	9.37	29.36	29.36	29.41
		March 2013	12.83	21.50	21.50	21.53
		May 2013	16.59	11.67	11.67	11.69
Chipmunk	Burned	July 2011	17.53	6.42	5.99	8.51
		November 2011	15.29	16.00	14.40	20.13
		March 2012	17.66	6.61	4.91	12.52
		May 2012	23.89	15.31	13.70	19.06
		July 2012	32.95	6.39	6.02	7.91
		November 2012	12.98	8.41	6.11	15.92
		March 2013	12.98	18.08	3.28	118.73
		May 2013	10.47	21.02	20.12	23.78
	Unburned	July 2011	22.88	1.27	1.17	2.29
		November 2011	31.62	0.29	0.25	0.98

		March 2012	31.62	0.38	0.26	1.63
		May 2012	19.30	4.23	3.66	6.37
		July 2012	35.11	3.19	2.99	4.31
		November 2012	35.11	0.37	0.24	1.65
		March 2013	0.00	0.00	0.00	0.00
		May 2013	13.77	4.94	4.68	6.50
Red-backed Vole	Burned	July 2011	26.67	0.35	0.27	1.32
		November 2011	26.67	1.40	1.13	2.92
		March 2012	26.49	3.17	2.62	5.21
		May 2012	26.49	0.35	0.28	1.32
		July 2012	26.49	0.70	0.56	1.92
		November 2012	10.60	3.53	2.90	6.19
		March 2013	10.60	2.02	1.63	4.20
		May 2013	10.60	0.50	0.39	1.89
	Unburned	July 2011	10.00	2.05	1.65	4.27
		November 2011	10.00	3.59	2.94	6.28
		March 2012	23.03	1.14	0.91	2.63
		May 2012	23.03	0.38	0.30	1.42
		July 2012	40.00	0.27	0.21	1.02
		November 2012	13.74	1.40	1.12	3.25
		March 2013	13.74	0.00	0.00	0.00
		May 2013	13.74	0.00	0.00	0.00
Meadow Vole	Field	November 2012	6.30	74.87	66.64	88.64
		March 2013	9.71	23.83	20.49	30.68
		May 2013	4.16	12.51	10.39	18.10
Jumping Mouse	Field	November 2012	0.86	0.00	0.00	0.00
		March 2013	1.86	0.00	0.00	0.00
		May 2013	2.86	16.93	16.93	16.93

Table 9: Expected monthly seasonal diet of a generalist predator based on estimates of food availability in Bath and Rockingham Counties, Virginia. * denotes higher occurrence potentially due to fawning season; + denotes higher occurrence potentially due to hunting season. NA is not available.

Month	Deer (BA)	Deer (RO)	Opossum	Cottontail	Raccoon	Squirrel	<i>Peromyscus spp.</i>	Meadow Vole	Chipmunk	Red-backed Vole	Soft Mast
January	Moderate	Moderate	Low	Moderate	Low	Moderate to Low	Moderate	Low	Low	Low	NA
February	Moderate	Moderate	Low	Moderate	Low	Moderate to Low	Moderate	Low	Low	Low	NA
March	Moderate	Moderate	Low	Moderate	Moderate	Moderate to Low	Moderate	Low	Low	Low	NA
April	Moderate	Moderate	Low	Moderate	Moderate	Moderate to Low	Moderate	Low	Low	Low	NA
May	Moderate	Moderate	Low	Moderate	Moderate	Moderate to Low	Moderate	Low	Low	Low	NA
June	High*	High*	Low	Moderate	High	Moderate to High	Moderate	Moderate	Low	Low	Moderate
July	Moderate	Moderate	Low	Moderate	High	Moderate to High	Moderate	Moderate	Low	Low	Moderate
August	Moderate	Moderate	Low	Moderate	High	Moderate to High	Moderate	Moderate	Low	Low‡	Moderate
September	Moderate	Moderate	Low	Moderate	High	Moderate to High	Moderate	Moderate	Low	Low	Moderate
October	Moderate	Moderate	Low	Moderate	High	High	Moderate	Moderate	Low	Low	Moderate
November	High ⁺	High ⁺	Low	Moderate	High	High	Moderate	Moderate	Low	Low	NA
December	High ⁺	High ⁺	Low	Moderate	Low	Moderate to Low	Moderate	Low	Low	Low	NA

NOTE: In chapter 3, these expectations are converted to ranks with 0 = NA, 1 = low, 2 = moderate, 3 = high, 4 = very high



Figure 1: Thermal images of deer as seen through forward-looking infrared (FLIR) imagery.

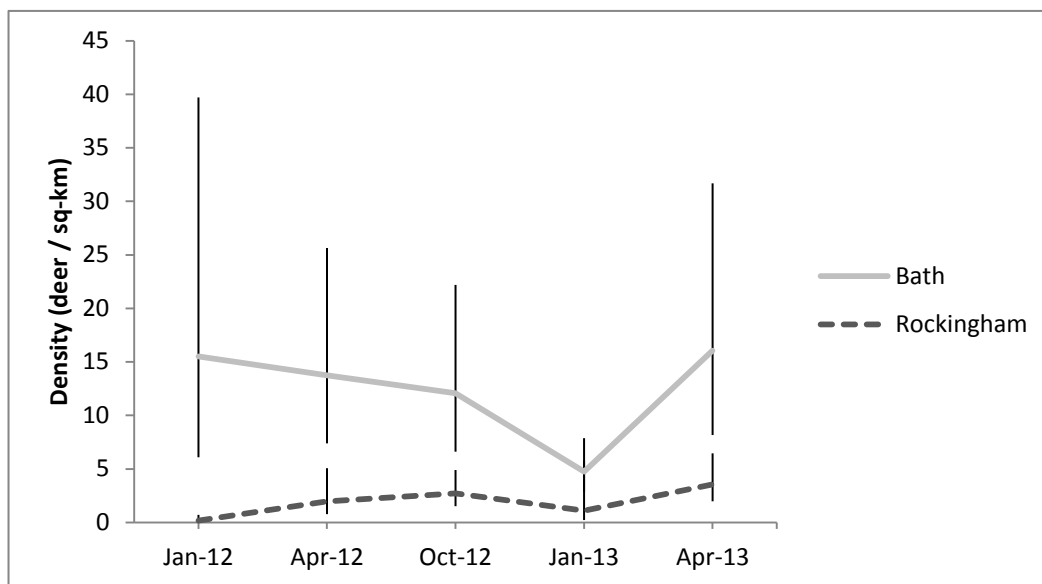


Figure 2: Seasonal deer density estimates with 95% confidence intervals for Bath and Rockingham Counties, Virginia from January 2012 to April 2013 as determined by distance estimation in Program DISTANCE.

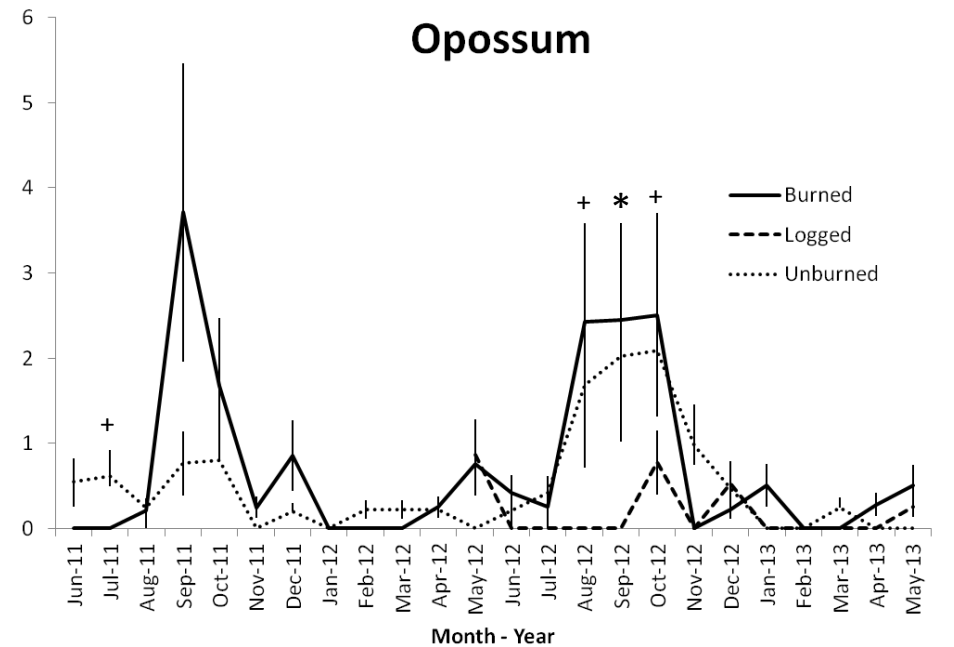
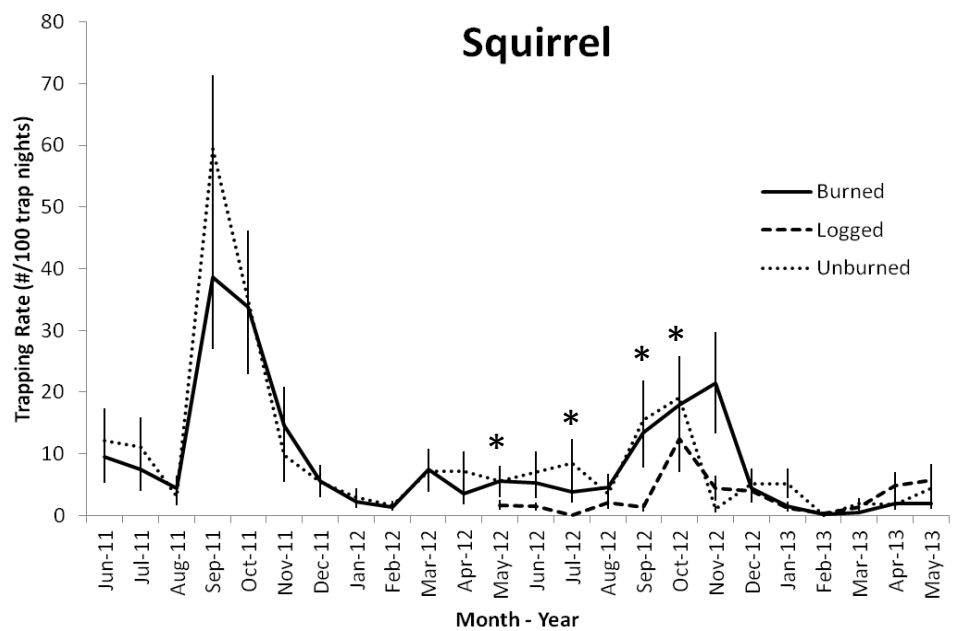
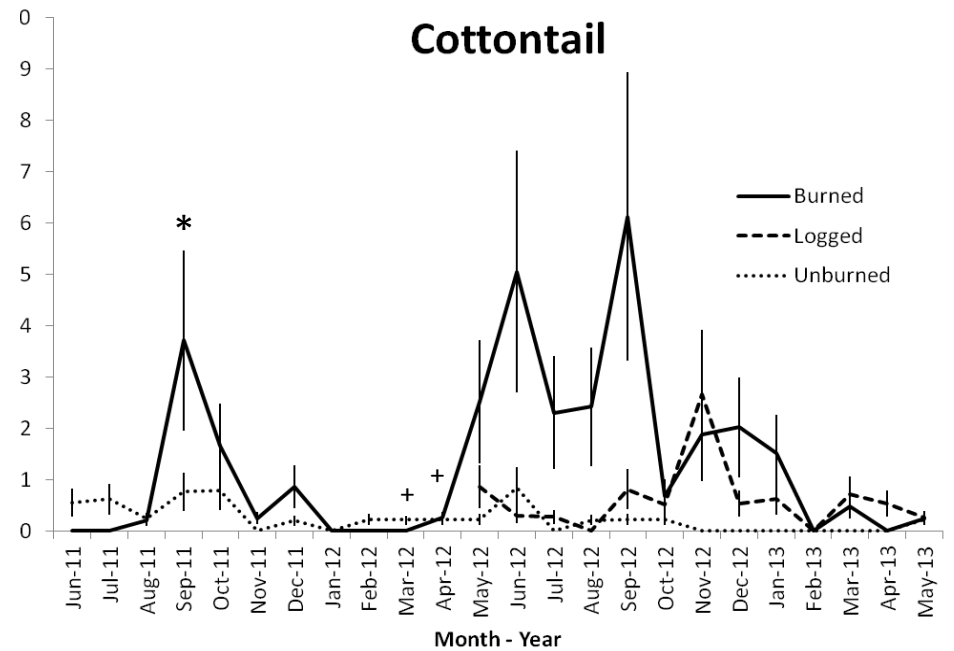
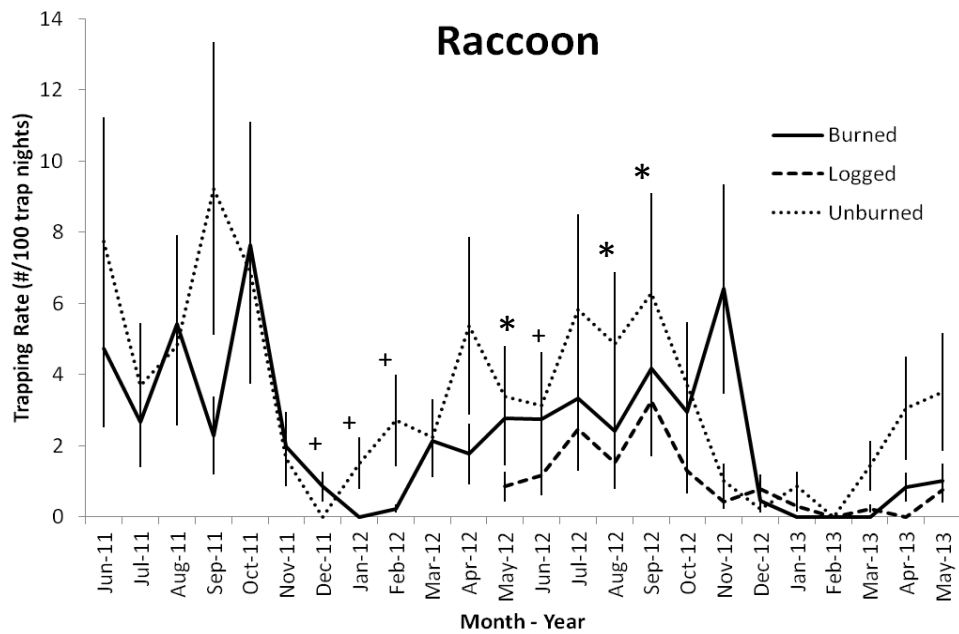


Figure 3: Seasonal activity by habitat type of 4 mid-sized mammal species in Bath County, Virginia as determined by trapping rates and 95% confidence intervals of trail cameras (n = 48) between June 2011 and May 2013. * denotes significance between habitat types; + denotes near-significance ($\alpha = 0.05$).

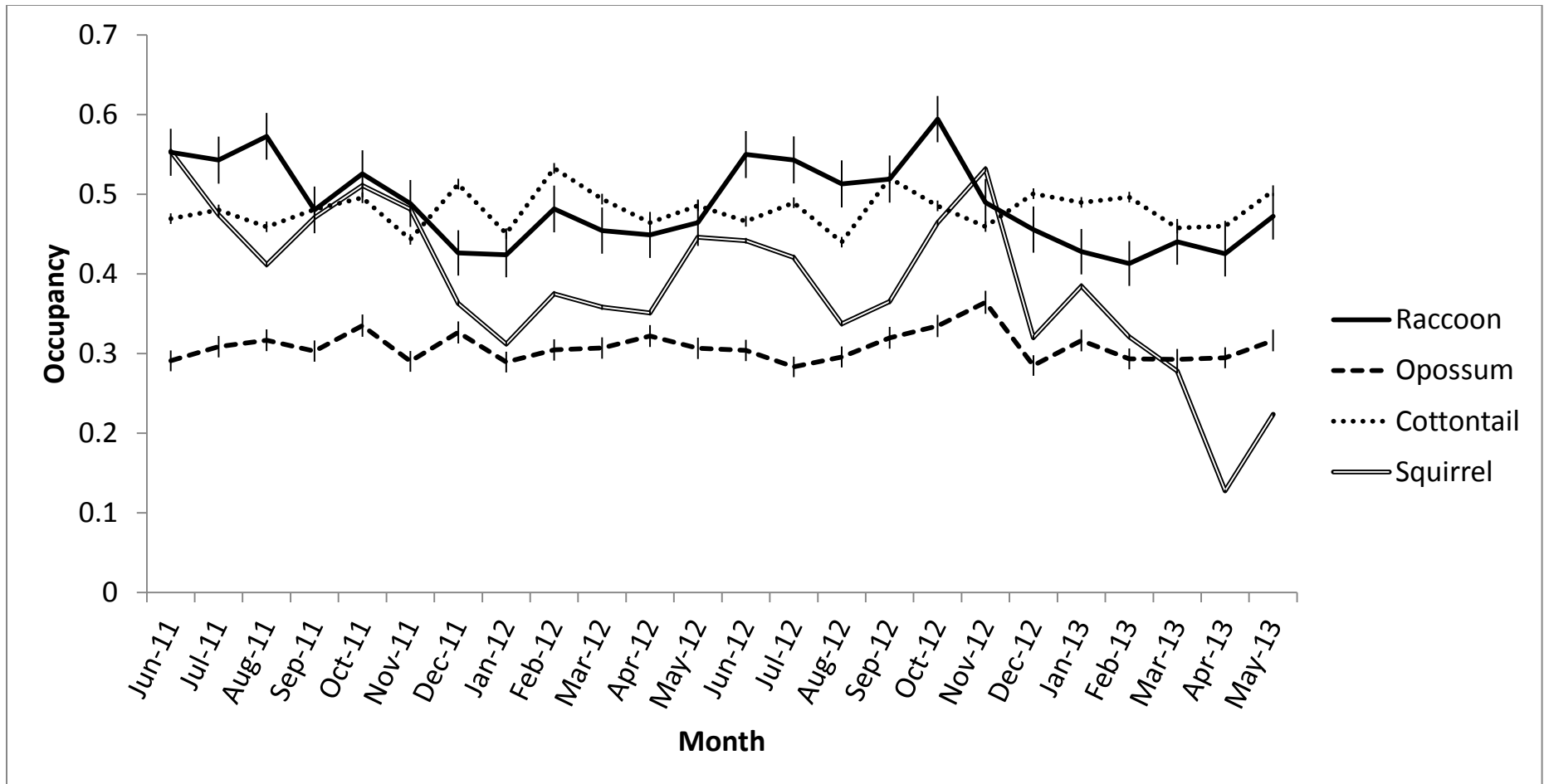


Figure 4: Monthly availability (occupancy) and 95% confidence intervals of 4 mid-sized prey species in Bath County, Virginia modeled in Program Presence with monthly data pooled from 2011, 2012, and 2013.

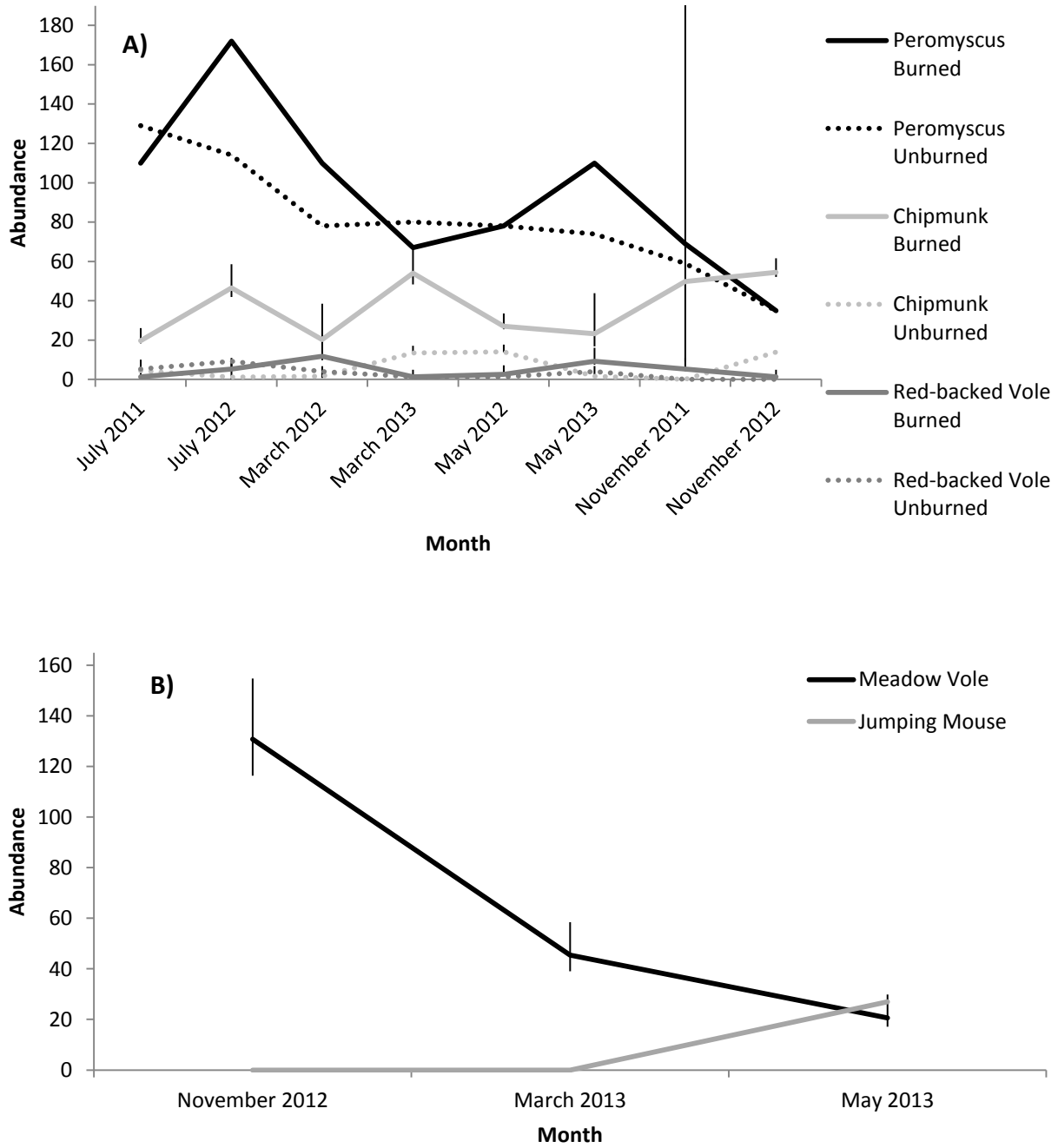


Figure 5: Estimates of seasonal population density and 95% confidence intervals of small mammal species trapped in Bath County in A) burned/unburned habitats and B) fields.

CHAPTER 3: SEASONAL DIETS OF COYOTES, BOBCATS, AND BLACK BEARS IN WESTERN VIRGINIA

ABSTRACT

Predation from coyotes, bobcats (*Lynx rufus*), and black bears (*Ursus americanus*), is believed to be a significant source of deer (*Odocoileus virginianus*) mortality in some regions and the cumulative predation effect may increase the potential for additive deer mortality. I analyzed scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107) from 2 counties in western Virginia collected over a 24 month period from 2011-2013. I ranked food availability each month from 0 (unavailable) to 4 (very high) and compared rankings to ranks of % occurrence and/or biomass consumed to determine if predators took food relative to availability (generalist) or targeted species regardless of availability (specialist). In all months, deer were the most frequently occurring food item represented in coyote scat regardless of availability (Bath: 60.0 % - 90.9 %; Rockingham: 55.6 % - 92.3 %). I did not estimate the availability of deer carcasses (carrion), which likely contributed to the lack of seasonality that I observed in deer occurrence. Deer occurrence in bobcat scat peaked in June (77.54 %). In black bear scat, deer occurrence was highest in February and March (100 %); however, sample sizes in these months were extremely low (n = 3 and n = 2, respectively). All 3 predators consumed deer more than expected in June and July, which may be indicative of fawn vulnerability to predation. In most months, coyotes consumed deer and soft mast more often than expected (1 rank higher) and they consumed deer much higher (2-3 ranks higher) than expected in January and February, probably due to scavenging. Mice (*Peromyscus* spp.) were consumed less than expected based on availability, whereas squirrels (*Sciurus* spp.) and chipmunks (*Tamias striatus*) were consumed by

bobcats more than expected. Voles (*Microtus* spp. and *Clethrionomys gapperi*) were consumed more than expected by both bobcats and coyotes. Mid-sized mammals occurred with expected frequency or lower in predator scats. Coyotes had the lowest diversity and variation in diet while bobcat and bear diets were more diverse including seasonal use of many species. Coyotes exhibited more selectivity based on changes, and magnitude of changes, in rankings for food occurrence versus availability, and appear more specialized on deer in all months than bobcats. However, if deer carcasses were highly available in the study area, coyotes may have behaved simply as opportunistic scavengers. Although deer are a major food source for all 3 predators, it is unclear whether this is from scavenging or predation. More research is needed on the interactions of sympatric predators in specific areas to gain further inferences regarding population-level impacts of predation on deer in western Virginia.

KEY WORDS: black bear diet, bobcat diet, *Canis latrans*, coyote diet, generalist predator, *Lynx rufus*, food selection, *Ursus americanus*, Virginia

INTRODUCTION

Although deer abundance is high throughout most areas of Virginia, parts of the western Virginia have comparatively low density deer populations, as inferred from trends in harvest data. In the mid-20th century, counties west of the Shenandoah Valley such as Bath and Rockingham routinely experienced an influx of tourism during deer hunting seasons as hunters from other parts of the state set up temporary camps to hunt the large tracts of public land in these areas. However, in recent decades, relatively few deer hunters have traveled to these counties, and those that do report few deer and poor quality deer hunting on public lands (N. Lafon, VDGIF,

personal comm.). Reductions in hunting tourism could be due to the lower deer density and poorer quality of deer hunting on public lands in Bath, Rockingham, and other western counties compared to 30+ years ago (VDGIF unpublished data). One hypothesized reason for declines in deer density is the increase in predators, specifically coyotes, and the effects of multiple sources of predation on a deer population that is already stressed by marginal habitat quality.

Numerous studies in the western US and the Northeast have emphasized the adaptability of the coyote. Some research suggests the coyote is a generalist predator, targeting whatever food is most abundant and readily available (Bowyer et al. 1983; Huebschman et al. 1997; Morey et al. 2007; Schrecengost et al. 2008). Other studies have shown a surprising degree of specialization in coyotes' diet, including a tendency to alternate between preferred food species while virtually ignoring other available food considered to be staples of coyote diets in other parts of their range (Patterson et al. 1998; Stoddart et al. 2001). Only two studies of coyote diet have occurred in Virginia in recent years. The first was an undergraduate research project (Gammons 2004) that provided a limited snapshot of coyote diet based on 17 scats (not confirmed by DNA) collected in Campbell and Bath Counties during a single fall season. In the second, Robinson (2005), described coyote diet at Marine Corps Base Quantico using 94 genetically confirmed coyote scats, and food items were grouped into broad categories of fur, vegetation, and insects. Neither of these studies provides an adequate description of the diet and feeding ecology of coyotes in Virginia. For more detailed information on coyote diet items across their range, see Chapter 1.

The diets of the other extant predators of large game in Virginia, black bears (*Ursus americanus*) and bobcats (*Lynx rufus*), are relatively unknown. Anecdotal evidence suggests that black bears may be a significant source of mortality for white-tailed deer fawns (C. Croy, U.S. Forest Service, personal communication), and bobcats are known to eat deer in parts of their range near

my study sites (McLean et al. 2005, Story et al. 1982). See Chapter 1 for more detail on bobcat and bear diets across the region. Because coyote predation is also believed to be a major source of fawn mortality (Stout 1982; Long et al. 1998), interspecific competition between these three predators, and the cumulative effects of predation from these sources, may increase the potential for additive mortality in deer populations.

Understanding the diet and feeding ecology of coyotes, bears, and bobcats in Virginia is a crucial first step toward understanding the impacts of coyote arrival in Virginia on predator and potential prey communities in the ecosystem at large. My goals in this study were to determine seasonal dietary patterns of coyotes, black bears, and bobcats in western Virginia; to relate predator diet to availability of multiple food species (Chapter 2) thus exploring where these carnivores fit along the generalist to specialist continuum, and to assess the potential that cumulative mortality from 3 predators, combined, may have on white-tailed deer populations.

METHODS

Field Collection

I collected scats monthly along 8, 5-km transects along roads and hiking trails in each study site (total of 16 transects; 80 kilometers) from June 2011 to May 2013 (Fig. 1). During the first month of the study (May 2011), I cleared transects of all scats, and no scat samples were collected at that time. By clearing transects of older scat, I attributed scats collected during the second month of the study (June 2011) to carnivore activity during the past month, and I linked food items identified in scats to carnivore diet during that time period. During the subsequent 24 months, observers collected all carnivore scats along each transect. I used genetic samples collected from each scat to confirm my morphology-based species identifications. Only scats

identified by genetic analysis as being coyote, black bear, or bobcat were included in diet analyses.

All complete scats were placed in individual plastic freezer bags and labeled with unique alphanumeric identifiers corresponding to a data sheet on which the observer recorded the transect name, date of collection, observer name, UTM coordinates as determined by GPS receiver, rank of observer certainty of scat identification based on morphology and associated tracks or sign, and rank of the approximate age of the scat (old or fresh).

Laboratory Analysis

Within 12 hours of collection in the field, I placed all scat samples in a standard – 20° C freezer for storage. Following confirmation of species identification by genetic analysis at the University of Idaho's Laboratory for Conservation and Ecological Genetics, I moved scat samples to a – 80° C freezer for 72 hours to reduce risk of infection from *Echinococcus spp.* and other potential zoonotic disease agents. During analysis, I thawed scats in the Alexander Wildlife Health Lab or the Black Bear Research Center lab at Virginia Tech. I washed the scats through a series of sieves of progressively finer mesh and manually separated them into piles of like materials such as bones, teeth, hair, feathers, fruits and seeds, and debris.

After weighing each pile of food material to the nearest 0.01 gram, I identified the food items using published dichotomous keys, field guides, and a reference collection of hair, bones, teeth, and seeds collected from the field (Spiers 1973; Tumlison 1983; Jones and Manning 1992). For hair samples, I prepared temporary slides to observe the hair's medulla by selecting 10-12 individual hairs, deliberately targeting hairs that differed in color, length, diameter, and texture to capture the fullest range of species present in the sample. I mounted the hairs on slides using tap

water and observed the medulla under 100X-400X magnification. I did not use any chemicals to lighten or clarify the hairs, and I had no difficulty observing the medulla, even of highly pigmented hairs. When slides of the medulla were insufficient for identification, I made additional slides by attaching hairs lengthwise to sheets of high-density foam or balsa wood and using razor blades to cut thin slices across the hair, wood, and foam. I placed these slices flat onto glass slides and observed them under the microscope to determine the shape of the hair in cross section. When necessary, I prepared slides of the cuticular scale patterns of hairs by mounting the hairs on microscope slides in Super Glue without cover slips, allowing up to 90 seconds of drying time, removing the hair from the glue, and observing the imprint of the scales left in the surface of the glue. These methods were adapted from Day (1966) and Wierzbowska (2009).

Although many authors describe using macro characteristics of hairs such as color, length, diameter, and cuticular scale patterns to distinguish fawn hair from adult deer hair, I was unable to find a conclusive method of distinguishing the two age classes (Patterson et al. 1998, Petrolje 2014, Schrecengost 2011). Hair color, length, and diameter vary considerably depending on the source location of the hair on the body. In my reference collection, I found hairs fitting the descriptions of both fawn and adult deer that came from different parts of a single individual. Cuticular scales of fawns and adults pictured in references frequently are distinctive (Konieczka 2014), but the majority of hairs recovered from scats had scale patterns that I was unable to match confidently to photographs of either age class. While some morphological characteristics may be distinctive when comparing neo-natal fawns to mature adults, the potential range of intermediate age classes recovered from scats can exhibit hairs with similarities to both extremes. As a result, I did not distinguish between fawn and adult deer hair in this study.

In the absence of teeth, I classified bones and bone fragments as either small, medium, or large mammals. When teeth were present, I attributed the bones of each size class to similarly-sized species identified from teeth. I observed occlusal patterns of teeth under a dissecting microscope and identified them using Hillson (2005). I attempted to identify feathers using nodes in the barbules as described by Day (1966), but feathers occurred rarely in scat and were typically too degraded for identification. Therefore, I lumped all bird remains into a single group for analysis, regardless of taxonomy.

I identified soft mast, hard mast, insects, and other diet items using field guides and reference collections. In the case of soft mast, I collected over 30 species of fruits and berries from the two study sites that could be eaten by predators. I compared seeds found in scats to these known seeds for identification.

In instances where piles of like materials included evidence of multiple species, I estimated the proportion of the total sample composed of each species to the nearest 5%. I adjusted the weight of each pile by multiplying the total weight by the proportion of each species. For example, if a sample contained 5 g of hair, and the hair was estimated as 80% Species A and 20% Species B, the adjusted weights would be $5 \times 0.80 = 4$ g of Species A and 1 g of Species B.

Data Analysis

I defined % occurrence as the number of times a food item occurs divided by the total number of samples ($\% \text{ occurrence} = \frac{\# \text{ of scats with food item}}{\text{total \# of scats}} \times 100$). I pooled data from both years of the study to increase samples sizes and compared % occurrence monthly for coyotes and bobcats using a Kruskal-Wallis nonparametric ranked sums test. Due to small samples sizes for bear scat, I pooled data from both counties and compared % occurrence in four calendar seasons:

winter (Dec - Feb), spring (March - May), summer (June - Aug), and fall (Sept. - Oct.). For coyotes and bobcats, I compared diet estimates from each month by study site using Wilcoxon Tests for nonparametric data comparisons of two samples. I used the same test to compare estimates for each site by season for bear samples.

In addition to % occurrence, I estimated consumed biomass by multiplying the weight of each diet item in scats by biomass coefficients from Jedrzejewska and Jedrzejewski (1998). I divided the estimated biomass of each diet item in each samples by the total biomass of the sample to obtain the % biomass consumed. I compared these estimates by month and by site using the same methods that I used for the % occurrence data.

In addition to seasonal estimates for bears and monthly estimates for coyotes and bobcats, I defined a “limited mobility period” (LMP) and “social mobility period” (SMP) for deer fawns according to methods proposed by Petroelje et al. (2014). I defined the LMP, when fawns rely on camouflage to hide from predators, as May 21 – June 21, and the SMP, when fawns stay close to their mothers and rely on flushing to escape predators, as June 22 – August 31. Because I collected samples once monthly, my collection dates were not as specific as my estimates of the LMP and SMP. In 2011, collection dates matched closely (depending on transect: May: 20 - 25; June: 20 - 30; August 26 - 30). In 2012, collection dates differed slightly from LMP and SMP estimates (depending on transect: May: 8 - 15; June: 10 - 11; August 9 - 12). I pooled data from both years to increase sample sizes and limit the effects of minor discrepancies in collection dates. I used Wilcoxon Tests to compare the % occurrence and % biomass of deer in scats of all three predators between the LMP (June collections) and SMP (July and August collections, combined). Unlike Petroelje et al. (2014), I did not distinguish between fawn and adult deer in

scat during these periods. As a result, I assume that any significant increase in the % occurrence or % biomass of deer during the SMP may be indicative of fawn predation.

Finally, I compared my monthly and seasonal estimates of coyote, bear, and bobcat diet to estimates of food availability (Chapter 2) in order to ascertain the extent to which the 3 predators exhibited generalist or specialist tendencies. I created a table of predictions for the relative ranking of 11 different food items in 12 months in the diet of a generalist predator in western Virginia (total 132 predictions). Ranks of occurrence in scat included 0 = none, 1 = low, 2 = moderate, 3 = high, 4 = very high. For coyotes and bobcats, I compared these predictions to the actual ranking (from 0 to very high %occurrence) of each food item in each month, as determined by scat analysis. I used the number of times food items occurred in the diet more than predicted based on availability as a metric of dietary specialization for each predator. In each instance of higher occurrence than expected, I multiplied the number of differences by the number of rank changes (e.g., I multiplied by 1 the number of times rank differed by 1; I multiplied by 2 the number of times rank changed by 2, etc.). I did not analyze bear diet using this method because the broad food categories and lumped seasons did not coincide with the monthly predictions based on food availability estimates by species.

RESULTS

Coyote Diet

From June 2011 – May 2013, I collected 1,679 fecal samples along 80 km of scat transects per month. Including backtracking, this amounts to 3,840 km traveled by the team in 24 months.

This is the equivalent of walking from Blacksburg, Virginia to Los Angeles, California. Results

of the 1,282 genetic samples that amplified successfully revealed that 429 were from coyotes, 166 were from black bears, and, surprisingly, 628 were from bobcats. Of these, I analyzed 334 coyote scats (78.2 %), 107 bear scats (66.3 %), and 258 bobcat scats (41.1 %).

In 334 coyote scats I found evidence of 21 mammal species. White-tailed deer, meadow voles (*Microtus pennsylvanicus*), squirrels (*Sciurus* spp.), eastern chipmunks (*Tamias striatus*), and cottontails (*Sylvilagus* spp.) were the mostly frequently occurring mammals (Fig. 2). Species that occurred infrequently included *Peromyscus* spp. (white-footed mice and deer mice combined), meadow jumping mice (*Zapus hudsonicus*), woodland jumping mice (*Napeozapus insignis*), harvest mice (*Reithrodontomys humilis*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), opossums (*Didelphis virginiana*), muskrats (*Ondatra zibethicus*), and short-tailed shrews (*Blarina brevicauda*). Domestic species occurred infrequently and consisted of cattle (*Bos taurus*; 0.9 % of scats) and sheep (*Ovis aries*; 0.6 % of scats). Black bears occurred in 4.2 % of coyote scats, sometimes comprising the majority of the total weight of the scat. I assume that black bears in coyote scats result from feeding on roadkills or carcasses left by hunters.

I found 12 types of soft mast in coyote scat. While no soft mast species occurred with high frequency, the most commonly occurring types of soft mast were grapes (*Vitis* spp.: 4.19 %) and apples (*Malus* spp.: 3.59 %). Soft mast types that occurred less frequently included blackberries (*Rubus* spp.), blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.), black gum (*Nyssa sylvatica*), hawthorn (*Crataegus phaenopyrum*), pokeberries (*Phytolacca americana*), cherries (*Prunus* spp.), autumn olives (*Eleagnathus umbellatum*), pawpaw (*Asimina triloba*), and sassafras (*Sassafras albidum*).

Acorns were the only hard mast found in coyote scats. Vegetation occurred relatively frequently in scat and consisted of grasses. Lichen, deer feces, and anthropogenics such as bits of plastic and cloth fibers occurred rarely and in small amounts. Reptiles occurred in only 0.60 % of scats and consisted of scales and fangs of timber rattlesnakes (*Crotalus horribilis*).

Among birds, wild turkeys, Passeriformes, Piciformes, and Falcoformes were found in coyote scats; however, the majority of birds in scats could not be identified, so birds were lumped into one group for analysis which comprised 7.3% of scats. Egg shells occurred in only one scat sample.

Insects were found in 15.27% of scats and included ants (Formicidae), Japanese beetles, peg beetles, June beetles, grasshoppers, crickets, cicadas, and mealworms. Ticks were not included in analyses of insects in scat, because most likely they were consumed during grooming and do not reflect consumption of insects as a food source. Similarly, dung beetles were not included in analyses because I assume they infiltrated the sample after defecation.

Results of the Wilcoxon test revealed that % occurrences of insects, soft mast, and birds were significantly higher in Rockingham County in some months, whereas voles occurred in coyote scat significantly more often in Bath County in some months. Occurrence of deer did not differ significantly between seasons or between the two study sites (Table 1; Fig. 3).

I applied biomass coefficients to the weights of food items in scat. Estimates of relative biomass consumed take into account the amount of each food item consumed (its “importance” to the animal’s diet) rather than giving equal weight to all food items. Biomass estimates altered the seasonal patterns in diet. Biomass of deer exhibited more seasonal variation than % occurrence of deer, with a peak in mean biomass consumed in June (82.04%) suggesting that while deer is

consumed with nearly constant frequency in all months, the amount of deer that is consumed varies significantly (Fig. 4). Similarly, vegetation, soft mast, insects, and birds occurred relatively frequently but contributed very little to the total biomass of coyotes' diets.

Wilcoxon tests revealed that the only month in which % biomass consumed varied significantly between counties was April, when biomass of cottontails was higher in Rockingham County (51.25% vs. 19.70%) and biomass of squirrels was higher in Bath County (40.59% vs. 7.69%) (Tables 2 and 3). In both counties, biomass of deer in June was significantly higher than in other months. In Bath County, biomass of squirrels was significantly lower in April than in other months, whereas in Rockingham County, biomass of cottontails was significantly lower in April than in other months. Although % occurrence did not vary significantly, Wilcoxon tests revealed significantly higher deer biomass in coyote scats during the limited mobility period (LMP) relative to the social mobility period (SMP) (Table 4).

Bobcat Diet

In 258 bobcat scats, I found evidence of the same 21 mammal species present in coyote scat with the exception of spotted skunk. As with coyotes, white-tailed deer, meadow voles, squirrels, eastern chipmunks, and cottontails were the mostly frequently occurring mammals (Fig. 5). Domestic species such as cattle and sheep did not occur in bobcat scats. Soft mast occurred in very few bobcat scats (4.26 %) and included species found in coyote scat such as blackberries, blueberries, huckleberries, and black gum as well as species that did not occur in coyote scat including sumac (*Rhus* sp.), serviceberry (*Amelanchier arboria*), rose (*Rosa* sp.), and a species of Cucurbitaceae. Hickory (*Carya* spp.) was the only type of hard mast found in bobcat scats. Insects included all species found in coyote scat as well as wasps, hornets, and wood grubs.

Only three samples contained anthropogenic “foods,” with one sample each containing a rubber band, scraps of plastic bag, and a cigarette butt (Marlboro sp.). The only bird species conclusively identified in bobcat scat was wild turkey, but the majority of bird samples were unidentifiable.

Wilcoxon tests revealed % occurrences of cottontails, voles, and insects were significantly higher in Bath County in some months, whereas deer, squirrels, and chipmunks occurred significantly more often in Rockingham County in some months (Table 1; Table 5).

% occurrence data indicated relatively even rates of occurrence of many food items among seasons. % biomass data suggest similar patterns among seasons. From the Wilcoxon test I found that biomass of voles was significantly higher and biomass of mice (*Peromyscus* spp., harvest mice, woodland jumping mice, and meadow jumping mice combined) was nearly significantly higher in Rockingham County in April (Table 2; Fig. 6). Biomass was significantly higher in Bath County for vegetation in July ($n = 26$, $z = 2.22$, $p = 0.026$), voles in September ($n = 24$, $z = 2.09$, $p = 0.037$), and cottontails in December ($n = 32$, $z = -2.21$, $p = 0.027$). In addition, biomass was nearly significantly higher in Bath County for squirrels ($n = 22$, $z = -1.76$, $p = 0.078$), chipmunks ($n = 22$, $z = -1.76$, $p = 0.078$), and voles ($n = 22$, $z = -1.76$, $p = 0.078$) in August, and hard mast in October ($n = 22$, $z = 1.93$, $p = 0.053$). In Bath County, % biomass consumed of vegetation was nearly significantly higher in July than in other months ($n = 131$, $z = 3.31$, $p = 0.061$). In Rockingham County, % biomass consumed of voles was nearly significantly higher in February than in other months ($n = 119$, $z = -3.16$, $p = 0.088$). Although % biomass consumed did not vary significantly, Wilcoxon tests revealed higher % occurrence of deer in bobcat scats during the LMP relative to the SMP (Table 4).

Bear Diet

In 107 bear scats, I found 6 species of mammals. Deer occurred most often (39.1 % of scats) (Fig. 7). Bear occurred in 14.5 % of scats; however, I did not find bear claws or other signs of infanticide commonly reported in bear diets (Clark and Smith 1994), therefore I assume that the bear hair found in scat was the result of grooming. Cottontails, squirrels, chipmunks, and meadow voles each occurred in < 10 % of scats.

I found 13 species of soft mast in bear scats. Huckleberries (12.0 %), grapes (10.0 %), blackberries (9.1 %), and black gum (8.2 %) were the most frequently occurring types of soft mast. Blueberries, apples, serviceberries, pokeberries, cherries, autumn olives, spicebush (*Lindera benzoin*), sassafras, Cucurbitaceae, and greenbriar (*Smilax* spp.) all occurred in < 5 % of scats.

Hard mast found in bear scats included acorns (*Quercus* spp.), hickories, corn, soybeans, and oats. All insect species found in coyote and bobcat scats also were found in bear scats. No birds were found in bear scat. One sample each contained aluminum foil, a rubber band, and crayfish. All food items in bear scat varied significantly among seasons with the exception of vegetation (Table 6).

Results of the Kruskal-Wallis test showed that estimated % biomass consumed did not vary significantly among seasons for any food item (Fig 8). This is in contrast to % occurrence data, which varied significantly by season in all food categories except for vegetation. These differences suggest that, in some seasons, bears consume many small meals of certain food categories, whereas in other seasons they eat fewer, larger meals which result in equal biomass, overall. This variation in meal size and frequency may be related to differences in the sizes of

food items pursued seasonally. Although % occurrence and % biomass consumed did not vary significantly in bear scats between the LMP and SMP, Wilcoxon tests revealed significantly higher deer biomass and % occurrence in Rockingham County during the SMP (Table 4).

Diet selectivity versus food availability

When I compared my rankings of coyote diet from scat analysis to my rankings of relative food availability (Chapter 2), several discrepancies arise from expectations of a typical generalist species (Table 7). Based on relatively lower availability, I predicted deer would occur in scat less frequently in Rockingham County relative to Bath County. However, I found no such difference in deer occurrence between the two counties and % occurrence in scat did not vary by month. However, biomass estimates were significantly higher in June compared to other months suggesting that deer comprise a much larger proportion of coyote diet in June. In both counties, % occurrence and % biomass of cottontails, squirrels, chipmunks, voles, birds and soft mast were lower in June than in many other months. In total, I observed 37 rank changes for coyotes in which rank increased and food was selected more often than expected based on availability (indicative of more specialization), or 28.0% higher than my predicted generalist predator diet. After multiplying the number of changes by the degree of the rank change, coyote had a total dietary specialist score of 53. In addition, I found that coyote diet agreed with my predicted generalist diet 37% of the time (49/132) (excluding instances of higher and lower occurrence than expected); and coyote deer % occurrence was higher than expected based on availability in 21 out of 24 predictions or 87.5% of instances.

For bobcats, I observed 33 rank changes of higher than expected (25.0%), from my predicted generalist predator diet (Table 7). After multiplying the number of changes by the degree of the

rank change, bobcats had a lower dietary specialist score (45) than coyotes. In addition, I found that bobcat diet agreed with my predicted generalist diet 42% of the time (56/132) (excluding instances of higher and lower occurrence than expected). Bobcat deer use was higher than predicted in 5 out of 24 predictions or 20.8% of instances.

DISCUSSION

Scat Misidentification

The rate of observer mis-identification of scats was high, with coyote and bobcat scats being confused most frequently (Kelly et al 2013). Preliminary findings based on mtDNA indicate that 70.3% of samples labeled in the field as being from coyotes actually came from other species, whereas 28.1 % of bobcat samples and 38.8% of bear samples similarly came from other species (Kelly et al 2013). This was true regardless of the observer's level of training or experience in the field. This finding seriously calls into question the reliability of previous diet studies that did not confirm the species of origin using DNA techniques and relied solely on morphological traits for identification. If mis-identification of scats in the presence of sympatric carnivores is a chronic problem in studies of coyote diet, comparisons between much of the published literature and my results may have limited utility. Throughout this discussion, results cited from other studies lacked genetic identification unless otherwise noted. The degree to which mis-identification may affect diet results inferred from scat is uncertain, but the difference in methodology between my study and most other scat-based studies, and potential for bias from mis-identification, should be highlighted.

Coyotes

The % occurrence data indicates coyotes in western Virginia utilize a wide array of potential food items. However, most food items occur in coyote diet very infrequently, and deer is the most frequent food item in all months. This indicates an unexpectedly low degree of dietary diversity and seasonal variation. The low occurrence of domestic species was expected since part of the selection criteria for the study sites was avoidance of heavily human-altered landscapes where livestock depredations alter coyote use of naturally occurring food items.

Coyotes' seasonal use of soft mast is consistent with other studies from southeastern states that found a sometimes high % occurrence of soft mast (Chamberlain and Leopold 1999, Schrecengost 2011, Thornton et al. 2004). The low occurrence of birds in coyote scat agrees with many other studies such as Henke (2003), Houchin (2005), and Wagner and Hill (1994). The occurrence of Falcoformes likely represents scavenging of roadkill or other carcasses. The spike in occurrence of black bear remains in coyote scat in both counties in January coincides with bear hunting season in Virginia, when bear carcass availability may be highest.

Based on my results, coyotes in my study area seem to be specializing on deer in all seasons, regardless of the availability of other food resources. However, my estimates of deer availability do not account for the availability of carcasses left by hunters or from deer/vehicle collisions. If carcass availability is high and relatively constant throughout the year, my estimates of coyote deer use may be in line with overall availability.

Reports of coyotes killing adult deer are uncommon, and most documented instances come from northern or western regions where deep winter snows prevent deer from escaping predators (Gese et al. 1988; Toweill and Anthony 1988; Patterson et al. 1998; Patterson and Messier 2000).

Since my study areas rarely are subject to deep snowfalls, coyotes in Virginia are unlikely to be efficient predators of adult deer. In New York State, including areas with deep winter snows, Frair et al. (2014) determined that 92% of deer carcasses ($n = 62$) visited by GPS-collared coyotes ($n = 15$) in winter were scavenged, whereas the remaining 8% ($n = 3$) of carcasses had previous injuries that may have increased vulnerability to predation. In an on-going, large-scale study of golden eagles, where remote cameras have been set on deer carcasses from New York through Alabama, 89% ($n = 120$) of the 135 camera sites recorded coyotes, and the Virginia and West Virginia sites often had daily visits by coyotes (Mark Ford, USGS Co-op Unit, personal comm.). During the winter in Wisconsin, Huegle and Rongstad (1985) observed 2 radio-collared juvenile coyotes and one adult coyote and found that white-tailed deer carrion comprised 43% and 69% of the juvenile diets. However, the adult coyote assisted other adults in killing adult deer on 3 separate occasions in late winter, although deep snow was noted as a factor in the success of deer killing.

The largest changes in rank (increases from expected food in diet) occurred for deer in January and February, which implies that coyotes are capitalizing on deer carcasses, perhaps dumped by hunter's following post-season game butchering, and these would not be reflected in my deer availability estimates since I targeted live deer with DISTANCE estimation techniques. If I consider the likely availability of deer carcasses, coyotes in this area may be behaving as highly opportunistic scavengers rather than specialists on live deer. However, without knowing the availability of deer carcasses, I am unable to make an exact determination.

The higher % occurrence of deer in both study areas in June is likely due to the availability of deer fawns since estimates of adult deer density did not differ significantly among months, which is documented in many studies (Wooding et al. 1984; Huebschman et al. 1997; Chamberlain and

Leopold 1999). Because of their vulnerability to predators, fawns may be easy meals for coyotes, leading coyotes to specialize on fawns when they are available. This specialization would be reflected in a lower % occurrence of other food items and a smaller proportion of the biomass in scat coming from non-deer sources in June. Coyotes' low use of other food sources during fawning season supports the suggestion that they are specializing on deer fawns during this time period. These conclusions are further supported by significantly higher deer occurrence during the LMP, when fawns are most vulnerable. Although I did not differentiate between fawn and adult deer hair, this is strong evidence of predation on fawns during the LMP. This is consistent with Frair et al. (2014), who found high rates of fawn predation taking the place of carcass scavenging in summer, with peak occurrence of deer in scat coinciding with peak fawning season. Further research is necessary to determine whether this level of predation is compensatory in deer populations or whether there is a discernible impact of predation at the population level.

Among small mammal species, mice occurred rarely in coyote scat, even though *Peromyscus* spp. were the most available small mammal in all seasons. By comparison, voles occurred more frequently in scat than other small mammals despite having low availability in most habitats. My estimates of vole density declined from November to May, but % occurrence of voles in scat remained relatively constant throughout this timeframe. Chipmunks were most available in summer and fall, which is relatively consistent with the timing of chipmunk occurrence in scat. All of this suggests that voles and chipmunks have greater benefits to coyotes than mice which makes specializing on them more profitable despite their lower availability. The larger body sizes of voles and chipmunks may make it more worthwhile for coyotes to expend additional time searching for less abundant species. In my small mammal trapping data, I found higher

vole densities in fields, and higher chipmunk densities in burned areas, suggesting coyotes spend more time foraging in these areas.

Bobcat Diet

Bobcats utilize many of the same food items as coyotes; however, compared to coyote diet, bobcats appear to consume a wider array of food items with greater frequency. Whereas coyote diet was dominated by deer in all months in both counties, bobcat diet was much more seasonal. Although deer occurred frequently in bobcat scat, in most months squirrels, chipmunks, and voles were the most frequently occurring food items (with nearly equal frequency). Deer occurrence peaked in June, again likely due to the availability of fawns. However, deer biomass was not significantly higher in June relative to other months, suggesting that the amount of deer consumed per meal was constant regardless of whether bobcats were scavenging, eating fawns, or potentially eating adult deer.

Compared to coyote diet, bobcat diet is much more similar to my estimate of a generalist predator diet (Chapter 2) (Tables 7 and 9). Deer occurred in scat less frequently in Rockingham County relative to Bath County, although the difference was only significant in one month.

In Rockingham County, squirrel occurrence in bobcat scat was highest from September to December and declined steadily until August. This is fairly consistent with my estimates of squirrel availability which predicted highest occurrence of squirrels in October and November followed by a steady decline until June. However, in Bath County, squirrel occurrence in bobcat scat did not fit my predictions as well. While squirrel occurrence was highest in September and October, a second peak occurred in April which coincided with relatively high occurrence of

deer, cottontails, voles, and insects in bobcat scat. Perhaps availability of alternative food in April resulted in greater diversity, and more opportunism, in bobcat scat.

While I observed some monthly variation in occurrence of cottontails, the differences were not statistically significant, consistent with my estimate of seasonally constant use of cottontails in a generalist predator. Opossums and raccoons did not occur in bobcat scat as their availability in the landscape predicted, but these species are rarely recorded in bobcat diets in other regions (Chamberlain and Leopold 1999, Tewes et al 2002, Tumlison and McDaniel 1990).

Because of high availability on the landscape, I predicted that *Peromyscus* spp. would occur more frequently in the scats of generalist predators than other small mammals. While mice occurred more frequently in bobcat scat than in coyote scat, chipmunks and voles still occurred more often. As with coyotes, the larger sizes of these species may make them more profitable for bobcats than *Peromyscus* spp.

As expected, occurrence of soft mast species was highly seasonal. I predicted that blueberries (*Vaccinium* sp.) would occur in the scat more frequently than other soft mast, and this was the case for bobcat scats in Bath County, but not in Rockingham County. However, since my data on relative % cover of soft mast species was collected in Bath County only, it is possible that blueberries are not as available relative to other species of soft mast in Rockingham County.

Bear Diet

Bear diets were diverse in all seasons. Mammals in the scat consisted mostly of deer; however, I found cottontails, squirrels, chipmunks, and voles in bear scat, also. Cottontail was reported in 2 out of 120 black bear scats collected in Pennsylvania by Bennett et al. (1943), and Cottam et al. (1939) reported cottontail in 3.5 % of stomachs dissected from Virginia black bears. Bull et al.

(2001) found vole remains in one of the 621 scats they analyzed. The occurrence of arboreal squirrels and chipmunks that I found has not been recorded previously in the central and southern Appalachians. The high rate of deer occurrence in February and March, and the absence of deer in November, are likely due to low sample sizes for bears in those months, but they may also reflect the low availability of alternative foods at the time of year coinciding with bears leaving their dens.

The high occurrence of soft mast in scat that I observed is consistent with other studies of bear diet. In particular, Eagle and Pelton (1983), Beeman and Pelton (1977), Bennett et al (1943), and Powell and Seaman (1990) all reported high occurrence of soft mast including blueberries, huckleberries, and blackberries in regions with resource availability that is very similar to my study area.

Of the three predators that I studied, bears exhibited the most seasonal variation in diet when comparing four broad seasons. Given the high proportion of soft mast in bear scat, and its inherently seasonal occurrence on the landscape, it is not surprising that bear use of soft mast – and the use of other food items in the absence of soft mast – was highly seasonal. However, even when I combined the two study sites and the two years, sample size was still small in some seasons. This likely was due to the dormancy of bears in cooler months which resulted in very low numbers of scats collected in winter and spring, in spite of the large amount of effort expended in searching for scats.

When examined at the food category scale used in my analyses, bears appear to have a very diverse diet. Within categories (mammals, soft mast, hard mast, insects, vegetation), bears specialized on deer as their primary mammalian prey. As I noted in my discussion of coyote use

of deer, this could be influenced by the availability of carcasses, which I did not account for in my estimates of deer availability. Furthermore, mammalian prey with the exception of large ungulates, are rarely reported in black bear diets (Cottam et al. 1939, Beeman and Pelton 1977, Hellgren et al. 1989), so it comes as no surprise that I found little evidence of non-ungulate mammals in bear scat. Aside from the mammal category, bears behaved as generalists, consuming soft mast species as they came into fruit, insects in season, and hard mast species when soft mast was no longer available.

Diet selectivity versus food availability

Perhaps surprisingly, I found that coyotes in my study area, had more and larger rank increases indicating higher food selectivity relative to food availability, compared to bobcats. They also agreed less often with the generalist diet predictions than bobcats did. This was driven primarily by much higher selection of deer in almost all months and secondarily by selection of voles at higher rates than expected. Coyotes therefore, appear to specialize on deer throughout the year whereas, bobcats appear to employ a mixed foraging strategy in which they behave as generalist predators in all months except during peak fawning season, when they specialize on deer. It should be noted however, that my data only account for deer consumed (which could include substantial scavenging) and I am unable to link consumption to direct deer predation.

Implications for Management of Predators and Potential Prey

My data indicate that coyotes, bobcats, and bears have broad dietary niches in Virginia. Contrary to my expectations, coyotes appear to have the least dietary diversity and seasonal variation in diet. Deer are a major diet item for all three predators, particularly during peak fawning season (Figs. 9 and 10). My inability to identify the source of the deer in scats, whether

from active predation events or from scavenging, seriously limits my ability to predict the impact of these three predators on deer populations. The fact that deer % biomass consumed was significantly higher in June for coyotes (Fig. 4), and % occurrence was significantly higher in June for bobcats (Figs. 5), suggests an increase in prey vulnerability, likely indicative of fawn predation at that time of year. Whether the number of fawns killed by predators is high enough to limit deer recruitment and lead to recent observed declines in deer populations in my study area is unknown. Research focusing on mortality causes of both adult deer and fawns, in conjunction with my results, would help to answer this question. However, my data show that the predation ecology of deer in western Virginia centers on a multi-predator environment, in which coyotes, bobcats, and black bears all play a role. The role of bears and bobcats as predators of deer in Virginia was larger than expected and the amount of specialization on deer by coyotes in all months was unexpected. However, the high % occurrences of deer in the scats of these predators could be due to carcass scavenging, which may help to explain the lack of seasonality I observed among coyote samples. Future studies in this region should include all three predators when considering effects on food species.

Furthermore, my results suggest that coyotes selected deer even when other food items are highly available on the landscape. This may be reflective of high availability of deer carcasses throughout the year. Meanwhile, bobcats and bears behaved more like generalist or opportunist predators with diets that change seasonally to mimic patterns in food abundance. Comparing expected versus observed diets for coyotes and bobcats, revealed a higher diet specialist score of 53 for coyotes compared to 45 for bobcats. In addition, coyote diet matched generalist diet less often than bobcat diet and coyote consumption of deer was higher than predicted for 87.5% of the rankings and only 20.8% of rankings for bobcats. My data suggest that coyotes have the most

specialized diets of the 3 predators in my study, followed by bobcats and black bears. However, if carcass availability is accounted for, coyotes may in fact be highly opportunistic scavengers rather than specialized predators on deer. This would be more consistent with known coyote behavior. Based on these behaviors, I anticipate that wildlife management designed to maximize potential prey species diversity, such as prescribed fire or timber harvest to create uneven-aged forest matrices, will have minimal impact on coyote diet or the rate of coyote predation on white-tailed deer. However, such management strategies may affect diet of bobcats and black bears, potentially decreasing seasonal use of deer by increasing availability of alternative prey such as voles, chipmunks, and cottontails. The decreased rate of predation from bobcats and black bears may reduce overall mortality of deer from predators. Such management may have the added benefit of increasing deer density as a result of improving the habitat quality for deer. To reduce potential impacts of coyote predation on deer populations, managers should focus on creation of large patches of fawning habitat and networks of escape cover to reduce vulnerability of deer to predators. Determining whether coyotes are actually preying on deer rather than scavenging is a very high priority. More research is necessary to link coyote, bobcat, and black bear food selection behavior to population-level impacts on deer in western Virginia.

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TABLES AND FIGURES

Table 1: Site comparisons of monthly % occurrence of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Wilcoxon Tests ($\alpha = 0.95$). Only months in which % occurrence varied significantly between sites are shown.

Predator	Month	Species	P-Value	Z	n	Score Mean	
						BA	Score Mean RO
Coyote	February	Voles	0.004	-2.895	34	20.6	12.5
		Soft Mast	0.043	2.021	34	15.8	20.2
	March	Insect	0.077	1.769	26	15.1	12.5
		Bird	0.077	0.077	26	15.1	12.5
	June	Chipmunk	0.061	1.871	56	28.0	30.3
		Insect	0.068	1.824	56	26.9	34.5
	October	Insect	0.024	2.260	18	8.5	12.1
	November	Veg	0.007	2.678	17	11.8	6.5
Bobcat	February	Cottontail	0.006	2.726	27	18.9	11.9
	May	Voles	0.067	1.833	10	4.0	7.0
	July	Cottontail	0.062	1.865	29	17.2	13.0
		Chipmunk	0.047	-1.991	29	12.1	17.7
	September	Deer	0.042	-2.038	24	10.0	14.3
		Voles	0.006	2.746	24	16.6	9.6
		Insect	0.069	1.821	24	15.0	10.7
		Veg	0.061	1.871	24	14.8	10.9
	October	Deer	0.066	-1.840	23	10.0	13.5
		Insect	0.044	2.018	23	14.0	10.5
December	Squirrel	0.006	2.751	32	12.8	20.7	

Table 2: Site comparisons of monthly % biomass consumed of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Wilcoxon Tests ($\alpha = 0.05$). Only months in which % biomass consumed varied significantly between sites are shown.

Predator	Month	Species	P-Value	Z	n	Score Mean	Score
						BA	Mean RO
Coyote	April	Cottontail	0.050	1.942	32	14.1	20.0
		Squirrel	0.006	-2.743	32	19.9	11.6
Bobcat	April	Voles	0.048	1.977	20	8.8	13.0
		Mice	0.089	1.703	20	9.5	12.0
	July	Veg	0.026	2.222	26	17.0	11.0
	August	Squirrel	0.078	-1.760	22	13.0	10.0
		Chipmunk	0.078	-1.760	22	13.0	10.0
		Voles	0.078	-1.760	22	13.0	10.0
	September	Voles	0.037	2.088	24	14.6	11.0
	October	Hard Mast	0.053	1.933	22	13.3	10.0
	December	Cottontail	0.027	-2.210	32	18.7	14.0

Table 3: Monthly comparisons of % biomass consumed of food items in coyote and bobcat scats collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 compared using Kruskal-Wallis Tests with Dunn's multiple comparisons ($\alpha = 0.05$). Only months in which % biomass consumed varied significantly are shown.

Predator	County	Species	Higher (n)	Lower (n)	P-Value	Z	Score Mean Higher	Score Mean Lower
Coyote	Bath	Deer	June (40)	February (22)	0.001	4.416	126.3	67.6
			June (40)	April (19)	0.009	3.817	126.3	73.0
			June (40)	October (13)	0.016	- 3.668	126.3	67.6
	Rockingham	Squirrel	April (19)	June (40)	0.003	- 4.049	124.8	74.8
			June (9)	February (18)	0.014	3.707	95.6	46.1
			June (9)	April (13)	0.005	3.955	95.6	39.5
		Cottontail	April (13)	June (9)	0.054	- 3.349	84.5	49.5
Bobcat	Bath	Veg	July (11)	June (30)	0.061	3.314	90.3	56.5
	Rockingham	Voles	February (19)	September (14)	0.088	- 3.156	74.5	45.5

Table 4: Seasonal and site comparisons of % occurrence and % biomass consumed of white-tailed deer in scats of coyotes, bobcats, and bears collected in Bath and Rockingham Counties, Virginia during the limited mobility period (LMP) and social mobility period (SMP) using Wilcoxon Tests ($\alpha = 0.95$), with sample sizes denoted (n). Only significant interactions are shown.

Predator	Type	County/Time	P-value	Z	Score Mean LMP (n)	Score Mean SMP (n)	Score Mean BA (n)	Score Mean RO (n)
Coyote	Biomass	Bath	0.006	2.774	38.0 (40)	25.0 (25)		
		Rockingham	0.090	1.695	22.9 (9)	16.3 (26)		
Bobcat	Occurrence	Rockingham	0.018	2.360	25.9 (13)	17.9 (27)		
Bear	Biomass	SMP	0.057	1.907				
	Occurrence	SMP	0.021	2.311			23.6 (22)	16.7 (18)

Table 5: Monthly comparisons of % occurrence of food items in bobcat scats, with sample sizes (n), collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 and compared using Kruskal-Wallis Tests with Dunn's multiple comparisons ($\alpha = 0.95$). Only months in which % occurrence varied significantly are shown.

Predator	County	Species	Higher (n)	Lower (n)	P-Value	Z	Score Mean Higher	Score Mean Lower
Bobcat	Bath	Deer	June (31)	September (10)	0.024	- 3.569	82.2	39.0
			June (31)	October (10)	0.024	- 3.569	82.2	39.0
		Squirrel	September (10)	December (17)	0.082	- 3.230	96.6	54.8
			October (10)	December (17)	0.082	- 3.230	96.6	54.8
		Voles	September (10)	December (17)	0.015	- 3.695	100.6	54.9
			September (10)	June (31)	0.010	3.791	100.6	57.8
	Rockingham	Chipmunk	July (15)	February (19)	0.035	3.415	82.8	48.0
			May (5)	March (8)	0.023	3.530	93.7	56.5
		Bird	May (5)	April (8)	0.023	3.530	93.7	56.5
			May (5)	February (19)	0.014	3.655	93.7	59.8
			May (5)	June (13)	0.047	- 3.334	93.7	61.3
			May (5)	October (13)	0.047	- 3.334	93.7	61.3
			May (5)	August (12)	0.009	- 3.783	93.7	56.5
			May (5)	July (15)	0.005	- 3.900	93.7	56.5

Table 6: Seasonal comparisons of % occurrence of food items in black bear scats, with sample sizes (n), collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 and compared using Kruskal-Wallis Tests with Dunn's multiple comparisons ($\alpha = 0.05$). Seasons include winter (Dec - Feb), spring (March - May), summer (June - Aug), and fall (Sept. - Oct.) Only seasons in which % occurrence varied significantly are shown.

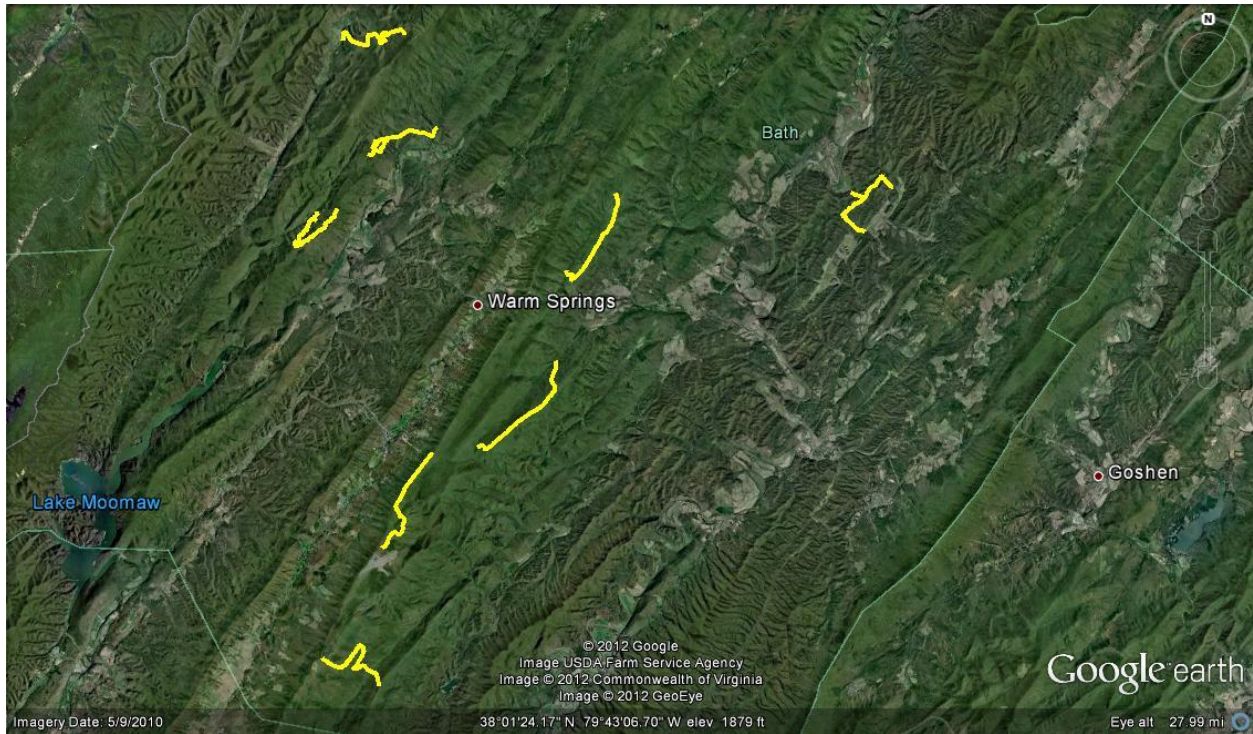
Speices	Higher (n)	Lower (n)	P-Value	Z	Score Mean Higher	Score Mean Lower
Mammal	Spring (11)	Summer (64)	0.0142	-3.039	75.9	49.6
Soft Mast	Summer (64)	Spring (11)	0.0096	3.157	61.2	33.0
Hard Mast	Summer (64)	Spring (11)	0.0453	2.672	53.8	30.0
	Fall (23)	Spring (11)	0.0003	-4.021	70.3	30.0
Insect	Summer (64)	Winter (11)	0.0043	-3.381	62.3	32.5

Table 7: Expected monthly seasonal diet of a generalist predator based on estimates of food availability in western Virginia (Chapter 2) compared to findings from diet analysis of scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107). Rankings are: 0 = none, 1 = low, 2 = moderate, 3 = high, 4 = very high. The first rank in each column is the expectation based on availability, the 2nd rank represents that found in coyote diet, denoted suffix “C”, and the 3rd rank represents that found in the bobcat diet, denoted with suffix “B”. The ranks within squares denote predator being more selective than availability with green for coyotes and orange for bobcats. The darker the color the bigger difference in selectivity (i.e. larger rank change from availability). “BA” indicates Bath County; “RO” indicates Rockingham County.

Month	Deer (BA)	Deer (RO)	Opossum	Raccoon	Cottontail	Squirrel	Chipmunk	<i>Peromyscus spp.</i>	Meadow Vole	Red-backed Vole	Soft Mast
January	2, 4C, 2B	1, 4C, 3B	1, 1C, 1B	2, 1C, 1B	2, 1C, 1B	1, 1C, 3B	1, 1C, 2B	3, 1C, 1B	1, 1C, 1B	1, 1C, 1B	0, 1C, 0B
February	2, 4C, 2B	1, 4C, 3B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	1, 1C, 2B	1, 1C, 1B	3, 1C, 2B	1, 2C, 3B	1, 1C, 1B	0, 2C, 1B
March	3, 4C, 1B	2, 4C, 2B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	1, 1C, 2B	1, 1C, 1B	3, 1C, 1B	1, 2C, 3B	1, 1C, 1B	0, 1C, 0B
April	3, 4C, 4B	2, 4C, 2B	1, 1C, 1B	2, 1C, 1B	2, 1C, 3B	1, 1C, 3B	1, 1C, 2B	3, 1C, 1B	1, 2C, 3B	1, 1C, 1B	0, 1C, 1B
May	3, 4C, 1B	2, 4C, 1B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	1, 1C, 2B	1, 1C, 1B	3, 1C, 1B	1, 2C, 2B	1, 1C, 1B	0, 1C, 0B
June	4*, 4C, 4B	3*, 4C, 4B	1, 1C, 1B	2, 1C, 1B	2, 1C, 1B	2, 1C, 2B	1, 1C, 2B	3, 1C, 1B	1, 1C, 1B	1, 1C, 1B	2, 1C, 0B
July	3, 4C, 3B	2, 4C, 3B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	2, 1C, 2B	1, 1C, 3B	3, 1C, 1B	1, 1C, 2B	1, 1C, 1B	2, 2C, 1B
August	3, 4C, 3B	2, 4C, 2B	1, 1C, 1B	2, 1C, 1B	2, 1C, 1B	1, 2C, 2B	1, 1C, 2B	3, 1C, 1B	1, 2C, 2B	1, 1C, 1B	2, 2C, 1B
September	3, 4C, 1B	2, 4C, 2B	1, 1C, 1B	2, 1C, 1B	2, 1C, 3B	2, 1C, 4B	1, 1C, 2B	3, 1C, 1B	2, 2C, 3B	1, 1C, 1B	2, 3C, 1B
October	3, 4C, 1B	2, 3C, 2B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	2, 1C, 4B	1, 1C, 3B	3, 1C, 2B	2, 2C, 2B	1, 1C, 1B	2, 4C, 0B
November	4+, 4C, 2B	3+, 4C, 1B	1, 1C, 1B	2, 1C, 1B	2, 1C, 1B	2, 1C, 1B	1, 1C, 1B	3, 1C, 2B	2, 3C, 2B	1, 1C, 1B	0, 2C, 0B
December	4+, 4C, 3B	3+, 4C, 3B	1, 1C, 1B	2, 1C, 1B	2, 1C, 2B	1, 1C, 3B	1, 1C, 2B	3, 1C, 1B	2, 2C, 1B	1, 1C, 1B	0, 2C, 0B

* denotes expected higher occurrence potentially due to fawning season; + denotes higher expected occurrence potentially due to hunting season.

a)



b)

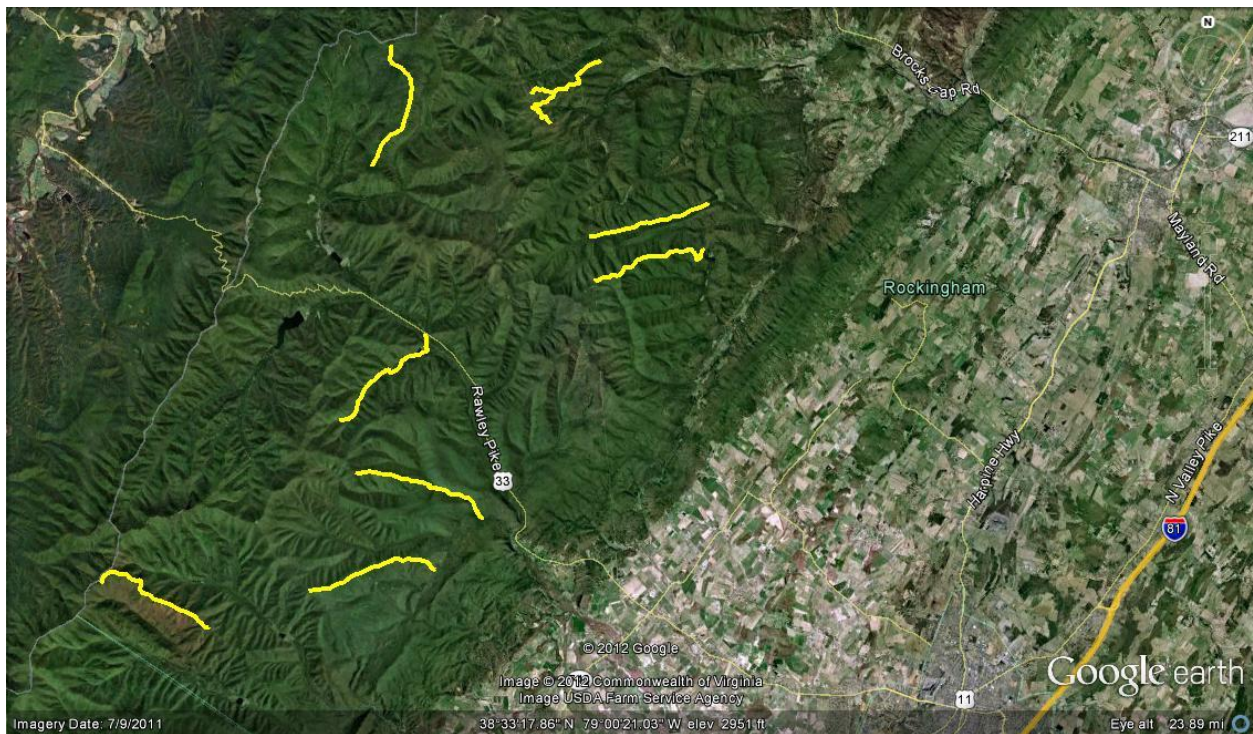


Figure 1: Locations of transects in (a) Bath and (b) Rockingham Counties, Virginia where carnivore scats were collected from June 2011 to May 2013. Note the hard edge between public and private lands in Rockingham County.

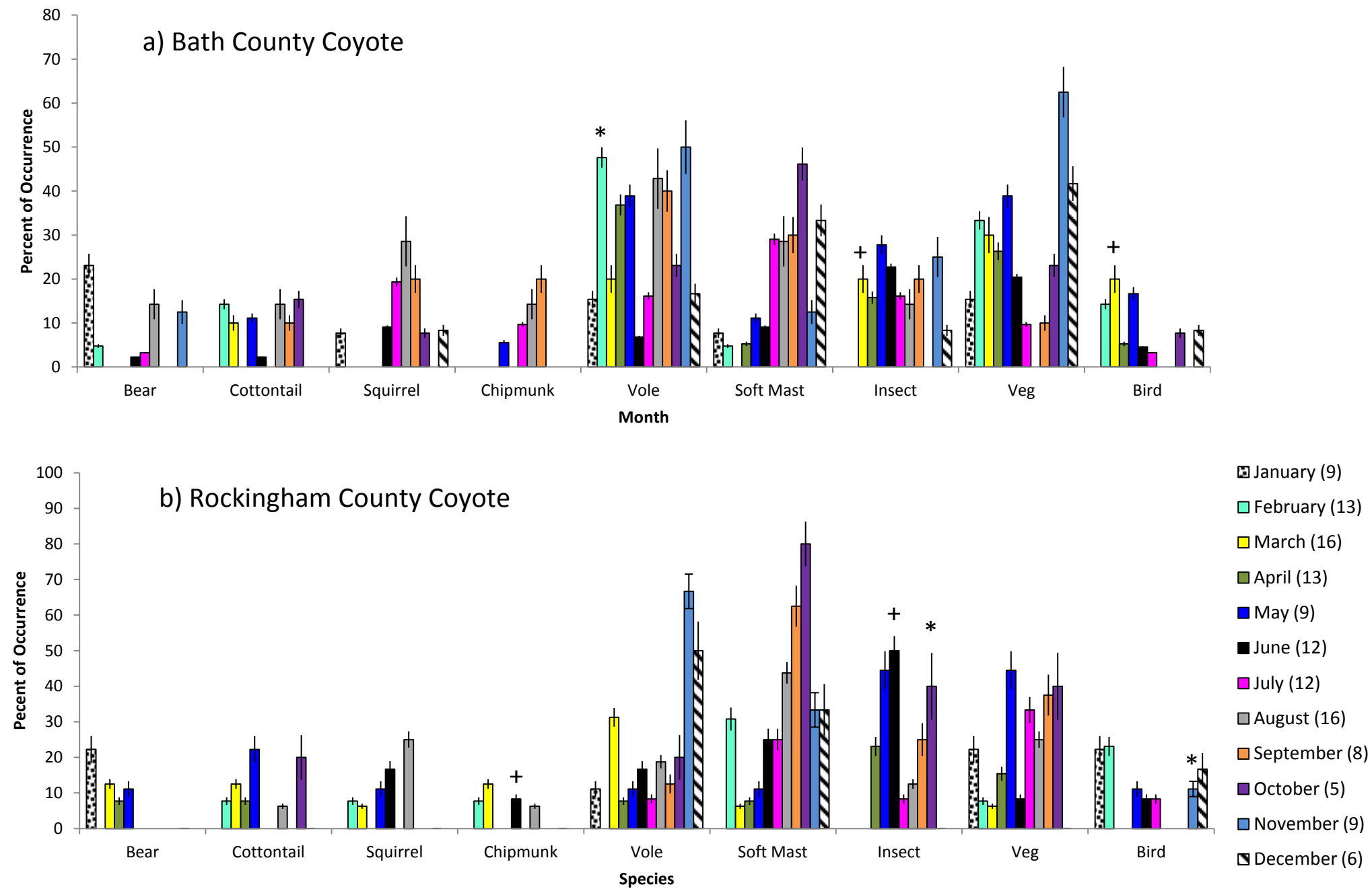


Figure 2: Monthly % occurrence and 95% confidence intervals of common prey items found in **coyote** scats (n = 334) in a) Bath County (n = 206) and b) Rockingham County (n = 128) from June 2011 to May 2013 (years combined). Deer occurrence is not shown (Fig. 3). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.

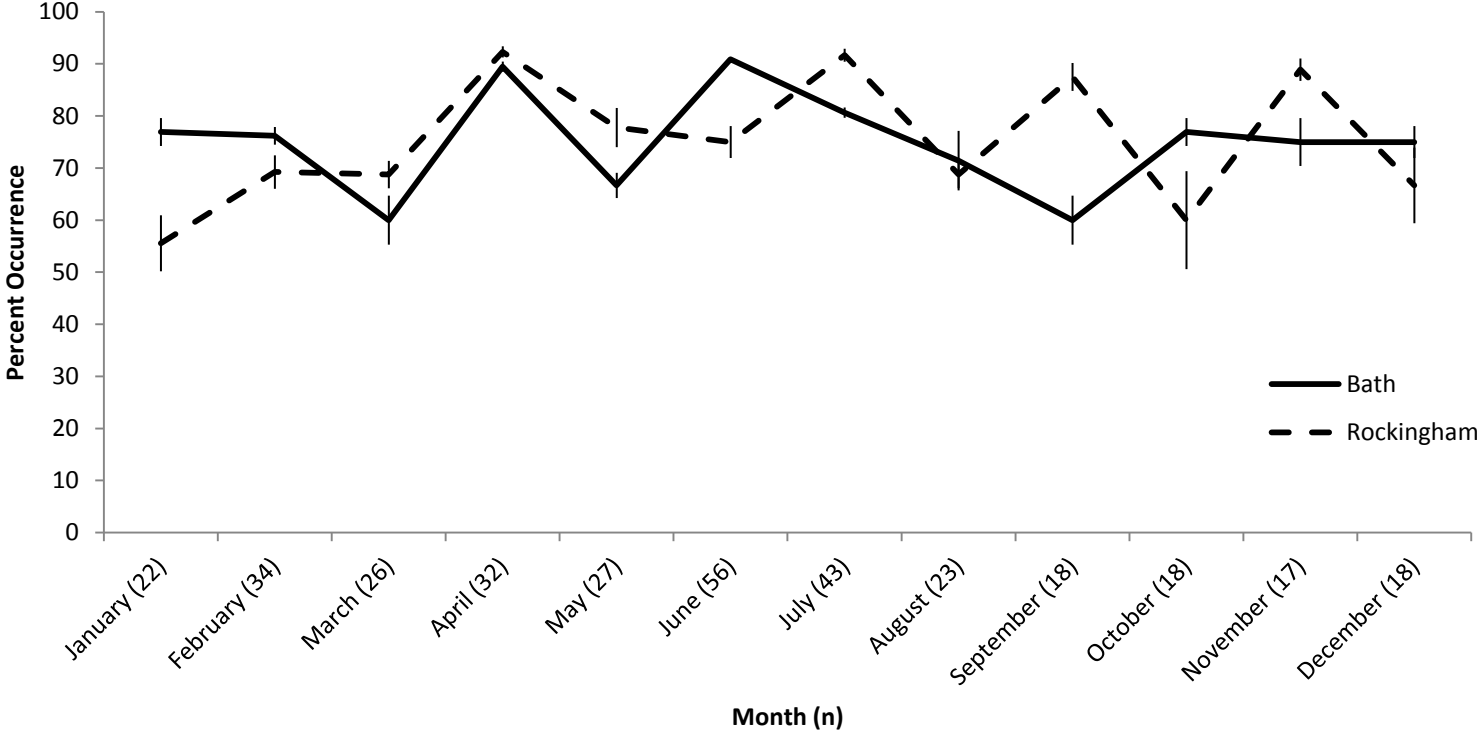


Figure 3: Monthly % occurrence of white-tailed deer with 95% confidence intervals found in **coyote** scats (n = 334) in Bath County (n = 206) and Rockingham County (n = 128) from June 2011 to May 2013 (years combined).

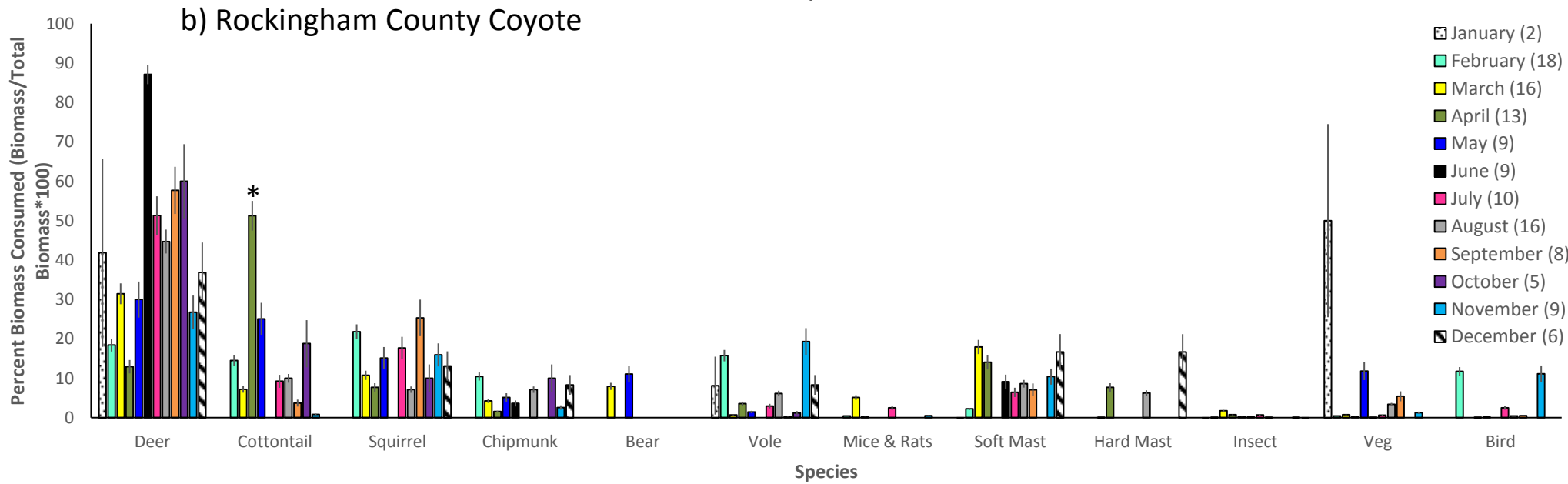
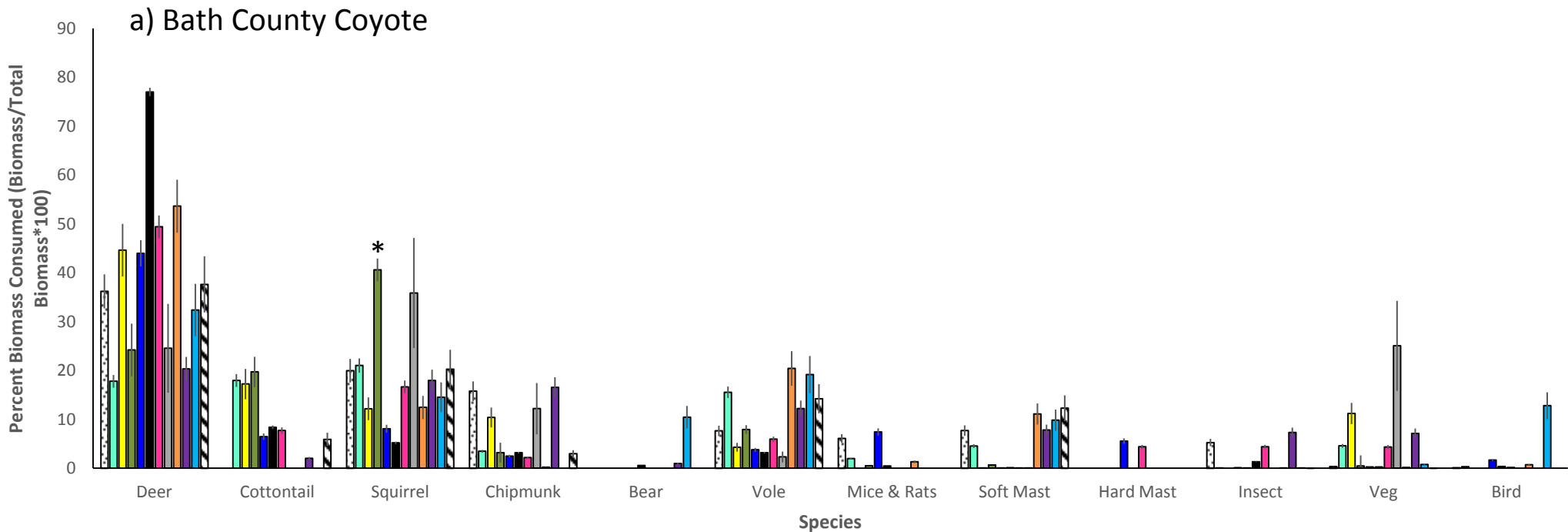


Figure 4: Estimated monthly % biomass consumed with 95% confidence intervals from **coyote** scats (n = 334) in a) Bath County and b) Rockingham County collected from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.

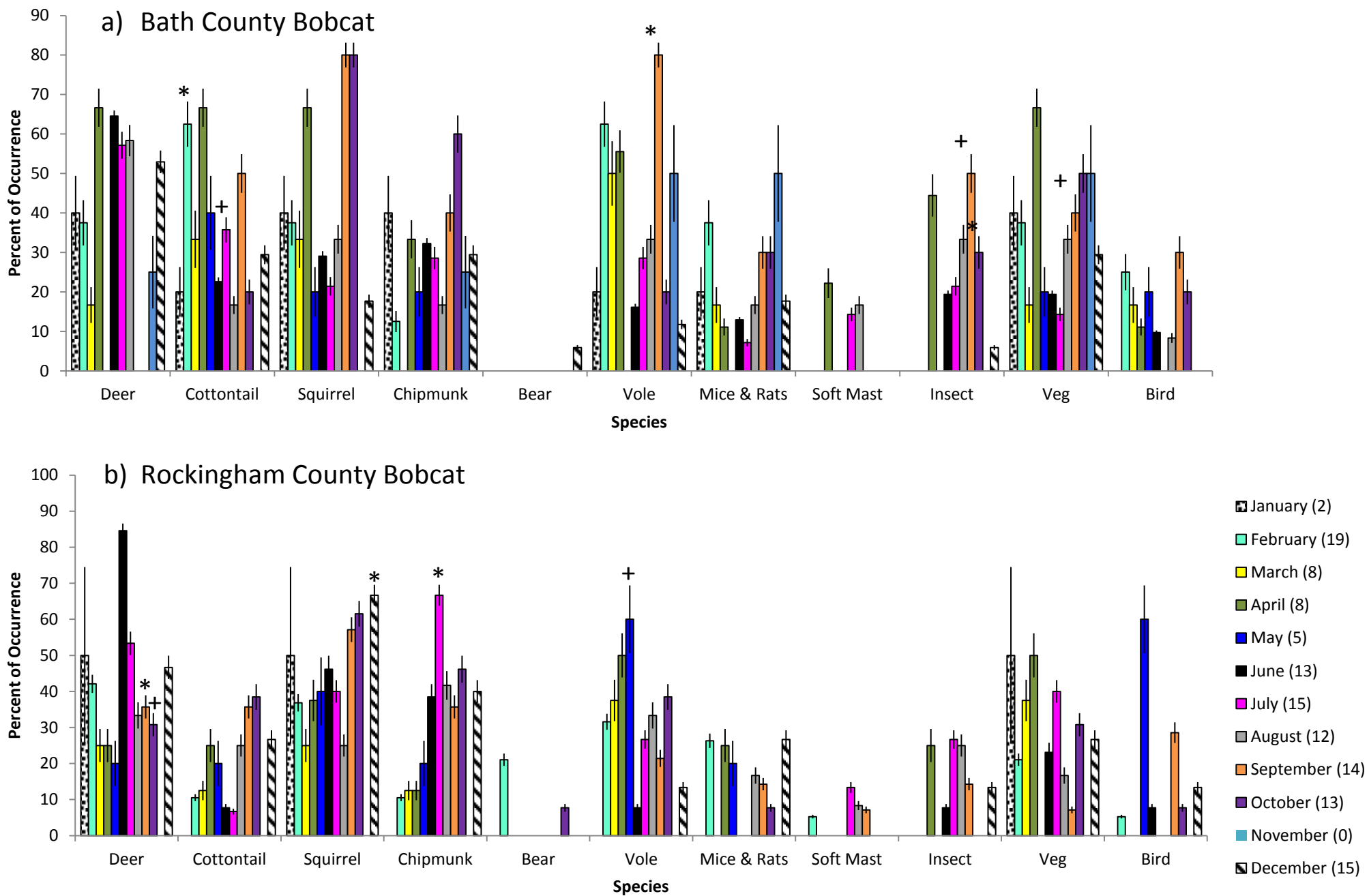


Figure 5: Monthly % occurrence and 95% confidence intervals of common prey items found in **bobcat** scat (n = 258) in a) Bath County (n = 134) and b) Rockingham County (n = 118) from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher % occurrence.

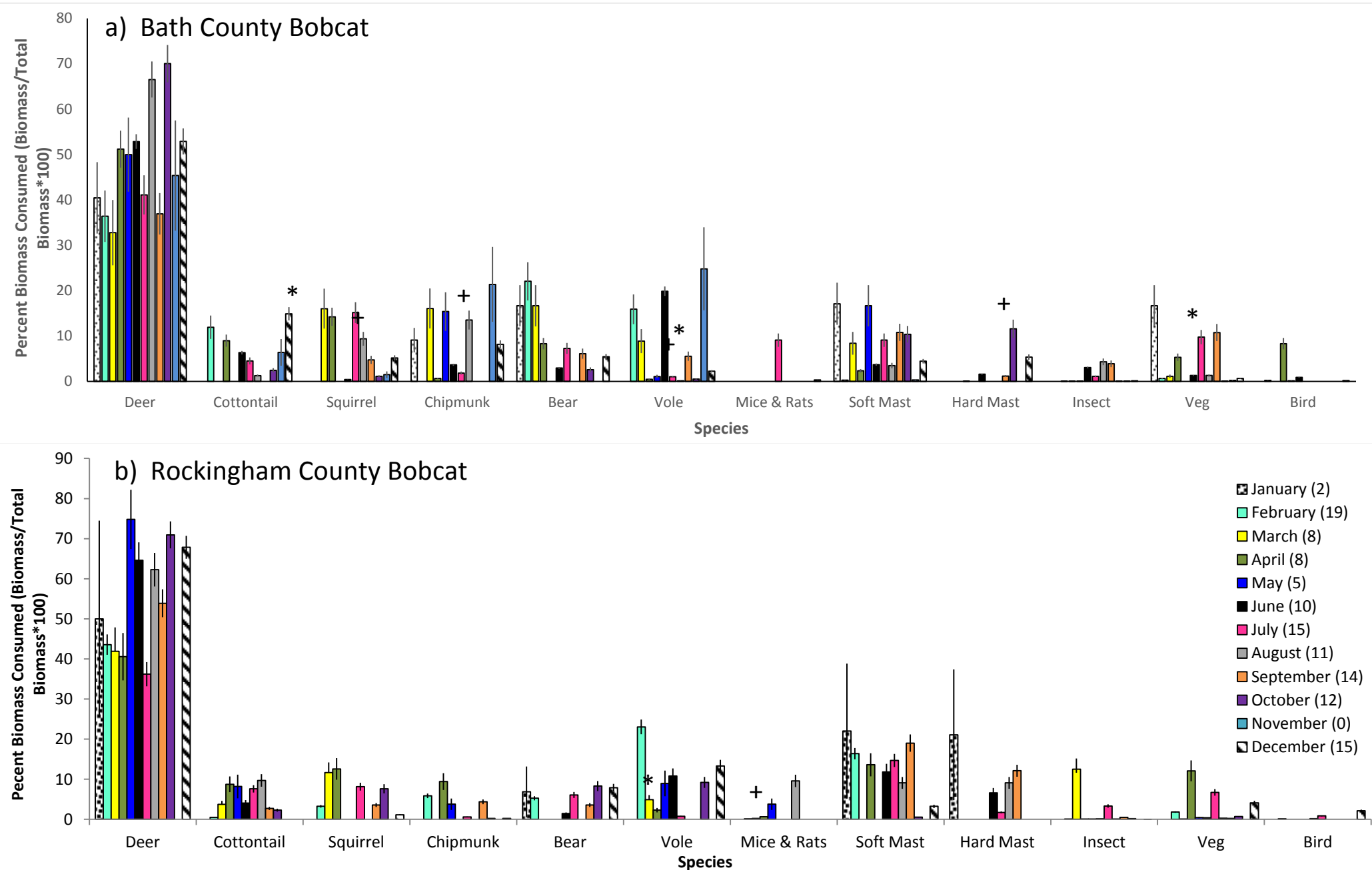


Figure 6: Estimated monthly % biomass consumed with 95% confidence intervals from **bobcat** scats (n = 258) in Bath County (a) and Rockingham County (b) collected from June 2011 to May 2013 (years combined). * denotes significance between counties; + denotes near-significance between counties. Symbol is placed over county with significantly higher occurrence.

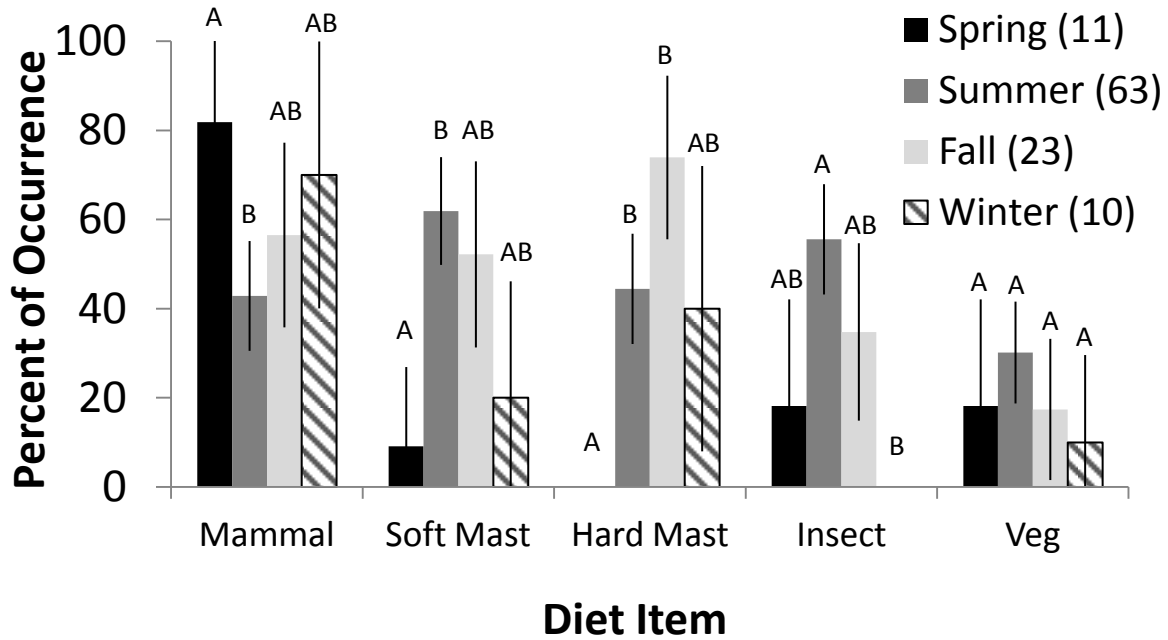


Figure 7: Seasonal % occurrence and 95% confidence intervals of broad diet categories found in **black bear** scats (n = 107) in western Virginia from June 2011 to May 2013 (years combined). Seasons include winter (Dec - Feb), spring (March - May), summer (June - Aug), and fall (Sept. - Oct.) Seasons not connected by same letters are significantly different.

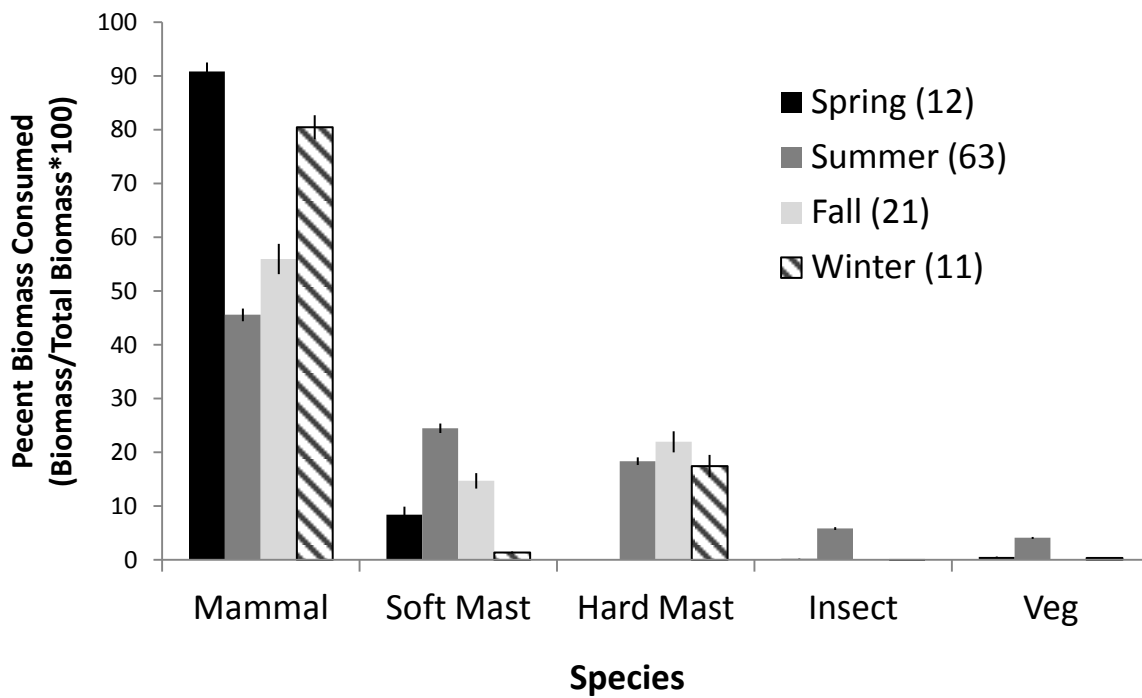


Figure 8: Estimated seasonal % biomass consumed with 95% confidence intervals from black bear scats (n = 107) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years combined). There were no significant differences between seasons.

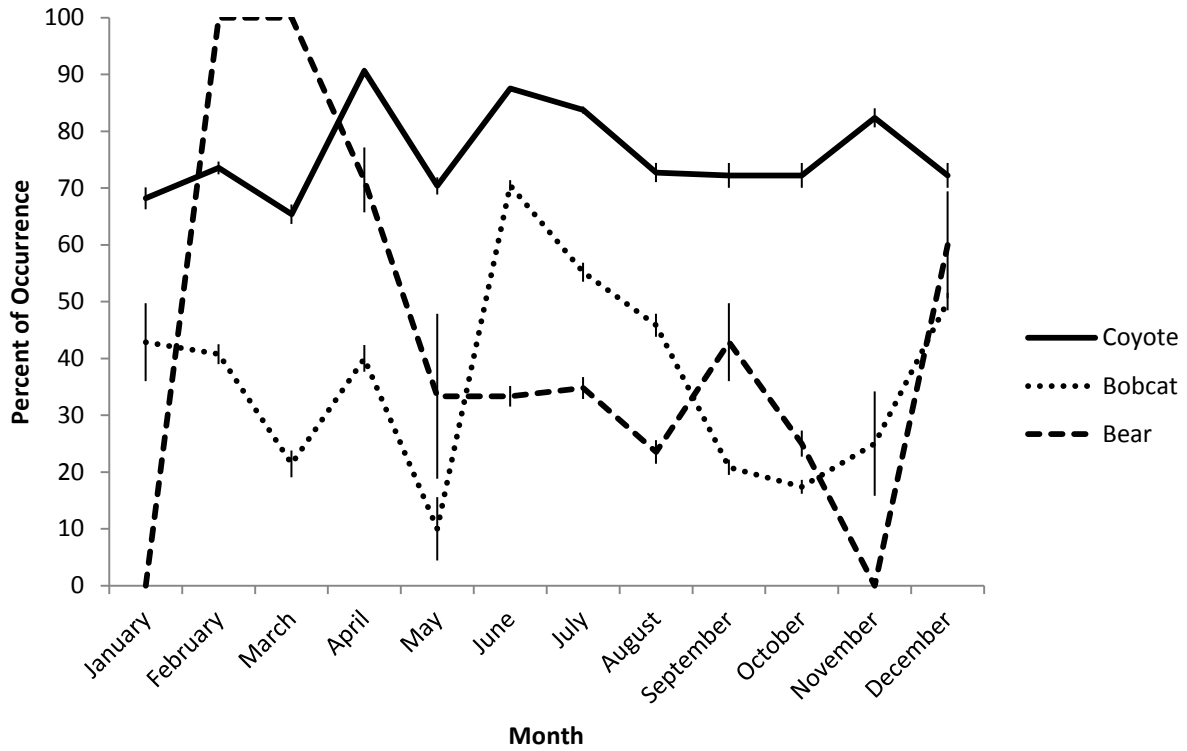


Figure 9: Monthly % occurrences of white-tailed deer with 95% confidence intervals found in scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years and sites combined)

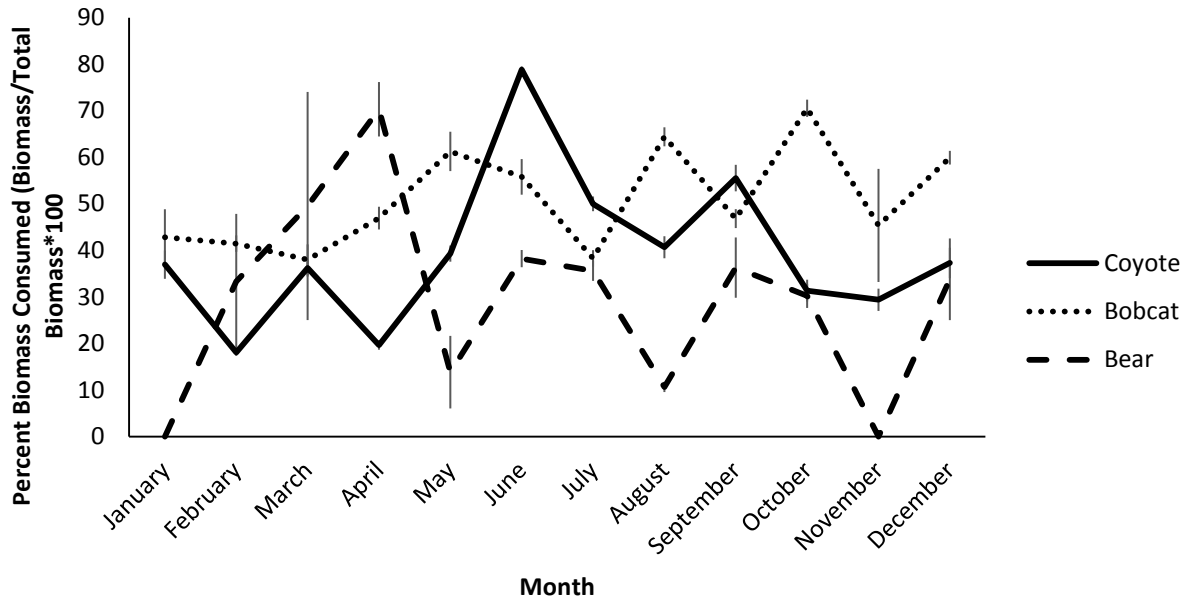


Figure 10: Monthly % biomass consumed of white-tailed deer with 95% confidence intervals found in scats of coyotes (n = 334), bobcats (n = 258), and black bears (n = 107) in Bath and Rockingham Counties, Virginia from June 2011 to May 2013 (years and sites combined).

CHAPTER 4: INTERNAL PARASITES OF COYOTES IN WESTERN VIRGINIA

ABSTRACT

The coyote (*Canis latrans*) is a relative newcomer to Virginia, having first appeared in the state in the 1950s and becoming an established fixture on the landscape only since the early 1970s. The parasites, parasite transmission dynamics, and the role of coyotes in disease ecology have not been studied previously in Virginia. I examined coyote fecal samples from the western part of the state to estimate the prevalence of parasites in the coyote population. I sought to identify spatial and temporal patterns of parasite occurrence in coyote feces. From June 2011-May 2013, I collected fecal samples monthly along 40 km of transects in each of two counties (Bath and Rockingham) for 80 km total in western Virginia. I only used fecal samples that were confirmed by DNA analyses to come from coyotes. I analyzed 203 randomly-selected coyote fecal samples using a modified Wisconsin fecal flotation technique. I identified 13 parasite taxa, 9 of which occurred with adequate frequency to permit statistical analysis. I used analysis of variance to test for seasonal (i.e. bi-monthly) and site differences for *Ancylostoma caninum*, capillarids, *Trichuris vulpis*, *Cystoisospora* spp., *Sarcocystis* spp., taeniids, *Physaloptera* spp., and *Toxocara canis*. No landscape patterns or statistically significant seasonal differences were found in prevalence of parasite taxa, *A. caninum* was significantly higher in Bath County, and *Cystoisospora* spp. was marginally significantly higher in Bath County. I used similar tests to compare spatial and seasonal prevalence of *Eimeria* spp., a spurious parasite which does not affect coyotes. I did not observe any landscape pattern in *Eimeria* spp., and it was significantly higher in Bath County. These descriptive data form a baseline from which to build a better

understanding of disease ecology of coyotes and the potential role of coyotes in the transmission dynamics of parasites in this region.

INTRODUCTION

Predators like coyotes often act as a mechanism of transmission of parasites in wildlife communities through the ingestion of prey that are intermediate or alternate hosts for indirectly or directly transmitted parasites (Schweiger et al. 2007). The spread of coyotes into Virginia in the latter half of the 20th century is hypothesized to have occurred along two fronts: one moving south from New England and the Ohio River Valley and the other moving north along the eastern edge of the Southern Appalachians (Parker 1995; Fig. 1). It is reasonable to assume that the parasite communities of coyotes in Virginia are a combination of the parasite diversity of coyote populations in states in both regions. Franson et al. (1978) found *Ancylostoma caninum* (hookworm), *Taenia* sp. (tapeworm), *Trichuris vulpis* (whipworm), *Toxascaris leonina* (roundworm), *Physaloptera* sp. (stomach worm), and coccidia in a fecal survey of Iowa coyotes. They demonstrated a high prevalence of *Taenia* sp. and low prevalence of *T. vulpis*, with prevalence of *A. caninum* inversely related to coyote age. More recently, Gompper et al. (2003) found a relatively high diversity of parasites in New York coyotes. In addition to the parasites observed by Franson et al. (1978), they also found three species of capillarids, *Toxocara canis*, *Uncinaria stenocephala*, and *Sarcocystis* sp. *Ancylostoma caninum*, which had high prevalence in Iowa, was not found in the New York coyotes.

On the southern front, a parasite fauna similar to that in Iowa was found in Georgia including *A. caninum*, *Physaloptera* sp., *Taenia* sp., and *Sarcocystis* sp. (Holtzman et al. 1992). Miller et al.

(2009) observed very low species richness in fecal samples of coyotes in South Carolina. *Ancylostoma* spp. was observed in more than 50% of samples, and *Trichuris* spp. and *Isospora* spp. were the only other fecal parasites that were found, both in extremely low prevalence. These studies from coyote populations both north and south of Virginia all indicate a relatively consistent parasite fauna with typically high prevalence of hookworms (*Ancylostoma* spp. or *Uncinaria* spp.), taeniids, *Isospora* (*Cystoisospora*) spp., *Physaloptera* spp., and *Sarcocystis* spp. capillarids, *Trichuris* spp., and ascarids (*T. canis* and *T. leonina*) also occurred in multiple nearby states. Prevalence of these parasites varied widely among studies, but parasite fauna composition was relatively consistent (Table 1).

Parasites that infect coyotes such as canine heartworm (*Dirofilaria immitis*) and hookworm (*Ancylostoma caninum*) can also infect domestic dogs, and others like *Echinococcus* spp. and *Toxocara canis* pose a zoonotic risk to humans (Wapenaar et al. 2013; Schweiger et al. 2007; Romig et al 2006). For example, Schweiger et al. (2007) suggested a link between a four-fold increase in fox populations in Switzerland and a dramatic increase in incidence in humans of *Echinococcus multiocularis* (alveolar tapeworm), a species currently unknown in Virginia but known to infect coyotes in other regions.

The parasites of coyotes in Virginia, and the role of coyotes in the transmission dynamics of parasites in Virginia, have not been studied previously. I examined coyote feces from the western part of the state to determine the prevalence of intestinal parasites in the coyote population. I defined parasite prevalence as the proportion of fecal samples containing each parasite taxa. In addition, I sought to identify spatial and temporal patterns of parasite occurrence in coyote feces across the landscape.

Methods

I collected coyote fecal samples along 5 km transects that followed dirt roads and trails used as travel corridors by coyotes in the George Washington National Forest and adjacent private lands. Eight transects were established in each of the 2 counties for a total of 16 transects, or 80 km in combined length. All feces were removed from these transects in May 2011 to ensure that feces collected in subsequent months had been deposited within the last month. Each transect was visited monthly from June 2011 to May 2013. All carnivore feces along the transects were collected and placed into plastic bags labeled with a unique sample number and the date of collection. Prior to bagging, a DNA sample was collected from every fecal sample by scraping a small amount of fecal matter from the outside of the feces with a tongue depressor and placing it into a plastic tube containing DET buffer solution. Fecal samples were stored frozen at -20°C for up to two years before being placed in a -80°C freezer for 72 hours to reduce the risk of zoonotic transmission of *Echinococcus* spp (Colli and Williams 1972).

Additional coyote fecal samples were collected from coyotes that were trapped in Bath County, VA and fitted with GPS collars for a concurrent study of coyote spatial ecology. These samples were collected at sites where coyotes were captured. The fecal samples were either defecated by coyotes while they were in the traps or while researchers were handling them. The same protocol that was used when collecting samples on transects was used for collecting samples from trapped coyotes. However, it was not necessary to collect genetic samples in order to confirm the species of origin of the feces.

Genetic samples were analyzed at the Laboratory for Ecological, Evolutionary and Conservation Genetics (LEECCG) at the University of Idaho by using mtDNA to determine the carnivore species that deposited each fecal sample. Although samples collected included feces of bobcats (*Lynx rufus*), black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), house cats (*Felis catus*), domestic dogs (*Canis familiaris*), and raccoons (*Procyon lotor*), only samples confirmed by mtDNA as coyote were analyzed for parasites.

I thawed samples and analyzed them using a modified Wisconsin fecal flotation technique (Liccioli et al. 2012) in the Zajac Parasitology Lab at the Center for Molecular Medicine and Infectious Diseases at the Virginia-Maryland College of Veterinary Medicine. Five grams of fecal material were weighed, suspended in water, and strained through two layers of bleached cheesecloth to remove solids like bones and hair which were reserved for later scat analysis. I centrifuged the suspension for 10 minutes at 500 rpms. The supernatant was poured off and the fecal material was re-suspended in Sheather's solution (specific gravity of 1.27) by stirring and vortexing. After resuspending the pellet, I added additional flotation solution to create a reverse meniscus. I placed a coverslip over the reverse meniscus of Sheather's solution and centrifuged the samples a second time for 10 minutes at 500 rpms. I scanned each slide at 100X magnification and used 400X when closer examination was needed. Parasite eggs, oocysts, etc. that were detected were identified using published resources (Zajac and Conboy 2006). I also used fecal sedimentation and fecal flotation with saturated ZnSO₄, but these did not result in detection of additional parasites, and therefore were discontinued. Many parasites cannot be identified to species using egg morphology. As a result, I could not differentiate some parasite taxa like *Taenia spp.* and *Echinococcus spp.* in this study.

I mapped the collection locations of all parasite samples across the landscape in geographic information systems (GIS) using Esri ArcMap 10.1. Because of low sample sizes in some months, I pooled from all years of sample collection into bi-monthly time periods and compared them by combining samples from January-February, March-April, May-June, July-August, September-October, and November-December. I compared seasonal prevalence of parasite taxa using one-way ANOVA ($\alpha = 0.05$) and t-tests of all pairs of comparisons with a Bonferroni correction in SAS JMP Pro 10 ($\alpha = 0.0033$ after correction). I also compared parasite prevalence between Bath and Rockingham Counties, regardless of season or collection year, using t-tests assuming unequal variance in SAS JMP Pro 10 ($\alpha = 0.05$).

RESULTS

From June 2011 – May 2013, I collected 1,679 fecal samples along 80 km of scat transects. Of these, DNA was successfully extracted from 1,282 samples and 429 were from coyotes. Of the 215 randomly-selected coyote fecal samples 131 were from transects in Bath County, 70 were from transects in Rockingham County, and 14 were from coyotes trapped in Bath County. Of the 215 random samples, 12 produced slides that were unreadable and could not be included in data analysis.

I identified 13 parasite taxa in coyote fecal samples, 9 of which occurred with sufficiently high prevalence to permit statistical analysis (Table 2). *Ancylostoma caninum* was the most prevalent species in both counties. *Trichuris vulpis*, capillarids, *Cystoisospora* sp., taeniids, *Toxocara canis*, *Toxascaris leonina*, *Physaloptera* sp., *Sarcocystis* sp., and *Spirometra* sp. were also found in both counties. In addition to these 9 species, which I analyzed statistically, I found *Alaria*

spp., *Paragonimus kellicotti*, and *Mesocestoides* sp. in very low prevalence in both counties. I found spurious coccidia (*Eimeria* sp.) in Bath County only, and with sufficient prevalence for analysis.

Although seasonal comparisons of parasite prevalence were not statistically significant, *A. caninum*, *Cystoisospora* sp., and *Sarcocystis* sp. all were most prevalent in July-August, whereas capillarids and *T. vulpis* were most prevalent in September-October (Fig. 5). By comparison, taeniids and *T. canis* were most prevalent in May-June, and only *Physaloptera* sp. had highest prevalence in November-December. Visual comparisons of fecal sample collection locations mapped in GIS did not reveal any pattern in the spatial occurrence of various parasite taxa (Fig. 3). I did not find any significant differences in parasite prevalence between the study sites for any species except for *Ancylostoma caninum* which was significantly higher in Bath County ($n = 140$; $\mu = 0.285$) than in Rockingham County ($n = 63$; $\mu = 0.182$, $t = 1.67$, $p = 0.048$) (Table 2; Fig. 4). In addition, *Cystoisospora* spp. was marginally significantly higher in prevalence in Bath County (Bath: $n = 140$, $\mu = 0.168$; Rockingham: $n = 63$, $\mu = 0.091$, $t = 1.606$, $p = 0.055$).

Although spurious in coyotes, *Eimeria* sp. was most prevalent in May-June. *Eimeria* spp. was significantly higher in Bath County ($n = 140$; $\mu = 0.044$) than in Rockingham County ($n = 63$; $\mu = 0$, $t = 2.50$, $p = 0.007$).

Bi-monthly comparisons of parasite prevalence pooled from both study sites revealed no significant differences among bi-monthly time periods (Table 3; Fig. 5). However, the occurrence of samples in which no parasites were detected differed significantly among bi-monthly time periods (one-way ANOVA, $p = 0.010$; Fig. 6). Multiple comparisons using Student's t-tests of all pairs with a Bonferroni correction for multiple comparisons revealed no

significant differences among seasons, suggesting that there is a weak seasonal effect in the proportion of samples in which no parasites were found. Although not significant according to the t-tests, there were more samples from winter months containing no parasites than there were in summer months.

DISCUSSION

In wild coyotes, parasites typically are studied by necropsy or scat analysis, which relies on identification of parasite eggs, oocysts, etc. that are shed in feces (Gompper et al. 2003; Trout et al. 2006; Miller et al. 2009). Fecal flotation is a common technique for identifying parasites in fecal samples. However, certain assumptions and limitations are associated with this technique. First, fecal flotation is limited to detection of parasites that live in the gastrointestinal tract (e.g. taeniids, *A. caninum*, etc.), shed eggs in the gastrointestinal tract (e.g. some capillarids), or have been ingested by the coyote (e.g. mites). Second, because a single adult parasite can release thousands of eggs in a host's digestive tract, the relative abundance of eggs in feces cannot be assumed to represent relative abundance of adult parasites within that host, but merely the presence of a particular species within the host (Villanua et al. 2006). Third, certain known parasites of coyotes (e.g. *Dirofilaria immitis*) do not spread through feces and therefore cannot be detected by scat analysis. Finally, the eggs of some parasites cannot be distinguished based on morphology alone, allowing identification only to genus or family in some cases (Trachsel et al. 2007).

The lack of any apparent differences in spatial distribution across the landscape in the occurrence of coyote fecal parasites suggests that either 1) the high mobility of coyotes negates any

influence of landscape variables at this scale, or 2) parasites within the two study areas are distributed relatively evenly and occur regardless of distance to urban development, rates of interaction with domestic canids, or differential availability of prey species acting as intermediate hosts. The significantly higher occurrence of *Ancylostoma caninum* and slightly significantly higher prevalence of *Cystoisospora* spp. in Bath County could be due to differences in the age structure of the coyote populations. *Ancylostoma caninum* and coccidia infections are more common in younger individuals (Franson et al. 1972). The higher prevalence of *A. caninum* eggs and *Cystoisospora* oocysts in samples from Bath County may be indicative of the presence of more young coyotes in this population, or it may indicate that sampling design and transect locations in Bath County resulted in more fecal samples from young coyotes. The occurrence of *Toxocara canis* eggs from May-August (pup rearing stage for coyotes) provides evidence that some of the samples that were collected came from pups, since the presence of patent (egg-producing) *T. canis* infections in domestic dogs decreases after 3 months of age (Morgan et al. 2013) and prevalence of *T. canis* in foxes (*Vulpes vulpes*) has been shown to be significantly higher among juveniles (Wapenaar et al. 2013). However, *T. canis* did not vary significantly between the two study sites, which does not support the suggestion that Bath County coyotes have a younger age structure. Nevertheless, anecdotal evidence suggests coyotes in Bath County may have a high rate of population turnover. If higher turnover in Bath County has resulted in density-dependent breeding and higher fecundity rates relative to Rockingham County, this could possibly explain the higher prevalence of parasites associated with juvenile canids.

Eimeria spp. also had significantly higher prevalence in Bath County than in Rockingham County. However, *Eimeria* is a genus of coccidia only occurring as spurious parasites in coyotes

– parasites of prey animals passing harmlessly through the coyote’s digestive tract – and therefore its presence in coyote feces does not indicate parasitism or disease among coyotes (Zajac and Conboy 2006). The higher prevalence of *Eimeria* in Bath County could be the result of differences in the composition of coyote diets due to differential prey species availability between the two study areas. If this is true, the *Eimeria* spp. observed in coyote scat may be associated with particular prey species comprising a higher proportion of coyote diets in Bath County. Alternatively, the observed difference in prevalence could be due to higher rates of parasitism among the prey community in Bath County. Results of scat analyses (chapter 3) reveal that all samples containing *Eimeria* spp also contained white-tailed deer remains. This suggests the parasites I found in could be one of several species of *Eimeria* reported in white-tailed deer including *E. madisoniensis*, *E. mccordocki*, *E. odocoilei*, *E. virginianus*, *E. ivensae*, or *E. zajacae* (Anderson and Samuel 1969; Lindsay et al. 1999). A link between *Eimeria* spp. in fecal samples and deer in coyote diets may help explain the higher prevalence of *Eimeria* spp. in Bath County, where I estimated higher deer population density than in Rockingham County.

I found no significant bi-monthly seasonal differences in parasite prevalence. One reason for the lack of any observed differences among seasons may be the pooling of data from multiple years. Samples were collected over the course of 24 months, and samples from the same month in each year were combined to increase sample size. Since parasite prevalence in a landscape can fluctuate from year to year depending on any number of internal and external factors, pooling data in this way may have masked seasonal effects. Additionally, data were combined into 2-month periods to increase sample size, which similarly may have masked seasonal effects, particularly if fluctuations in parasite prevalence occurred over very short durations. Aside from issues of sample size and seasonal lumping, the lack of seasonal variation may be due to low

seasonal variation observed in use of food resources (chapter 3). High % occurrence of deer in coyote feces in all months may correspond with a lack of seasonal variation in parasite prevalence.

These data provide a baseline of coyote fecal parasite prevalence in western Virginia and raise many questions for future study. Larger sample sizes, perhaps from focused sampling during a shorter period, may improve seasonal estimates of parasite prevalence and reveal significant seasonal differences in coyote parasite prevalence. Both study areas have low human populations and a high proportion of the landscape in mature, even-aged forest, so it is unclear whether coyote populations in areas with more agriculture, livestock, or urbanization might have differing rates of infection from parasites. Molecular studies identifying parasites such as taeniids to the level of species could help us understand the diversity of parasites in Virginia. Detailed studies of the seasonal and spatial prevalence of parasites in various species of coyote prey in Virginia are needed to understand the sources of coyote parasitic infections and their prevalence in the landscape. Finally, forthcoming research on the demographics of these coyote populations may supplement these findings and reveal new insights into the dynamics of disease transmission and prevalence in the wildlife of western Virginia.

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TABLES AND FIGURES

Table 1: Parasite species detected in fecal surveys of coyotes (n = 215) collected in Bath and Rockingham Counties, Virginia from June 2011 to May 2013. x = presence; + = high prevalence; - = low prevalence.

Location	Nematode							Cestode		Protozoa	
	<i>Ancylostoma caninum</i>	<i>Uncinaria stenocephala</i>	<i>Trichuris vulpis</i>	capillarids	<i>Toxascaris leonina</i>	<i>Toxocara canis</i>	<i>Physaloptera</i> spp.	<i>Taenia</i> spp.	<i>Spirometra</i> spp.	<i>Sarcocystis</i> spp.	coccidia
Iowa*	+ (pups)		-		x		x	+			x
New York†		x	x	x	x	x	x	x	x	x	x
Georgia‡	x						x	x		x	
South Carolina**	+		-								-
Virginia***	+		x	x		x	x	x	x	x	+
Adult Worm Location	Intestinal tract	Intestinal tract	Intestinal tract	Lungs and nasal passages	Intestinal tract	Liver, lungs, brain, heart, striated muscle	Stomach	Intestinal tract	Intestinal tract	Intestinal tract	Spurious

* Franson et al. 1978; † Gompper et al. 2003; ‡ Holtzman et al. 1992; ** Miller et al. 2009; *** This study 2014

Table 2: Prevalence of common parasites of coyotes (n = 215) collected in Bath and Rockingham Counties, VA from June 2011 to May 2013 and results of t-tests comparing prevalence between counties ($\alpha = 0.05$).

Species	Bath (n = 137)		Rockingham (n = 66)		p-value
	Prevalence	SE	Prevalence	SE	
<i>A. caninum</i>	28.47	7.56	18.18	6.46	0.048*
capillariids	11.68	5.38	10.61	5.16	0.410
<i>T. vulpis</i>	12.41	5.52	13.64	5.75	0.595
<i>Cystoisospora</i> spp.	16.79	6.26	9.09	4.81	0.055
<i>Sarcocystis</i> spp.	10.22	5.07	7.58	4.43	0.264
taeniids	14.60	5.91	10.61	5.16	0.207
<i>Toxocara canis</i>	2.92	2.82	1.52	3.43	0.252
<i>Physaloptera</i> spp.	4.38	2.05	4.55	3.49	0.521

Table 3: Bi-monthly prevalences of common parasites of coyotes (n = 215) collected in Bath and Rockingham Counties, VA from June 2011 to May 2013 (years combined), with results of a one-way analysis of variance ($\alpha = 0.05$).

Species	Jan - Feb (n = 20)	March-April (n = 40)	May - June (n = 72)	July-August (n = 39)	Sept - Oct (n = 21)	Nov - Dec (n = 11)	p-value
<i>Ancylostoma caninum</i>	25.00	12.50	30.56	35.90	9.52	27.27	0.08
Capillarid	20.00	10.00	6.94	10.26	23.81	9.09	0.19
<i>Trichuris vulpis</i>	0.00	12.50	12.50	12.82	23.81	18.18	0.50
<i>Cystoisospora</i> spp.	10.00	5.00	18.06	20.51	19.05	0.00	0.36
<i>Sarcocystis</i> spp.	5.00	5.00	11.11	15.38	9.52	0.00	0.26
taeniid	0.00	17.50	18.06	12.82	4.76	9.09	0.28
<i>Toxocara canis</i>	0.00	0.00	5.56	2.56	0.00	0.00	0.40
<i>Physaloptera</i> spp.	5.00	0.00	5.56	5.13	0.00	18.18	0.16

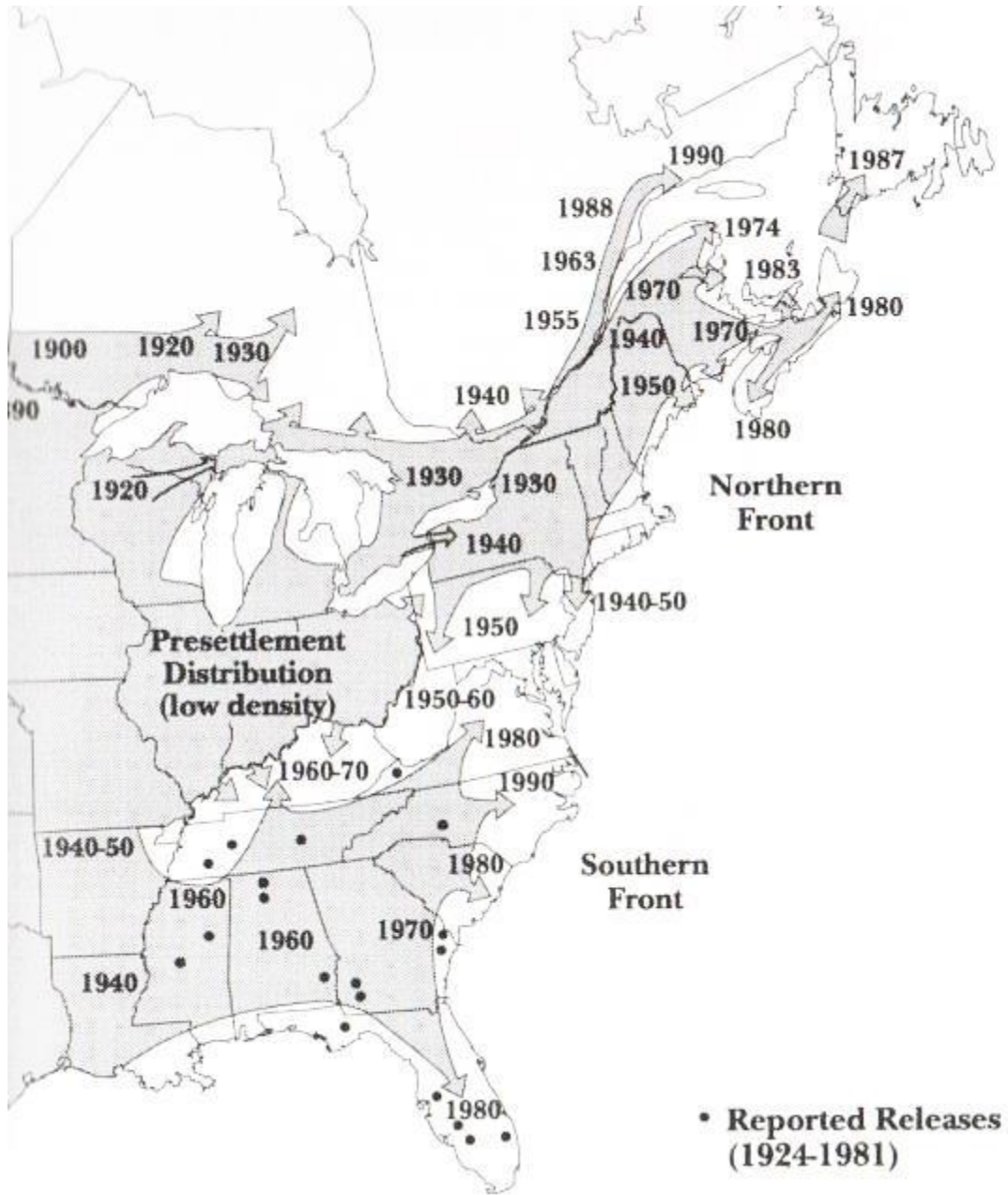


Figure 1: Mode and timeline of coyote range expansion in the eastern United States (Parker 1995).

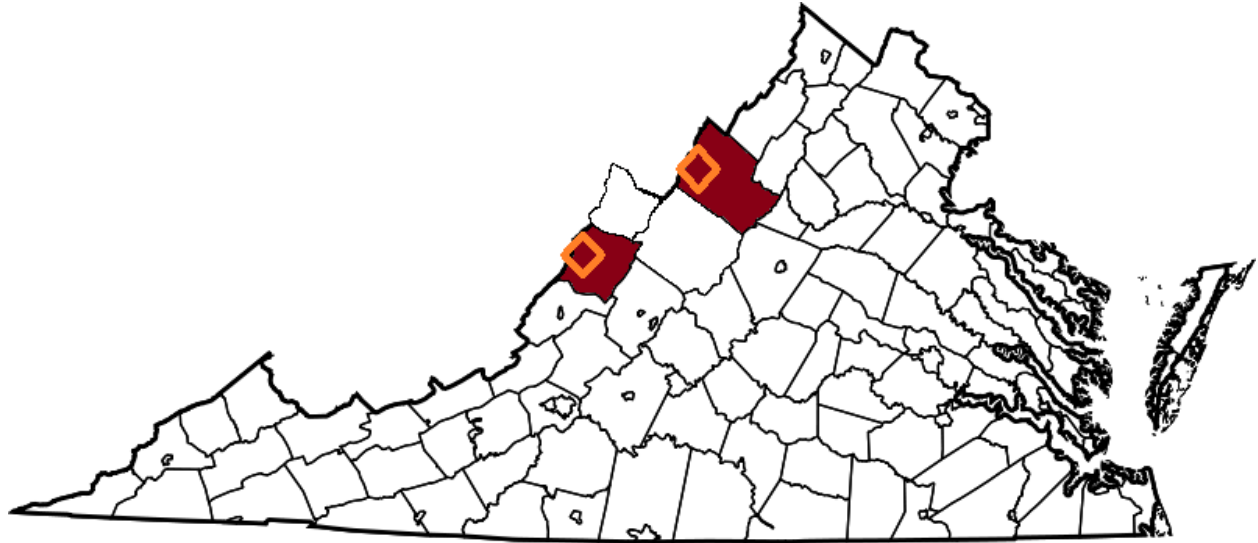
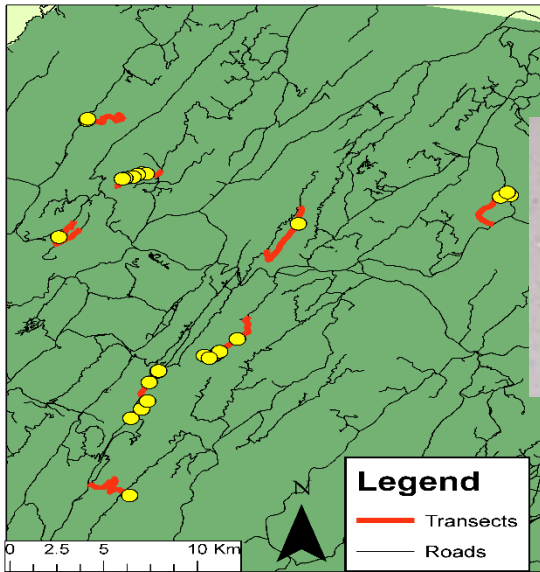
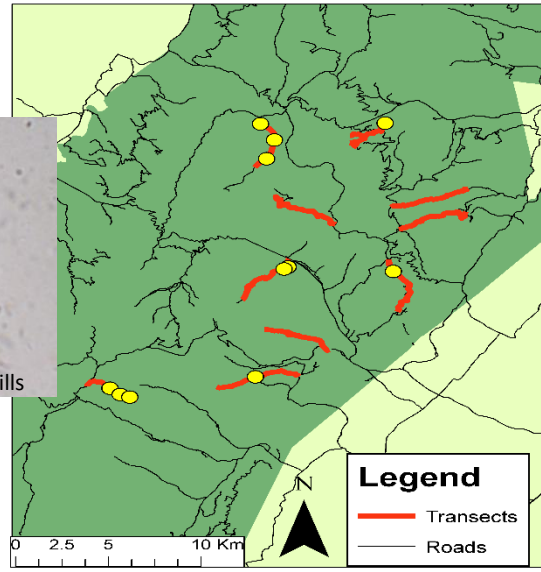


Figure 2: Map of the study areas highlighting (L to R) Bath and Rockingham Counties. Orange boxes denote the general region of each county studied.

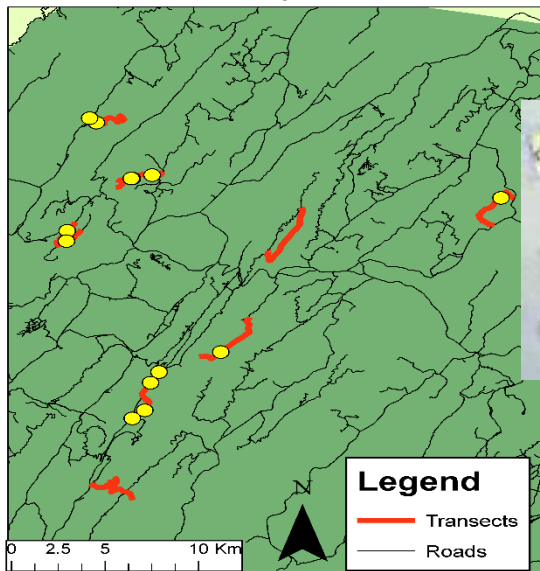
Bath: *Ancylostoma caninum*



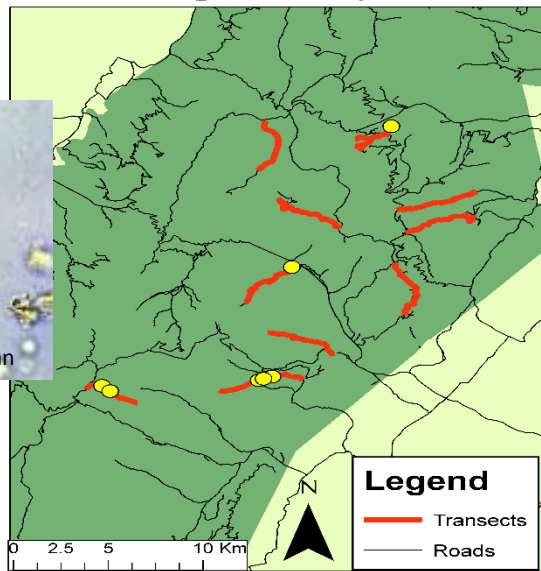
Rockingham: *Ancylostoma caninum*



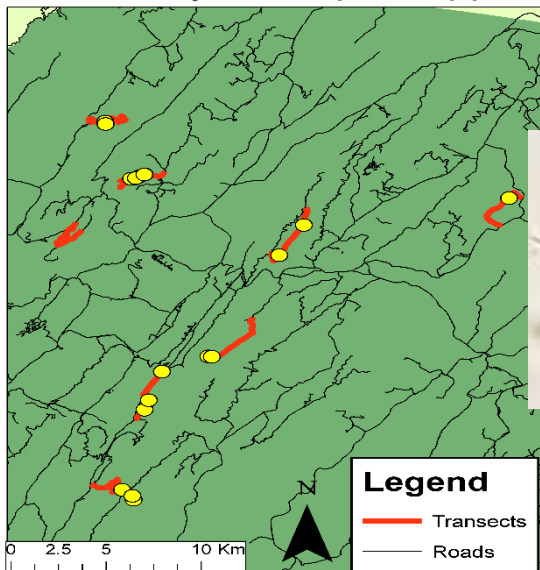
Bath: capillarids



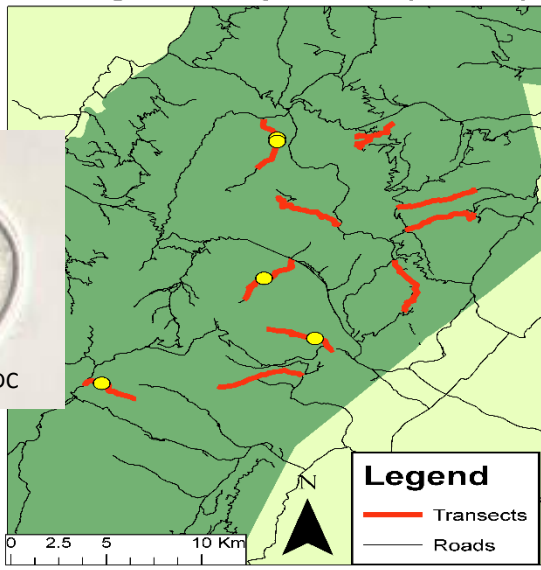
Rockingham: capillarids



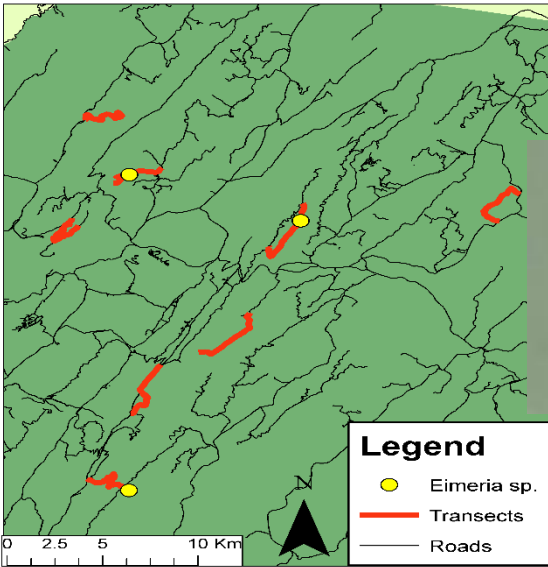
Bath: *Cystoisospora* spp.



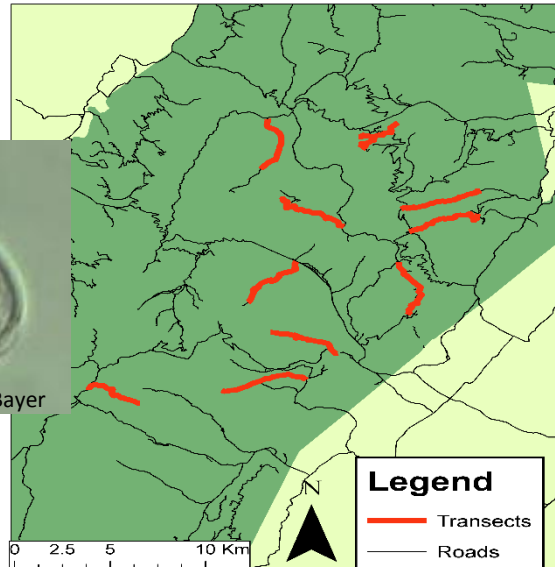
Rockingham: *Cystoisospora* spp.



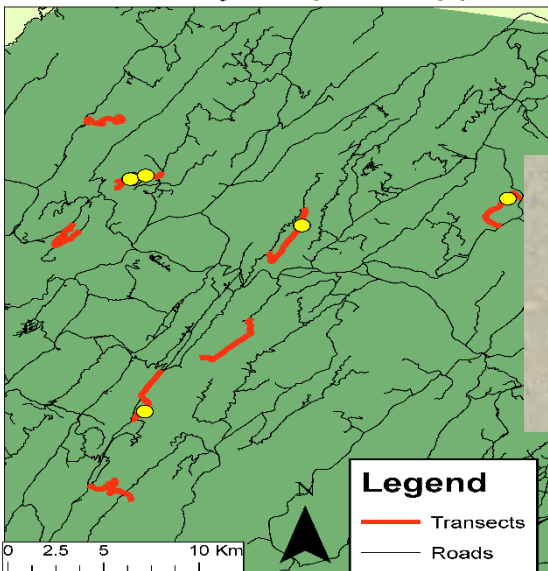
Bath: Eimeria sp.



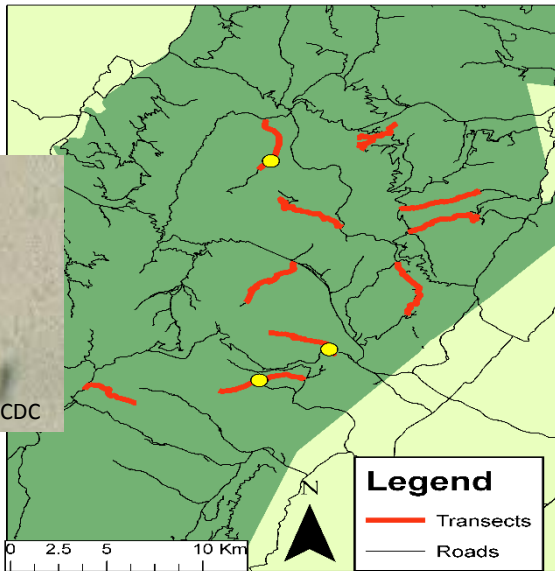
Rockingham: Eimeria spp.



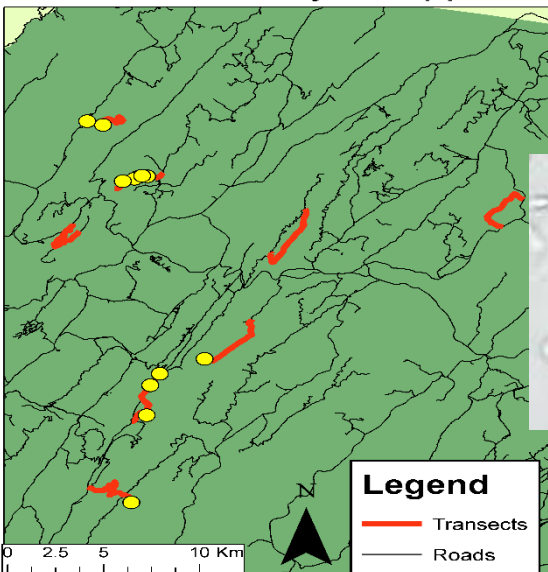
Bath: Physaloptera spp.



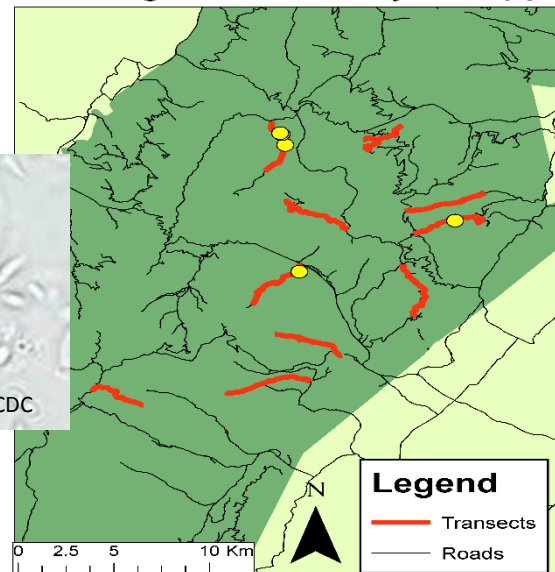
Rockingham: Physaloptera spp.



Bath: Sarcocystis spp.



Rockingham: Sarcocystis spp.



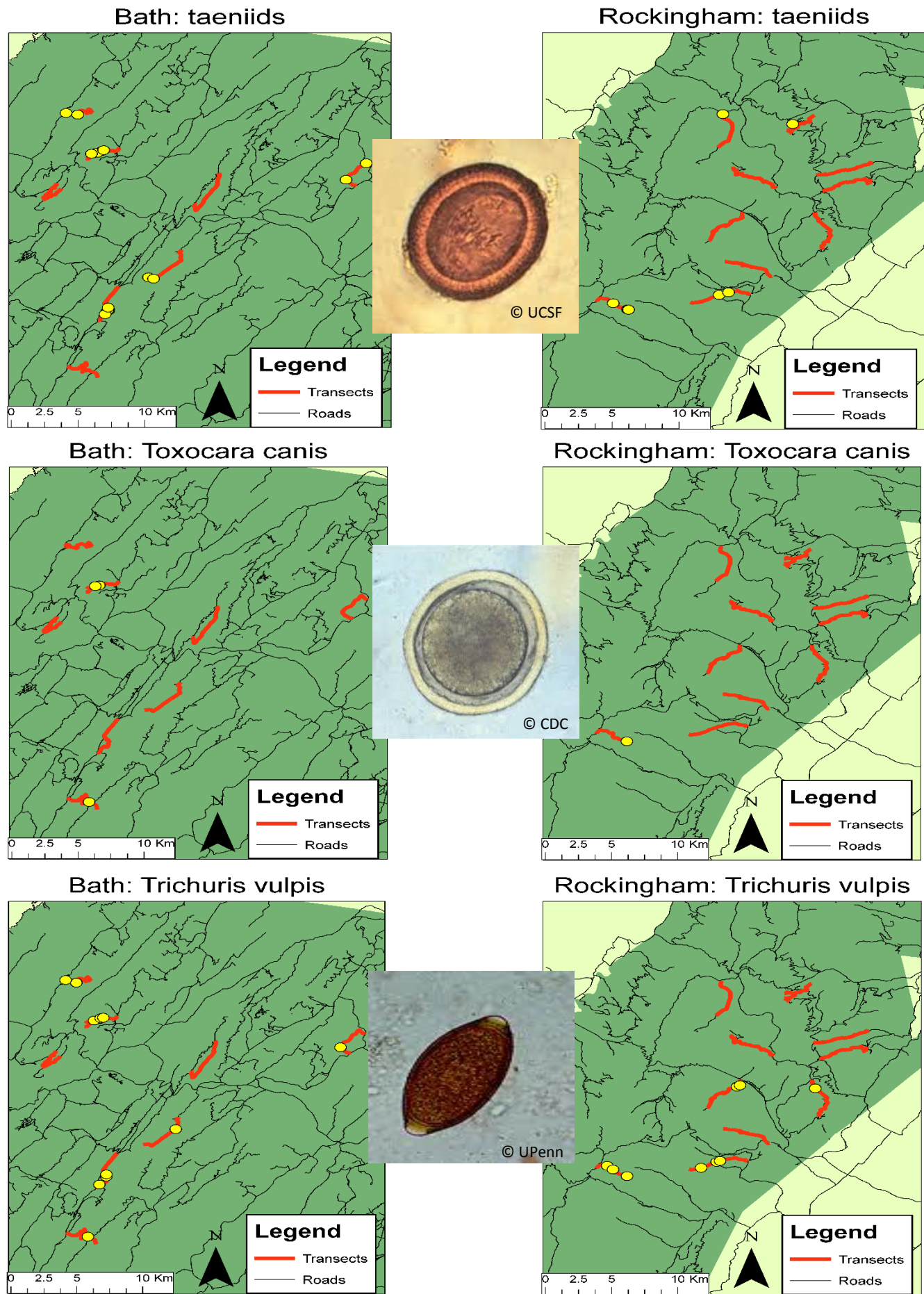


Figure 3: Locations of coyote feces (n = 215) containing 9 different parasite species in Bath (left panel) and Rockingham (right panel) Counties, Virginia relative to survey transects.

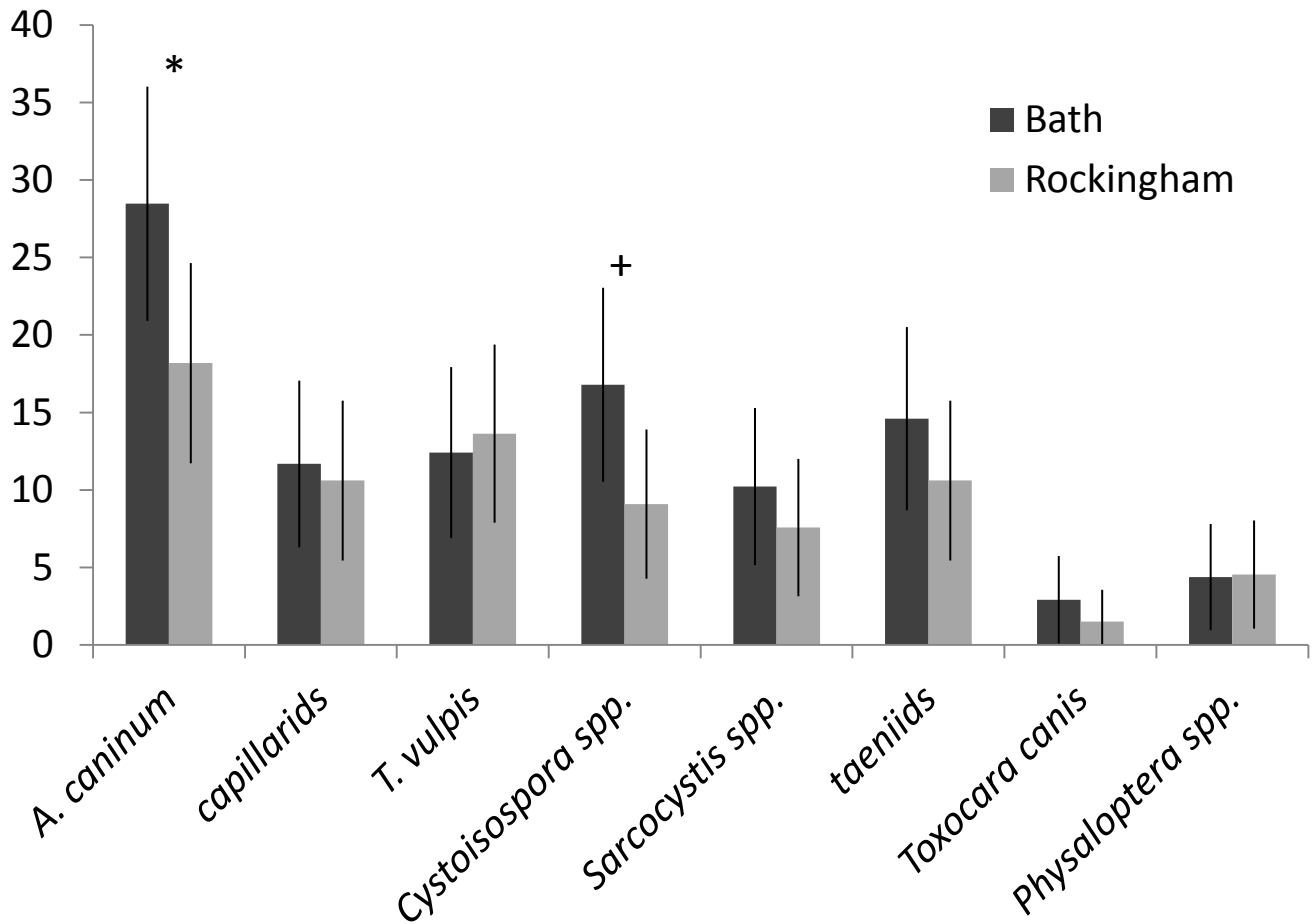


Figure 4: Prevalence and 95% confidence intervals of fecal parasites of coyotes (n = 215) in Bath and Rockingham Counties, VA, collected from June 2011 to May 2013 (years and months comined). * denotes significance. + denotes near significance.

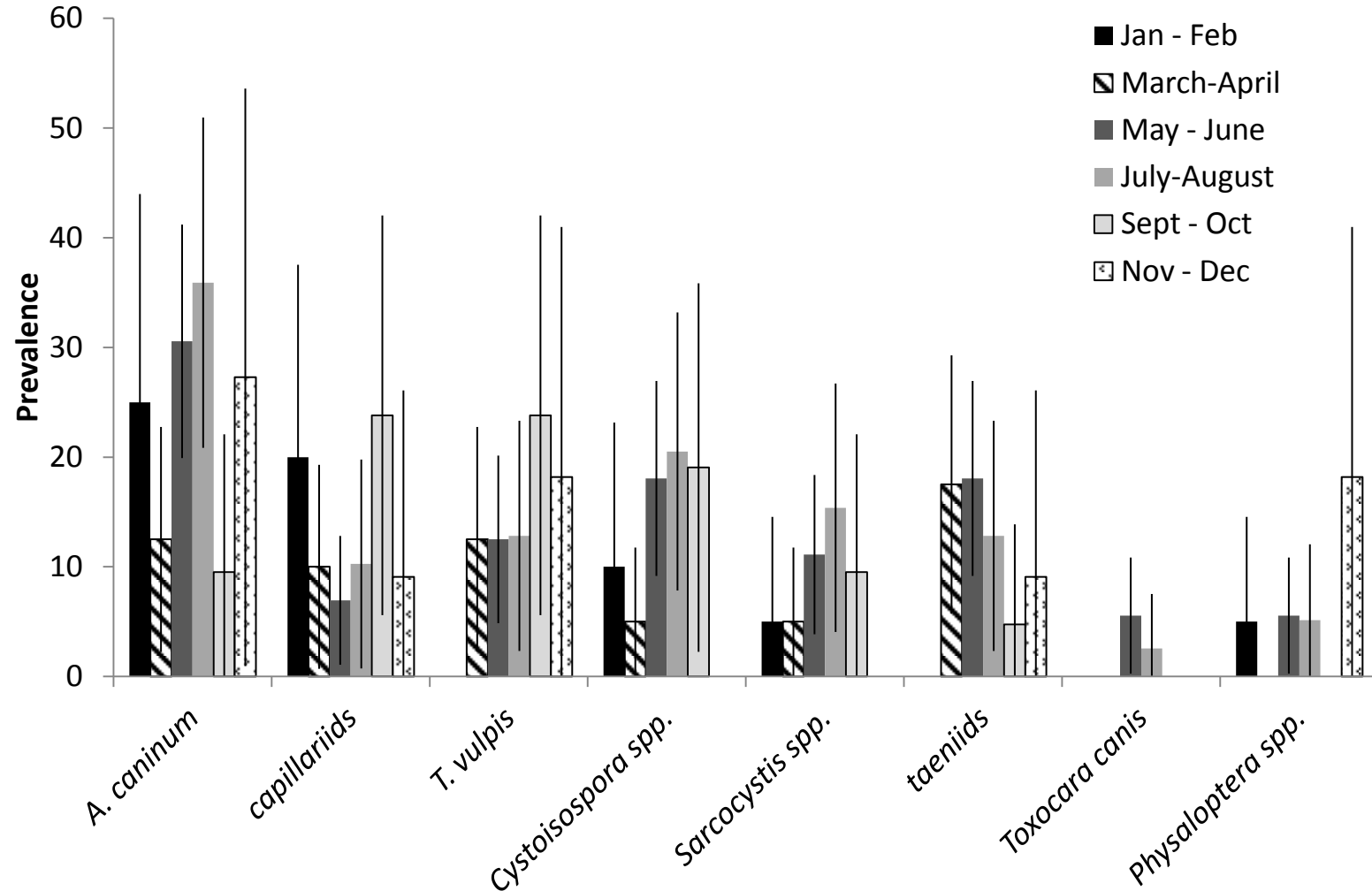


Figure 5: Bi-monthly prevalence and 95% confidence intervals of common fecal parasites of coyotes (n = 215) in Bath and Rockingham Counties, VA from June 2011 to May 2013 (years and counties combined)

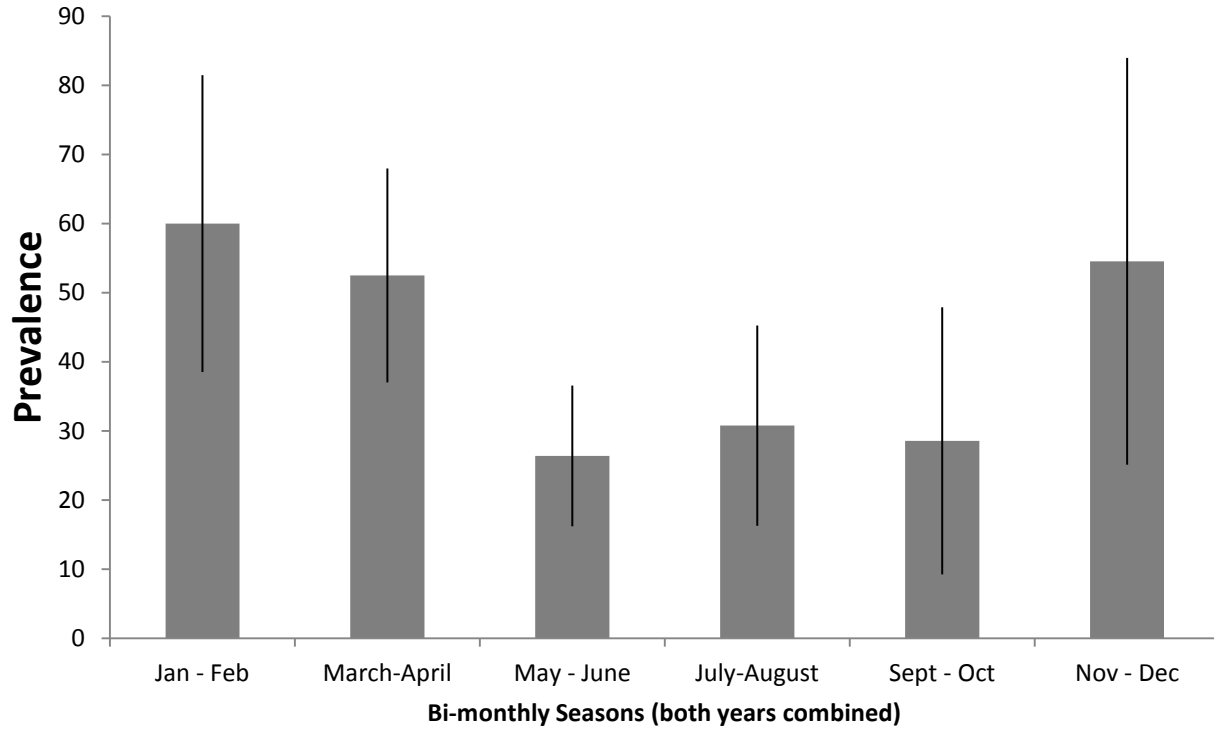


Figure 6: Seasonal proportion and 95% confidence intervals of coyote fecal samples (n = 215) from June 2011 to May 2013 in which no parasites were detected.

CHAPTER 5: CONCLUSION

I estimated food item availability and carnivore diet in Bath and Rockingham Counties, Virginia, for 24 consecutive months. In addition, I studied fecal parasites of coyotes during the same time period. These datasets provide baseline information on carnivore ecology in the Appalachian Mountains of Virginia, which can be used to guide future research.

My estimates of food item availability in Bath and Rockingham Counties indicate a food base that varies substantially both seasonally and annually. I also confirmed internal VDGIF reports that had suggested that deer densities in Bath County, while lower overall than other regions of Virginia, substantially are higher than those in Rockingham County. Based on my estimates of food availability, I would expect a generalist predator to have a diverse diet that is highly seasonal. Based on density estimates of live, adult deer in the 2 study areas, I would expect scats of generalist predators to have a higher % occurrence of deer in Bath County than scats of predators in Rockingham County, with deer consumed in relatively constant amounts throughout the year in both counties. However, there are several complications. First, my methods for estimating deer density provide data only on the availability of live deer, not on total deer biomass that exists. Because deer carcasses are easier to “predate” than live deer, estimates of % occurrence of deer in predator scats are subject to misinterpretations about where the deer remains in the diet are coming from, especially where predators shift to using seasonally available deer carcasses (e.g., carcasses or remains of field dressed deer during the hunting season, carcasses arising from a greater number of deer-vehicle collisions during the rut, or carcasses arising from late winter deer mortality) rather than consuming deer obtained from predation on live deer. Secondly, I did not collect data on deer fawn availability. Fawns represent a vulnerable seasonal prey item that predators will take advantage of. Given this

seasonally vulnerable resource available to predators, one might expect that the % occurrence of deer in predator scats overall would increase, reflecting this seasonal spike in availability of deer. However, because fawns are more available, predators may abandon efforts to prey on adults as they focus on finding fawns; as a result, one may not observe any spike in the % occurrence of deer biomass in scats due to this form of prey switching.

Given my findings on mid-sized mammals, generalist predators in this region should display seasonally-constant, but low, rates of utilization of opossum, as evidenced by presence in their scats, and a higher, but similarly constant, utilization of cottontail rabbits. Utilization of raccoons as a food resource by generalist predators should be higher in summer and fall and lower in winter. Finally, availability of squirrels to generalist predators peaks in October and November, but declines steadily thereafter until June.

If all habitat types are foraged equally, *Peromyscus* spp. and meadow voles should constitute the largest proportion, among small mammals, of the diet of generalist predators. Chipmunks and red-backed voles would provide a constant, but lower, component, except when predators expend greater effort foraging in burned habitats; here, chipmunks would be expected to comprise a larger component.

Among generalist predators, use of soft mast should be correlated with its availability during its fruiting season. If total biomass of fruit available corresponds with relative % cover of soft mast plants, *Vaccinium* spp. should comprise a dominant proportion of fruits consumed when its fruiting season overlaps with other soft mast producing species.

To reduce the suspected impacts of predation on species of special management interest, such as deer, managers should provide a high diversity of food alternatives. Based on my results, this

can be achieved in the mountains of western Virginia by using periodic prescribed fire or conducting timber harvests to increase the acreage of young forest types that provide habitat for cottontails, opossums, and small mammals that prefer these younger seral stages. This management strategy is neither desirable nor feasible in all areas of western Virginia; however, providing more acreage of young forest, where viable, would have the additional benefit of improving habitat quality for deer and allowing for more robust deer populations. Wildlife management designed to maximize food item diversity, such as prescribed fire or timber harvest to create uneven-aged forest matrices, may have little impact on coyote diet or the rate of coyote predation (or scavenging) on deer because my data indicate high % occurrence of deer in coyote scat despite availability of alternative foods. A possible management scenario to reduce potential impacts of coyote predation on deer populations would be to create large patches of fawning habitat and networks of escape cover to reduce vulnerability of deer to predators. However, continued monitoring would be needed to determine if such management practices were effective.

Although my data (based on scat analysis) suggests that coyotes, bobcats, and bears all have broad dietary niches in this region of Virginia, coyotes exhibit less dietary diversity and seasonal variation in prey utilization, contrary to expectations. In fact, coyotes selected deer and/or deer carcasses almost exclusively, even when other foods were more available on the landscape. Deer obviously represents a major food resource for all 3 predators, particularly during peak fawning season. Yet, among these 3 predators, deer comprised a higher % occurrence in coyote scats (21 of my 24 predictions based on availability), indicating that they, in fact, may be selecting for deer. My inability to identify accurately the source of deer being reflected in scats (i.e., from active predation or scavenging) seriously limits my ability to predict the true impact of predation

on deer populations. The fact that % biomass of deer consumed and % occurrence of deer in scats were higher in June for coyotes, bears, and bobcats suggests these predators may be profiting from the seasonal availability and vulnerability of fawns. Whether the number of fawns killed by predators is high enough to limit deer recruitment and lead to observed declines in deer populations in my study area is unclear. The discrepancy between low availability of deer contrasted against high % occurrence of deer in coyote and bobcat scats during late winter, especially in Rockingham County, suggests high selectivity for deer at a time when deer density is lowest. But, again, I am unable to determine whether this apparent high utilization simply results from scavenging on carcasses or predation on adult or sub-adult deer. Research focusing on mortality causes of both adult deer and fawns, in conjunction with my results, would help answer this question. My data do suggest that predation by coyotes, bobcats, and black bears collectively may exert a substantial influence on western Virginia deer populations, but additional future research is needed to define more precisely the effects of all 3 predators on white-tailed deer.

In contrast to coyotes, bobcats and bears behaved more like generalist or opportunist predators, exhibiting diets that changed seasonally and followed patterns of food availability. Given these dietary traits, management strategies that enhance habitat diversity, and thus food diversity, likely would expand food resources available to bobcats and black bears, thus potentially decreasing their seasonal use of deer and reducing mortality of deer induced by these predators. My baseline data of coyote fecal parasite prevalence in western Virginia raise many questions for future study. Larger sample sizes, perhaps from focused sampling during a shorter period of time, would improve the quality of seasonal estimates of parasite prevalence and better reveal seasonal differences in prevalence. My 2 study areas displayed similar patterns of land use and

resource availability; it is unclear whether my findings in these habitats accurately describe coyote populations in other areas characterized by more agriculture, livestock production, or urbanization, some of which may display differing rates of parasite prevalence. Molecular studies identifying parasites such as taeniids to the level of species are needed to determine whether coyotes play a significant role in the life histories or transmission dynamics of *Echinococcus* spp. or other potential zoonoses. Detailed studies of the seasonal and spatial prevalence of parasites in various prey species of coyotes in Virginia are needed to understand the sources of parasitic infections in coyotes and their prevalence in the landscape. Forthcoming research on the demographics of these coyote populations may supplement my findings and reveal new insights into the prevalence and dynamics of disease transmission in wildlife of western Virginia.

The high rate of scat mis-identification in the field that I observed emphasizes the importance of using mtDNA to confirm the species of origin of samples used in diet analyses. The results of studies that do not identify scats using mtDNA should be treated with great skepticism. The fact that this technique is relatively new and still uncommon among carnivore diet studies suggests the classic diets of carnivores such as coyotes, bobcats, and foxes may be based on biased or inaccurate samples. The issue of chronic mis-identification of scats calls into question the accuracy of basic elements of the life histories of these species. It is necessary to re-examine the diets of carnivores using samples whose origins are confirmed by genetic analyses. Extensive research is needed to correct potential inaccuracies in baseline carnivore diet data.

By comparing data on spatio-temporal patterns of food item availability to the occurrence of food items in the scats of predators, opportunities for targeted management may be identified that to balance predator-prey dynamics with human needs and values. Although my work

establishes a baseline for the western mountain region of Virginia, additional research is necessary to link coyote, bobcat, and black bear foraging behavior to population-level impacts on deer and other prey populations in western Virginia.