Spatial ecology and demography of eastern coyotes (*Canis latrans*) in western Virginia

Dana Janine Morin

Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State
University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
In
Fisheries and Wildlife

Marcella J. Kelly
Lisette P. Waits
Sarah M. Karpanty
James A. Parkhurst
James D. Nichols
Dave E. Steffen

June 19, 2015
Blacksburg, VA

Keywords: *Canis latrans*; class structure; compensatory immigration; coyote; demography; density dependence; habitat selection; mortality; noninvasive genetics; optimal foraging theory; spatial capture-recapture; territoriality; transients

Spatial ecology and demography of eastern coyotes (*Canis latrans*) in western Virginia

Dana Janine Morin

ABSTRACT

Coyote (*Canis latrans*) range expansion in the Central Appalachian Mountains has stimulated interest in ecology of this predator and potential impacts to prey populations. This is particularly true in the Ridge and Valley Region in western Virginia where white-tailed deer (*Odocoileus virginianus*) populations are restricted by low nutritional carrying capacity and are subject to two other predators, bobcats (*Lynx rufus*) and American black bears (*Ursus americanus*), in addition to an active hunter community. I address two primary objectives of the Virginia Appalachian Coyote Study: to investigate 1) spatial ecology and 2) population dynamics of coyote populations in Bath and Rockingham counties. I deployed 21 GPS satellite collars on 19 coyotes over 32 months. I estimated home range size (mean = 13.46 km^2, range = 1.23 km^2 - 38.24 km^2) across months using biased-random bridges and second-order habitat selection at four scales using eigenanalysis of selection ratios. I developed a metric to classify social status of individuals as either resident or transient based on stability of home range centers over time. I found evidence for class substructure for selection of territories where adult residents had a higher probability of mortality in high productivity/high risk habitats, compared to subadults and transients that were restricted to less productive habitats. I collected scat samples over five scat surveys across 2.5 years and extracted fecal DNA to identify individual coyotes in a mark-recapture framework. I estimated coyote densities in Bath (5.53 – 9.04 coyotes/100 km^2) and Rockingham Counties (2.41 – 8.53

coyotes/100 km^2) using a spatial capture-recapture model. Six-month apparent survival was lower in Bath County (ϕ_{Bath} = 0.442, 0.259 – 0.643; $\phi_{\text{Rockingham}}$ = 0.863, 0.269 – 0.991). The Bath County population demonstrated persistence despite high mortality and the Rockingham population demonstrated boundedness with recruitment inverse of changes in density. Findings at both sites suggest density-dependence, and tests of territoriality, presence of transients, and territory turnover demonstrate a capacity for immediate local immigration in response to high mortality in Bath County. I suggest that landscape-level habitat management may be a viable strategy to reduce potential conflicts with coyotes in the region.

ACKNOWLEDGEMENTS

Financial support provided by the Virginia Department of Game & Inland Fisheries came from the U.S. Fish & Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. This project was extensive and would not have been possible without the additional financial and logistical support of our collaborators, the US Forest Service, USDA Wildlife Services, and The Nature Conservancy, as well as several additional sources including the Appalachian members of the Virginia Deer Hunters Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).

Thank you to all of the students and technicians that worked on this project: Robert Alonso, David Montague, Sarah Webster, Josh Kinkead, Stephen Perkins, Jake Estienne, Sean Hovendon, Roxzanna Montague, James Hody, Summer Higdon, and Casey Maynard (Casey, I am so proud of you!). In addition, an uncountable number of graduate and undergraduate students volunteered and contributed to the success of this project, collecting scat. Thank you!

I am grateful to my committee, Marcella Kelly, Lisette Waits, Sarah Karpanty, Jim Parkhurst, Dave Steffen, and Jim Nichols, for their support, assistance, and encouragement.

I am deeply indebted to my cohort, colleagues, and mentors at Virginia Tech, collaboration agencies and groups, University of Idaho, and across the Southeast for thoughtful conversations and assistance with the project:

Robert Alonso, Mike Cherry, Marcus Lashley, Colter Chitwood, Joey Hinton, Will Gulsby, Jim Nichols, Andy Royle, Mike Conner, Mike Fies, Dave Steffen, Nelson Lafon, Matt Knox, Al Bourgeois, Dave Kocka, Megan Kirchgessner, Carol Croy, Steve Tanguay, Terry Slater, Lauren Mastro, Marek Smith, Nicole Swaney, Colleen Olfenbuttel, Ed Bangs, Eric Hallerman, Claudia Wultsch, Keri Parker, Sunarto, Greg Anderson, Alex Silvis, Cathy Jachowski, Chris Latimer, Anne Hilborn, Lindsey Rich, Erin Poor, Asia Murphy, Zach Farris, Chris Rowe, Chris Satter, Ben Augustine, Kanchan Thapa, Mamadou Kane, Dan Schilling, Matt Johnson, Amanda Hyman, Tyler Fox, Meghan Sheppard, Mike St Germain, Bernardo Mesa, Christine Proctor, Tom McNamara, Jen Adams, Caren Goldberg, Rob Lonsinger, Carisa Stansbury, Susannah Woodruff, Kate Cleary, Matt Mumma, Steve Spear, and David Roon.

Finally, much of the success of this project is due to the enthusiasm and encouragement of the residents of the Bath County study area. While I could not possibly acknowledge all, I am indebted to Jason Woods for public relations and carcass/collar retrieval; Jaime and (Chef) Ed McArdle for logistical support, especially after the county laundromat was closed; Maggie and Wayne Anderson for the unwavering support of the Appalachian Members of the Virginia Deer Hunters Association; John and Kate Loeffler at the Inn at Gristmill Square, Peter and Tricia at the Warm Springs Inn, and Sarah and Bruce McWilliams at the Bridge for morale; Marion Kober for companion animal support; Glen

Criser, Franklin Johnson, and the Men’s Group at the Ashwood United Methodist Church; Burns Garage for performing miracles with trucks, The Homestead Preserve, Dominion Power, Bill and Lee Elliot, John Pound, Nancy and Scott Miller, Michael Blakely, Jim Taylor, Kevin Frye, Cliff Gilchrist, Matt and Linda Caughley, Dot and Ron Pozun, Craig Robertson, and many more.

…and again, Robert Alonso, thanks for teaching me the ropes and being a fantastic trapping partner, a curious and thoughtful ecologist, and a dependable and considerate friend. I hope I can return the favor when it is your turn.

Attribution

Below is a brief description of the contributions made by colleagues that assisted with the preparation of manuscripts for the following chapters. Contributions rose to the level of co-author for manuscript publication for four chapters.

Chapter 2. The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment

Robert Alonso provided assistance with safe capture and handling of coyotes. Carol Croy, Lindsay Curtain, and Russ McFarlane (US Forest Service) provided assistance with GIS data. The Virginia Department of Game and Inland Fisheries, the US Forest Service, The Nature Conservancy provided financial and logistic assistance. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided logistic assistance and edits to the manuscript. Jim Nichols (US Geological Survey) and Dave Steffen (VDGIF) provided statistical consultation and assistance and edits to the manuscript.

Chapter 3. Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest, Virginia

Lisette Waits (University of Idaho) provided training, materials, and logistic assistance and provided edits to the manuscript. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial and logistic assistance, and edits to the manuscript. Jim Nichols and Andy Royle (US Geological Survey) provided study design, and statistical consultation.

Chapter 4. The Spatial Component of Density Dependence: Evidence for Coyote Population Regulation through Competition for Territories and Compensatory Immigration

The Virginia Department of Game and Inland Fisheries, the US Forest Service, The Nature Conservancy provided financial and logistic assistance. Lisette Waits (University of Idaho) provided training, materials, and logistic assistance and provided edits to the manuscript. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided financial and logistic assistance and edits to the manuscript. Jim Nichols and (US Geological Survey) and Mike Conner (Joseph W. Jones Ecological Center) and Dave Steffen (VDGIF) provided study design, and statistical consultation.

Chapter 5. Can landscape level habitat management reduce human-coyote conflict?

Robert Alonso provided assistance with safe capture and handling of coyotes. Carol Croy, Lindsay Curtain, and Russ McFarlane (US Forest Service) provided assistance with GIS data. The Virginia Department of Game and Inland Fisheries, the US Forest Service, The Nature Conservancy provided financial and logistic assistance. Marcella Kelly (Department of Fish & Wildlife Conservation, Virginia Tech) provided logistic assistance and edits to the manuscript. Jim Nichols (US Geological Survey) and Dave Steffen (VDGIF) provided statistical consultation and assistance and edits to the manuscript.

TABLE OF CONTENTS

List of Figures

CHAPTER 2.
The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment

CHAPTER 3
Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest, Virginia

CHAPTER 4
The Spatial Component of Density Dependence: Evidence for Coyote Population Regulation through Competition for Territories and Compensatory Immigration

CHAPTER 5.
Can landscape level habitat management reduce human-coyote conflict?

List of Tables

CHAPTER 2.
The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment

CHAPTER 3
Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest, Virginia

CHAPTER 4
The Spatial Component of Density Dependence: Evidence for Coyote Population Regulation through Competition for Territories and Compensatory Immigration

CHAPTER 5.
Can landscape level habitat management reduce human-coyote conflict?

List of Appendices

CHAPTER 2.
The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment

CHAPTER 3
Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest, Virginia

CHAPTER 5.
Can landscape level habitat management reduce human-coyote conflict?

CHAPTER 1.

Introduction

The North American canid species complex is relatively young (~3 million years) and characterized by repeated contrasting expansions and contractions in response to changing climate and associated habitat and prey base conditions (Wang et al. 2004, Hinton et al. in press). When cooler climates allowed dense and diverse megaherbivore populations to develop and prosper, selection in canid species favored larger body size, hypercarnivory, and more complex social structure, leading to an expansion of large-bodied wolf populations. However, these selected traits increased extinction vulnerability to stochastic events (Van Valkenburgh 1991, Creel 1998) and, when the climate became warmer and megaherbivore populations declined, smaller, more adaptable, generalist canids were favored and their populations expanded.

The most recent coyote range expansion has been rapid, hastened by human-caused alterations of the landscape (e.g. through converting dense forests to agriculture) and through effective removal of aggressive competitors such as wolves. Over the last two centuries coyotes have expanded their range from an area restricted to the central plains of the United States prior to European settlement to one that now encompasses all 49 continental states of the United States, and most of Canada and Central America (Bekoff 1978, Parker 1995, Gompper 2002a, Dennis 2010, Kays et al. 2010). As a result, human-coyote conflicts have increased (Gompper 2002a) and multiple studies have examined the potential impacts to prey and competitors (Etheredge and Yarrow 2013, Cherry 2014, Hinton 2014, Kilgo et al. 2014, Chitwood et al. 2015, Gulsby et al. 2015) and the possible role of coyotes in filling the extirpated wolf niche in eastern North America (Benson and Patterson 2013).

As coyote populations have expanded into each new state, the natural resource agencies and state legislature have attempted to limit expansion or manage populations or conflict, typically by attempting to reduce coyote populations through removals, with little to no success. Thus, there is a need for a better understanding of coyote population dynamics and space use to allow managers to make informed decisions concerning potential human-coyote conflict.

Coyotes exhibit phenotypic and behavioral plasticity (Bekoff 19771978; Boer 1992, Parker 1995, Gehrt 2007). Therefore, spatial ecology and population demography must be assessed at local or regional spatial scales in order to understand potential conflicts, population responses, and ecological roles. The most recent coyote range expansion occurred in three directions from the central plains, first expanding to the west, then to the northeast, and finally to the southeast, with both eastern expansions converging in the mid-Atlantic/Central Appalachian Mountains region (Parker 1995, Loweny et al. 1997, Houben 2004, Bozarth et al. 2015).

The Ridge and Valley region of the Central Appalachian Mountains was one of the last areas to be colonized, with coyote populations becoming established in the 1980s (Parker 1995). This area consists of predominantly mature deciduous hardwood forests within the George Washington National Forest along mountainsides and ridgetops and a mixture of forested and agrarian private inholdings along valley bottoms, and low human densities. The contiguous, even-aged mature hardwood forests, with small, scattered wildlife clearings provide low nutritional carrying capacity for many game species (DeCalesta 1997, Diefenbach et al. 1997). Not surprisingly, as the forests in the area have continued to age, game species populations appear to have declined. This spurred interest in the potential role of the coyote as an additional predator in the region. Typically predation mortality is compensatory and not a strong regulatory mechanism for prey populations (Robinson et al. 2014). However, when nutritional carrying capacity is low, predation mortality can be additive (Kilgo et al. 2014, Chitwood et al. 2015). The western mountains of Virginia already support two healthy populations of predators, bobcats (*Lynx rufus*) and American black bear (*Ursus americanus*), in addition to an active hunter population and outdoor recreation industry. Thus, concerns about shared harvest of declining white-tailed deer (*Odocoileus virginianus*) herds resulted in the initiation of this study of coyote ecology in Bath and Rockingham Counties, Virginia, to provide a better understanding of the local coyote populations for state wildlife managers.

The Virginia Appalachian Coyote Study (VACS) was contracted by the Virginia Department of Game and Inland Fisheries in December 2010 to better understand coyote ecology in the Ridge and Valley Region of Virginia, including space use, population dynamics, and feeding ecology. This dissertation addresses two of three components of VACS: 1) the spatial ecology and 2) population structure and dynamics of the local coyote populations in Bath and Rockingham counties. In Chapter 2, “The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment”, I first consider space use and second-order habitat selection (Johnson 1980, Manly et al. 2002) of coyotes in the Bath County study area using relocation data from 19 coyotes collared over three years. Coyotes are often described as habitat generalists because they can occupy most habitats (Bekoff 1978). However, coyotes prefer some habitats over others based on observed differences in densities in across regions and in the general pattern of range expansion; dense forests appear to act as a barrier to dispersal (Parker 1995, Gompper 2002b, Dennis 2010) representing the last areas to be colonized (Bozarth et al. 2015). In previous studies, coyotes have generally selected for more open habitat types compared to forests (Tremblay et al. 1998, Crete et al. 2001, Kays et al. 2008, Schrecengost et al. 2009), and mature hardwood forests are typically considered to support low densities of coyotes (Samson and Crete 1997, Richer et al. 2002, Kays et al. 2008). Thus, I expected coyote home ranges in the Bath County study area would be relatively large as coyotes would need to travel and defend large areas to obtain necessary resources (Wilson and Shivik 2011). Although most studies relate coyote habitat selection to food availability (Perkins and Mautz 1990, Richer et al. 2002, Randa and Yunger 2004, Thibault and Oullet 2005, Kays et al. 2008), coyote populations may be heavily “exploited” through unrestricted harvest (Knowlton et al. 1999), experience interspecific interference competition (Palomares and Caro 1999), and are also territorial social carnivores that compete for, and defend, territories (Knowlton et al. 1999, Kamler and Gipson 2000, Gese 2001). Thus, coyote decisions about habitat selection should also consider risk of mortality (Caraco 1980, Brown 1988, Abrahams and Dill 1989) and population class structure (Kamler and Gipson 2000, Patterson and Messier 2001, Hinton et al. in press).

I found very high coyote mortality in Bath County, with 63% of collared coyotes confirmed killed during the 32 months collars were deployed. This high level of mortality, combined with the distribution of small patches of productive habitats concentrated in valley bottoms where increased opportunities for human interactions occur, created a unique opportunity to test hypotheses about optimal foraging theory (MacAurthur and Pianka 1966, Emlen 1968, Charnov 1976, Pyke et al. 1977). To examine coyote optimal foraging strategy within a risk versus reward framework, I used second-order habitat selection and examined how social class structure within coyote populations related to risk of mortality. By considering how different coyotes select for habitat to incorporate in their territories and home range areas based on class structure, I aimed to identify possible population level impacts and potential strategies relevant to management of human-coyote conflict.

Estimating coyote density and population dynamics in the Bath and Rockingham County study areas were primary objectives of VACS. In Chapter 3, "Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest", I used recent advances in noninvasive genetics and spatial capture-recapture (SCR) models to estimate coyote density at both study sites over five scat collection surveys (July 2011, February 2012, July 2013, March 2013, and July 2013). Coyote populations in other regions are often density dependent and demonstrate a negative feedback compensatory mechanism (Knowlton et al. 1999, Hixon et al. 2002) in response to changes in population density. Assessing density-dependence in local populations is critical, as it would dictate the expected effectiveness of current attempts to reduce coyote density through unrestricted harvest and provide baseline population information for future management decisions. Thus, I used a Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) combined with the SCR density estimates in an ad hoc robust design approach (Pollock et al. 1990, Williams et al. 2002) to estimate apparent survival, net and per capita recruitment, population growth, and test for evidence of density-dependent regulation.

In Chapter 4, "The Spatial Component of Density Dependence: Evidence for Coyote Population Regulation through Competition for Territories", I used both the relocation data and fecal DNA genotype detections from the Bath County scat surveys to address questions raised by the findings in chapters 2 and 3. I developed hypotheses to identify the capacity of the Bath County coyote population to immediately replace individuals killed through local immigration, and tested for evidence of territoriality, a transient population in biding areas, and territory turnover among residents.

In Chapter 5, “Can Landscape-level Habitat Management Reduce Human-Coyote Conflict?”, I review the results of the previous three chapters and highlight local findings in the greater context of limitations to the effectiveness of predator control. I then expand on the findings of class structure in second-order habitat selection in Bath County in Chapter 2 to assess differences in third-order habitat selection, or within home range selection, along the risk and reward gradient. I conclude with an evaluation of landscape-level habitat management as an additional or alternative strategy to reduce potential conflicts with coyotes in the region.

Literature Cited

Abrahams, M. V., L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70(4): 999-1007.

Bekoff, M. 1977. Canis latrans. Mammalian species 1-9.

Bekoff, M. (Ed.). 1978. Coyotes: biology, behavior, and management. Academic Press, New York.

Benson, J. F., and B.R. Patterson. 2013. Inter-specific territoriality in a Canis hybrid zone: spatial segregation between wolves, coyotes, and hybrids. Oecologia 173(4): 1539-1550.

Boer, A.H. 1992. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick

Bozarth, C. A., B. Gardner, L. L. Rockwood, and J. E. Maldonado. 2015. Using Fecal DNA and Spatial Capture-Recapture to Characterize a Recent Coyote Colonization. Northeastern Naturalist 22(1): 144-162.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22(1): 37-47.

Caraco, T., S. Martindale, and T. S. Whittam. 1980. An empirical demonstration of risk-sensitive foraging preferences. Animal Behaviour 28(3): 820-830.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9(2): 129-136.

Cherry, M. J. 2014. Coyotes, deer and the ecology of fear in a longleaf pine savanna. PhD dissertation. University of Georgia, Athens.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2015. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer?. PloS one 10(3): e0119070.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika: 429-438.

Creel, S. 1998. Social organization and effective population size in carnivores. Behavioral Ecology and Conservation Biology: 246-265.

Crete, M., J.P. Ouellet, J.P. Tremblay, and R. Arsenault. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. Ecoscience: 311-319.

DeCalesta, D. S. 1997. Deer and ecosystem management. Pages 267-279 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institute Press, Washington, D.C.

Dennis, D. L. 2010. Genetic analysis of dispersal and population dynamics of the southeastern Coyote (*Canis latrans*). PhD Dissertation, Auburn University, Auburn, Alabama.

Diefenbach, D. R., W. L. Palmer, and W. K. Shope. 1997. Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. Wildlife Society Bulletin: 244-251.

Emlen, J. M. 1968. Optimal choice in animals. American Naturalist: 385-389.

Etheredge, C., and G. K. Yarrow. 2013. Lack of support for coyote control of raccoon populations predicted by the mesopredator release hypothesis. Proceedings of the 15th Wildlife Damage Management Conference.

Gehrt, S. D. 2007. Ecology of coyotes in urban landscapes. Pages 303-311 *in* D.L. Nolte, W.M. Arjo, D.H. Stalman, editors. Proceedings of the 12th Wildlife Damage Management Conference. University of Nebraska Digital Commons, Lincoln, Nebraska.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Canadian Journal of Zoology 79(6): 980-987.

Gompper, M. E. 2002a. The ecology of northeast coyotes. Wildlife Conservation Society 17: 1-47.

Gompper, M. E. 2002b. Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of North-eastern North America by Coyotes The expansion of the coyote's geographical range may broadly influence community structure, and rising coyote densities in the suburbs may alter how the general public views wildlife. Bioscience 52(2): 185-190.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39(2): 248-255.

Hinton, J. W. 2014. Red wolf (*Canis rufus*) and coyote (*Canis latrans*) ecology and interactions in northeastern North Carolina. PhD Dissertation. University of Georgia, Athens, Georgia.

Hinton, J.W., F.T. van Manen, and M.J. Chamberlain. *In Press*. Space use and habitat selection by resident and transient coyotes. PlosOne.

Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83(6): 1490-1508.

Houben, J.M. 2004. Status and management of coyote depredations in the eastern United States. Sheep and Goat Research Journal 19:16-22.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1): 65-71.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika: 225-247.

Kamler, J. F., and P. S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78(12): 2106-2111.

Kays, R. W., M. E. Gompper, and J. C. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications 18(4): 1014-1027.

Kays, R., A. Curtis, and J. J. Kirchman. 2010. Rapid adaptive evolution of northeastern coyotes via hybridization with wolves. Biology Letters 6(1): 89-93.

Kilgo, J. C., M. Vukovich, H. Scott Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. The Journal of Wildlife Management 78(7): 1261-1271.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52(5): 398-412.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62(1): 67-118.

Lowney, M., J. Houben, and P. Eggborn. 1997. Development of the Virginia Cooperative Control Program to protect livestock. Proceedings of the Eastern Wildlife Damage Management Conference 8:41-49.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100: 603-609.

Manly, B.F., L.L. McDonald, D. L. Thomas, T. L. McDonald, W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. 2nd edition. Kluwer Academic, Boston, Massachusetts.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153(5): 492-508.

Patterson, B.R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463-477.

Parker, G.E. 1995. Eastern coyote: the story of its success. Nimbus, Halifax, Nova Scotia, Canada.

Perkins, P. J., and W. W. Mautz. 1990. Energy requirements of eastern coyotes. Canadian Journal of Zoology 68(4): 656-659.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 3-97.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology: 137-154.

Randa, L. A., and J. A. Yunger. 2004. The influence of prey availability and vegetation characteristics on scent station visitation rates of coyotes, *Canis latrans*, in a heterogeneous environment. Canadian Field-Naturalist 118(3): 341-353.

Richer, M.C., M. Crête, J.P. Ouellet, L.P. Pirest, and J. Huot. 2002. The low performance of forest versus rural coyotes in northeastern North America: inequality between presence and availability of prey. Ecoscience 9(1): 44-54.

Robinson, K. F., D. R. Diefenbach, A. K. Fuller, J. E. Hurst, and C. S. Rosenberry. 2014. Can managers compensate for coyote predation of white-tailed deer?. The Journal of Wildlife Management 78(4): 571-579.

Samson, C., and M. Crete. 1997. Summer food habits and population density of coyotes, *Canis latrans* in boreal forests of southeastern Quebec. Canadian Field Naturalist 111(2): 227-233.

Schrecengost, J. D., J. C. Kilgo, H. S. Ray, and K. V. Miller. 2009. Home range, habitat use and survival of coyotes in western South Carolina. The American Midland Naturalist 162(2): 346-355.

Seber, G. A. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.

Thibault, I., and J. P. Ouellet. 2005. Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. Ecoscience 12(4): 466-475.

Tremblay, J. P., M. Crete, and J. Huot. 1998. Summer foraging behaviour of eastern coyotes in rural versus forest landscape: a possible mechanism of source-sink dynamics. Ecoscience 5(2): 172-182.

Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology17(4): 340-362.

Wang, X., R. H. Tedford, B. Van Valkenburgh, and R. K. Wayne. 2004. Evolutionary history, molecular systematics, and evolutionary ecology of Canidae. Pages 39-54 *in* D. W. Macdonald and C. Sillero-Zubiri, editors. Biology and Conservation of Wild Canids. Oxford University Press, Oxford, United Kingdom.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.

Wilson, R. R., and J. A. Shivik. 2011. Contender pressure versus resource dispersion as predictors of territory size of coyotes (*Canis latrans*). Canadian Journal of Zoology 89(10): 960-967.

CHAPTER 2.

The Role of Coyote Population Class Substructure and Probability of Survival in Determining Second-order Habitat Selection in a Low-resource Environment

Target Journal: Ecological Applications

ABSTRACT

The success of coyote range expansion often is attributed to generalist behaviors and resource selection explained by prey densities. However, coyotes are social canids and populations display complex interactions in competition for and defense of territories. In addition to intraspecific competition, coyotes must also consider threats from larger competitors and they are commonly persecuted by humans. Thus, while coyotes at the population level may appear to be habitat generalists, resource selection likely involves class substructure and resource-associated risk. We deployed 21 satellite GPS collars on 19 coyotes in the western mountains of Virginia in a highly exploited population over 2.5 years and used biased-random bridges to estimate home range size and resource selection of coyotes using telemetry relocation data. We classified status of individuals as either resident or transient by stability of home range centers over time and considered home range use over monthly intervals as representative of changing resources and risk in the region. We used eigenanalysis for second-order resource selection ratios to assess differences in partitioning habitats among individuals of the population at multiple levels of space use (overall home range/territory, core home range, intensively used areas, and frequently visited areas). We used linear mixed models to account for individual variation in home range size and habitat selection compared to differences over months and due to class membership including sex, age, and status. Known-fate survival models with habitat selection as explanatory variables showed support for increased mortality among individuals that established territories with predicted high risk/high productivity habitats (primarily adult residents). Linear mixed models with habitat selection as response variables indicate transients and subadults select for or are restricted to low/productivity/low risk habitats. Our results indicate habitat selection strategies are dictated by optimal foraging theory and changing life histories, given the disparity between low risk/low productivity mature forest stands compared to high risk/high productivity habitats associated with moderate human density in our study area. We suggest coyote space use, from a risk-reward perspective, can provide insightful remediation options for potential effects on prey populations and competitors, and human-coyote conflicts.

Key words: biased-random bridge; *Canis latrans*; class structure; coyote; dynamic space use; eigenanalysis of selection ratios; habitat generalist; habitat selection; optimal foraging theory; resident; risk; space use; survival; transient

INTRODUCTION

Coyotes (*Canis latrans*) are considered behaviorally adaptable habitat generalists (Litvaitis and Harrison 1989, Chamberlain et al. 2000) and can be found in almost all habitats across their range (Bekoff 1978, Parker 1995). Most studies on eastern coyotes relate habitat use to food and prey availability (Perkins and Mautz 1990, Richer et al. 2002, Randa and Yunger 2004, Thibault and Oullet 2005, Kays et al. 2008). However, resource productivity is not the only basis on which most animals make selection decisions (Caraco et al. 1980, Brown 1988, Abrahams and Dill 1989). Resource selection, even for predators, is also determined by costs and real or perceived risks (Brown et al. 1999, Brown and Kotler 2004, Mukherjee and Heithaus 2013). As omnivorous, opportunistic predators, coyotes likely make decisions about resource selection by balancing risk and reward with overall resource availability. Further complicating space use dynamics, coyotes are territorial social canids (Knowlton et al. 1999, Gese 2001) and are often classified by social status: residents defending an established territory, or transients overlapping with, or interspersed among, several other territories (Gese et al. 1988, Kamler and Gipson 2000, Hinton et al. 2012). The transient phase, typical of animals pre- and post-dispersal, is thought to be a critical component of coyote population dynamics across space, as individuals search for available territories, a central limiting resource for coyotes (Messier and Barrette 1982, Harrison 1992, Windberg and Knowlton 1988, Knowlton et al. 1999, Hinton 2014). High value resource patches are often fought over in territorial boundary disputes (Crete et al. 2001, Patterson and Messier 2001, Wilson and Shivik 2011). Thus, while coyotes may be habitat generalists at the population level, distinct differences exist in how individual coyotes select resources based on intraspecific competition and degree of resource-associated risk.

Optimal foraging theory is based on the assumption that an animal's foraging strategy is a result of behaviors that maximize individual fitness (Emlen 1968, MacAurthur and Pianka 1966, Pyke et al. 1977). For wide-ranging generalists like coyotes, this can be reflected by space use over time and selection among habitat patches of varying quality (Charnov 1976). Traditionally in optimal foraging theory models, fitness has been measured by surrogates such as energetic costs and benefits of different foraging behaviors (Abraham and Dill 1989, Perry and Pianka 1997). However, in our study area the high rate of human-related coyote mortality coupled with substantial differences in productivity among available habitat types sets up a natural experiment to compare individual coyote habitat selection of risky, high productivity habitats compared to safer, low productivity habitats.

Bath County, Virginia is located in the Ridge and Valley region of the central Appalachian Mountain range and consists predominantly of late-successional National Forest habitat interspersed with private lands (Figure 1). Outdoor recreation, particularly hunting, has significant economic and cultural value within the region. However, forest structure and composition have changed over the decades with concurrent declines in game and non-game populations. Typically mature forests are also low quality habitat for coyotes (Tremblay et al. 1998, Crete et al. 2001, Kelly and Holub 2008). Thus, we expected coyote densities to be low and home range sizes to be relatively large in our study area (Wilson and Shivik 2011), with preferential selection for pockets of high productivity including agricultural lands, edges of developed areas, grassland openings, and early successional forests (Fedriani et al. 2000, Kays et al. 2008, Schrecengost et al. 2009, Ordenana et al. 2010, and Newsome et al. 2015). However, we predicted many of these habitats would also be associated with higher mortality risk, as selection for these habitats would directly or indirectly place coyotes in conflict with humans.

Generally home range studies evaluate space requirements and habitat selection at broad temporal scales, averaging over different time periods to provide an overall picture of what a coyote home range looks like. However, coyotes are highly vagile and responsive to their environment. They exhibit a variety of seasonal activities that can affect home range use and habitat selection, including reduced home range size and concentrated resource selection during denning and pup rearing (Parker and Maxwell 1989, Harrison et al. 1991) compared to expansive home range movements in the winter when exploring dispersal opportunities, aggressively defending territory boundaries, and/or searching for potential mates (Parker and Maxwell 1989, Patterson and Messier 2001, Gosselink et al. 2003). In addition, the environment in the western Virginia mountains is continually changing, both with meteorological seasons and associated resource pulses. Finally, home range movements are also a function of memory (Spencer 2012) and are shaped by past experiences of individuals. Therefore, coyote space use is dynamic and should be evaluated over time (Fieburg and Börger 2012).

Biased-random bridge (BRB) is a movement-based kernel density estimator (MKDE, Benhamou 2011). BRBs explicitly incorporate an animal's movement using serial autocorrelation between successive relocations to estimate trajectory by considering the relocations recorded one time step prior, and one time step after, the focal relocation (Benhamou 2011). Active utilization distributions (UD), or the probability of an animal using an area, can be divided into two components: 1) the mean residence time per visit to a resource or an area estimated by the intensity distribution (ID), and 2) the frequency of visits to a resource or area estimated by the recursion distribution (RD). Both the ID and RD can be estimated from the active UD because the animal's trajectory is accounted for in the BRB (Benhamou and Riotte-Lambert 2012). Thus, by considering the dynamic movement of an animal, we are better able to make inferences about the way individuals use their home ranges and different resources therein (Monsarrat et al. 2013).

Eigenanalysis of selection ratios has been proposed as an optimal method to assess habitat selection when there is variability in habitat use by individuals or class and when there is a variety of available habitats (Calenge and Dufour 2006). Improving on selection ratios, which quantify use compared to availability and estimate selection for or avoidance of each habitat singularly, eigenanalysis considers all available and used habitats simultaneously for multivariate inference along factorial axes representing maximized similarities and differences in selection or avoidance of habitats among individuals and groups. This method exploits the commonly violated assumption of selection ratios that all individuals select for habitat similarly (Manly et al. 2002) to allow for a more realistic and coherent depiction of space use among individuals in a population.

We used relocation data from 19 coyotes collared in the study area over 33 months to estimate coyote space use and habitat selection using BRBs over multiple time intervals. We classified available habitats into 10 general types that can broadly be considered to vary in both productivity and risk, to allow for inference considering optimal foraging theory. Our objective for this analysis was to identify differences in how coyotes partitioned available habitat amongst themselves in establishment of territories and in defense of limited resource patches, and how this affects risk of mortality. Thus, we chose to evaluate second-order eigenanalysis of resource selection (Johnson, 1980, Manly et al. 2002) at different levels of space use (95% UD, 50% UD, 50% ID, and 50% RD), and used the resulting habitat selection scores to test hypotheses about differences in space use as a result of class substructure and risk of mortality.

We predicted home range size and habitat selection would differ by class structure and season. We expected to find differences in how individuals and groups select for habitat based on associated productivity and risk. In particular, we hypothesized females, subadults, and transients would be more risk averse due to life history strategies that would favor prioritizing future reproductive opportunities over current risks (Post 1975, Abraham and Dill 1989, Holzman et al. 1992). In addition, we expected residents would be more likely to include productive habitats within territories (Hinton et al. 2012), and that overall territories would remain relatively constant but we would observe seasonal differences in core home range use (Knowlton et al. 1999). Finally, we expected the best known-fate model would predict higher mortality rates for individuals selecting for habitats we hypothesized to be high risk.

MATERIALS AND METHODS

Study Area

The study area was located primarily in western Bath County, in the Ridge and Valley region of Virginia (Figure 1). This area was approximately 43% private land., Including low-density residential areas and small townships (~4,300 residents countywide; U.S. Census Bureau 2010), and small-scale livestock operations and hay farms, private land was found mostly along valley bottoms, rivers, and roadways. These private inholdings were interspersed within small state wildlife management areas and large federal tracts comprising the George Washington National Forest. Public land primarily consisted of mountain sides and ridgetops of contiguous, even-aged mature hardwood forests, with small wildlife clearings. Overall, the public areas were considered to be low-productivity mature forests and provide low nutritional carrying capacity for many game species (DeCalesta 1997, Diefenbach et al. 1997).

Field Methods

Approved for safe capture and permitted by the Virginia Department of Game and Inland Fisheries (permit #041503), we trapped coyotes using Victor #3 Softcatch padded foothold traps (Lititz, PA) with Paws-I-Trip™ pan adjustments (Homer City, PA) set to require 3 pounds of pressure to spring the trap (Association of Fish and Wildlife Agencies BMP) and free-standing nonlethal Michigan regulation coyote neck snares. We physically immobilized coyotes and then weighed, determined sex, and estimated age based on tooth wear (Gier 1968). Coyotes estimated to be less than two years old were classified as subadults; adults were two years old or greater. We fit each individual with an African Wildlife Tracking (Pretoria, South Africa) two-way satellite communication GPS collar designed specifically for coyotes in our study area. We programmed collars to record 4 to 5 relocations each day on rotating schedules. We released all non-target captures. Animal handling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (permit #10-117-FIW).

Space Use Analyses

Home Range Stability and Status Classification

Coyotes are often classified as residents or transients in a population and this distinction has traditionally been made by overall home range size or overlap with several other territories (Kamler and Gipson 2000, Hinton et al. 2012). However, home range size can vary with age, sex, resource availability, local density, and season. For our purposes, the transient designation refers to a lack of a defensible territory, or instability in home range. Thus, we developed a novel method for classifying coyote status based on the stability or shifting of the activity center of the estimated home range over time. Residents were assumed to have a more stable home range represented by smaller distances between successive activity centers. We defined an individual's activity center (s_t) as the centroid of locations over a given time period (t), and described territory stability by the distance (d) between two successive activity centers over the defined time interval (s_t to s_{t+1}), calculated using the Pythagorean Theorem ($d = \mathrm{sqrt}(s_t^2 + s_{t+1}^2)$). We plotted the frequency of distances between successive activity centers across individuals at three different time intervals (1 week, 2 weeks, and one month) and visually inspected the density plots for an obvious threshold between successive distances that could be used to distinguish individuals as residents or transients. We also calculated the mean, range, quartiles, and median values for successive distances for each time designation and used this information to make a final determination of home range status classification criteria for this region.

Estimating Biased Random Bridges, Utilization Distributions and Home Range Size

We used the biased random bridge (BRB) function in adehabitatHR and adehabitatLT packages (Calenge 2006) in R (R Core Team 2013) to compute an active utilization distribution (UD) for each coyote during one-month time periods. To build home ranges using BRBs, we first created estimated trajectories for each coyote for each month using the as.ltraj function in adehabitatLT. We estimated the diffusion parameter, or the probability of direction of movement for the estimated trajectory path, using the maximum likelihood function (BRB.likD) in adehabitatHR with the upper and lower bounds of the diffusion coefficient (Dr) widely set at 0.01 and 100. Because this method is dependent on serial autocorrelation in the data, we defined "bursts" of trajectories as consecutive relocations within the 4 - 5 hour relocation collar schedule, and defined a new burst if a scheduled relocation was not obtained (Tmax = 5.5 hours). However, missed relocations were very infrequent due to the use of satellite collars. While movement-based kernel density estimators (MKDE) are more commonly used for fine-scale movement data (e.g., ~30 minute relocation schedules), we felt that the interpretation of the trajectory as an indication of behavior for highly mobile, wide-ranging coyotes was appropriate at a 4 – 5 hour schedule. A previous study inferred behavioral differences in a coyote using two-hour time steps divided in two parts over a 14-hour time window (Byrne et al. 2014), and thus potentially much larger than the 4-5 hour interval we used. Given the biology of the animal, we were comfortable making inferences assuming serial autocorrelation in relocations and that trajectory was representative of coyote behavior at a broad temporal scale. Even with the assumption of serial autocorrelation of relocations, any given location was a random sample of many adjacent points at which an animal may have been located at the general time of relocation (Benhamou 2011) and typically contained some degree of error in GPS-estimated location

(Laver and Kelly 2008). Thus, we set standard error (hmin) at 100 meters (the one-dimensional resolution of habitat raster cells). The smoothing parameter for the estimated trajectory paths is estimated using the diffusion parameter and the error term. We used 20 meters as the minimum distance between successive locations for the animal to be considered resting, as we found very small location error with collars placed in known locations with repeated relocations (mean distance between 10 and 20 meters depending on habitat). We set filtershort = FALSE as we consider den and resting location as resource utilization, so all bursts including those indicating rest were used. We used the constructed BRBs to estimate the suite of distributions (UD, ID, and RD) based on estimated movement and trajectories to directly address hypotheses about coyote space use in the western mountains of Virginia. We defined home range size or total territory as the 95% UD isopleths and core home range size as the 50% UD isopleths (Hinton et al. 2012). Intensity of use and recursion were evaluated at the 50% scale (Benhamou and Riotte-Lambert 2012).

Compilation of Geospatial Layers and Habitat Selection

We compiled geospatial layers using QGIS (Quantum GIS Development Team 2014) and the raster (Hijmans 2014), sp (Pebesma and Bivand 2005, Bivand et al. 2013), maptools (Bivand and Lewin-Koh 2014), and rgdal (Bivand et al. 2014) packages in R (R Core Team 2013). For the habitat layer, we combined raster data at 100 m X 100 m resolution from the National Land Cover Gap Analysis Project for Virginia and West Virginia (USGS 2011). This resulted in 53 possible fine-scale habitat types. We bounded the extent by the x-axis and y-axis limits of the coyote relocation data buffered by 2 km and reclassified habitat types into 10 general habitat classes (hardwood, softwood, mixed softwood/hardwood, grass dominated habitats, shrub dominated habitats, open/barren, rocky habitat including outcrops and cliffs, agriculture, riparian, and disturbed/developed habitat) for the final habitat layer (Appendix 1). We then classified each of these habitats in terms of productivity for coyotes based on findings of previous coyote studies and hypothesized the general risk associated with the habitat type. Because all coyote mortality in the study was a result of human actions, we considered upland areas and ridgelines farther from human population density to be low risk habitats, and areas along valley bottoms with greater human population density to be high risk habitats. . This resulted in three categories: 1) low risk/low productivity including hardwood and rocky habitat often associated with National Forest lands, 2) low risk/moderate productivity including softwood and mixed forest stands and grassland dominated stand regenerations comprised of areas still some distance from human population density but improved habitat due to management activities and associated regeneration; and 3) high risk/high productivity including agricultural areas consisting primarily of pastures and hay farms, and open/barren, riparian, disturbed/developed, and shrub habitats associated with valley bottoms and moderate human population density (Figure 2). One final habitat type, small grass openings created for wildlife management on the public lands, were designated high productivity/low risk, but accounted for only 0.1% of the available habitat (Appendix 1). We did not consider open water and any residual raster cells unclassified as an artifact of bounding the extent in further analyses. We compiled the estimated coyote space use layers including 95% UD, 50% UD, 50% ID, and 50% RD polygon layers generated from BRBs, as well as a dissolved 2-km buffer layer constructed from all coyote relocations during the study. We converted polygon layers to raster using the rasterize function in the raster package (100-m resolution using the Gap Analysis raster as a template). We stacked the space use layers with the coarse habitat layer using the stack() function in the raster package. Finally, we combined the stacked raster layers in a list with the coyote relocation data to be converted to a SpatialPixelDataFrame object using the sp package for use in adehabitatHS and masked the extent with the 2-km relocation buffer layer to minimize memory and computational requirements. The appropriate home range isopleth rasters (95% UD, 50% UD, 50% ID, and 50% RD) were used as a final mask (Figure 3) for each distribution type for within home range analyses, described below.

We evaluated second-order resource selection of the four space use classifications (Manly et al. 2002) using eigenanalysis (Calenge and Dufour 2006). The 95% UD home range level demonstrated how individuals partition available habitat into overall territories and the 50% UD core home range level indicated how coyotes partition habitat amongst themselves into core territory resources. The 50% ID and 50% RD are complementary components of the active 50% UD, and second-order analyses of these distributions reflected how coyotes partition the areas they most intensively use and those they most frequently visit, respectively, amongst themselves. As a result, second-order analysis of each of the four space use classifications elucidated differences in how individual coyotes partition resources available to the population for different purposes or activities. We used the appropriately masked habitat classification raster layer to tabulate the number of raster cells for each habitat type available to the population for each space use classification. We then used the individual monthly 95% UD, 50% UD, 50% ID, and 50% RD to count the number of raster cells of each classification used by each individual in each month they were tracked. These counts, performed for each space use classification, comprised the “available” and “use” designations for second-order analysis (Calenge 2011). We performed eigenanalysis of selection ratios (Calenge and Dufour 2006) using the eisera() function in adehabitatHS (Calenge 2006).

Accounting for Variability in Coyote Space Use

Home range, while generally described as a unit of space, inherently incorporates the unit of time over which it is estimated and thus is a rate (Fieburg and Börger 2012). Calculating home range estimates and habitat selection for an individual for each month (sample unit = coyote-month) allowed for general comparisons of how coyote home range use changed during different seasons (e.g., the denning period following the April birth of pups) and during concentrated resource pulses (e.g., peak hunting season in November when game carcass availability may be greater). Grouping individuals by attributes such as stage (adult or subadult) or sex, and quantifying variability as a function of home range stability status (resident or transient), allowed us to explore hypotheses about class structure and investigate differences in home range size and second-order habitat selection across and within classes.

We used two methods to assess sources of variability in home range size and second-order habitat selection across the four space-use classifications: 1) visual inspection of variability and 2) cumulative model weights estimated using AIC (Burnham and Anderson 2002) from linear mixed models (LMMs). We used boxplots and scatterplots to evaluate variability in ranges of values for estimated home range size for each coyote in each month, and second-order habitat selection factor component scores for each coyote in each month grouped by potential sources of variability. For all four eigenanalyses (one each for the four utilization classifications), we compared the resulting resource selection functions for each habitat type by assessment of resource selection values across each axis and visual inspection of biplots.

In addition, we created several candidate model sets for LMMs using the factor scores and selection ratios from each analysis above as response variables, grouping factors and month as fixed effects, and individual as a random effect (Table 1). Including 95% UD, 50% UD home range sizes, and two extracted resource selection axes for each of the four eigenanalyses, we evaluated a total of 10 model sets, one for each response variable, each set consisting of the same 11 candidate models. This approach allowed us to investigate differences and variation in resource use as a function of individual variation, compared to differences over months and between classes of individuals (stage, sex, status), at different scales of space use (95% UD, 50% UD, 50% ID, and 50% RD). We restricted model sets to include no more than two fixed effects and did not test for interactions due to the limits of the total sample size (137 coyote-month observations). We recognized that the restricted model set and small sample size may reduce our ability to identify the “best” model or provide strong predictions based on resulting models. But our goal was to calculate cumulative model weights for each fixed effect explanatory variable compared to the individual random effect intercept, and the resulting balanced model sets were sufficient to account for relative sources of variability.

For all comparisons we fit LMMs in R using the lmer() function in the lmer4 package (Bates et al. 2014) with individual as a random effect to account for autocorrelation as a result of repeatedly sampling the same coyotes over different months (Börger et al. 2006). When necessary, we transformed variables to best meet assumptions of normality. We estimated the dispersion factor (c-hat) by dividing the model deviance for the global model including all covariates by the number of residual degrees of freedom using the MuMIn package in R (Barton 2014) and compared models using AIC_c, or QAICc when c-hat > 1. We calculated cumulative weights by summing the model weights for each model including the factor (Burnham and Anderson 2002), and compared these to the model weight of the random effect individual intercept-only model. Interpretation of variability in home range size is straightforward. However, when comparing component factor scores for each eigenanalysis axis, greater variation in habitat selection scores did not represent uncertainty, but rather represented greater diversity and varying strengths of selection; less variation indicated more consistency in habitats selected for at each scale.

Known Fate Model to Validate Habitat Risk Assignments

Finally, we attempted to test our designation of high-risk habitats using a known-fate approach. We fit a null known-fate model with constant probability of mortality in program MARK (White and Burnham 1999) implemented through the RMark Package (Laake 2013) to estimate the monthly survival rate for our study area. Because the known-fate model is simply a binomial model assuming prefect detection, we used a binomial generalized linear mixed model (GLMM) to test habitat selection axes as explanatory variables for survival using the glmer() function in the lme4 package (Bates et al. 2014). We coded the response variable as a 1 if an individual survived from the first of the month to the end of the month, and a 0 if it was confirmed killed during the month, and used the individual monthly factor scores extracted from the eigenanalyses axes as explanatory covariates to test what level (95% UD, 50% UD, 50% ID, and 50% RD) best predicted probability of survival. We selected the best model based on AICc and used the beta estimates for the best model to predict probability of survival for the range of possible values along the eigenanalysis factor scores for the selected axis. We identified the factor score equivalent to the mean monthly survival estimated by the null known-fate model in MARK, and expected high-risk habitats would have lower probability of survival predicted from factor scores on the selected axis.

RESULTS

We captured and fitted collars on a total of 19 coyotes over short trapping sessions spanning 2 years from July 2011 to June 2013. Of the coyotes captured, eight were male (six adults ≥ 2 years of age, two subadults <2 years of age) and eleven were female (six adults and five subadults). No coyotes transitioned from subadult to adult during the time their collars were active. Coyote mortality was very high in the study area and 63% of coyotes were confirmed killed during the time they were tracked with a collar. One individual was hit by a vehicle, three were killed by recreational trappers, six were shot, and two were killed by authorized devices used by US Department of Agriculture, Wildlife Services, to reduce potential damage to livestock. The fates of the remaining seven collared coyotes were unknown. Collars were operational on individual coyotes over different intervals from July 2011 through March 2014. Tracking duration ranged from one month (four coyotes were killed within approximately one month of initial capture) to 16 months for a male (C07) and 18 months for a female (C10), both of whom were recaptured in successive years and fitted with new collars.

Home Range Stability and Status Classification

We found a consistent distinct threshold at 2 km for successive distances between home range activity centers at one week, two week, and one month intervals (Figure 4). Approximately 75% (3rd Quartile) of all distances moved between successive activity centers were less than 2 km regardless of time interval considered (Table 2). Thus, we classified coyotes with distances less than 2 km between successive activity centers as residents during that time period, and those with distances greater than 2 km between successive home range centers as transients during that time interval. For all following analyses we used status designation based on monthly differences in distances between successive activity centers. For the purposes of classification for variability assessment in space use, there was no designation of status for the first month a coyote was collared. However, we did not want to reduce our observation count further by removing one month for each coyote, so we assumed distance between activity centers for the first month a coyote was collared to be the same as the distance calculated for the second month. One individual male (C11) was only tracked for two weeks before being shot, so we assumed the mean for male adults for that month, which classified him as a resident, consistent with observed concentration of relocations over the time the animal was collared. Finally, we confirmed the assigned monthly classification using the distance between successive centers estimated at the one-week and two-week scales for the first month each individual was tracked to ensure the assigned first month classification was representative of the individual's home range stability for that month. The final classification resulted in 103 total coyote-month observations when coyotes were classified as residents and 34 total coyote-month observations when coyotes were classified as transients. Eight coyotes were classified as residents over the entirety of the duration they were collared, and two coyotes were classified primarily as transients during the time they were collared. The remaining nine coyotes were classified as both residents and transients for one to multiple months over the time they were tracked.

Coyote Home Range Size and Habitat Selection

Overall Home Range/Territory (95% UD)

Overall home range or territory size varied widely across months with a mean area of 13.46 km^2 and a range from 1.23 km^2 to 38.24 km^2 (Figure 5). Monthly mean home range size ranged from 19.92 km^2 in December to 9.14 km^2 in April when pups were born in the study area. When autocorrelation from monthly estimates were considered using LMMs, model selection suggested individual differences were a greater source of variation in total home range size (random effect intercept only ω= 0.254, Table 3, Appendix 2). However, based model rankings and cumulative model weights ($\Sigma\omega$), there is some support for individual grouping attributes (Table 3) including home range stability represented as the distance between monthly successive activity centers ($\Sigma\omega = 0.406$) and stage ($\Sigma\omega = 0.392$). Individuals classified as transients based on home range stability between months accounted for larger 95% UD areas (median = 19.16 km^2) compared to residents (median = 11.71 km^2), and subadults (median 7.63 km^2) maintained smaller total monthly home range areas than adults (median 15.04 km^2). There was no model support for variability over months suggesting the overall home range or territory a coyote maintains is relatively constant in size, and variability is a function of individual or class structure attributes including stage and status.

At the 95% UD overall home range or territory level, second-order eigenanalysis consisted of two high-loading factors which differentiated how coyotes partitioned available habitat into territories (Figure 6). Small positive values for axis 1 indicated selection for hardwood forests and rocky habitats, and negative values on axis 1 (38.67% of variation explained) represented comparatively strong selection for all other habitat types. Positive values for axis 2 (26.15% of variation explained) demonstrated selection for agriculture-, disturbed/developed-, open/barren-, and shrub-dominated habitats compared to selection for mixed and softwood forest stands and riparian, rocky, and grassy habitats. We were unable to fit a linear mixed model to axis 1 (Appendix 3) due to poor transformations and inadequate goodness of fit (c-hat = 18.49), however when we evaluated total variability in axis 1 based on individual attributes and month, we identified differences in how individuals select for habitat in establishing 95% UD home range territories. Several individuals consistently selected to maintain territories in hardwood forests and rocky habitats, whereas other individuals showed strong selection for more open habitats or agriculture at more extreme negative values along axis 1. In addition, individuals classified as transients tended to have positive values on axis 1 and showed less variability in selection, suggesting transients were selecting for hardwood forest stands and rocky habitats. Model selection for axis 2 (Appendix 3), provided overwhelming support for LMMs including distance between successive home range centers ($\Sigma\omega = 0.995$, Table 3). Resident coyotes with stable home ranges scored more positive values for axis 2, indicating selection to incorporate agriculture, disturbed/developed, open/barren, and shrub dominated habitats within territories.

Core Home Range (50% UD)

Core home range size (50% UD isopleths) varied dramatically by month (Figure 7), even when individual was included as a random effect, indicating strong seasonal trends in the size of core home range use throughout the coyote population ($\Sigma\omega= 0.987$, Table 3). The best model accounted for 75% of the model weights and included month and stage as explanatory variables (Appendix 2). Subadults (median = 1.19 km^2) tended to have smaller core home ranges than adults (median = 1.88 km^2), and showed less variability in core home range size (0.07 – 3.18 km^2 for subadults compared to 0.15 – 5.78 km^2 for adults).

At the 50% UD core home range level, second-order eigenanalysis representing individual selection for habitat among home ranges consisted of two high-loading axes (Figure 8). Positive scores on axis 1 (27.52% of variation explained) represented selection for softwood forest and open/barren areas, whereas negative scores on axis 1 represented selection for shrub habitats, agriculture, riparian, grass dominated habitats, and mixed forests. There were no strong trends for other habitat types on axis 1. Positive scores on axis 2 (20.25% of variation explained) represented selection to incorporate mixed and softwood forests and riparian habitats in core home range areas and negative values represented selection of open/barren, disturbed/developed, rock, shrub, and agriculture. Model selection of LMMs using QAICc suggested individual differences were the greatest source of variance in core home range habitat selection for both axis 1 and axis 2 (Appendix 4). Visual inspection of variability of axis 1 and 2 suggested most individuals selected for softwood stands, mixed stands, and riparian and grass habitats in core home range areas, as can be seen by the high proportion of positive factor scores for individuals. Overall, second-order analysis of habitat selection suggested most coyotes in the study area were selecting to establish core home range areas based on the same habitat factors (softwood and mixed stands, grass, and riparian habitats), regardless of sex, stage, status, or season.

Intensity of Use and Habitat Selection (50% ID)

The intensity distribution is a component of the utilization distribution that uses the trajectory of an individual to account for how long individuals spend in a given area (Benhamou and Riotte-Lambert 2012). Second-order eigenanalysis of the 50% ID describes how the habitats intensively used by individuals were partitioned among individuals at different times (Figure 9). Axis 1 (27.82% of variation explained) reflects selection for softwood and mixed stands, riparian and grass-dominated habitats at positive values compared to selection for open/barren, disturbed/developed, and shrub-dominated habitats, and agriculture at negative values. Axis 2 (26.24% of variation explained) describes selection for softwood forest stands at positive values and riparian, grass-dominated habitats, and mixed forest stands at negative values. Home range stability explained most variation in habitat selection (Appendix 5) with individuals classified as transients more often showing intensive use of softwood forest stands and open/barren and rocky habitats compared to resident coyotes ($\Sigma\omega = 0.833$, Table 3). In addition, we found support for models including stage as an explanatory variable ($\Sigma\omega = 0.495$, Table 3) with subadults also selecting more for softwood stands, open/barren and rocky habitats. We were unable to use LMMs to evaluate axis 2 due to extremely poor model fit (c-hat = 15.88), but visual inspection of boxplots and scatterplots suggest individual differences were the greatest source of variation.

Frequency of Use and Habitat Selection (50% RD)

The recursion distribution is the complementary component to the intensity distribution and accounts for how frequently individuals visit areas based on estimated trajectory. Second-order eigenanalysis of the 50% RD shows strong evidence for differential partitioning between the areas individuals visit frequently across the available landscape (Figure 10). Axis 1 (41.28% of variation explained) distinguished between selection for rocky habitats and weak selection for hardwood forest stands at positive values, moderate selection for softwood and mixed forest stands at intermediate negative values, and stronger selection for all other habitat types at more extreme negative values. Axis 2 (19.11% of variation explained) differentiated between selection for softwood and mixed forest stands, riparian and grass dominated habitats at positive values, selection for agriculture, disturbed/developed, and rocky habitats at intermediate negative values, and strong selection for open/barren, and shrub dominated habitats at extreme negative values. The random effect intercept-only model was ranked highest for the axis 1 ($\omega = 0.416$) and axis 2 ($\omega = 0.348$, Table 3.) LMM candidate sets and the high degree of individual selection in partitioning habitats visited frequently is evident (Appendix 6). However there was some support for moderate differences based on status ($\Sigma\omega = 0.341$, axis 2), where individuals classified as residents demonstrated greater variability in selection of habitat types frequently visited.

Known-Fate Model to Validate Habitat Risk Assignments

Monthly survival from the null known-fate model estimated in Program MARK was 0.91 (SE = 0.02, 95% CI = 0.86 – 0.95). The binomial GLMM survival model that received the most support included the secondary axis of the 95% UD (Table 4, $\omega = 0.406$) and predicted probability of survival decreased with increasingly positive eigenanalysis factor scores. Monthly predicted probability of survival ranged from 0.997 at the lowest observed factor scores for 95%

UD axis 2 (-0.81) to 0.596 at the highest observed factor scores for 95% UD axis 2 (0.77). A factor score of 0.20 (95% CIs = 0.00 – 0.35) on the second axis of the 95% UD represented the predicted probability of monthly survival for the estimated mean survival (0.91) based on the null known-fate model. Thus, selection for habitat types with factor scores for the axis 2 for the 95% UD greater than 0.20 are associated with greater risk of mortality. These habitat types include agriculture, shrub dominated habitats, open/barren, and disturbed/developed habitats (Figure 6). All of these habitat types were associated with increased human density along the valley bottoms. Differences along the 95% UD secondary axis were best described by status (Table 3), with transients consistently selecting for low productivity/low risk habitats, and some residents selecting for high productivity/high risk habitats associated with a lower survival probability.

DISCUSSION

We found evidence for differences in coyote habitat selection and probability of survival based on class structure. In particular, our results suggested differences in selection of territories and in associated risk of mortality based on social status (residents and transients), providing insight into population interactions of a social carnivore in a low-resource, high-risk environment. Although coyote status (resident or transient) has typically been defined by home range size based on the assumption that transients occupy larger areas than residents with defensible home ranges (Gese et al. 1988, Kamler and Gipson 2000, Hinton et al. 2012), we propose that the behavior associated with transience is not necessarily that of requiring larger areas, but rather a reflection of home range instability, or temporal variation in home range location, and a lack of territorial behavior. We found distinct differences among coyotes in the distance between monthly activity centers and suggest that classification of individuals as residents or transients based on monthly home range stability is more informative than overall home range size. While transients tended to have larger overall home ranges (Figure 5), we did not detect a size threshold for transients when we evaluated monthly home range stability, and several individuals with stable home ranges had larger territories than some coyotes with unstable home ranges at this monthly scale. In addition, we did not detect a difference in core area size between coyotes with stable home ranges and coyotes with unstable home ranges (Figure 7), suggesting residents and transients were both able to find the resources required within the same size areas, but individuals lacking a well-defined, defensible territory may be ranging at a larger scale beyond the 50% core UD.

Another advantage to using monthly home range stability to assess status was that it allowed us to detect individual shifting between transient or resident behaviors (i.e., we could identify residents that experienced short periods of transient behavior). We found evidence that some individuals moved to adjacent territories. For example, C7, a male captured at 3 years old in April 2012, was classified as a resident based on distance between successive activity centers until mid-September 2012, where he entered a transient phase for 2 months and then returned to a resident phase in an adjacent territory 2.25 km away in mid-November 2012. Previous methods of estimating and classifying home ranges would have likely resulted in the C7's relocation data being discarded or classifying him as a transient for the length of the study. Our method revealed that C7 predominantly behaved as a resident with a stable monthly home range but made a distinct home range shift following a brief transient period. Other individuals were initially classified as residents, but then entered an extended transient phase before the collar stopped transmitting or they were killed. This typically occurred in fall and early winter which we attribute to exploratory movements and transition into a transient phase during dispersal.

Overall, the cumulative view of the total coyote population portrayed a high level of individual differences in home range size and habitat use. We did not observe strong seasonal differences in monthly home range sizes when individuals were accounted for as a random effect, suggesting monthly consistency in territory size (95% UD). However, the size of the core home range (50% UD) did change among months indicating that core home range may have been the scale at which coyotes responded to biological seasons and changes in resource availability (Knowlton et al. 1999). This was also reflected by the greater variability in habitats individuals selected to incorporate within their overall home ranges (95% UD second order, Figure 6). Conversely, at the core home range scale (Figure 8) we noted more consistent selection across the population for incorporation of softwood and mixed forests stands, and riparian and grass dominated habitats regardless of age, sex, stage, or status. These habitat types comprised only 11% of the available habitat (Appendix 1) and were all considered more productive than the most commonly available habitat, hardwood forest stands, for which there was no evidence of selection (~75% of available habitat).

The known-fate models confirmed most of our risk designations for habitat types. Agriculture, shrub dominated habitats, open/barren, and disturbed/developed habitats associated with human density along the valley bottoms all had eigenanalysis factor scores that predicted a greater risk of mortality than the estimated mean monthly survival (0.91% monthly survival ~ 0.2 factor score on axis 2, Figure 6). However, riparian habitat, which we predicted to be associated with risk due to location, did not have positive values for habitat selection along axis 2 for the 95% UD; as a result, predicted probability of survival for riparian habitat was greater than the estimated mean monthly survival. Thus, the limited areas of riparian habitat (0.80% of the area evaluated) may have provided some level of refuge for coyotes in the study area, similar to findings in urban areas (Tigas et al. 2002) and agricultural areas (Gosselink et al. 2003) where riparian networks are protected from encroaching development. The very low negative values on the secondary axis for both riparian habitat and the few small grassland areas, maintained wildlife clearings within the National Forest (0.10% of area evaluated), indicated very strong selection by individuals to incorporate these habitats within their overall (95% UD) monthly home range territories proportional to availability and resulted in higher probability of survival.

When we evaluated coyote space use at multiple types of use and partitioned variability by grouping variables, we were able to extract several trends that suggested the habitat generalist population was composed of different types of coyotes with distinct selection strategies based on life history and acceptable risk with respect to potential reward as dictated by class membership. Generally, based on the 95% UD secondary habitat selection axis that determines probability of survival, we found three "types" of coyotes: 1) transient coyotes with large or unstable territories that selected for low productivity, low risk habitats; 2) resident coyotes with stable home ranges that selected for low productivity, low risk habitats; and 3) resident coyotes that incorporated risky areas that may be more productive. We found that subadults tended to behave as adults, only at a smaller scale and with less variation, and tended to group with residents, but made less risky decisions based on habitat selection. At both the overall home range (95% UD) and core home range (50% UD) scales, subadults did not use as much area as adults. However we did not find differences in habitat selection between these two stages.

We detected a trade-off pattern between risk and productivity in the eigenanalysis results for all levels of space use evaluated as indicated by the order of habitat type component loadings along axis 1, the primary axis explaining the most variability compared to axis 2, the secondary axis. This allowed us to make some inference about how coyotes were behaving, given risk and reward, at different levels of space use. Divergent choices along axis 1 described a greater amount of variability compared to divergent choices along axis 2 and this allowed us to presume priorities in habitat selection by comparing whether habitats loading on axis 1 distinguish differences in selection for habitats based on productivity or risk (Table 5).

At the 95% UD level coyotes first choose between productive and unproductive habitats along axis 1 (hardwood and rocky habitats at small positive values, softwood and mixed forest stands at moderate negative values, and high risk/high productivity habitats at extreme negative values), and then selected for habitats based on risk on axis 2 (less risky softwood and mixed wood stands at moderate negative values, and riparian, and grassland habitats at extreme negative values compared to high risk agriculture, disturbed/developed, open/barren and shrub habitats at positive values). There is additional evidence of risk associated with these choices as three coyotes killed within a month of being collared scored consistently negative second-order 95% UD axis 1 values and positive axis 2 values, indicating they established their home ranges in high-risk/high-productivity areas that were more likely to result in conflict with humans (agriculture and habitats associated with valley bottoms).

At the 50% ID level coyotes were not selecting low-productivity habitats in the areas they use intensively (second-order component scores for rocky habitats and hardwood forest are very close to the origin, Figure 9), but rather were selecting habitats with relatively greater productivity in all areas they use intensively. Axis 1, the highest loading component of second-order analysis of the ID, demonstrated selection of high-risk, high-reward habitats at negative values (agriculture, open/barren, shrub and disturbed/developed) compared to selection for moderate risk, moderate reward habitats at positive values (mixed and softwood forest stands).

At the 50% RD second-order level there is very strong differentiation between habitats frequently visited (Figure 10), with productivity prioritized over risk.

These dichotomous patterns in how coyotes account for (or do not account for) risk, beg the question, “why do animals take risks?”. Previous experimental studies (Caraco et al. 1980, Abraham and Dill 1989) suggested that we should find differences in the eigenanalysis axes of risk based on individual attributes and class membership, and indeed we do detect patterns. Subadults and transients often selected for safer, more moderate productivity areas such as softwood and mixed forest stands (Table 3), as would be expected for the life history of animals that have future opportunities for reproduction, spreading risk across time. However, this may also occur if less competitive individuals were excluded from high-risk, high-reward areas by more dominant residents. We did not find strong evidence for differences in second-order habitat selection based on sex as predicted. However, dispersal was not sex-biased and male and female resident coyotes did not defend separate territories, but typically jointly defended home ranges. Thus, it is not surprising that we did not detect sex-specific differences in selection for territories and home range areas. However, it is possible that risk perception may differ by sex at the third-order level, which would distinguish how individuals used the habitats already within established home ranges.

Adult residents demonstrated differential selection for risky habitats among territories (second order), a pattern also detected in urban coyotes (Newsome et al. 2015). In the high-density urban environment of Chicago, some individuals restricted movements to safer areas such as parks and reserves, while other individuals selected more high-risk areas and heavily exploited anthropogenic resources, as determined through isotope analysis. Support for the known-fate binomial GLMM including axis 2 of the 95% UD suggested probability of survival was related to where individuals established overall home range or territories. There was very strong cumulative AICc model weight for the social status (resident or transient) class structure variable in the LMMs when axis 2 for the 95% UD was the response variable ($\omega = 0.995$), and coyotes identified as transients did not have factor scores greater than 0.2, suggesting they selected for safe habitats or were excluded from the riskier high productivity habitats when attempting to establish overall home range areas (Figure 6). However, residents demonstrated a large amount of variability in selection for habitats to defend as territories along axis 2. This may be due to individual differences in risk perception and behavior or dominance, and is likely it is the result of the very limited and locally concentrated high productivity areas associated with high risk. As most LMMs for the primary axis factor scores indicated selection first occurred along a gradient of habitat productivity, it is likely that these few high quality but high risk habitats are highly desirable for residents to incorporate within territories and defend, excluding other residents and transients. Thus, it may be the territory, more so than the individual coyote that is risky and associated with a higher probability of mortality.

CONCLUSIONS

Even with small sample sizes (19 individuals collared for 1 – 18 months for a total of 137 total coyote-month observations), we were able to detect patterns including selection along gradients of risk and rewards, and core home range seasonal changes in response to changing availability in resources and requirements. Compiling data sources across multiple studies in this framework may provide greater insight into levels of variability. Many recent studies focus on predation impacts attributed to coyotes, but few investigate the ecology and behavior of this species. Furthermore, while the risk of predation at the habitat scale of a prey animal has often been examined (Chitwood et al. 2014, Kilgo et al. 2014, Gulsby et al. 2015), rarely have landscape variables at an appropriate scale been considered for habitat selection by a highly mobile predator in combination with potential impacts to prey. To do this, we need a broader perspective and meta-analysis incorporating many regions, which is logistically difficult, but the flexibility of eigenanalysis and LMMs offers potential means towards achievement. Finally, potential risk and reward behavior of predators, including the use of optimal foraging theory, should be considered when attempting to understand highly adaptable, density-dependent predator species such as coyotes. Coyote management is rife with challenges, and there is no single silver bullet solution, but potential avenues of success may be identified by viewing perceived and real conflict through the behavior of the predator.

ACKNOWLEDGEMENTS

We would like to thank collaborators Robert Alonso, the Virginia Department of Game and Inland Fisheries, including Mike Fies, Dave Steffen, Al Bourgeois, and Nelson Lafon, US Forest Service, including Steve Tanguay, Carol Croy, Russ MacFarlane, and Lindsey Curtain, the Nature Conservancy and Marek Smith at the Warm Springs Mountain Preserve. In addition, we thank Mike Cherry, Joey Hinton, and Jim Nichols for conversations critical to converting pattern to process, Lisa Lyren, Ed and Jaime McArdle for logistic support, and Jason Woods for public relations and carcass/collar retrieval. Financial support provided by the Virginia Department of Game & Inland Fisheries came from the U.S. Fish & Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Finally, we appreciated additional funding and support from the Appalachian members of the Virginia Deer Hunter Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).

LITERATURE CITED

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70(4): 999-1007.

Association of Fish and Wildlife Agencies. Best management practices: Trapping coyotes in the eastern United States.

Bates D, M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4_. R package version 1.1-7, <URL: http://CRAN.R-project.org/package=lme4>.

Barton, K. 2014. MuMIn: Multi-Model Inference. R package version 1.12.1. http://CRAN.R-project.org/package=MuMIn.

Bekoff, M. 1978. Coyotes: biology, behavior, and management. 2001, reprint. Blackburn Press Caldwell, New Jersey, USA.

Benhamou, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PloS one 6(1):e14592.

Benhamou, S., and L. Riotte-Lambert. 2012. Beyond the Utilization Distribution: Identifying home range areas that are intensively exploited or repeatedly visited. Ecological Modelling 227:112-116.

Bivand, R.S., T. Keitt, and B. Rowlingson. 2014. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.9-1. http://CRAN.R-project.org/package=rgdal

Bivand, R.S., and N. Lewin-Koh. 2014. maptools: Tools for reading and handling spatial objects. R package version 0.8-30. http://CRAN.R-project.org/package=maptools

Bivand, R.S., E. Pebesma, and V. Gomez-Rubio. 2013. Applied spatial data analysis with R, Second edition. Springer, New York.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist 168(4):471-485.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22(1):37-47.

Brown, J. S., and Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. Ecology letters 7(10):999-1014.

Brown, J. S., Laundré, J. W., and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80(2):385-399.

Burnham, K. P., and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer, New York.

Byrne, M. E., J. C. McCoy, J. W. Hinton, and M. J. Chamberlain, B. A. Collier. 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83(5):1234-1243.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.

Calenge, C. 2011. Adehabitat: Analysis of habitat selection by animals. R package version, 1(10).

Calenge, C., and A. B. Dufour. 2006. Eigenanalysis of selection ratios from animal radio-tracking data. Ecology 87(9):2349-2355.

Caraco, T., S. Martindale, and T. S. Whittam. An empirical demonstration of risk-sensitive foraging preferences. Animal Behavior 28: 820-830.

Chamberlain, M. J., C.D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78(12):2087-2095.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical population biology 9(2):129-136.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2014. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer?. PloS one 10(3):e0119070-e0119070.

Crete, M., J. P. Ouellet, J. P. Tremblay, and R. Arsenault. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. Ecoscience 8:311-319.

DeCalesta, D. S. 1997. Deer and ecosystem management. Pages 267-279 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institute Press, Washington, D.C.

Diefenbach, D. R., W.L. Palmer, and W.K. Shope. 1997. Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. Wildlife Society Bulletin: 25(2):244-251.

Emlen, J. M. 1968. Optimal choice in animals. American Naturalist 102(926):385-389.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258-270.

Fenneman, N.M. and D.W. Johnson. 1946. Physiographic divisions of the conterminous U. S. US Geological Survey, Reston VA.

Fieberg, J., and L. Börger. 2012. Could you please phrase "home range" as a question?. Journal of Mammalogy 93(4):890-902.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. The Journal of Wildlife Management 52(4):640-646.

Gese, E. M. 2001. Territorial defense by coyotes (Canis latrans) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Canadian Journal of Zoology 79(6):980-987.

Gier, H.T. 1968. Coyotes in Kansas. Kansas State College Agricultural Experiment Station

465 Bulletin 393. Kansas State University, Manhattan, Kansas, USA.

Gosselink, T.E., T.R. Van Deelen, R.E. Warner, and M.G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 67:90-103.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39(2):248-255.

Harrison, D.J. 1992. Social ecology of coyotes in northeastern North America: relationships to dispersal, food resources, and human exploitation. Pages 53-72 *in* Boer A. H., editor. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, Fredericton. New Brunswick, Canada.

Harrison, D. J., J. A. Harrison, and M. O'Donoghue. 1991. Predispersal movements of coyote (*Canis latrans*) pups in eastern Maine. Journal of Mammalogy 72:756-763.

Hijmans, R. J. 2014. raster: Geographic data analysis and modeling. R package version 2.3-12. http://CRAN.R-project.org/package=raster

Hinton, J. W. 2014. Red wolf (*Canis rufus*) and coyote (*Canis latrans*) ecology and interactions in northeastern North Carolina. PhD Dissertation. University of Georgia, Athens, Georgia, USA.

Hinton, J. W., M. J. Chamberlain, and F. T. van Manen. 2012. Long-distance movements of transient coyotes in eastern North Carolina. American Midland Naturalist 168(2): 281-288.

Holzman, S., M. J. Conroy, and W. R. Davidson. 1992. Diseases, parasites and survival of coyotes in south-central Georgia. Journal of Wildlife Diseases 28(4):572-580.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1):65-71.

Kamler, J.F., and P.S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78:2106–2111.

Kays, R.W., M.E. Gompper, and J.C. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications 18:1014-1027.

Kelly, M. J., and E. L. Holub. 2008. Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist 15:249-262.

Kilgo, J. C., M. Vukovich, H. S. Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. The Journal of Wildlife Management 78(7):1261-1271.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52(5):398-412.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. The Journal of Wildlife Management 72(1):290-298.

Litvaitis, J.A., and D. J. Harrison. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology-Revue Canadienne De Zoologie 67:1180-1188.

MacArthur, R. H., E. R. Pianka, E. R. 1966. On optimal use of a patchy environment. American Naturalist 100(916): 603-609.

Manly, B.F., L.L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. 2nd edition. Kluwer Academic, Boston, Massachusetts, USA.

Messier, F., and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60:1743-1753.

Monsarrat, S., S. Benhamou, F. Sarrazin, C. Bessa-Gomes, W. Bouten, and O. Duriez. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers?. PloS one 8(1):e53077.

Mukherjee, S., and M. R. Heithaus. 2013. Dangerous prey and daring predators: a review. Biological Reviews 88(3):550-563.

Newsome, S. D., H. M. Garbe, E. C. Wilson, and S. D. Gehrt. 2015. Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178(1):115-128.

Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and Van Vuren, D. H. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91(6):1322-1331.

Parker, G.E. 1995. Eastern coyote: the story of its success. Nimbus. Halifax, Nova Scotia, Canada.

Parker, G. R., and J. W. Maxwell. 1989. Seasonal movements and winter ecology of the coyote, *Canis latrans*, in northern New Brunswick. Canadian Field-Naturalist 103:1-11.

Patterson, B.R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463-477.

Pebesma, E.J., and R.S. Bivand. 2005. Classes and methods for spatial data in R. R News 5 (2), http://cran.r-project.org/doc/Rnews/.

Perkins, P.J., and W.W. Mautz. 1990. Energy requirements of eastern coyotes. Canadian Journal of Zoology 66:656-659.

Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present and future. Trends in Ecology and Evolution 12(9):360-364.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52(2):137-154.

Quantum GIS Development Team, 2014. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Randa, L.A., and J.A. Yunger. 2004. The influence of prey availability and vegetation characteristics on scent station visitation rates of coyotes, *Canis latrans*, in a heterogeneous environment. Canadian Field-Naturalist 118:341-353.

Richer, M.C., M. Crête, J.P. Ouellet, L.P. Priest, and J. Huot. 2002. The low performance of forest versus rural coyotes in northeastern North America: Inequality between presence and availability of prey. Ecoscience 9:44-54.

Schrecengost, J. D., J.C. Kilgo, D. Mallard, H.S. Ray, and K.V. Miller. 2009. Home range, habitat use and survival of coyotes in western South Carolina. American Midland Naturalist 162:346-355.

Spencer, W.D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93:929-947.

Thibault, I., and J.P. Ouellet. 2005. Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. Ecoscience 12:466-475.

Tigas, L. A., Van Vuren, D. H., and Sauvajot, R. M. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108(3):299-306.

Tremblay, J.P., M. Crete, and J. Huot. 1998. Summer foraging behaviour of eastern coyotes in rural versus forest landscape: A possible mechanism of source-sink dynamics. Ecoscience 5:172-182.

U.S. Census Bureau. 2010 Census. <http://factfinder.census.gov>. Accessed 20 April 2011.

US Geological Survey, Gap Analysis Program (GAP). August 2011. National Land Cover, Version 2.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

Wilson, R. R., and J. A. Shivik. 2011. Contender pressure versus resource dispersion as predictors of territory size of coyotes (*Canis latrans*). Canadian Journal of Zoology 89(10):960-967.

Windberg, L. A., and F. F. Knowlton. 1988. Management implications of coyote spacing patterns in southern Texas. The Journal of Wildlife Management 52(4):632-640.

TABLES

Table 1. Linear Mixed Model (LMM) candidate sets of multiple working hypotheses for sources of variability in coyote monthly home range size and habitat selection. There are 10 response variables for which the same candidate set composed of 11 models was applied. Response and explanatory variables were transformed as necessary to approximate normality and c-hat was estimated using the global model deviance and residual degrees of freedom, although this model was not included in the restricted candidate model sets due to the excessive number of parameters for a relatively small sample size (137 total observations of coyote home ranges over months).

Space Use Classification	Space Use Type	Response Variable	Candidate Set and model number used for each response variable
Overall Home Range Size	Size	95% UD area	**model 1** ~ (1 | individual) **model 2** ~log(Successive Distance) + (1 | individual) **model 3** ~month + (1 | individual) **model 4** ~log(Successive Distance) + month + (1 | individual) **model 5** ~sex + (1 | individual) **model 6** ~log(Successive Distance) + sex + (1 | individual) **model 7** ~month + sex + (1 | individual) **model 8** ~stage + (1 | individual) **model 9** ~log(Successive Distance) + stage + (1 | individual) **model 10** ~month + stage + (1 | individual) **model 11** ~sex + stage + (1 | individual)
Overall Home Range Habitat Selection	Partitioning of available habitat for territories among individuals	95% UD second order eigenanalysis axis 1	
		95% UD second order eigenanalysis axis 2	
Core Home Range Size	Size	50% UD area	
Core Home Range Habitat Selection	Partitioning of available habitat for core home range areas among individuals	50% UD second order eigenanalysis axis 1	
		50% UD second order eigenanalysis axis 2	
Core Home Range Areas Used Intensively	Partitioning of available habitat for intensive use (long durations) among individuals	50% ID second order eigenanalysis axis 1	
		50% ID second order eigenanalysis axis 2	
Core Home Range Areas Frequently Used	Partitioning of available habitat for core home range areas among individuals	50% RD second order eigenanalysis axis 1	
		50% RD second order eigenanalysis axis 2	

Table 2. Summary of distances between successive estimated activity centers by three different time intervals: 1 week, 2 weeks, and 1 month. Approximately 75% (3rd Quartile) of all distances moved were under 2000 meters.

Time interval	Minimum (m)	1stQuartile (m)	Median (m)	Mean (m)	3rd Quartile (m)	Maximum (m)	Total Observation Units
1 week	41.99	494.10	941.90	1860	1903	19410	494
2 week	15.13	447.50	811.80	1836	1813	20790	247
1 month	19.96	476.60	1035.00	2124	1913	28890	111

Table 3. Support for differential coyote space use by individual (random effect intercept), month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by log(distance between successive activity centers)) for 10 model sets (one model set for each response variable, with each model set consisting of 11 candidate models). Values are cumulative (Q)AICc weights, and bolded fields represent best supported variables based on cumulative (Q)AICc weights listed from linear mixed model (LMM) selection.

Candidate model response variable	**Axis[1]**	**status**	**month**	**sex**	**stage**	**Individual intercept only**	**Level of Inference**
95% UD Home Range Size		**0.406**	0	0.238	**0.392**	0.254	overall home range/territory
95% UD second order habitat	1	NA[2]	NA	NA	NA	NA	selection between overall home ranges/territories
95% UD second order habitat	2	**0.995**	0.001	0.25	0.19	0.002	
50% UD Home Range Size		0.053	**0.987**	0.044	**0.763**	0.001	core home range area
50% UD second order habitat	1	0.263	0	0.238	0.276	**0.389**	selection between core home range areas
50% UD second order habitat	2	0.293	0	0.239	0.239	**0.393**	
50% ID second order habitat	1	**0.833**	0.001	0.223	**0.495**	0.069	selection between intensively used areas
50% ID second order habitat	2	NA[2]	NA	NA	NA	NA	
50% RD second order habitat	1	0.241	0	0.246	0.249	**0.416**	selection between frequently visited areas
50% RD second order habitat	2	**0.341**	0	0.238	0.265	**0.348**	

[1] Axis refers to the primary (Axis 1 - x) and secondary (Axis 2 - y) component factor scores from each eigenanalysis of habitat selection ratios.

[2] Unable to fit LMM due to poor transformations and inadequate goodness of fit.

Table 4. Model Selection for known-fate binomial Generalized Linear Mixed Model. The response variable indicates survival from the beginning of one month to the next and the factor scores for each eigenanalysis axis were compared as explanatory variables (eight total, two eigenanalysis axes for each level of space use). Individual coyote was included as a random effect.

Model	Intercept (SE)	Eigenanalysis axis beta estimate (SE)	logLikelihood	Deviance	df	AICc	delta AICc	AICc model weight
95% UD Axis 2	3.03 (0.48)	- 3.51 (1.60)	-35.6	71.2	134	77.399	0.000	0.406
50% RD Axis 1	2.55 (0.39)	0.83 (0.50)	-36.7	73.3	134	79.496	2.097	0.142
50% ID Axis 2	2.54 (0.45)	1.47 (1.00)	-36.9	73.9	134	80.056	2.657	0.107
95% UD Axis 1	2.54 (0.34)	0.81 (0.48)	-37.0	74.0	134	80.219	2.820	0.099
50% ID Axis 1	2.55 (0.42)	1.48 (1.09)	-37.1	74.2	134	80.399	3.000	0.091
50% UD Axis 2	2.58 (0.43)	1.04 (0.89)	-37.3	74.7	134	80.867	3.468	0.072
50% RD Axis 2	2.50 (0.41)	0.74 (1.28)	-37.8	75.6	134	81.800	4.401	0.045
50% UD Axis 1	2.46 (0.49)	0.12 (1.12)	-38.0	75.9	134	82.124	4.725	0.038

Table 5. Summary of findings regarding risk compared and productivity prioritization of habitat selection at multiple levels of space use as determined by eigenanalysis of selection ratios. Second-order selection refers to how individuals select for habitat to incorporate in a home range unit. The primary axis is in bold and explains the greatest trend in variability.

Space Use Scale	Component axis	Dichotomy for axes	% Variation explained
95% utilization distribution (UD), overall home range/territory	**Primary (axis 1: x)**	**productivity**	**38.67%**
	Secondary (axis 2: y)	risk	26.15%
50% utilization distribution (UD), core home range	**Primary (axis 1: x)**	**productivity**	**27.51%**
	Secondary (axis 2: y)	risk	20.25%
50% intensity distribution (ID), intensive use areas	**Primary (axis 1: x)**	**risk (only productive habitats selected)**	**27.82%**
	Secondary (axis 2: y)	risk	26.24%
50% recursion distribution (RD), frequent use areas	**Primary (axis 1: x)**	**productivity**	**41.28%**
	Secondary (axis 2: y)	risk	19.11%

FIGURES

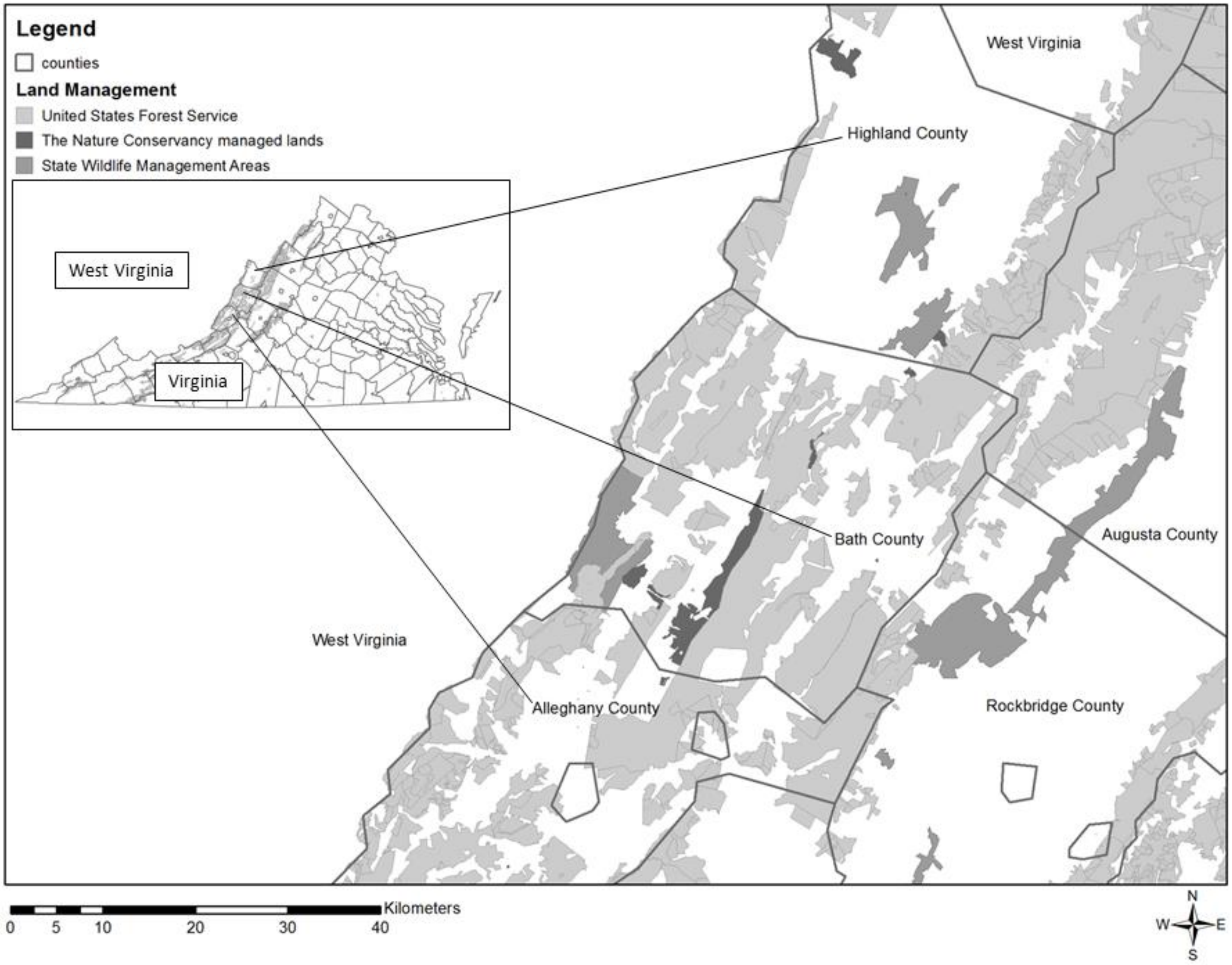

Legend
counties
Land Management
United States Forest Service
The Nature Conservancy managed lands
State Wildlife Management Areas
West Virginia
Virginia
West Virginia
Highland County
Bath County
Augusta County
West Virginia
Alleghany County
Rockbridge County
Kilometers
0
5
10
20
30
40
N
W
E
S

Figure 1. The study area is located in the western mountains of Virginia along the Virginia/West Virginia border in the Ridge and Valley province of the Middle section of the Appalachian Highlands (Fenneman and Johnson 1946). Coyote trap lines were concentrated in the western portion of Bath County, Virginia, and collared coyotes used areas in Bath County as well as in Highland and Allegheny Counties, Virginia, to the north and south, and neighboring Pocahontas and Greenbrier Counties to the west in West Virginia.

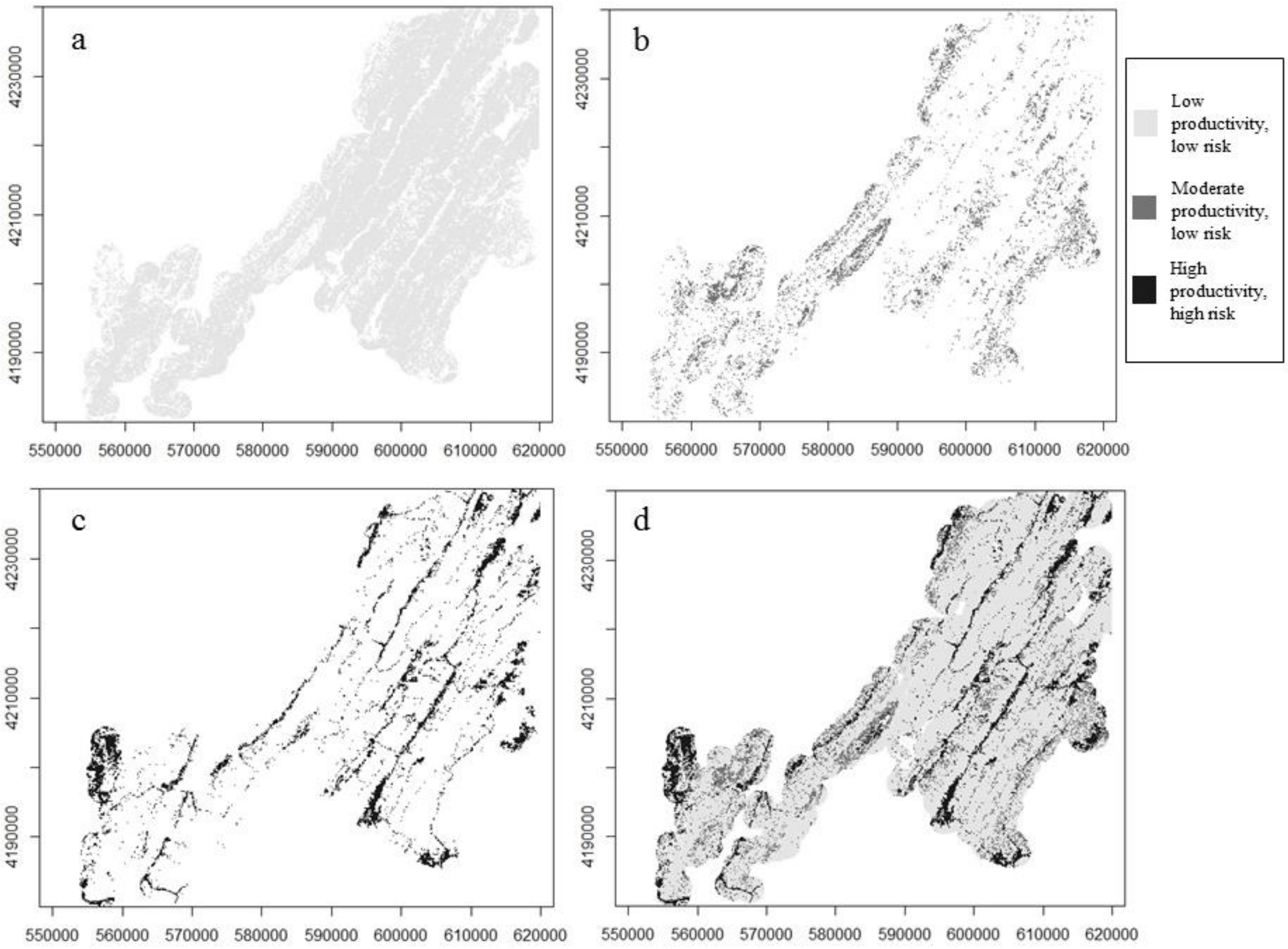

a
b
c
d
4230000
4210000
4190000
550000
560000
570000
580000
590000
600000
610000
620000
Low productivity, low risk
Moderate productivity, low risk
High productivity, high risk

Figure 2. Habitat map classified by (a) low productivity/low risk areas, including hardwood forest stands and rocky habitats associated with ridgelines, (b) moderate productivity/low risk areas, including softwood and mixed forest stands and grass regeneration from timber harvests, (c) high productivity/high risk areas, including agricultural fields, disturbed/developed, open/barren, and shrub and riparian habitats associated with valley bottoms and increased human activity, and (d) all three productivity/risk classifications merged. Habitat raster files were masked by a 2-km buffer around collared coyote relocations so that habitat availability reflects only that available to collared animals. Low productivity/low risk accounts for 78.6% of the available habitat in the study area, whereas moderate productivity/low risk and high productivity/high risk habitats account for 10.3% and 10.9% of available habitat, respectively.

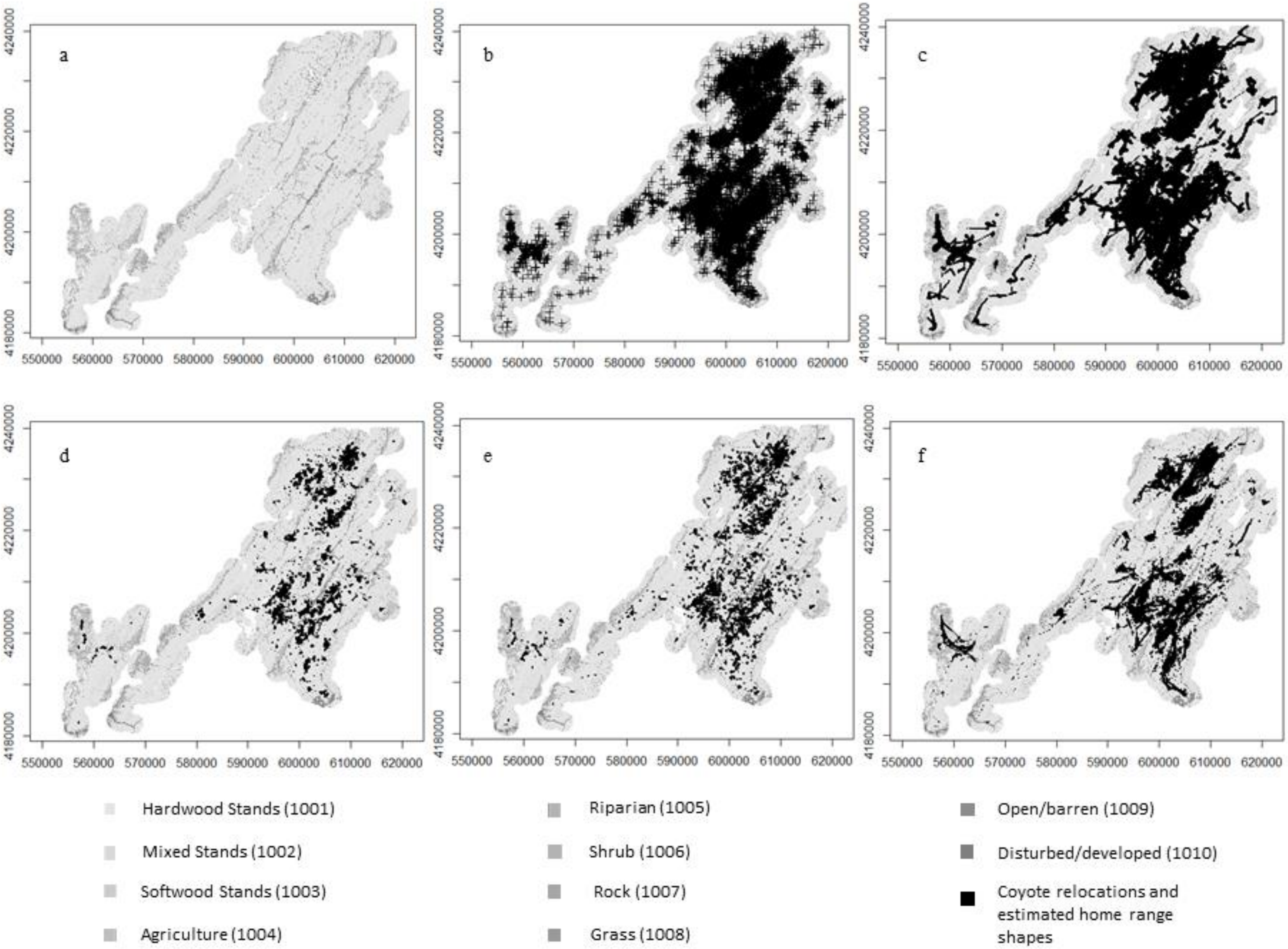

a
b
c
d
e
f
4240000
4220000
4200000
4180000
550000
560000
570000
580000
590000
600000
610000
620000
Hardwood Stands (1001)
Mixed Stands (1002)
Softwood Stands (1003)
Agriculture (1004)
Riparian (1005)
Shrub (1006)
Rock (1007)
Grass (1008)
Open/barren (1009)
Disturbed/developed (1010)
Coyote relocations and estimated home range shapes

Figure 3. Ten coarse habitat classifications were based on the 53 fine-scale habitat types identified across the study area (a) by the National Land Cover Gap Analysis Project for Virginia and West Virginia (USGS 2011). The 100-m resolution raster layer was masked several different ways to quantify availability appropriately at different levels of analysis. These levels included a 2-km dissolved buffer around relocations for all 19 individual coyotes tracked shown here (b). The 95% UD home range polygons (c), 50% UD core home range polygons (d), 50% ID polygons (e), and 50% RD polygons (f) are overlaid in black.

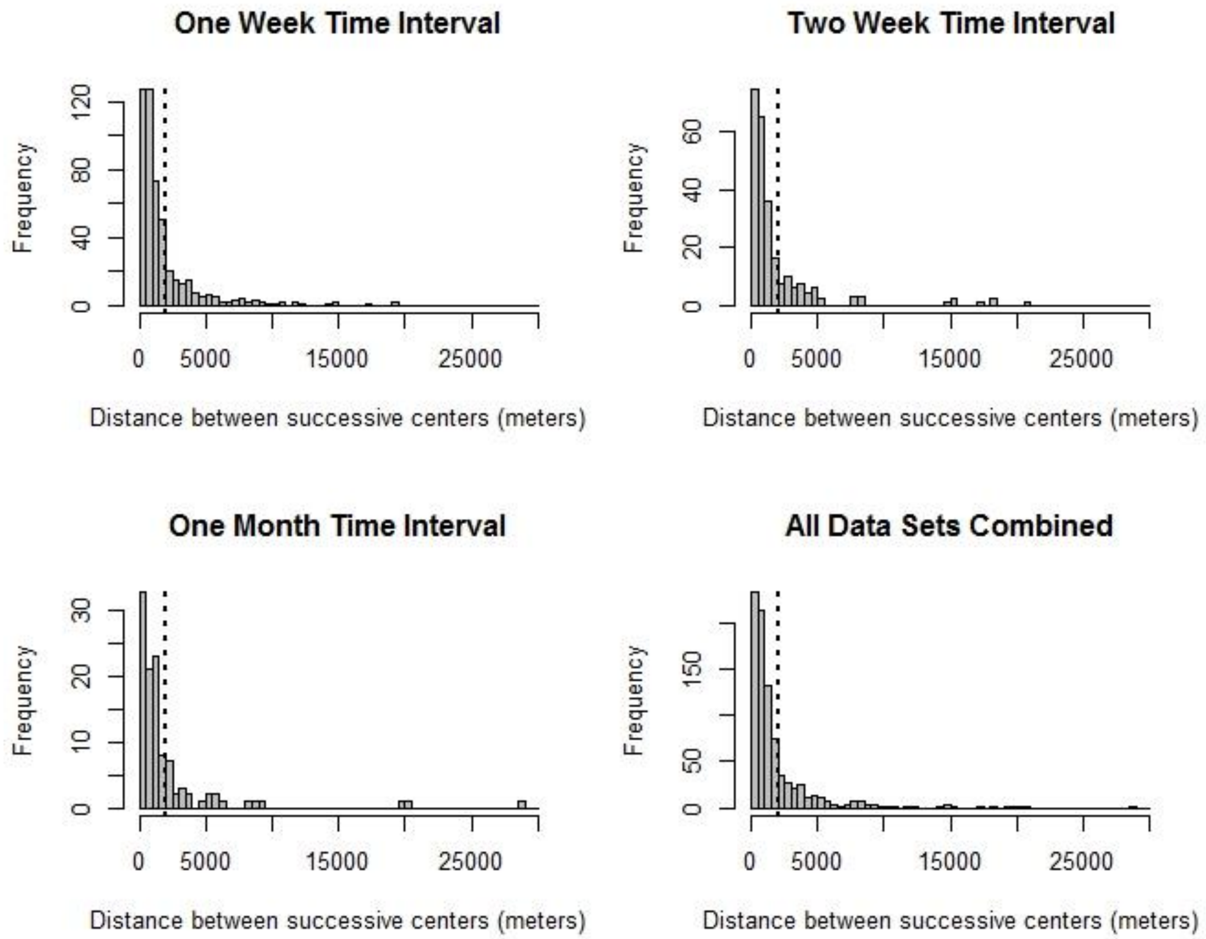


Figure 4. Histograms of distances between successive estimated activity centers demonstrate a distinct threshold at 2000 meters (dashed vertical line) at all time intervals evaluated. This cut-off represented the approximate third quartile for each of the time intervals and all three data sets combined. We used this threshold to distinguish between residents and transients based on home range stability for each month.

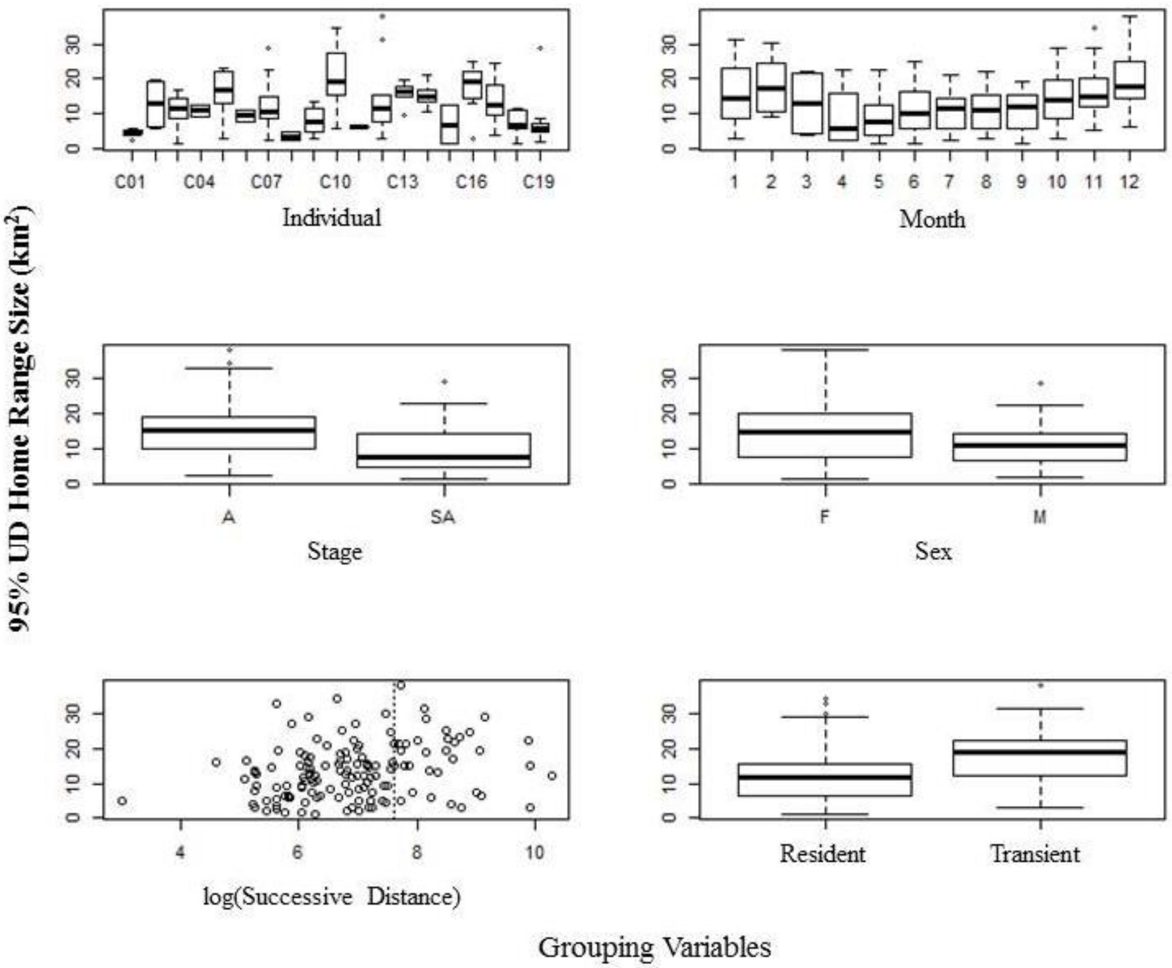
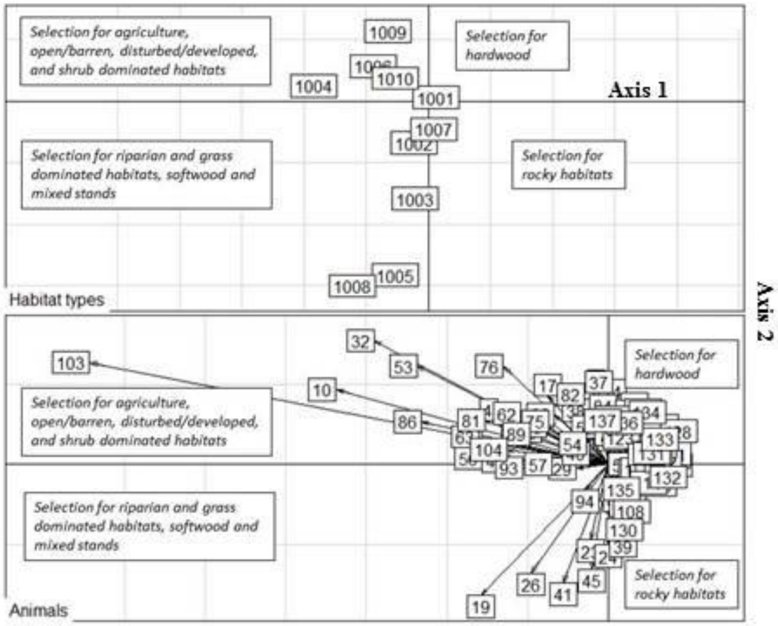
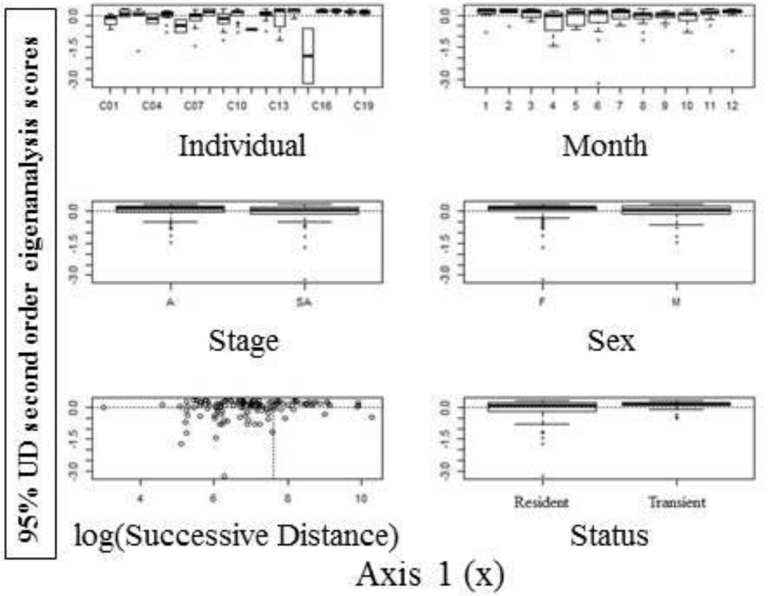


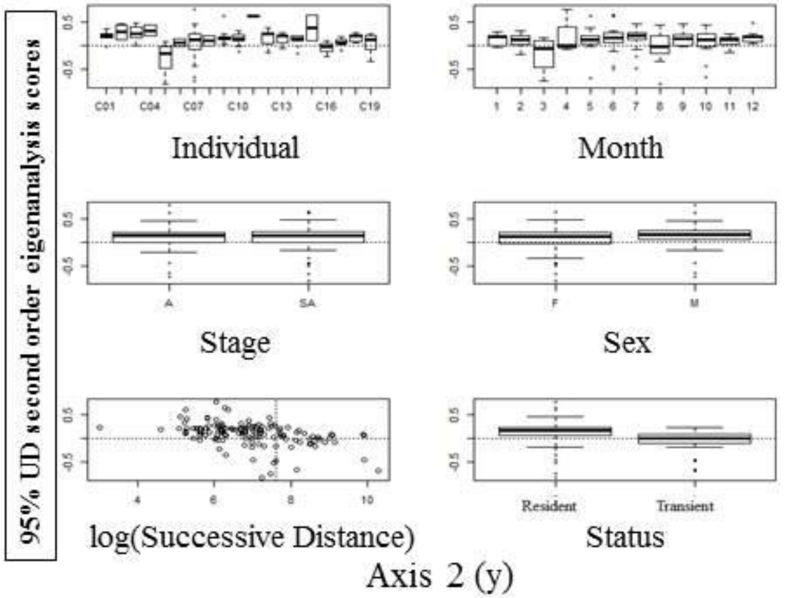
Figure 5. 95% utilization distribution (UD) home range size estimates for 137 coyote-month observations (y-axis) by individual attributes, month, and class structure grouping variables (x-axis). Difference among individuals, and between stages (adult and subadult) and status (resident or transient as classified by distance between successive home ranges) accounted for the majority of variability in overall monthly home range or territory size.

	Eigenanalysis Factor Scores	
Habitat Type	**95% UD second order Axis 1 (x)**	**95% UD second order Axis 2 (y)**
Hardwood Forest **1001**	23.780	11.936
Mixed-Hardwood/Softwood **1002**	-45.417	-136.867
Softwood Forest **1003**	-44.339	-317.852
Agriculture **1004**	-369.255	49.019
Riparian **1005**	-106.492	-566.882
Shrub **1006**	-179.389	113.830
Rock **1007**	16.171	-91.491
Grass **1008**	-244.809	-601.313
Open/Barren **1009**	-132.124	226.9127
Disturbed/Developed **1010**	-108.221	74.631





Axis 1 (x)



Axis 2 (y)

Figure 6. Second-order habitat selection eigenanalysis biplots (top right) for 95% utilization distribution (UD) overall home range by habitat type (boxed numbers in top right pane) and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for habitat types for each axis (top left pane) demonstrated differentiation and relative strength of selection of habitat among areas individuals used to establish monthly home ranges. Values near zero (the origin in the biplots, top and central right panes) represented similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Most individuals established home ranges in either low productivity hardwood stands and rocky habitats (positive values on axis 1, lower left pane) or showed selection for more open, shrub or grass dominated habitats and agriculture (negative values on axis 1). There appears to be greater selection for maintaining territories in hardwood and rocky habitats in winter months and by transients. On axis 2 (lower right) residents with stable territories tended to select to establish home ranges in more open and productive habitats, including agriculture, disturbed/developed, and shrub habitats (negative values on axis 2). Box 103 (right central pane) represents individual C15, a female in June 2013 who demonstrated strong selection for agriculture in the month it was killed.

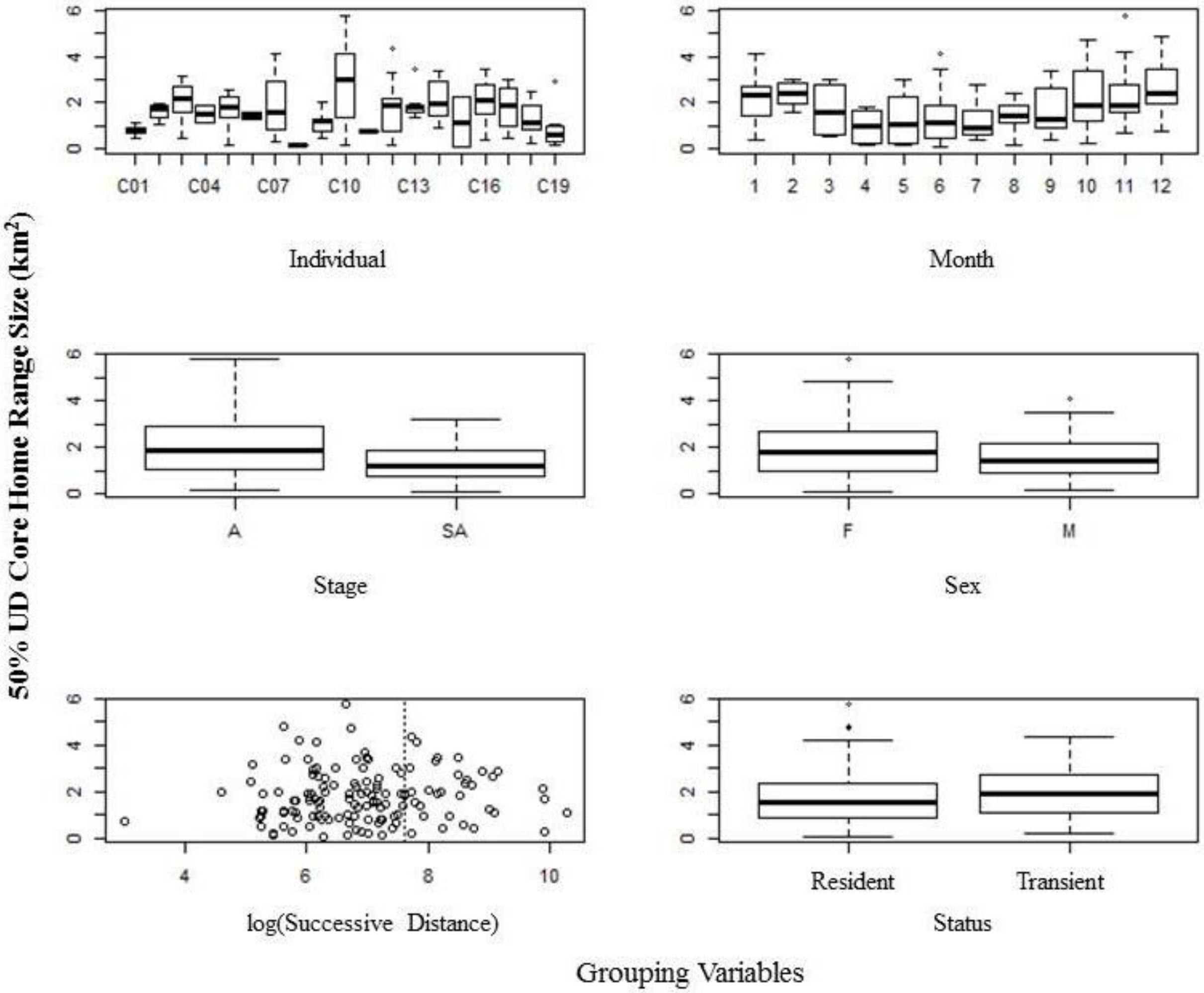
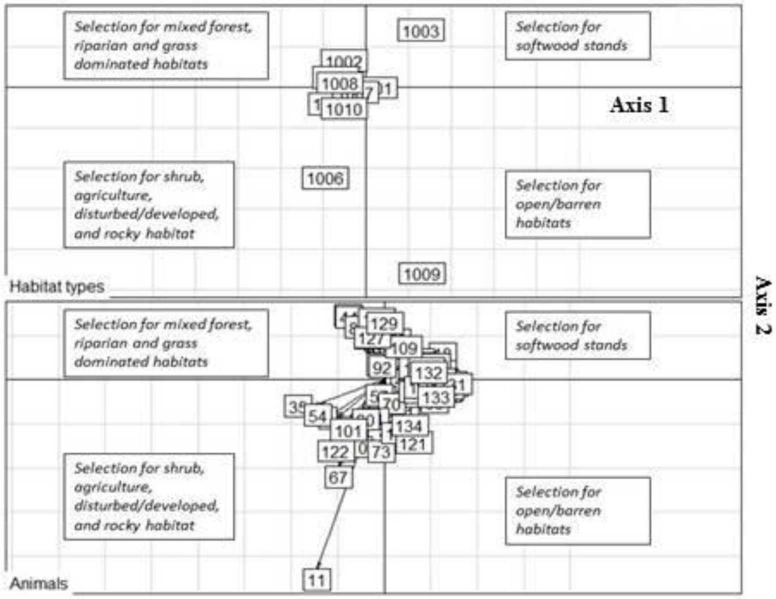
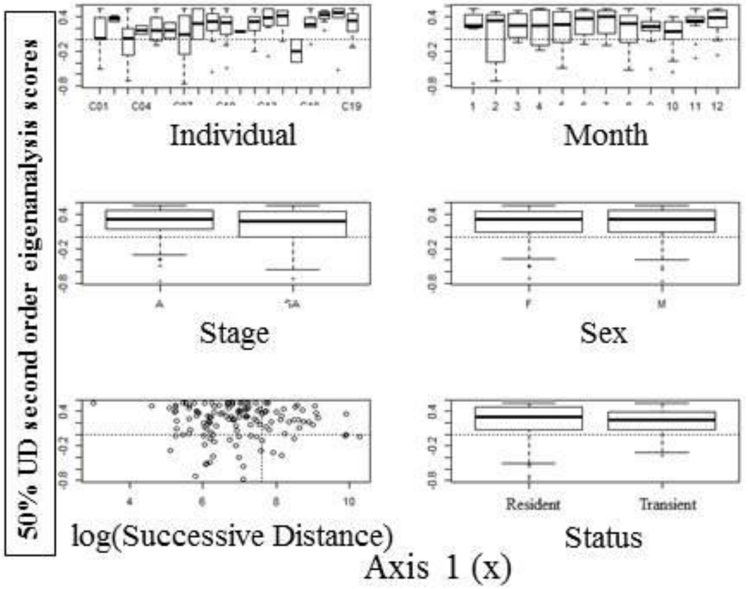


Figure 7. 50% utilization distribution (UD) home range size estimates for 137 coyote-month observations (y-axis) by individual attributes, month, and class-structure grouping variables (x-axis). Difference in core home range size by month and stage (adult and subadult) accounted for the majority of variability with largest monthly core home range sizes in the winter and for adults.

Habitat Type	Eigenanalysis Factor Scores 50% UD second order Axis 1 (x)	 50% UD second order Axis 2 (y)
Hardwood Forest **1001**	18.447	-1.465
Mixed-Hardwood/Softwood **1002**	-52.380	65.365
Softwood Forest **1003**	128.492	141.250
Agriculture **1004**	-80.160	-41.035
Riparian **1005**	-70.455	24.7401
Shrub **1006**	-95.145	-224.181
Rock **1007**	-25.463	-12.839
Grass **1008**	-62.459	10.939
Open/Barren **1009**	131.073	-460.369
Disturbed/Developed **1010**	-52.596	-52.689





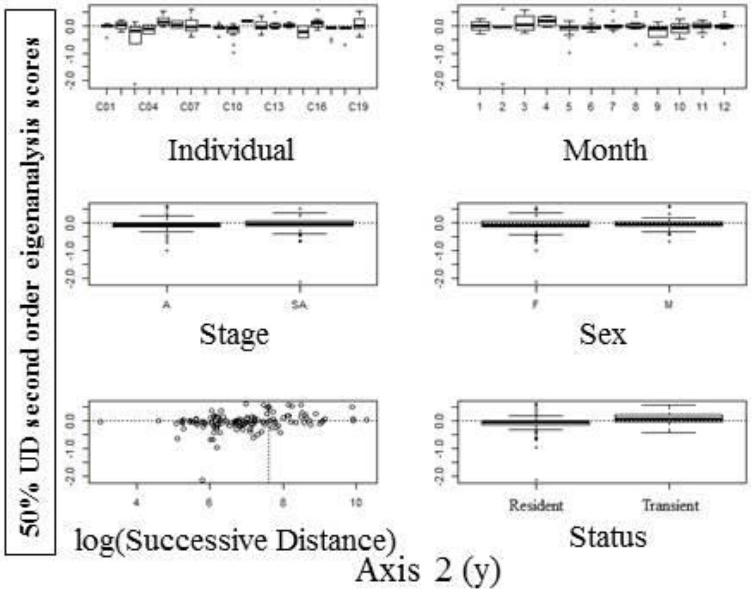
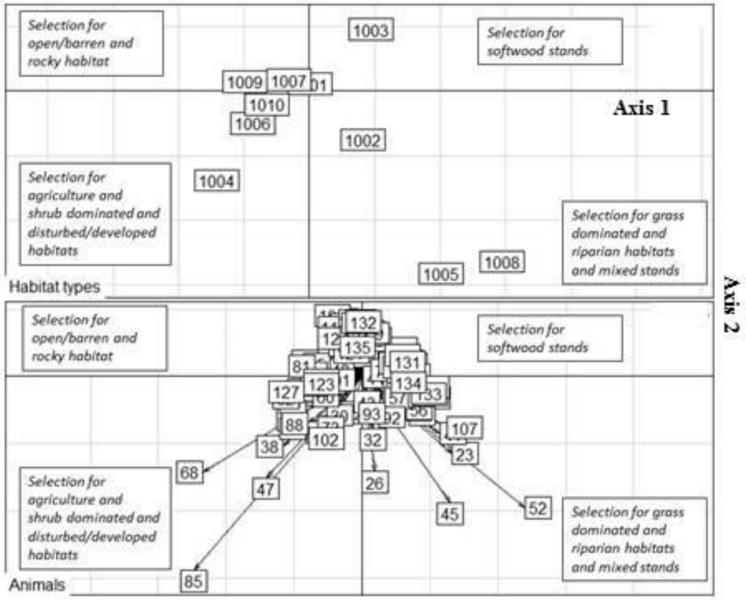
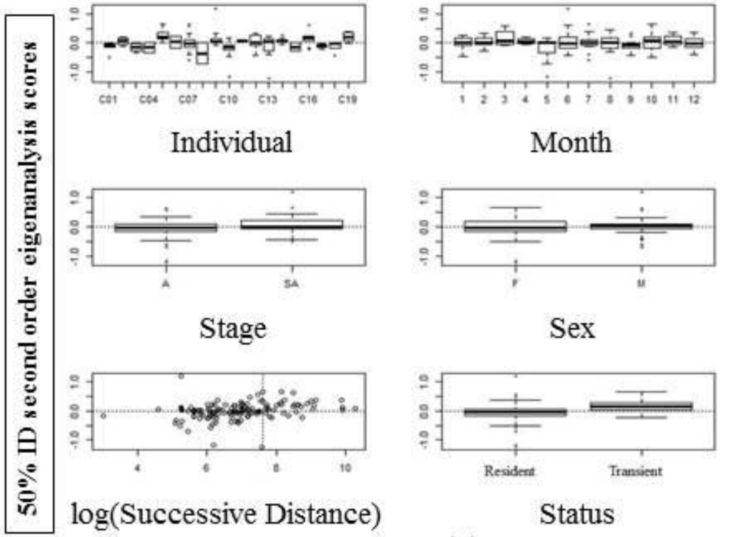


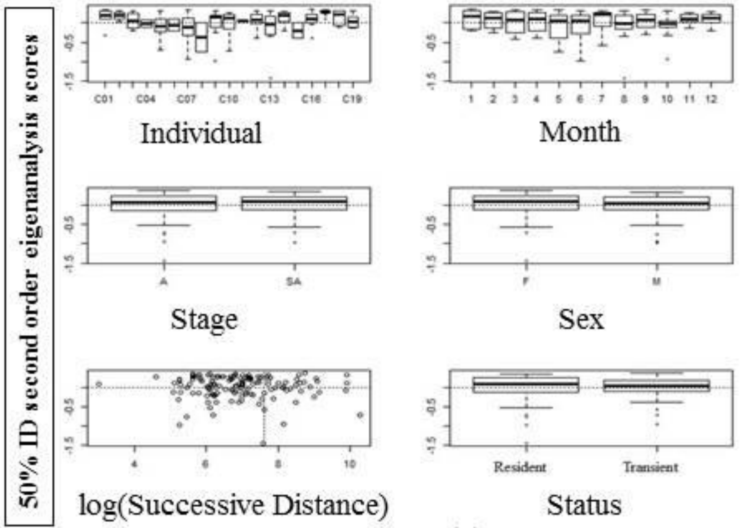
Figure 8. Second-order habitat selection eigenanalysis biplots (top right) for 50% utilization distribution (UD) core home range by habitat type (boxed numbers in top right pane) and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for habitat types for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat among areas individuals used to establish monthly core home ranges. Values near zero (the origin in the biplots, top and central right panes) represented similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Individual was the greatest source of variation along axis 1 (lower left). Most individuals demonstrated positive values for axis 1 in most months, representing selection for establishing core home range areas in relatively safe softwood forest, mixed forests, riparian, and grass habitats, regardless of age, sex, stage, or home range stability. Generally, there was weak evidence for individual as a source of variation along axis 2 (lower right). However, there are exceptional negative outliers representing individuals establishing core areas in high risk/high productivity open/barren, shrub, agriculture, and disturbed/developed habitats in some months. Habitat selection for C03 in February 2011 (box 11 in right central pane), the month it was killed, is the dominant negative value for axis 2.

Habitat Type	Eigenanalysis Factor Scores	
	50% ID second order Axis 1 (x)	50% ID second order Axis 2 (y)
Hardwood Forest **1001**	0.392	10.834
Mixed-Hardwood/Softwood **1002**	81.352	-75.453
Softwood Forest **1003**	94.196	95.447
Agriculture **1004**	-141.402	-138.317
Riparian **1005**	201.367	-281.962
Shrub **1006**	-86.018	-49.573
Rock **1007**	-30.828	17.189
Grass **1008**	294.640	-263.616
Open/Barren **1009**	-98.080	14.720
Disturbed/Developed **1010**	-64.509	-20.729





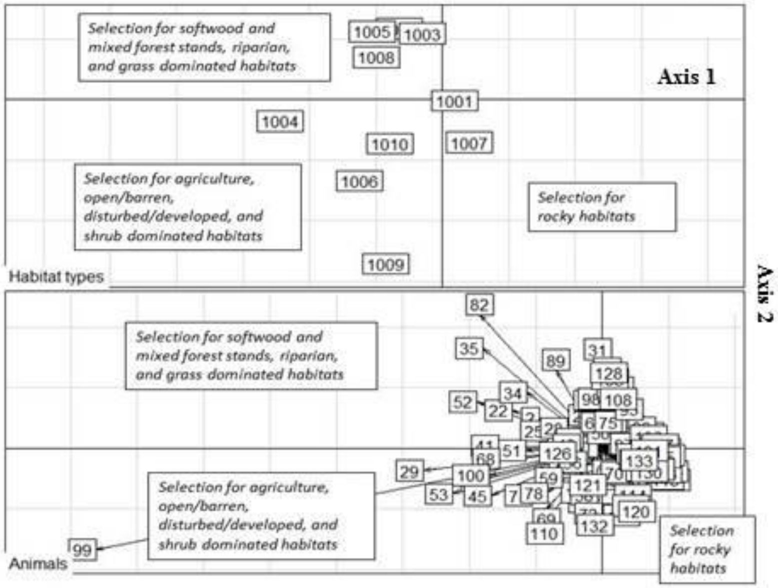
Axis 1 (x)

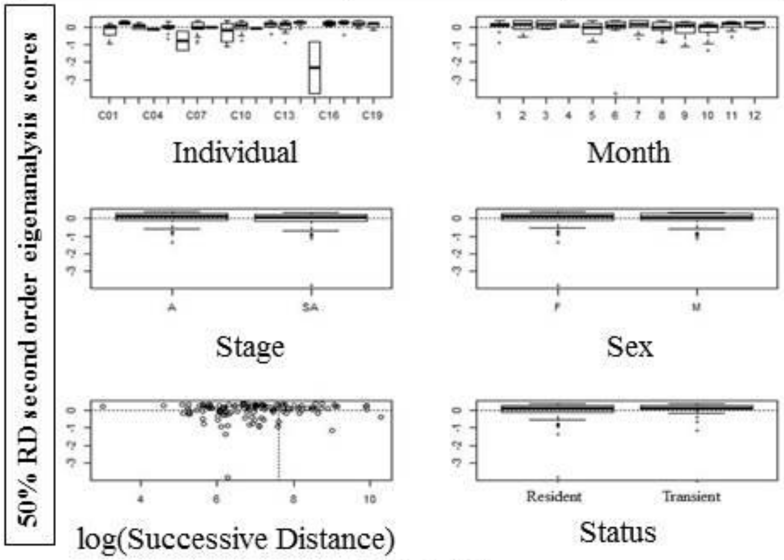


Axis 2 (y)

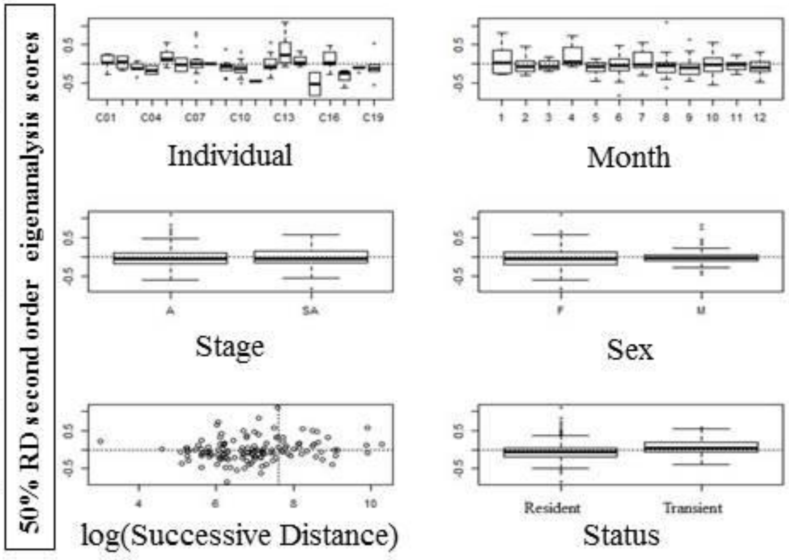
Figure 9. Second-order habitat selection eigenanalysis biplots (top right) for 50% intensity distribution (ID) for intensively used areas by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for habitat types for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat among areas individuals incorporate into monthly home ranges for intensive use. Values near zero (origin in the biplots, top and central right panes) represented similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Subadults and individuals classified as transients showed intensive use of softwood and mixed forest stands in establishing the areas they intensively use across the available landscape as shown by the consistently positive values along axis 1 (lower left). Individual was the greatest source of variation along axis 2 (lower right).

Habitat Type	Eigenanalysis Factor Scores 50% RD second order Axis 1 (x)	 50% RD second order Axis 2 (y)
Hardwood Forest **1001**	19.058	-2.199
Mixed-Hardwood/Softwood **1002**	-64.923	116.599
Softwood Forest **1003**	-30.031	108.694
Agriculture **1004**	-243.857	-35.675
Riparian **1005**	-105.250	112.090
Shrub **1006**	-123.923	-134.039
Rock **1007**	40.138	-70.635
Grass **1008**	-99.534	69.591
Open/Barren **1009**	-85.354	-271.048
Disturbed/Developed **1010**	-79.418	-73.087





Axis 1 (x)



Axis 2 (y)

Figure 10. Second order habitat selection eigenanalysis biplots (top right) for 50% recursion distribution (RD) for frequently used areas by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for habitat types for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat between areas individuals incorporate into monthly home ranges for frequent use. Values near zero (the origin in the biplots, top and central right panes) represent similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Individual was the greatest source of variation along both axis 1 (lower left) and axis 2 (lower right).

APPENDICES

Appendix A. General habitat types and availability based on reclassification of National Land Cover Gap Analysis Project for West Virginia and Virginia (USGS 2011). Raster cells are 1 km^2 and area is masked by a 2-km buffer around all coyote relocations.

Habitat Type	Code	Number of Raster Cells	Area (km^2)	Proportion of Available Habitat
Hardwood Forest	1001	130526	13052.60	0.754
Mixed-Hardwood/Softwood	1002	17738	1773.80	0.102
Softwood Forest	1003	39	3.90	0.0002
Agriculture	1004	10136	1013.60	0.059
Riparian	1005	1466	146.60	0.008
Shrub	1006	704	70.40	0.004
Rock	1007	5624	562.40	0.032
Grass	1008	228	22.80	0.001
Open/Barren	1009	38	3.80	0.0002
Disturbed/Developed	1010	6625	662.50	0.038
Total Area Available		173124	17312.4	

Appendix B. Linear mixed model (LMM) selection for 95% utilization distribution (UD) overall and 50% core monthly home range size based on QAICc (95% UD candidate set) and AICc (50% UD candidate set) with individual as a random effect. Model number refers to the 11 candidate models defined in Table 1. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	(Q)AICc	delta (Q)AICc	QAICc model weight
95% UD Overall Home Range Size	1	3.306					3	-199.188	93.5	0	0.254
	2	1.706	+ (0.239)				4	-195.577	94.1	0.61	0.187
	8	3.674				+	4	-196.06	94.3	0.82	0.169
	9	2.002	+ (0.250)			+	5	-191.425	94.6	1.02	0.152
	5	3.458			+		4	-198.529	95.4	1.87	0.1
	11	3.832			+	+	5	-194.988	96.1	2.55	0.071
	6	1.876	+ (0.228)		+		5	-195.285	96.2	2.67	0.067
	3	2.584		+			14	-183.969	112.7	19.15	0
	10	2.851		+		+	15	-180.651	113.8	20.3	0
	4	1.444	+ (0.183)	+			15	-181.656	114.3	20.73	0
	7	2.712		+	+		15	-183.653	115.1	21.58	0
50% UD Core Home Range Size	10	0.943		+		+	15	-58.022	150	0	0.753
	3	0.867		+			14	-60.937	153.3	3.31	0.144
	4	0.745	+ (0.019)	+			15	-60.764	155.5	5.49	0.048
	7	0.882		+	+		15	-60.899	155.8	5.75	0.042
	8	1.333				+	4	-76.065	160.4	10.42	0.004
	9	1.024	+ (0.045)			+	5	-75.129	160.7	10.71	0.004
	11	1.360			+	+	5	-75.745	161.9	11.94	0.002
	1	1.220					3	-78.631	163.4	13.43	0.001
	2	0.875	+ (0.051)				4	-77.622	163.5	13.54	0.001
	5	1.249			+		4	-78.372	165	15.04	0
	6	0.916	+ (0.047)		+		5	-77.523	165.5	15.49	0

Appendix C. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from second order eigenanalysis (home range selection among individuals) at the 95% utilization distribution (UD) overall monthly home range level based on AICc. Model number refers to the 11 candidate models defined in Table 1. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	AICc	delta AICc	AICc model weight
Second Order 95% UD Overall Home Range Axis 1	NA[1]	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Second Order 95% UD Overall Home Range Axis 2	2	0.637	(+) -0.077				4	13.742	-19.2	0	0.556
	6	0.600	(+) -0.077		+		5	14.016	-17.6	1.61	0.249
	9	0.637	(+) -0.077			+	5	13.742	-17	2.15	0.189
	1	0.124					3	6.860	-7.5	11.64	0.002
	5	0.087			+		4	7.767	-7.2	11.95	0.001
	4	0.693	(+) -0.066	+			15	20.556	-7.1	12.04	0.001
	8	0.122				+	4	6.863	-5.4	13.76	0.001
	11	0.085			+	+	5	7.769	-5.1	14.10	0
	3	0.319		+			14	15.793	-0.1	19.04	0
	7	0.269		+	+		15	16.566	0.8	20.02	0
	10	0.314		+		+	15	15.815	2.3	21.52	0

[1] Unable to fit LMM due to poor transformations and inadequate goodness of fit.

Appendix D. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from second order eigenanalysis (home range selection among individuals) at the 50% utilization distribution (UD) core home range level based on (Q)AICc. Model number refers to the 11 candidate models defined in Table 1. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	AICc	delta AICc	AICc model weight
Second Order 50% UD Core Home Range Axis 1	1	1.689					3	-146.348	99.9	0	0.389
	8	1.750				+	4	-145.723	101.7	1.76	0.161
	2	2.034	(+) -0.050				4	-145.919	101.8	1.89	0.151
	5	1.680			+		4	-146.335	102.1	2.15	0.133
	9	2.075	(+) -0.048			+	5	-145.335	103.6	3.71	0.061
	11	1.742			+	+	5	-145.71	103.9	3.94	0.054
	6	2.037	(+) -0.051		+		5	-145.918	104	4.07	0.051
	3	1.748		+			14	-141.145	122.3	22.41	0
	10	1.784		+		+	15	-140.577	124.5	24.62	0
	4	2.067	(+) -0.048	+			15	-140.752	124.6	24.73	0
	7	1.724		+	+		15	-141.101	124.9	24.95	0
Second Order 50% UD Corel Home Range Axis 2	1	26.300					3	-454.183	72.5	0	0.393
	2	15.630	(+) 1.565				4	-450.459	74.1	1.63	0.174
	8	26.680				+	4	-454.039	74.6	2.13	0.135
	5	26.220			+		4	-454.177	74.7	2.15	0.134
	6	13.860	(+) 1.747		+		5	-449.993	76.3	3.75	0.06
	9	15.930	(+) 1.563			+	5	-450.328	76.3	3.80	0.059
	11	26.600			+	+	5	-454.032	76.8	4.32	0.045
	3	29.940		+			14	-448.512	97.4	24.86	0
	4	20.220	(+) 1.588	+			15	-444.589	99.4	26.87	0
	10	30.140		+		+	15	-448.428	99.9	27.42	0
	7	29.750		+	+		15	-448.492	99.9	27.43	0

Appendix E. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from second order eigenanalysis (intensive use area selection among individuals) at the 50% intensity distribution (ID) home range level based on (Q)AICc. Model number refers to the 11 candidate models defined in Table 1. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	AICc	delta AICc	AICc model weight
Second Order 50% ID Intensive Use Axis 1	9	-0.475	(+) 0.063			+	5	-16.668	43.8	0	0.421
	2	-0.386	(+) 0.056				4	-18.22	44.7	0.95	0.262
	6	-0.477	(+) 0.066		+		5	-17.708	45.9	2.08	0.149
	1	-0.007					3	-20.612	47.4	3.61	0.069
	8	-0.045				+	4	-19.783	47.9	4.08	0.055
	5	-0.012			+		4	-20.595	49.5	5.7	0.024
	11	-0.051			+	+	5	-19.759	50	6.18	0.019
	4	-0.243	(+) 0.045	+			15	-11.519	57	13.21	0.001
	3	0.042		+			14	-12.946	57.3	13.54	0
	10	0.009		+		+	15	-12.039	58	14.25	0
	7	0.026		+	+		15	-12.871	59.7	15.91	0
Second Order 50% ID Intensive Use Axis 2	NA[1]	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

[1] Unable to fit LMM due to poor transformations and inadequate goodness of fit.

Appendix F. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from second order eigenanalysis (frequent use area selection among individuals) at the 50% recursion distribution (RD) home range level based on (Q)AICc. Model number refers to the 11 candidate models defined in Table 1. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	QAICc	delta QAICc	QAICc model weight
Second Order 50% RD Frequent Use Axis 1	1	-0.119					3	-82.063	21.6	0	0.416
	8	-0.015				+	4	-81.534	23.7	2.07	0.148
	5	-0.198			+		4	-81.710	23.7	2.10	0.146
	2	-0.059	(+) -0.009				4	-82.037	23.8	2.15	0.142
	11	-0.093			+	+	5	-81.206	25.8	4.20	0.051
	9	0.037	(+) -0.008			+	5	-81.514	25.9	4.25	0.050
	6	-0.163	(+) -0.005		+		5	-81.701	25.9	4.28	0.049
	3	0.081		+			14	-76.676	46.4	24.79	0
	10	0.166		+		+	15	-76.277	48.9	27.29	0
	7	-0.005		+	+		15	-76.367	48.9	27.30	0
	4	0.146	(+) -0.011	+			15	-76.641	49.0	27.35	0
Second Order 50% RD Frequent Use Axis 2	1	-0.027					3	-13.020	32.2	0	0.348
	2	-0.182	(+) 0.023				4	-12.532	33.4	1.15	0.196
	8	-0.008				+	4	-12.873	34.0	1.83	0.139
	5	-0.020			+		4	-12.999	34.3	2.08	0.123
	9	-0.164	(+) 0.023			+	5	-12.373	35.2	2.98	0.078
	6	-0.180	(+) 0.023		+		5	-12.532	35.5	3.30	0.067
	11	-0.001			+	+	5	-12.852	36.2	3.94	0.048
	3	0.137		+			14	-8.998	49.4	17.22	0
	4	-0.036	(+) 0.028	+			15	-8.305	50.6	18.36	0
	10	0.150		+		+	15	-8.895	51.8	19.54	0
	7	0.149		+	+		15	-8.957	51.9	19.66	0

CHAPTER 3.

Population Dynamics and Density Dependence of Eastern Coyotes in the Central Appalachian Forest, Virginia

Target Journal: Journal of Wildlife Management

ABSTRACT Coyote populations often show signs of density dependent regulation through competition for territories. However, estimating coyote density and other demographic parameters are difficult, especially for populations that exist at low density. This may be especially true for recently established eastern coyote populations in the eastern United States that may still be unregulated as they grow to approach population limitations. We used non-invasive fecal DNA collected from 5 scat sampling sessions over 2.5 years to estimate population parameters for coyotes at 2 different sites (Bath and Rockingham Counties) in the Ridge and Valley region of the central Appalachians in Virginia. We identified individuals using microsatellite genotypes and estimated apparent survival for the local population in both sites across the 5 sessions in a single Cormack-Jolly-Seber model. We estimated density for each site and session separately using spatial replicates of 0.5- km transect segments as “traps” in a spatial capture recapture model. Finally, we derived estimates of recruitment and population growth using an ad hoc approach based on the robust design. We found indications of population regulation, even at low densities (median density Bath County = 8.02 coyotes/100 km^2, median density Rockingham County = 4.68 coyotes/100 km^2). Generally recruitment and apparent survival were inversely related across sites with low apparent survival, but consistent density across seasons and years at the Bath County site. In contrast at the Rockingham site, density fluctuated and recruitment was inversely related to density in the previous sampling period. Our results indicated that the recently established coyote populations in our study areas existed at low density, but still demonstrated boundedness and return rates indicative of density-dependent regulation that were likely limited by competition for territories. In addition, varying levels of apparent survival and recruitment suggested spatial structure with source-sink dynamics across sites. Thus, current attempts to reduce populations are unlikely to be effective and alternative management strategies should be explored.

KEY WORDS ad hoc robust design, apparent survival, *Canis latrans*, coyote, demography, density estimation, density dependence, noninvasive genetics, recruitment, spatial capture-recapture

Journal of Wildlife Management 00: 000-000

INTRODUCTION

Populations are considered regulated if they exhibit boundedness (Murdoch 1994), persistence, and a negative feedback loop where population inputs are inverse to population outputs (Turchin 1995, Hixon et al. 2002). Studies on western coyote (*Canis latrans*) populations have determined that most populations exhibit density dependence and are limited by recruitment based on availability of prey and intraspecific competition for territories (Windberg 1995, Knowlton et al. 1999). Saturated populations with no available territories demonstrated dramatically reduced local recruitment (Knowlton et al. 1999) with reproductive rates determined by the percent of females in a population successfully breeding (Knowlton 1972, Parker 1995) and litter size (Knowlton et al. 1999, Pitt et al. 2003). Reproductive rates were positively related to prey abundance (Clark 1972, Geffen et al. 1996, Gese et al. 1996, Knowlton et al. 1999), negatively related to survival (Crete and Lemieux 1996), lower in saturated populations (Andelt 1985, Parker 1995, Knowlton and Gese 1995), and positively related to removal of adults from the population (Knowlton 1972, Knowlton et al. 1999). Reproduction is typically low in saturated populations characterized by high territoriality and social structure (Parker 1995, Knowlton and Gese 1995); high-ranking individuals are philopatric and low-ranking individuals are dispersers in these saturated populations (Gese 1995, Knowlton and Gese 1995). Finally, reproductive rates were reduced during parasitic outbreaks, typical of populations approaching carrying capacity (Pence and Winberg 1994, Nelson et al. 2003).

While density dependence has been difficult to identify in single studies from expanding and recently established eastern coyote populations, trends in survival, recruitment, and density can be identified from a review and comparison of studies. First, coyote survival in western states and urbanized areas has been relatively high (Bogan 2004, Gehrt 2007, Grubbs and Krausman 2009) compared to survival rates of eastern coyotes. Mortality in eastern studies was mostly human-caused, including trapping, shooting, other forms of lethal removal, road mortality, and incidental poisoning (Post 1975, Smith 1984, Harrison 1986, Crete et al. 2001, Bogan 2004, Houben 2004, Van Deelen and Gosselink 2006, Gehrt 2007, Schrecengost et al. 2009). Even in an eastern population where annual survival was unusually high (0.80 – 0.98), the prevalent cause of mortality was incidental harvest (Chamberlain and Leopold 2001). Annual survival was found to be higher during the colonization period (0.60 – 0.70) and decreased after population establishment (0.50) due to increased human-caused mortality (Crete and Lemieux 1996). Finally, mortality was often determined to be age specific, with high mortality rates for juveniles and individuals < 1 year of age (Hilton 1978, Harrison 1986, Crete and Lemieux 1996, Lloyd 1998, Crete et al. 2001, Van Deelen and Gosselink 2006) and dependent on natal population density, and increasing with dispersal risks (Messier and Barrette 1982, Harrison 1986, Atwood 2006).

In addition, estimates of reproductive recruitment into eastern coyote populations were highly variable. Estimates of annual percentage of breeding females in eastern coyote populations varied from 23% to 72% (Smith 1984, Priest 1986, Poulle et al. 1995, Lloyd 1998, Mahan and Mahan 2007), litter sizes brought to term ranged from 3 to 12 pups per litter (Smith 1984, Stephenson and Kennedy 1993, Parker 1995, Lloyd 1998, Nelson and Lloyd 2005, Mahan and Mahan 2007), and pups surviving to one year of age ranged from 4% to 50% (Hilton 1978, Priest 1986, Parker 1995,). In aggregate, these studies suggest that mortality and likely, emigration, may increase with density and reproduction can be variable according to local conditions, demonstrating capacity for a density-dependent negative-feedback mechanism for population regulation based on competition (Hixon et al. 2002).

We conducted population monitoring surveys at 2 study sites in the western mountains of Virginia to estimate population density and examine population dynamics to evaluate evidence of local coyote population density dependence. The study occurred in Bath County and Rockingham Counties, in the Allegheny Highlands of Virginia on the eastern divide and bordering West Virginia. Both study areas consisted primarily of mature hardwood forest habitat with low expected coyote densities (Samson and Crete 1997, Richer et al. 2002, Kays et al. 2008). However, the Rockingham County study area was located in a large block of contiguous forest in the western portion of the county while the Bath County study area contained forest interspersed with veins of more productive pasture, hayfields, and human development along linear valley bottoms (Chapter 2).

We extracted fecal DNA from scat samples collected along established scat transects for 5 sampling sessions over 2.5 years. We identified and matched individual coyotes based on genotypes to construct capture histories and estimated apparent survival, density, recruitment, and population growth rates for each site. Coyotes were first sighted in the western part of Virginia as early as the 1950s and populations became established in the 1980s (Parker 1995). Therefore we assumed the local populations are established, and no longer colonizing. We hypothesized coyote population dynamics will indicate density-dependent regulation with recruitment inverse of apparent survival over time. We predicted that both mortality and recruitment would be higher at the Bath County study site due to the higher human population density throughout western Bath County compared to western Rockingham County. Because annual density is also expected to be dependent on prey availability (Knowlton et al. 1999), we predicted density will be greater at the Bath study site as there is greater habitat diversity and potential anthropogenic food resources from interspersed human and agricultural habitats (Rose and Polis 1999, Fedriani and Kohn 2001). Finally, we predicted local densities would fluctuate seasonally as a result of reproductive pulses and dispersals (Knowlton et al. 1999) with greater densities in the summer following birth of pups and lower densities in the winter following dispersal.

METHODS

Study Area and Sample Collection

Bath and Rockingham Counties, Virginia are located in the northern Ridge and Valley region of the central Appalachians bordering West Virginia (Figure 1). We collected fecal DNA samples over 5 sessions, three summer sessions (July 2011, 2012, and 2013) and two winter sessions (February 2012, and March 2013), to estimate rates of change over intervals with expected population inputs (spring) and population outputs (fall). We established approximately 200 km of scat transects along dirt roads, hiking trails, and well-defined game trails on publicly managed lands (predominantly George Washington National Forest) in each study area: 213 km in Bath County, 208.5 km in Rockingham County. Scat accumulation rates can be slow for highly mobile, low-density populations. Conducting repeated secondary sampling sessions in order to estimate detection within sessions can violate closure assumptions when accumulation periods are lengthy, especially if apparent survival is low. However, these are the populations we are often most interested in monitoring. Thus, we chose to use single-session detections over spatial replicates during a single month for each sampling session to satisfy the population closure assumption. We first cleared scat from all transects and then collected fecal DNA samples and recorded GPS locations for all newly accumulated scats one month later.

Identifying Individual Coyotes from Scat Samples

We extracted DNA from feces using Qiagen QIAmp DNA stool kit (Qiagen Inc., Valencia, CA) in a lab designated for low-quality, low-quantity DNA. We included an extraction negative in each extraction batch to allow for identification of reagent contamination. We screened all samples using a species identification multiplex that allows co-amplification and fragment analysis of two segments of the mitochondrial DNA (mtDNA) control region for scoring species-specific fragment sizes (DeBarba et al. 2014). The 2 study sites were located in the assumed convergence zone of the northern and southern fronts of eastern coyote range expansion (Parker 1995, Kays et al. 2008) which indicated gray wolf (*Canis lupus*) mtDNA haplotypes may occur in the population. In addition, Adams et al. (2003) found domestic dog (*Canis familiaris*) mtDNA haplotypes in coyotes in the southeastern US. Two tissue samples collected from 19 different individual coyotes captured in the Bath County study area (Chapter 2) were identified as possible domestic dog or gray wolf based on amplified fragment sizes from the mtDNA test. Thus, we attempted to genotype all samples identified as canid (*Canis sp.*) and screened for domestic dogs using a more sensitive nuclear DNA (nDNA) genotype assignment test as described below. To identify individual genotypes, we combined 9 nuclear microsatellite loci primers (FH2001, FH2054, FH2088, FH2137, FH2611, FH2670, FH3725, C09.173, and Cxx.119 – Holmes et al. 1994; Breen et al. 2001; Guyon et al. 2003) and 2 canid specific-sex identification primers (Seddon 2005) in a multiplex for polymerase chain reaction (PCR) amplification under conditions described in Stenglein et al. (2011). We included a PCR positive (known coyote tissue sample) and PCR negative control in each PCR plate to identify PCR failure or potential contamination.

We analyzed PCR products using an Applied Biosystems 3130xl ABI capillary machine (Applied Biosystems, Inc., Foster City, California) and scored alleles by viewing amplification peak fragment sizes in Genemapper 4.0 (Applied Biosystems). We initially performed PCR for each sample twice to cull poor quality nDNA samples (samples with <50% amplification across the nine loci not associated with sex chromosomes). We then repeated PCR 1 – 3 more times for each sample to confirm alleles for each locus. We required two repetitions to confirm heterozygous loci and three repetitions to confirm homozygous loci to correct for potential genotype errors in low quality-low quantity DNA samples from allelic dropout and polymerase errors (Taberlet et al. 1996). We used RELIOTYPE (Miller et al. 2002) to confirm 95% accuracy of genotypes observed in only a single sample.

Finally, scat sample genotypes collected for this study (closed sessions for population monitoring) were added to scat sample genotypes identified from simultaneous monitoring efforts to estimate coyote diet and scat accumulation rates in both study areas and from coyote home range use in the Bath County study area. Although these other samples were not collected during the established closed-density monitoring sessions, we combined samples from all scat collection efforts in the 2 study areas only for genetic analyses to improve sample sizes for assignment tests and estimation of summary population genetics statistics required to estimate of $P_{ID(sibs)}$ (Waits et al. 2001). The additional samples were not included in models to estimate population demographic parameters described below. We calculated $P_{ID(sibs)}$ (Waits et al. 2001) in GenAlEx 6.501 (Peakall and Smouse 2006) using an allele frequency data set consisting of individual coyotes identified with fecal DNA with alleles confirmed at all loci and tissue samples from known captured individuals in the study area (Chapter 2). We matched genotypes from different scat samples to the same individual canid using GenAlEx 6.501 and the calculated $P_{ID(sibs)}$ (Waits et al. 2001) to conservatively distinguish between genetically similar siblings ($P_{ID(sibs)} < 0.001$ at 7 loci required for a match, $P_{ID(sibs)} = 0.000069$ at all 9 codominant loci). We combined all individual canid genotypes with genotypes from 19 coyotes captured in the Bath County study area and 28 domestic dogs (*Canis familiaris*) and screened the canid genotypes in STRUCTURE version 2.3.4 (Pritchard et al. 2000) with 9 loci, 2 assumed populations, 100,000 burnin and 200,000 iterations. We removed all genotypes that clustered with known domestic dog samples and used the remaining confirmed individual genotypes from the 5 closed-session population monitoring surveys to construct spatial capture-recapture data sets for both study sites resulting in a total of 10 SCR data sets to estimate density (five sessions for each site). To estimate survival, we created a capture history by recording whether an individual was detected during a session and noted site as a grouping factor.

Population Parameter Estimates

Apparent Survival. -We estimated apparent survival (ϕ) and detection (p) using the Cormack-Jolly-Seber (CJS) model in program MARK (White and Burnham 1999) implemented through the RMark Package (Laake 2013) in Program R (R Core Team 2013) with individual encounters for 5 sessions grouped by both sites. We constructed a candidate model set consisting of 25 candidate models testing whether survival and detection were best estimated by site (Bath or Rockingham), session (July 2011, February 2012, July 2012, March 2013, and July 2013), season (winter or summer), or combinations of site and session or season (site * session or site * season). We imported the full model [ϕ(site*session) *p*(site*session)] to MARK and estimated goodness of fit using parametric bootstrap with 999 simulations and estimated the overdispersion parameter ($\hat{c}$) by dividing the observed $\hat{c}$ by the mean $\hat{c}$ for the simulations. We selected the best model using (Q)AICc and assessed usefulness of estimates of survival based on precision.

Density.-We estimated coyote density for each site for all 5 sessions separately. We used a hierarchical spatial capture-recapture (SCR) single occasion model for each closed session at each site. We used 0.5- km transect segments as spatial replicates and fit the SCR_0 model (Royle et al. 2013a, Sutherland et al. 2014). The model consists of encounter histories of individuals detected by fecal DNA at specific transect segment locations (J) over a single sampling occasion ($K = 1$). The process model assumes that individual animals use space around an individual activity center (s), and that probability of detection at a specific trap decreases with distance of that trap from activity centers, represented by a scaling parameter (σ). We assumed a bivariate Gaussian (half-normal) distribution detection function defined by parameter σ. We recognize a monotonically decaying detection rate from an activity center may not be ideal for detection of scat for territorial animals. Thus, estimates of σ may be biased by this assumption and 95% home range should not be inferred from σ. However, our primary interest is estimating density, and while the size of estimated home ranges may be biased by violation of this assumption, the estimate of the number of activity centers in the state space should not be, and the bivariate Gaussian detection function has been well tested and density estimates from models employing the bivariate Gaussian detection function have proven robust to most assumption violations (Royle et al. 2013a).

We used data augmentation to account for individuals present but not detected during the study (Royle and Young 2008). For each of the 10 data sets we set a maximum number of possible activity centers (M) within an area (*S*) for each site- and session-specific state space (Table 1). We associated an indicator variable (z_i, outcome of a Bernoulli trial) with each possible unobserved activity center to estimate whether those possible activity centers are representative of individuals that were present in the area but that had capture histories consisting of all zeros, or whether they are structural zeros (not representative of undetected individuals), with a binomial distribution characterizing all trials (ψ). All activity centers (detected and estimated nonstructural zeros) are summed and density is derived by dividing the sum of activity centers within the state space by the total area of the state space. The choice of *S* is not arbitrary, but is a prior of the binomial point process model and is determined by testing the sensitivity of resulting parameter estimates to changes in the size of *S*, and thus may vary by site and session (Table 1).

We formatted data using the SCR23darray() function analysis package scrbook (Royle et al. 2014) in R (Core Development Team 2013) and implemented each model using the rjags (Plummer 2014), and coda (Plummer 2006) packages. We ran each model with 3 Markov chain Monte Carlo (MCMC) chains with 100 adaptations for the Metropolis-within-Gibbs algorithm, and then used coda to sample 200,000 iterations from the posterior distributions of each monitored parameter (λ_0, σ, ψ, *N*, and *D*) at a thinning rate of 1 (no thinning), including a burn-in of 100,000 iterations. We assessed MCMC convergence by visually inspecting trace plots for each monitored parameter, and comparing $\hat{R}$ statistics to1.1 (Gelman and Rubin 1992). In addition, we subset 30,000 iteration posteriors from different locations within each 100,000 iteration posterior and confirmed similar estimates within reasonable MCMC error. We reported the posterior means and standard deviation, medians, and 95% credible intervals for λ_0, σ, and ψ, and we report the posterior mode for *D* as it is unbiased compared to the posterior mean in SCR models (Chandler and Royle 2013).

Recruitment. - We used an ad hoc robust design approach combining the apparent survival estimates from the CJS model and the site and session specific density estimates from the SCR models to derive estimates of net new recruits to the population (B_i) and per capita recruitment (f_i) over each interval (Pollock 1981, 1982; Williams et al. 2002). We estimated B_i using a Jolly-Seber estimator (Jolly 1965, Seber 1965, Pollock et al. 1990) where $\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i)$, and $f_i = \frac{\hat{B}_i}{\hat{N}_i}$, or the number of new animals at session $i + 1$ per the number present at i. We estimated approximate variance for B_i following Pollock et al. (1990) where $var(\hat{B}_i) = var(\hat{N}_{i+1}) + \phi_i^2 * var(\hat{N}_i) + N_i^2 * var(\hat{\phi}_i) + var(\hat{\phi}_i) * var(\hat{N}_i)$. We estimated variance for f_i by calculating the variance of a ratio of random variables (Mood et al. 1974) where $var(f_i) = f_i^2 * (\frac{var(B_i)}{\hat{B}_i^2} + \frac{var(N_i)}{\hat{N}_i^2})$.

Population Growth Rate. - We derived population growth as the ratio of posterior mode density estimates from the SCR model ($\hat{\lambda}_i = \frac{\hat{D}_{i+1}}{\hat{D}_i}$) between each session. We estimated variance for λ_i by calculating the variance of a ratio of random variables (Mood et al. 1974) where $var(\lambda_i) = \lambda_i^2 * (\frac{var(N_t)}{\hat{N}_t^2} + \frac{var(N_{t+1})}{\hat{N}_{t+1}^2})$.

RESULTS

Individual Coyote Identification from Scat

We collected a total of 5048 fecal samples across all simultaneous scat collection monitoring efforts and identified 1003 (19.87%) as canid using mtDNA species identification. We successfully amplified nDNA microsatellites and confirmed genotypes at 7 loci for 579 of 1,003 samples (57.7%). After removing genotypes identified as domestic dog (39 samples, 32 individuals) we identified 146 individual genotypes across the 2 study sites. For the closed session population monitoring we genotyped 347 total scat samples and confirmed 107 individual coyotes over 5 sessions at the 2 study sites.

Population Parameter Estimates

Apparent Survival. – Bootstrap goodness of fit indicated evidence of lack of fit ($p < 0.001$) so we used $\hat{c} = 2.20$ (observed deviance of most parameterized model/mean simulation deviance) to estimate a quasilikelihood adjustment to (QAICc) for model selection. There were several competing models that all included site-specific survival and nested parameterizations of detection including site and season (Table 2). These models indicated detection was higher in the summer than the winter at the Bath County site, but lower in the summer compared to winter at the Rockingham County site, so we did not attempt to constrain detection with a post hoc additive model (Appendix 1). As the top 3 models were all nested and had approximately equivalent model weights (Table 2), we chose to use the [ϕ(site) p(site*season)] model ($\phi_{Bath} = 0.442$, 95% CI = 0.259 – 0.643, and $\phi_{Rockingham} = 0.863$, 95% CI = 0.269 – 0.991) for further population parameter estimates (Table 3), as this model produced practical estimates of apparent survival and would not be affected by constraints on detection.

Density. - Density estimates appeared to vary between the 2 sites among sessions at the Rockingham study area (Figure 2, Table 3, Appendix 2). At the Rockingham County study area, density was higher and less precise during the winter sessions (February 2012 posterior mode = 7.53/100 km^2, 95% credible interval = 4.52 – 14.46; March 2013 posterior mode = 8.53/100 km^2, 95% credible interval = 6.43 – 15.16) than during the summer sessions (July 2011 = 2.41/100 km^2, 95% credible interval = 1.21 - 10.54; July 2012 = 4.68/100 km^2, 95% credible interval = 2.51 - 16.07; July 2013 = 3.77/100 km^2, 95% credible interval = 2.74 - 6.51). The Bath County study area reflected higher but more consistent density estimates than Rockingham across all sessions regardless of season (median density for Bath County study area = 8.02/100 km^2; minimum density July 2013 = 5.53/100 km^2, 95% credible interval = 2.76 – 19.72; maximum density March 2013 = 9.04, 95% credible interval = 7.32 – 14.18).

Recruitment. - Both net recruitment (B_i) and per capita recruitment (f_i) were consistently positive for the Bath County study area over each season interval (Figure 2, Table 3). Over 6-month intervals, recruitment and per capita recruitment in Bath County ranged from 1.53 to 5.56 new recruits and from 0.17 to 0.71 recruits per capita, respectively. At the Rockingham County study area, recruitment alternated between seasons with greater numbers of recruits between the summer and winter sessions and negative estimates of recruits between winter and summer sessions (range = -3.59 – 5.45) suggesting no recruitment into the population over these intervals. Per capita recruitment demonstrated the same fluctuating seasonal pattern in the Rockingham County study area (range = -0.42 – 2.26).

Population Growth Rate. - Population growth rate ($\hat{\lambda}_i$) at the Bath County study area was near or above 1 for the first three 6-month intervals (range = 0.91 – 1.15), and then may have declined for the fourth interval between March and July 2013 (0.61, SE = 0.12) (Table 3). At the

Rockingham County study area population growth rate was greater than 1 in the 6-month intervals between the summer and winter sessions and less than 1 between the winter and summer sessions (range = 0.44 – 3.12) (Table 3).

DISCUSSION

The Bath County study area had generally higher densities than the Rockingham County study area as predicted, likely due to greater availability of resources. Except for the final summer session, the higher estimated densities in Bath were relatively consistent across seasons and years (~8 coyotes/100 km^2) and the population growth rate was approximately 1 between each season. The estimate for the final session is lower but less precise due to the small sample size and very small number of recaptures (Table 1). This may be a result of excessive rainfall during the accumulation period following initial clearing for the session in Bath County which likely removed scats and decreased DNA success rates for remaining scats. Clearing for the Rockingham transects followed clearing for Bath County and occurred during the persistent heavy rains and individuals detected and recapture rates were much higher. Thus, we do not have as much confidence in the final density estimate for Bath County. For the first four sessions in Bath County, we found unvarying density estimates despite very low 6-month apparent survival estimates (0.442) across seasons suggesting population persistence and a possible negative compensatory feedback mechanism. We did not detect any seasonal variability in density, suggesting immigration may be an important density-dependent response mechanism (Lieury et al. 2015), in addition to any increases in reproductive rates. New recruits estimates for the Bath County study area were greater than for the Rockingham study area, which had higher apparent survival (0.863), and per capita recruitment in Bath County was always greater than 0 for each session, regardless of season, further highlighting the possible role of local immigration in population persistence.

The dynamics at the Rockingham study area demonstrate an inverse relationship between density and per capita recruitment and number of recruits in the population (Figure 2), although this may also be an artifact of negative sampling covariance if density estimates were biased. Interestingly, density estimates were more than twice as high for the winter sessions than the summer, opposite of our initial predictions. In addition, per capita recruitment was greater than 0 over fall intervals compared to no new recruits over spring intervals, and population growth rate estimates were greater than 1 for the period between summer and winter sessions and less than 1 for the period between winter and summer sessions. It is possible this is a reflection of the detection sensitivity of our sampling method. Previous studies found whelping to occur in late March to late May and dens are abandoned after 2-3 months of age, with increasing pup independence at 4 months of age (Priest 1986, Parker 1995). In our study area, births seemed to occur in mid-late April, which would mean pups are not moving around independently until August, after our summer sampling session. Because we were sampling transects, and not rendezvous sites (Stenglein et al. 2011), it is possible we were not detecting the reproductive pulse in the summer, but were detecting new individuals in the winter resulting in increased densities. Because apparent survival was relatively high (0.863) in the Rockingham study area, it is possible those individuals dispersed out of the population before the following summer session, reflected in reduced recruitment and lower densities (Knowlton et al. 1999). One way to test this hypothesis would be to determine if individuals first detected in the winter sessions are offspring of individuals in the previous summer session, however this would require more loci and likely greater sample sizes. In addition, it is also possible the higher density in winter is a result of increased transients or individuals attempting to immigrate into the study area and that the summer population is comprised of fewer individuals that are residents and defending territories.

Density is a central parameter of interest in ecology and wildlife management (Kéry and Schaub 2012), and there have been several recent attempts to quantify coyote densities (Bozarth et al. 2015) to allow for comparisons across regions (Hansen et al. 2015) or changes in populations over time (Gulsby et al. 2015). However these studies often required problematic assumptions about closure, counts, or detection that may bias estimates, particularly in coyote populations that had high mortality and complex adaptive social structures. We found combining single-season scat surveys with non-invasive genetics and a spatial replicate SCR model (Sutherland et al. 2014) was a successful approach for estimating coyote density and population growth in our study area. We were also able to combine SCR model estimates with CJS apparent survival estimates to derive recruitment estimates using an ad hoc robust design approach to address hypotheses concerning population regulation.

However, there is room for improvement based on the lessons learned here. Sample sizes and detection could be improved by extending the length of the closed session slightly. Recapture rates were highest for both sites during the winter 2013 session. This session was completed prior to denning, but was slightly later than intended because of periods of high snowfall that prohibited detection of scats for both the clearing and the collection sessions. Thus, the accumulation period was one to two weeks longer for this session and that likely contributed to larger sample sizes, better recapture rates, and more precise estimates. For our study area, it may be preferable to increase the length of the closed session to 6 weeks to improve estimates. In addition, we found initially clearing transects to be a critical step as test samples collected during clearing sessions detected individuals known to be killed 1-4 months before. Thus it is important to consider closure and accumulation rates to provide an adequate sample for density estimates (Lonsinger et al. 2014).

There are several other considerations that could improve estimates from the SCR models. First, coyote space use and home range were variable, and often determined by class structure (Chapter 2). Including habitat covariates could result in some improvement to model estimates (Royle et al. 2013a). However, biases or uncertainty due to differences in habitat, especially in our study area, were likely less important than the challenges associated with class structure. While there was no evidence for differences in home range size by sex, there was support for differences in home range size between adults and subadults, and especially between residents and transients (Chapter 2). Estimates of the spatial scalar, σ, could be dramatically improved if allowed to differ for residents and transients (Royle et al. *in revision*). In addition, incorporating resource selection functions (Royle et al. 2013b) could also improve accuracy and precision. Estimates of σ may also be biased by the chosen detection function (Gaussian bivariate "half-normal"). The initial Gaussian bivariate SCR model (Royle et al. 2013a) was developed to estimate carnivore densities from camera-trap photographs which are direct observation of the animals, so the assumption that detection is highest at an individual's activity center is often reasonable. However, detection based on collection of fecal DNA from transects may result in behavioral biases if detection is uniform throughout a home range or greater towards the outer portions of the home range for territorial animals such as coyotes (Allen et al. 1999, Gese 2001). In addition, there may be a sampling bias as detections can only occur along transects. Validation of detection functions for this sampling method could dramatically improve identifiability, accuracy, and precision for estimates of all parameters within the model. Finally, recent developments for SCR CJS (Gardner et al. 2010a) would likely allow for more useful session-specific estimates for apparent survival compared to the maximum likelihood estimates we used here. This would be especially true for low-density populations and would improve derived estimates and our ability to identify trends over time and across sites.

CONCLUSIONS

Our findings align with demographic expectations if the local populations in both study areas were established and regulated by density dependence. The Bath County study area demonstrated persistence, despite very low, 6-month apparent survival and there was evidence of compensatory recruitment over 6-month intervals. In addition, lower densities, higher apparent survival, and seasonal population fluctuations in density and recruitment indicate boundedness at the Rockingham study area (Murdoch 1994; see also Windberg 1995, Knowlton et al. 1999). Although the two study areas were only approximately 100-km apart, there were indications of demographic spatial structure within the region. This finding was surprising as the habitat is similar across our study areas and the only discernible difference is increased year round interaction with humans in Bath County.

Overall, our findings were similar to recent studies documenting the ineffectiveness of culling efforts for red foxes (*Vulpes vulpes*) in agricultural areas in England (Baker and Harris 2006) and France (Lieury et al. 2015) due to compensatory immigration. Our results suggest human-coyote conflicts will be more difficult to be resolve, and current local control efforts in the region including nuisance species designation, indiscriminant harvest, bounties, and lotteries may be insufficient. If management of coyote populations is a priority for the area, we suggest that alternative landscape-level and conflict-specific solutions need to be considered.

ACKNOWLEDGMENTS

We would like to thank collaborators Robert Alonso, the Virginia Department of Game and Inland Fisheries, including Mike Fies, Dave Steffen, Al Bourgeois, and Nelson Lafon, US Forest Service, including Steve Tanguay, Carol Croy, the Nature Conservancy and Marek Smith at the Warm Springs Mountain Preserve, and the Laboratory for Ecological and Evolutionary Conservation Genetics, including Jen Adams, Caren Goldberg, Claudia Wultsch, Rob Lonsinger, Susannah Woodruff, Kate Cleary, Matt Mumma, Joel Tebbenkamp, and Carisa Stansbury. In addition, we thank Mike Cherry, Mike Conner, Jim Nichols, and Andy Royle for invaluable discussions on model implementation and interpretation. Financial support provided by the Virginia Department of Game & Inland Fisheries came from the U.S. Fish & Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Finally, we appreciated additional funding and support from the Appalachian members of the Virginia Deer Hunter Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).

LITERATURE CITED

Adams J. R., J. A. Leonard, and L. P. Waits. 2003. Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern coyotes. Molecular Ecology 12:541-546.

Allen, J. J., M. Bekoff, and R. L. Crabtree. 1999. An Observational Study of Coyote (*Canis latrans*) Scent-marking and Territoriality in Yellowstone National Park. Ethology 105:289-302.

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:1-45.

Atwood, T. C. 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. Canadian Journal of Zoology-Revue Canadienne De Zoologie 84:80-87.

Baker, P. J., and S. Harris. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? European Journal of Wildlife Research 52:99-108.

Bogan, D. A. 2004. Eastern coyote (*Canis latrans*) home range, habitat selection, and survival rates in the suburban Albany pine bush landscape of New York. Thesis, State University of New York, Albany, USA.

Bozarth, C. A., B. Gardner, L. L. Rockwood, and J. E. Maldonado. 2015. Using Fecal DNA and Spatial Capture-Recapture to Characterize a Recent Coyote Colonization. Northeastern Naturalist 22:144-162.

Breen, M., S. Jouquand, C. Renier, C. S. Mellersh, C. Hitte, N. G. Holmes, A. Cheron, N. Suter, F. Vignaux, A. E. Bristow, C. Priat, E. McCann, C. Andre, S. Boundy, P. Gitsham, R. Thomas, W. L. Bridge, H. F. Spriggs, E. J. Ryder, A. Curson, J. Sampson, E. A. Ostrander, M. M. Binns, and F. Galibert. 2001. Chromosome-specific single-locus FISH probes allow anchorage of an 1800-marker integrated radiation-hybrid/linkage map of the domestic dog genome to all chromosomes. Genome Research 11:1784-1795.

Chamberlain, M.J., and B.D. Leopold. 2001. Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. American Midland Naturalist 145:414-418.

Chandler, R. B., J. A. Royle. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. Annals of Applied Statistics 7:936-954.

Clark, F. W. 1972. Influence of Jackrabbit Density on Coyote Population Change. Journal of Wildlife Management 36:343-356.

Crête, M., and R. Lemieux 1996. Population dynamics of coyotes colonizing the boreal forest of southeastern Québec. Journal of Wildlife Resources 1:99-105.

Crete, M., J. P. Ouellet, J. P. Tremblay, and R. Arsenault. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. Ecoscience 8:311-319.

DeBarba, M., J. R. Adams, C. S. Goldberg, C. R. Stansbury, D. Arias, R. Cisneros, and L. P. Waits. 2014. Molecular species identification for multiple carnivores. Conservation Genetics Resources 6:821-824.

Fedriani, J. M., and M. H. Kohn. 2001. Genotyping faeces links individuals to their diet. Ecology Letters 4:477-483.

Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010. Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91:3376-3383.

Geffen, E., M. E. Gompper, J. L. Gittleman, H. K. Luh, D. W. MacDonald, and R. K. Wayne. 1996. Size, Life-History Traits, and Social Organization in the Canidae: A Reevaluation. The American Naturalist 147:140-160.

Gehrt, S. D. 2007. Ecology of coyotes in urban landscapes. Proceedings of the 12th Wildlife Damage Management Conference 12:303-311.

Gelman A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7(4):457-472.

Gese, E. M. 1995. Foraging ecology of coyotes in Yellowstone National Park. Dissertation, University of Wisconsin, Madison, USA.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Canadian Journal of Zoology 79:980-987.

Gese, E. M., T. E. Stotts, and S. Grothe. 1996. Interactions between Coyotes and Red Foxes in Yellowstone National Park, Wyoming. Journal of Mammalogy 77:377-382.

Grubbs, S. E., and P. R. Krausman. 2009. Use of Urban Landscape by coyotes. Southwestern Naturalist 54:1-12.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39(2):248-255.

Guyon, R., T. D. Lorentzen, C. Hitte, L. Kim, E. Cadieu, H. G. Parker, P. Quignon, J. K. Lowe, C. Renier, B. Gelfenbeyn, F. Vignaux, H. B. DeFrance, S. Gloux, G. G. Mahairas, C. Andre, F. Galibert, and E. A. Ostrander. 2003. A 1-Mb resolution radiation hybrid map of the canine genome. Proceedings of the National Academy of Sciences, 100:5296-5301.

Hansen, S. J., J. L. Frair, H. B. Underwood, and J. P. Gibbs. 2015. Pairing call-response surveys and distance sampling for a mammalian carnivore. Journal of Wildlife Management 79:662-671.

Harrison, D. J. 1986. Coyote dispersal, mortality, and spatial relationships with red foxes in Maine. Dissertation, University of Maine, Orono, USA.

Hilton, H. 1978. Systematics and ecology of the eastern coyote. Pages 210-228 *in* Bekoff M, ed. Coyotes: biology, behavior, and management. Caldwell, New Jersey, USA: Blackburn Press.

Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490-1508.

Holmes, N. G., N. J. Strange, M. M. Binns, C. S. Mellersh, and J.Sampson. 1994. Three polymorphic canine microsatellites. Animal Genetics 25:200.

Houben, J. M. 2004. Status and management of coyote depredations in the eastern United States. Sheep and Goat Research Journal 19:16-22.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Kays, R., W., M. E. Gompper, and J. C. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications 18:1014-1027.

Kéry M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, San Diego, California, USA.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369-382.

Knowlton, F. F., and E. M. Gese. 1995. Coyote population processes revisited. Pages 1-6 *in* Rollins D., C. Richardson, T. Blankenship, K. Canon, and S. Henke, Editors. Coyotes in the southwest: a compendium of our knowledge. Texas Parks and Wildlife Department, Austin, USA.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52:398-412.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. National Oceanographic and Atmospheric Administration, Alaska Fisheries Science Center, Seattle, Washington, USA.

Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015. Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. Journal of Wildlife Management 79:425-434.

Lloyd, D. M. 1998. Demographics and condition of coyotes in Illinois. Thesis, Eastern Illinois University, Charleston, USA.

Lonsinger, R. C., E. M. Gese, S. J. Dempsey, B. M., Kluever, T. R. Johnson, and L. P. Waits. 2014. Balancing sample accumulation and DNA degradation rates to optimize noninvasive genetic sampling of sympatric carnivores. Molecular Ecology Resources 15(4):831-842.

Mahan, B. R., and E. C. Mahan. 2007. Demographics of coyotes (*Canis latrans*) during the late 1970s and 1990s in southwestern Illinois. Transactions of the Illinois State Academy of Science 100:251-257.

Messier, F., and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60:1743-1753.

Miller, C. R., P. Joyce, and L. P. Waits. 2002. Assessing allelic dropout and genotype reliability using maximum likelihood. Genetics 160:357–366.

Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the Theory of Statistics. Third Edition. McGraw-Hill, New York, New York, USA.

Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology 75:271-287.

Nelson, T. A., and D. M. Lloyd. 2005. Demographics and Condition of Coyotes in Illinois. The American Midland Naturalist 153:418-427.

Nelson, T. A., D. G. Gregory, and J. R. Laursen. 2003. Canine heartworms in coyotes in Illinois. Journal of Wildlife Diseases 39:593-599.

Parker, G. E. 1995. Eastern coyote: the story of its success. Nimbus, Halifax, Nova Scotia, Canada.

Peakall, R., and P. E. Smouse. 2006. GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Pence, D. B., and L. A. Windberg. 1994. Impact of a sarcoptic mange epizootic on a coyote population. Journal of Wildlife Management 58:624-633.

Pitt, W. C., P. W. Box, and F. F. Knowlton. 2003. An individual-based model of canid populations: modelling territoriality and social structure. Ecological Modelling 166:109-121.

Plummer M. 2014. rjags: Bayesian graphical models using MCMC. R package version 3-13. http://CRAN.R-project.org/package=rjags.

Plummer M., N. Best, K. Cowles, and K. Vines. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News 6: 7-11.

Pollock, K. H. 1981. Capture-recapture models: a review of current methods, assumptions, and experimental design. Pages 426-435 *in* C. M. Ralph and J. M. Scott, Editors. Estimating numbers of terrestrial birds, Studies in Avian Biology, Allen Press, Lawrence, Kansas, USA.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. The Journal of Wildlife Management 46:757-760.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3-97.

Post, R. A. 1975. Movements and home ranges of coyotes in New York: preliminary observations. Paper presented at Transactions of the Eastern Coyote Workshop. Northeast Fish and Wildlife Conference, New Haven, Connecticut, USA.

Poulle, M. L., M. Crete, and J. Huot. 1995. Seasonal variation in body mass and composition of eastern coyotes. Canadian Journal of Zoology-Revue Canadienne De Zoologie 73:1625-1633.

Priest, J. M. 1986. Some aspects of the ecology of the coyote: Dixon Springs Agricultural Center, S.E. Illinois. Thesis, Southern Illinois University, Carbondale, USA.

Pritchard, J. K., M. Stephens, M., and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Richer, M. C., M. Crête, J. P. Ouellet, L. P. Pirest, and J. Huot. 2002. The low performance of forest versus rural coyotes in northeastern North America: Inequality between presence and availability of prey. Ecoscience 9:44-54.

Rose, M. D., and G. A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998-1007.

Royle, J. A., and K. V. Young. 2008. A hierarchical model for spatial capture-recapture data. Ecology 89: 2281-2289.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013a. Spatial capture-recapture. Academic Press, San Diego, California, USA.

Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013b. Integrating resource selection information with spatial capture–recapture. Methods in Ecology and Evolution 4:520-530.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. scrbook: Companion to the book: Spatial Capture Recapture. R package version 0.21-0.

Royle, J. A., A. K. Fuller, and C. Sutherland. *In revision*. Spatial capture-recapture models allowing Markovian transience or dispersal. Population Ecology.

Samson, C., and M. Crete. 1997. Summer food habits and population density of coyotes, *Canis latrans*, in boreal forests of southeastern Quebec. Canadian Field-Naturalist 111:227-233.

Schrecengost, J. D., J. C. Kilgo, H. S. Ray, and K. V. Miller. 2009. Home Range, Habitat Use and Survival of Coyotes in Western South Carolina. American Midland Naturalist 162:346-355.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 26:13-22.

Seddon, J. M. 2005. Canid-specific primers for molecular sexing using tissue or non-invasive samples. Conservation Genetics 6:147–149.

Smith, G. J. 1984. Coyote ecology in northern Wisconsin and Minnesota. Dissertation, University of Wisconsin, Madison, USA.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784-795.

Stephenson, S. W., and M. L. Kennedy. 1993. Demography of a coyote population in western Tennessee. Journal of the Tennessee Academy of Science 68:122-124.

Sutherland, C., A. K. Fuller, and J.A. Royle. 2014. Modeling non-Euclidean movement and landscape connectivity in highly structured ecological networks. Methods in Ecology and Evolution 6:169–177.

Taberlet P., S. Friffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. P. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research 24:3189–3194

Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84(1):153-159.

Van Deelen, T. R., and T. E. Gosselink. 2006. Coyote survival in a row-crop agricultural landscape. Canadian Journal of Zoology 84:1630-1636.

Waits, L. P., G. Luikart, and P. Taberlet. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10:249–256.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46:S120-S139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California, USA.

Windberg, LA. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology-Revue Canadienne De Zoologie 73:942-954.

FIGURES

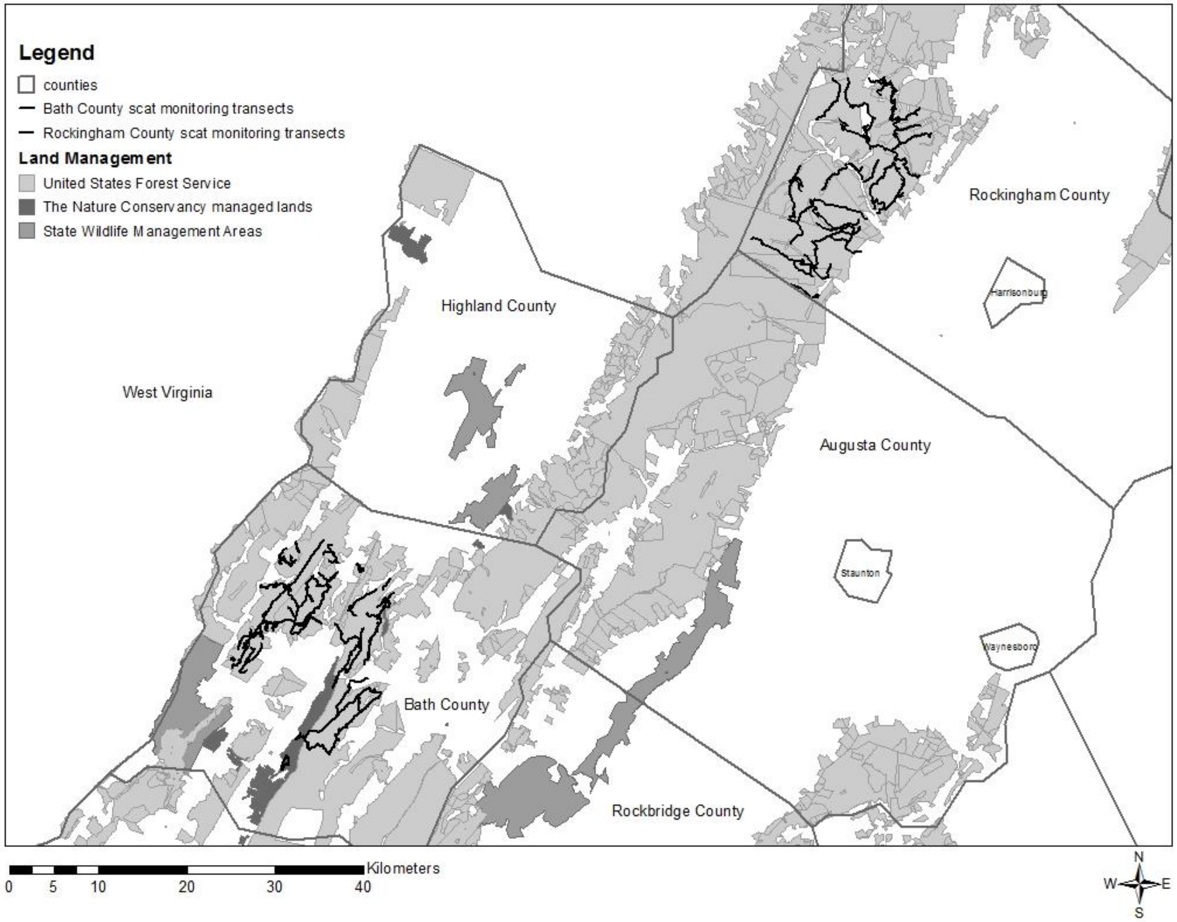


Figure 1. Locations of ~ 200 km of scat transects in each of 2 study areas (Bath County to the south, and Rockingham County to the north) in western Virginia. Transects were located on existing dirt roads and trails on public managed lands and surveys repeated over 5 surveys from 2011 - 2013 to estimate density and population demographics for coyotes.

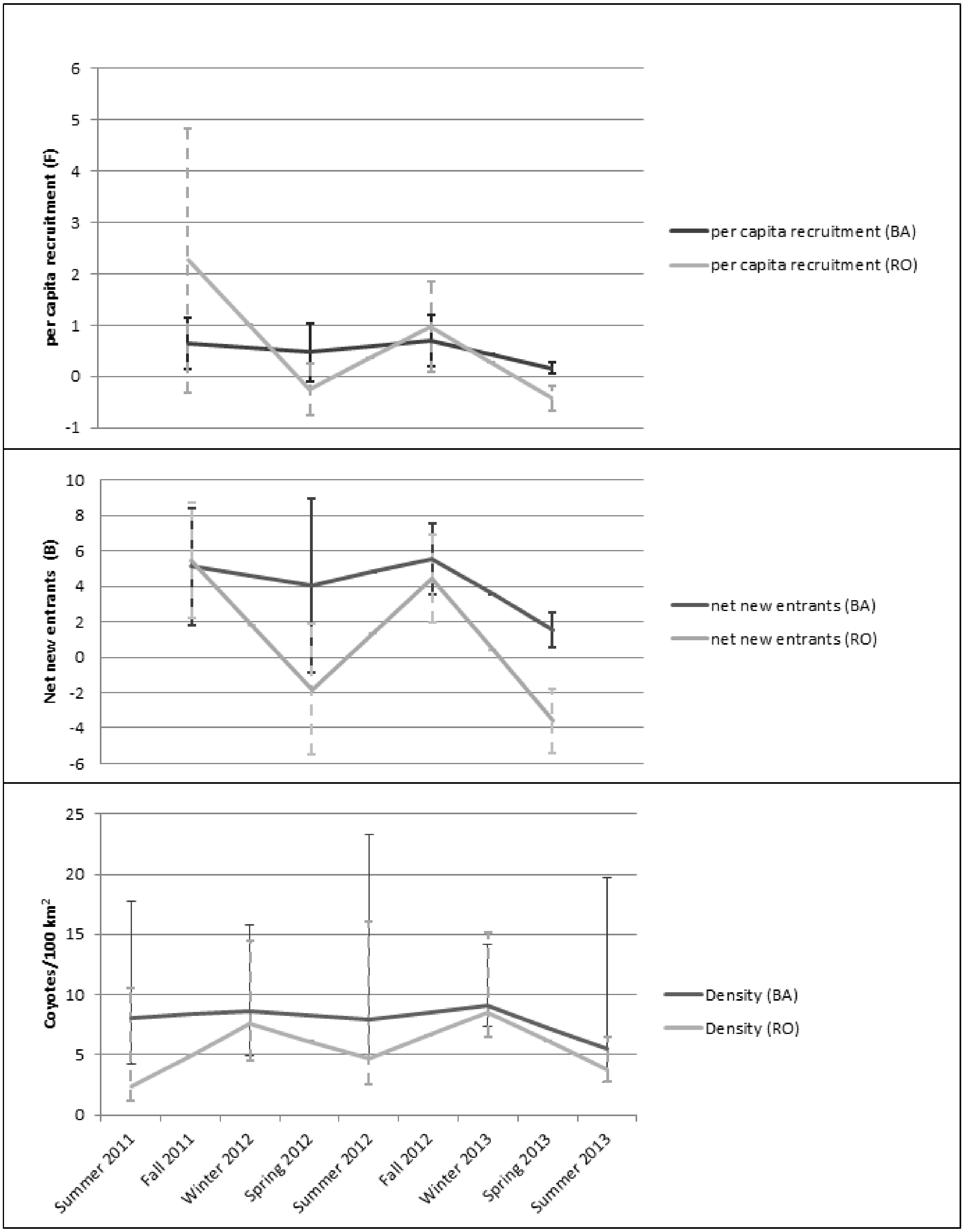

6
5
4
3
2
1
0
-1
per capita recruitment (F)
per capita recruitment (BA)
per capita recruitment (RO)
10
8
6
4
2
0
-2
-4
-6
Net new entrants (B)
net new entrants (BA)
net new entrants (RO)
25
20
15
10
5
0
Coyotes/100 km^2
Density (BA)
Density (RO)
Summer 2011
Fall 2011
Winter 2012
Spring 2012
Summer 2012
Fall 2012
Winter 2013
Spring 2013
Summer 2013

Figure 2. Per capita recruitment (F_i), new recruits into the population (B_i), and density (D = coyotes/100 km^2) estimates for the two sites, Bath County (BA) and Rockingham County (RO) for the five scat sampling sessions (D) and the four intervals between sampling sessions (F_i and B_i). Error bars for D represent the 95% credible intervals for estimates and error bars for F_i and B_i represent standard errors.

TABLES

Table 1. Recapture rates, priors, and parameter values used in the SCR_0 model to estimate coyote density for each site and session in Bath and Rockingham Counties, Virginia.

Site session	Captures (total detections)	Individuals recaptured (range of # of times recaptured)	M (maximum number of possible individuals)	S (area of site- and session- specific state space).	σ prior
Bath July 2011	15 (21)	4 (2 – 3)	200	997.50 km^2 ~5.0 km buffer	uniform(0,5)
Bath February 2012	22 (41)	8 (2 – 10)	250	934.89 km^2 ~4.5 km buffer	uniform(0,5)
Bath July 2012	14 (21)	5 (2 – 4)	240	874.29 km^2 ~4.0 km buffer	uniform(0,3)
Bath March 2013	31 (79)	17 (2 – 12)	165	874.29 km^2 ~4.0 km buffer	uniform(0,4)
Bath July 2013	14 (18)	2 (2 – 4)	280	1267.92 ~7 km buffer	uniform(0,8)
Rockingham July 2011	7 (11)	3 (2 – 3)	150	995.80 km^2 ~4.5 km buffer	uniform(0,5)
Rockingham February 2012	19 (33)	8 (2 – 4)	175	995.80 km^2 ~4.5 km buffer	uniform(0,4)
Rockingham July 2012	12 (16)	4 (2)	225	1194.67 km^2 ~6.0 km buffer	uniform(0,6)
Rockingham March 2013	25 (51)	14 (5)	175	995.80 km^2 ~4.5 km buffer	uniform(0,4)
Rockingham July 2013	17 (52)	11 (2 – 13)	175	1060.09 km^2 ~5.0 km buffer	uniform(0,4)

Table 2. Model selection for Cormack-Jolly-Seber (CJS) models of apparent survival (Phi) and detection (p) over 5 scat sampling sessions for coyotes in Bath and Rockingham Counties, Virginia (sites). Time models allows parameters for each session or interval to be estimated and season constrains survival or detection to be the same for each season (winter or summer).

Model	K	QAICc	ΔQAICc	weight	QDeviance
Phi(~site)p(~season)	4	126.84	0.00	0.19	26.73
Phi(~site)p(~site)	4	127.15	0.31	0.16	27.04
Phi(~site)p(~site * season)	6	127.41	0.57	0.14	22.96
Phi(~site * season)p(~site * season)	7	127.93	1.09	0.11	21.26
Phi(~season)p(~site)	4	128.78	1.94	0.07	28.67
Phi(~season)p(~season)	4	128.92	2.08	0.07	28.81
Phi(~season)p(~site * season)	6	129.49	2.65	0.05	25.04
Phi(~site)p(~time)	6	130.17	3.33	0.04	25.72
Phi(~time)p(~season)	6	130.26	3.42	0.03	25.81
Phi(~time)p(~site)	6	130.66	3.82	0.03	26.21
Phi(~site * season)p(~site)	6	130.93	4.09	0.02	26.48
Phi(~time)p(~site * season)	8	131.02	4.18	0.02	22.10
Phi(~site * season)p(~season)	6	131.11	4.27	0.02	26.66
Phi(~season)p(~time)	6	132.10	5.26	0.01	27.65
Phi(~time)p(~time)	7	132.13	5.29	0.01	25.46
Phi(~site * season)p(~time)	8	134.38	7.54	0.00	25.45
Phi(~site)p(~site * time)	10	135.27	8.43	0.00	21.73
Phi(~site * time)p(~time)	10	136.32	9.48	0.00	22.78
Phi(~site * time)p(~site)	10	137.13	10.29	0.00	23.59
Phi(~season)p(~site * time)	10	137.27	10.43	0.00	23.73
Phi(~site * time)p(~season)	10	137.28	10.44	0.00	23.74
Phi(~site * time)p(~site * season)	12	138.23	11.39	0.00	19.92
Phi(~site * season)p(~site * time)	12	138.37	11.53	0.00	20.07
Phi(~time)p(~site * time)	12	139.88	13.04	0.00	21.58
Phi(~site * time)p(~site * time)	13	140.55	13.71	0.00	19.81

Table 3. Population parameter estimates for coyotes in Bath and Rockingham Counties, Virginia for 6-month seasonal intervals, and for each session from July 2011 to July 2013.

Site	Session	Apparent survival (ϕ)[1]	Density (D, per 100 km^2)[2]	Births (B_i)[3]	Recruitment (F_i)[4]	Population growth rate (λ)[5]
Bath	July 2011	0.442 (0.103, 0.259 – 0.643)	8.02 (4.21 – 17.74)	5.12 (3.31)	0.64 (0.50)	1.08 (0.58)
	February 2012		8.66 (4.92 – 15.83)	4.05 (4.87)	0.47 (0.58)	0.91 (0.63)
	July 2012		7.88 (4.69 – 23.33)	5.56 (2.01)	0.71 (0.50)	1.15 (0.73)
	March 2013		9.04 (7.32 – 14.18)	1.53 (0.95)	0.17 (0.11)	0.61 (0.12)
	July 2013		5.53 (2.76 – 19.72)			
Rockingham	July 2011	0.863 (0.172, 0.269 – 0.991)	2.41 (1.21 - 10.54	5.45 (3.27)	2.26 (2.57)	3.12 (3.20)
	February 2012		7.53 (4.52 – 14.5)	-1.82 (3.70)	-0.24 (0.50)	0.62 (0.50)
	July 2012		4.68 (2.51 - 16.07)	4.45 (2.45)	0.96 (0.88)	1.82 (1.42)
	March 2013		8.53 (6.43 – 15.16)	-3.59 (1.80)	-0.42 (0.24)	0.44 (0.16)
	July 2013		3.77 (2.74 - 6.51)			

[1] Maximum likelihood point estimate (standard error, 95% lower confidence limit – 95% upper confidence limit)

[2] Posterior mode from 1 chain (lower 95% credible interval, upper 95% credible interval)

[3] Net new entrants in the population between i and $i + 1$

$$(SE(\hat{B}_i) = \sqrt{var(\hat{N}_{i+1}) + \phi_i^2 * var(\hat{N}_i) + N_i^2 * var(\hat{\phi}_i) + var(\hat{\phi}_i) * var(\hat{N}_i)})$$

[4] Number of new animals at session $i + 1$ per the number present at i $(SE(f_i) = \sqrt{f_i^{\,2} * (\frac{var(B_i)}{\hat{B}_i^2} + \frac{var(N_i)}{\hat{N}_i^2}}))$

[5] ratio of posterior mode density estimates from the SCR model ($\hat{\lambda}_i = \frac{\hat{D}_{i+1}}{\hat{D}_i}$) between each session ($SE(\lambda_i) = \sqrt{\lambda_i^2 * (\frac{var(N_t)}{\hat{N}_t^2} + \frac{var(N_{t+1})}{\hat{N}_{t+1}^2})}$)

APPENDICES

Appendix G. Real parameter estimates from the two competing Cormack-Jolly-Seber models of apparent survival for coyotes in Bath and Rockingham Counties, Virginia.

Model	Parameter	Estimate	Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Phi(site) p(site*season)	Phi(Bath)	0.442	0.103	0.259	0.643
	Phi(Rockingham)	0.863	0.172	0.269	0.991
	p(Bath, summer)	0.711	0.140	0.393	0.903
	p(Bath, winter)	0.342	0.090	0.192	0.531
	p(Rockingham, summer)	0.294	0.095	0.145	0.505
	p(Rockingham, winter)	0.415	0.112	0.223	0.636
Phi(site*season) p(site*season)	Phi(Bath, summer)	0.267	0.116	0.102	0.537
	Phi(Bath, winter)	0.897	0.469	<0.001	>0.999
	Phi(Rockingham, summer)	1[1]	0	1	1
	Phi(Rockingham, winter)	0.555	0.223	0.175	0.880
	p(Bath, summer)	0.782	0.130	0.447	0.941
	p(Bath, winter)	0.257	0.089	0.122	0.463
	p(Rockingham, summer)	0.300	0.087	0.160	0.492
	p(Rockingham, winter)	0.521	0.145	0.259	0.772

[1] The beta estimate is a singular value

Appendix H. SCR model parameter estimates, standard errors, and credible intervals for coyotes in the Bath and Rockingham County study areas of Virginia.

Site Session	Parameter	Mean	SE	Mode	Q 0.025	Q 0.50	Q 0.975
Bath July 2011	σ^1	1.544	0.455		0.946	1.450	2.694
	$\lambda_0{}^2$	0.050	0.030		0.012	0.043	0.125
	ψ^3	0.465	0.174		0.204	0.436	0.883
	D^4		3.45	**8.02/100 km^2**	4.21/100 km^2	8.72/100 km^2	17.74/100 km^2
Bath February 2012	σ	1.974	0.398		1.375	1.912	2.926
	λ_0	0.045	0.018		0.019	0.043	0.088
	ψ	0.338	0.108		0.178	0.322	0.596
	D		2.80	**8.66/100 km^2**	4.92/100 km^2	8.56/100 km^2	15.83/100 km^2
Bath July 2012	σ	1.301	0.376		0.785	1.227	2.271
	λ_0	0.051	0.029		0.014	0.045	0.123
	ψ	0.414	0.175		0.165	0.379	0.851
	D		4.78	**7.88/100 km^2**	4.69/100 km^2	10.29/100 km^2	23.33/100 km^2
Bath March 2013	σ	1.543	0.150		1.284	1.531	1.871
	λ_0	0.109	0.024		0.069	0.107	0.160
	ψ	0.545	0.100		0.369	0.539	0.760
	D		1.77	**9.04/100 km^2**	7.32/100 km^2	10.18/100 km^2	14.18/100 km^2
Bath July 2013	σ	3.615	1.313		1.868	3.306	7.010
	λ_0	0.009	0.007		0.002	0.008	0.026
	ψ	0.394	0.202		0.121	0.349	0.892
	D			**5.53/100 km^2**	2.76/100 km^2	7.65/100 km^2	19.72/100 km^2
Rockingham July 2011	σ	2.516	0.834		1.376	2.327	4.564
	λ_0	0.030	0.024		0.005	0.024	0.093
	ψ	0.255	0.156		0.075	0.214	0.705
	D		2.3	**2.41/100 km^2**	1.72/100 km^2	3.20/100 km^2	5.57/100 km^2
Rockingham February 2012	σ	2.081	0.418		1.450	2.016	3.089
	λ_0	0.040	0.018		0.015	0.037	0.083
	ψ	0.468	0.146		0.243	0.447	0.824
	D		2.5	**7.53/100 km^2**	4.52/100 km^2	7.83/100 km^2	14.5/100 km^2
Rockingham July 2012	σ	2.408	0.806		1.326	2.238	4.503
	λ_0	0.026	0.019		0.005	0.021	0.075
	ψ	0.373	0.183		0.130	0.330	0.853
	D		3.44	**4.68/100**	2.51/100	6.19/100	16.07/100

				km^2	km^2	km^2	km^2
Rockingham March 2013	σ	1.629	0.228		1.260	1.602	2.152
	λ_0	0.071	0.021		0.037	0.069	0.120
	ψ	0.576	0.131		0.354	0.563	0.867
	D		2.23	**8.53/100 km^2**	6.43/100 km^2	9.84/100 km^2	15.16/100 km^2
Rockingham July 2013	σ	2.208	0.289		1.738	2.176	2.871
	λ_0	0.093	0.026		0.051	0.090	0.151
	ψ	0.266	0.067		0.153	0.260	0.413
	D		0.97	**3.77/100 km^2**	2.74/100 km^2	4.25/100 km^2	6.51/100 km^2

[1] scaling parameter for Gaussian bivariate detection model

[2] encounter rate at hypothetical activity center

[3] data augmentation parameter

[4] density

CHAPTER 4.

The Spatial Component of Density Dependence: Evidence for Coyote Population Regulation through Competition for Territories and Compensatory Immigration

Target Journal: Southeastern Naturalist

Abstract – *Canis latrans* (Coyote) populations can be density dependent and recruitment limited by number of available territories (territory saturation). Increased reproductive rates have been documented in response to increased mortality rates, however less attention has been directed towards recruitment through immigration to a local population. We investigated lines of evidence for population regulation through competition for territories and recruitment through immigration in a highly exploited Coyote population. We used non-invasive fecal DNA from scat transects and GPS relocation data collected from individuals tracked in the western mountains of Virginia. We found evidence of resident territorial behavior and evidence of territory turnover amongst residents indicating competition for space as a limiting resource. We also found strong support for the presence of transients resulting in populations of potential recruits in biding areas, with recruitment occurring either through immigration or delayed dispersal. Our results suggested the spatial component of density-dependent regulation may offset attempts to even temporarily reduce local Coyote populations, and that spatial structure of Coyote competition could potentially regulate Coyote populations, even at low densities.

Introduction

Previous studies found *Canis latrans* (Say) (Coyote) populations are often density dependent and population growth rate was positively related to prey abundance and negatively related to Coyote abundance (Windberg 1995, Knowlton and Gese 1995, Knowlton et al. 1999). In particular, recruitment was limited by available territories with very little recruitment when available territories were “saturated”. These studies focused on reproductive recruitment and found increased reproductive rates in populations with higher mortality rates and demonstrated Coyote populations can be regulated by competition through reproductive mechanisms. However, less attention has been directed towards recruitment through immigration into a local population (Lieury et al. 2015).

Density is a spatial parameter and other population inputs (e.g., temporary immigration, permanent immigration), may also respond to changes in outputs (mortality and emigrations). The spatial structure of Coyote populations, consisting of residents (small groups of individuals actively defending territories) and transients (individuals without stable, defensible territories), likely allows Coyote populations to quickly respond to temporary reductions in density (Camenzind 1978, Kamler and Gipson 2000). Hinton et al. (2015) suggested that the transient phase, individuals with home ranges overlapping resident territories or moving through the interstitial spaces between territories, was a critical part of Coyote life history. They argued that the transient phase resulted in nomadic individuals occupying “biding areas”, or areas where nonresidents lie in wait, ready to fill vacant territories. However, this may not be the only form of biding areas in highly exploited Coyote populations. Selection for coyote life history strategies appears to be flexible across coyote populations (Knowlton and Gese 1995). In areas with high mortality, resident Coyotes may be more tolerant of yearlings remaining in natal territories for an additional year resulting in delayed dispersal (Messier and Barrette 1982, Patterson and Messier 2001, Atwood and Weeks 2002b, Atwood 2006). This alternative form of a “biding area” within the resident adult parents’ territory would minimize the associated risk of long-distance dispersal to novel areas. Delayed dispersal may increase foraging efficiency of parents, alleviate reproductive costs through cooperative breeding, and reduce subadult mortality during high-risk dispersal (Messier and Barrette 1982, Patterson and Messier 2001, Atwood and Weeks 2002b, Atwood 2006). Late-dispersing young could increase their chance of assuming a nearby territory or the natal territory when residents are removed, likely improving reproductive fitness. Finally, there is often intensive competition for territories containing more productive patches of habitat (Chapter 2, Patterson and Messier 2001). If more productive habitats are also characterized by greater potential mortality as found in Chapter 2, individual behavior may result in rapid territory turnover in these more productive areas, resulting in a third form biding. All three forms of biding areas increase the potential for compensatory immigration as a negative feedback mechanism to mortality in density dependent populations.

The Coyote population in the western part of Bath County, VA, experienced very high anthropogenic mortality rates (Chapter 2). The estimated monthly survival probability from the known-fate model (0.91, Chapter 2) and would result in an approximate 0.57 survival probability over a 6-month period (0.91^6, Pollock et al. 1989). In Chapter 3, we estimated 6-month apparent survival (i.e., 1-death rate - emigration rate) in Bath County to be 0.44. This estimate approaches the calculated 6-month known-fate survival estimate (which did not include emigration). Thus, it appeared that the majority of the losses to the local population were due to mortality, and not dispersal and emigration. Yet despite local efforts by hunters and trappers to reduce Coyote density, the population continued to persist via additional recruitment (Chapter 3) which might be evidence of density-dependent negative feedback (Murdoch 1994, Turchin 1999, Hixon et al. 2002). These density-dependent inputs to the population seemed to occur in Bath County even between summer and winter seasons, even though reproduction only occurs in the spring (Chapter 3). Conversely, in a second study area with higher apparent survival (western

Rockingham County, Chapter 3), density fluctuated between seasons with reduced densities and recruitment in the population.

Our objective was to test for evidence of three spatial mechanisms (territoriality, presence of transients, and territory turnover) in the Bath County study area as indicators of population regulation through competition with other Coyotes for territories and resultant compensatory recruitment through local immigration. To better understand the interplay between Coyote space use and demographic processes, we collected two different types of data: 1) satellite collar data from individual captured Coyotes in Bath County, and 2) fecal DNA genotypes and locations from scat collection surveys in Bath County. We predicted we would observe the presence of transients in the local population indicating competition for space and expected differences in territoriality based on social status (we expected residents to be more territorial compared to transients). We also hypothesized subadults would be more likely to display transient behavior than adults as indicated by home range stability, and that we would observe territory turnover following periods when residents began behaving as transients.

Field-Site Description

The study area was located in western Bath County, in the Ridge and Valley region of the western mountains of Virginia (Figure 1). The area was primarily US Forest Service parcels of low productivity, mature hardwood forests with veins of more productive habitat along valley bottoms, often privately owned and coinciding with increased human population density (Chapter 2).

Methods

Data Collection

We used a subset of data from trapped and processed Coyotes previously described in Chapter 2. We fit each Coyote with an African Wildlife Tracking (Pretoria, South Africa) two-way satellite communication GPS collar and programmed collars to record 4 to 5 relocations each day on rotating schedules. In addition, we used the Bath County study area scat collection data (five scat collection surveys conducted to estimate density over time: July 2011, February 2012, July 2012, March 2013, July 2013), as previously described in Chapter 3, as well as targeted home range scat collection surveys in June and July 2012. For the targeted home range scat collection surveys we searched and recorded lengths of additional transects (dirt roads and trails) in areas where collared individuals were known to be during May through July 2012. We collected fecal DNA samples from all scats encountered. We collected samples and cleared scats found during the June 2012 session, and then collected fecal DNA samples from the same transects in July 2012 representing a closed session. We analyzed fecal DNA samples, identified individual Coyotes, and matched samples to collared individuals using methods described in Chapter 3 and Stenglein et al. (2011). Animal handling methods were approved by the Virginia Tech Institutional Animal Care and Use Committee (permit #10-117-FIW).

Statistical Analyses

We used several different approaches to test hypotheses concerning transients, individual territoriality, and territory turnover. We expected we would find evidence of spatial mechanisms that would describe density-dependent processes as a result of competition for space and compensatory immigration.

Transients. We identified transients by measuring the distance between successive activity centers as described in Chapter 2. We determined resident or transient status each month a Coyote was tracked using the 2-km threshold for home range stability identified for the Bath County study area. We summarized transient months for individual Coyotes and attempted to identify trends in transient activity. We hypothesized subadult residents would become transients as part of dispersal (Hinton et al. 2012). To test this, we used the log-transformed home range stability measure as a response variable and compared two linear mixed models (LMM) using AICc. The first model incorporated home range stability as determined only by differences between individuals {stability ~ (1|individual)} (i.e., the null model) and the alternative model also included stage as a subadult or adult {stability ~ (1|individual) * stage}.

Territoriality. Scent marking, including defecation, is a form of communication in carnivores and there is often a positive correlation between scent marking and territoriality (Allen et al. 1999, Gese 2001). Thus we hypothesized transients would be more difficult to detect with scat compared to residents. We used the samples collected from the targeted home range scat surveys to estimate an encounter rate given search effort in the home ranges of the seven collared individuals. We also expanded this analysis to include collared individuals known to overlap with the Bath County density monitoring grid during seasonal scat collection sessions (Chapter 3). We extracted the transect lengths that overlapped with a polygon surrounding relocations for an individual during scat collection surveys to account for search effort. Encounter rate was estimated as the number of detections/length of transects, and we compared encounter rates for individuals classified as residents and transients during the given scat collection session.

In addition, we hypothesized resident Coyotes would deposit scats in the outer portions of their territories as a form of communication with other individuals about territory boundaries. We tested distribution of scat within a home range by using collar locations for Coyotes classified as residents from May through July 2012 and corresponding scat detections for both June and July 2012 scat collection sessions. Although we cannot assume closure for the June 2012 scat detection session, we found in Chapter 2 that overall home ranges (95% UD) did not vary seasonally (see also Knowlton et al. 1999, Gese 2001). We assumed that even if scat persisted from several months prior to June 2012 collection period, the distribution of those scats in the overall home range would remain indicative of marking patterns within a home range. We used the estimated minimum convex polygons (MCP) surrounding all relocations for collared residents from May 2012 (spring 2012 trapping session) to July 2012 to represent a conservative home range boundary. To test our hypothesis we estimated two minimum convex polygon (MCP) shapes, a 50% MCP and a 100% MCP, for each collared Coyote classified as a resident May through July 2012, and counted the number of scats detected in the outer band (i.e., in the area from the50% MCP boundary to the100% MCP boundary), similar to Nichols and Haramis (1980). We compared the observed number of scats in the outer band (50% - 100% MCP) to the expected number of scats (1/2 observed number of scats based on number of relocations in each MCP) and computed a chi-square statistic with a Yates correction to test our hypothesis. We predicted we would observe a greater proportion of scats in the outer band (50% - 100% MCP) than expected if scat deposition was simply correlated with density of relocations throughout a territory.

Territory Turnover. We hypothesized that when residents demonstrated periods of transient behavior, as reflected by home range instability, they transitioned into a new territory.

To evaluate this hypothesis we measured the distance between activity centers between the last month an individual was first considered a resident and the next month that individual was again considered a resident. If the distance between those activity centers was greater than the 2-km home range stability threshold in Chapter 2, we considered that a transition between territories.

Results

Transients

We determined that nine of the 19 collared individuals behaved as residents for the entire length of time they were collared (Table 1) (Coyotes were collared from 1 month to 18 months) and one adult female (C17) was a resident for nine months before demonstrating transient behavior in the tenth month (the last month the collar was functional). Two individuals were primarily classified as transients (C05: transient 8/10 months, C16: transient 7/8 months). Three subadults were initially classified as residents and then began behaving as transients. Of those, two were killed and one fate was unknown as the collar stopped functioning and was not recovered. Finally, four individuals were primarily classified as residents but periodically demonstrated transient movement for one to two months before becoming residents again. This included early movements of one of the subadults described as transitioning to transient status above (C12). One individual (C11: adult male) only survived little over two weeks, and we were not able to assess social status using distance between monthly successive activity centers, although distance between one-week and two-week successive centers indicate it was behaving as a resident. Classification of residents did not appear to show bias by sex or stage. However, a smaller proportion of the collared population was classified as transient in the summer months (14% for June, July, and August), compared to fall and winter months (Figure 2).

Using a log-transformation for distance between home range centers, we did not find strong support for differences in home range stability (as measured by distance between successive home range centers) by stage (adult or subadult), as the model including stage as an explanatory variable (delta AICc = 2.10, ω = 0.259, AICc = 342.10, n = 180, groups = 18, logLikelihood = -166.9, residual degrees of freedom = 114) received less support compared to the null model including only individual variability (delta AICc = 0, ω = 0.741, AICc = 340.00, n = 180, groups = 18, logLikelihood = -166.9, residual degrees of freedom = 115). However, there was a much wider range in subadult home range stability (0.02 km – 28.89 km) compared to adults (0.10 km - 8.51 km). Mean distance between successive distances was much greater for subadults (3.60 km) compared to adults (1.60 km), and larger than the 2-km threshold distinguishing residents from transients. However, the medians for subadults (1.27 km) and adults (1.07 km) were much more similar, suggesting subadult female (C05), a transient that eventually dispersed to a neighboring county, was exceptional. When C05 is not considered, mean distance between activity centers for subadults was smaller (1.71 km) and home range stability was more similar between subadults and adults as suggested by the LMM results. In addition the means for both adults and subadults (when omitting C05) were less than the 2-km threshold considered to distinguish residents from transients.

Territoriality

We detected 10 of 19 collared individuals a total of 86 times across all scat collection sessions. However, we did not always detect them during closed sessions or during sessions when they were tracked. Seven collared individuals (one transient and six residents) were monitored during the July 2012 density surveys and the targeted home range scat collection survey. We detected two female residents (C12 and C13) during the July 2012 session, and one female that was a resident during the July 2013 session, and behaved as a transient during the March 2013 session (Table 1). Of nine individuals collared at some point in time from May – July 2012, we detected six of those individuals during June and July 2012. Of these detections, we counted 20 scats in the outer 50% - 100% MCP ring (Figure 3), providing support for our hypothesis that individuals are more likely to deposit scats in the outer portion of their territories ($\chi^2 = 5.14$, df = 1, p = 0.03).

Territory Turnover

There were eight total instances where five individuals with stable home ranges began to behave as transients, and then returned to stable home range behavior, as determined by distance between successive activity centers (three individuals did this twice). Of the eight instances, six resulted in the Coyote occupying a different territory following transient activity as indicated by an activity center greater than 2 km from the last resident activity center: adult male C07 twice, adult male C09 twice, and adult female C10, and subadult female C19 once each. Of the two instances where the individual did not ultimately occupy a new territory, the first appears to be an exploratory movement by adult female C12 before it attempted to disperse one month later. The second was C10 again, moving in the direction of the area in the territory it denned with pups in the previous year. Unfortunately, the collar was not operational for most of April so we were unable to determine if she was attempting to use the same den site. C10 was recaptured and fitted with a new collar in June 2013 at which point it had returned as a resident in its second territory from February 2013.

Discussion

We found evidence of territorial behavior, identified a proportion of the population as transient, and a revealed a high amount of territory turnover in the Bath County Coyote population. We were unable to test for differences in scat detection probabilities for residents and transients due to small sample sizes during our study (only one transient and six residents in July 2012), and an insufficient duration of scat accumulation to allow for detection in the summer in our study area. We found individual detection via scat transects was lower in summer sessions compared to winter sessions in the Bath County study area (Chapter 3). However, we did find evidence that Coyotes were marking the outer portions of their territories at a greater rate than expected based on relocation density, and thus residents appeared to be demonstrating territorial behavior.

Transients were present in all months although there appeared to be a smaller proportion of transients in the summer months when food resources peak in safer habitats in the National Forest and core home range size decreases (Chapter 2). This may be an artifact of the available sample of collared Coyotes and further research is needed to determine if there is a seasonal trend in transient behavior. Both adults and subadults were identified as transients and we did not detect a difference in home range stability between subadult and residents. However, three of four individuals originally classified as residents and that transitioned to transients before tracking ended were subadults. In addition, we identified several adult residents that moved into different territories during the time they were tracked. This territory transition was detectable at the one-month resolution and was likely the result of residents being displaced from a territory by another individual or group of individuals, or residents moving into a better territory that becomes vacant when the territory holder was removed.

Presence of transients and residents displaying transient behavior and territory turnover provides evidence that Coyotes were spatially prepared to quickly replace individuals removed in the study area (Windberg and Knowlton 1988). The traditional transient phase defined by a large home range overlapping several resident territories was proposed as a transitional stage following natal dispersal while individuals sought out available territories (Camerzind 1978, Kamler and Gipson 2000, Hinton et al. 2015). These large home ranges were not defensible territories and the term "biding area" has been proposed to describe the role of the wide-ranging space use by transients (Hinton et al. 2012). However, we propose the high mortality rate in our study area established conditions for three different types of "biding" populations. First, we identified two individuals that behaved as large-ranging transients for most of the time they were tracked. One subadult female did appear to establish a possible territory in Greenbrier County, West Virginia, before confirmed killed in that area by USDA Wildlife Services.

Second, high-value habitats were limited in the study area as the predominant habitat type, mature deciduous hardwood forest, is low productivity and comprises over 75% of available habitat (Chapter 2). We identified a dichotomy in resident Coyotes second-order selection for habitats for overall territories, with some resident Coyotes selecting for territories with safe but unproductive habitats, and other residents selecting for limited high-productivity habitats with greater mortality risk (Chapter 2). These findings suggest a dynamic demographic spatial structure (Levins 1968, Pulliam 1988) at the territory scale, with high mortality of Coyotes in resource-desirable territories and rapid subsequent "colonization" by individuals in adjacent territories. Thus, residents in poor habitat territories may constitute a second type of biding population.

Finally, we find support for delayed dispersal in the study area. We did not capture or track any individuals under 1.5 years of age, and yet we still documented several attempts (C02, C12, and C19) at what appeared to be subadult dispersal from a natal area by individuals estimated to be 2 years old based on tooth wear (Geir 1968). In addition, two of these three dispersal attempts resulted in confirmed deaths, and the result of the third is unknown as the collar stopped functioning at this time. Thus, dispersal is dangerous in the study area (see also Harrison 1986, Sacks et al. 1999), creating a situation where there would be selection for breeding residents to tolerate related yearlings and increase potential reproductive fitness (Messier and Barrette 1982). Delayed dispersal may result in increased group size within territories and creates a third potential "biding" populations prepared to annex or subsume adjacent or natal territories when residents are removed. Delayed dispersal may also explain why we did not detect a difference in subadult and adult home range stability, as subadult individuals may opt to remain relatively safe behaving as residents within natal territories for an additional year.

We contend these results provide evidence of a spatially structured population capable of rapid recruitment and population regulation through compensatory local immigration. Therefore, most local Coyote control efforts (e.g., bounties and lotteries), as currently implemented in Virginia, will not reduce local Coyote populations, minimize potential impacts to prey species, or mitigate potential human-Coyote conflicts, even over short time intervals, if resident Coyotes removed are rapidly replaced with individuals in biding areas (Baker and Harrison 2006, and Lieury et al. 2015). However, this territorial behavior and transitions toward territories of greater perceived value suggest that local Coyote populations are regulated through competition for space and territories, similar to findings of previous studies established Coyote populations in the western US. In these studies, lightly exploited populations exhibited boundedness (Murdoch 1994) where recruitment was highly limited by available territories and “reproductive rates fall far short of the biotic potential of the species” (Knowlton and Gese 1995). Thus, it is not surprising that current removal rates do not reduce population numbers. In fact, Coyote populations appear to be increasing or are stable in Virginia (USDA 2013, Virginia Department of Game and Inland Fisheries 2012) because attempted broad scale removals are reducing or negating the effects of the intraspecific competition regulation mechanism.

Acknowledgements

We would like to thank collaborators Robert Alonso, the Virginia Department of Game and Inland Fisheries, including Mike Fies, Dave Steffen, Al Bourgeois, and Nelson Lafon, US Forest Service, including Steve Tanguay, Carol Croy, the Nature Conservancy and Marek Smith at the Warm Springs Mountain Preserve, and the Laboratory for Ecological and Evolutionary Conservation Genetics, including Jen Adams, Caren Goldberg, Claudia Wultsch, Rob Lonsinger, Susannah Woodruff, Kate Cleary, Matt Mumma, Joel Tebbenkamp, and Carisa Stansbury. In addition, we thank Mike Cherry, Mike Conner, Jim Nichols, and Andy Royle for invaluable discussions on model implementation and interpretation. Financial support provided by the Virginia Department of Game & Inland Fisheries came from the U.S. Fish & Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Finally, we appreciated additional funding and support from the Appalachian members of the Virginia Deer Hunter Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).

Literature Cited

Allen, J.J., M. Bekoff, and R.L. Crabtree. 1999. An Observational Study of Coyote (*Canis latrans*) Scent-marking and Territoriality in Yellowstone National Park. Ethology 105(4):289-302.

Atwood, T.C. 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. Canadian Journal of Zoology-Revue Canadienne De Zoologie 84:80-87.

Atwood, T.C., and H.P. Weeks. 2002. Facultative dyad formation in adult male coyotes. Northeastern Naturalist 9:353-358.

Baker, P.J., and S. Harris. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? European Journal of Wildlife Research 52:99-108.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the national elk refuge, Jackson, Wyoming. Pp. 267-294 *In* M. Bekoff, Editor. Coyotes: biology, behavior, and management. Academic Press, New York, NY, USA.

Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Canadian Journal of Zoology, 79(6):980-987.

Gier, H.T. 1968. Coyotes in Kansas. Kansas State College Agricultural Experiment Station 465 Bulletin 393. Kansas State University, Manhattan, KS, USA.

Harrison, D.J. 1986. Coyote dispersal, mortality, and spatial relationships with red foxes in Maine. Ph.D Dissertation. University of Maine, Orono, ME, USA.

Hinton, J.W., M.J. Chamberlain, and F.T. van Manen. 2012. Long-distance movements of transient coyotes in eastern North Carolina. American Midland Naturalist 168(2):281-288.

Hinton J.W., F.T. van Manen, and M.J. Chamberlain. 2015. Space Use and Habitat Selection of Resident and Transient Coyotes. PlosOne. In Press.

Hixon, M. A., S.W. Pacala, and S.A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83(6):1490-1508.

Kamler, J.F., and P.S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78:2106–2111.

Knowlton, F.F., and E.M. Gese. 1995. Coyote population processes revisited. Pp 1-6 *In* D. Rollins, C. Richardson, T. Blankenship, K. Canon, and S. Henke, ed. Coyotes in the southwest: a compendium of our knowledge. Texas Parks and Wildlife Department. Austin, Texas, USA.

Knowlton, F.F., E.M. Gese, and M.M. Jaeger. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52:398-412.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations (No. 2). Princeton University Press, Princeton. NJ, USA.

Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015. Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. Journal of Wildlife Management 79:425-434.

Messier, F. and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60:1743-1753.

Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology 75(2):271-287.

Nichols, J.D., and G.M. Haramis. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. Condor 82(4):406-416.

Patterson, B.R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463-477.

Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53(1):7-15.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132(5):652-661.

Sacks, B.N., M.M. Jaeger, J.C. Neale, and D.R. McCullough.1999. Territoriality and breeding status of coyotes relative to sheep predation. Journal of Wildlife Management 63(2):593-605.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. Journal of Mammalogy 92:784-795.

Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84(1):153-159.

USDA. 2013. Status of the Virginia Cooperative Coyote Damage Control Program, Fiscal Year 2013.

Virginia Department of Game and Inland Fisheries. 2012. Virginia bowhunter survey, hunter harvest, and pelt harvest data.

Windberg, L.A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology-Revue Canadienne De Zoologie 73:942-954.

Windberg, L.A., and F.F. Knowlton. 1988. Management implications of coyote spacing patterns in southern Texas. The Journal of Wildlife Management: 632-640.

TABLES

Table 1. Class structure and fates of Coyotes collared in Bath County, VA, July 2011 – March 2014. Coyotes were classified as resident based on stability of monthly home range centers (< 2km distance between centers).

Status	Coyote	Sex	Stage	Months tracked (month/year)	Total fecal DNA detections[1]	Session: Scat Encounter Rate during May – July 2012 scat collection session (detections/km search effort)	Fate
Resident	C04	Male	Adult	1+ (10/11 – 11/11)	0		Killed (opportunistic shooting)
Resident	C08	Male	Adult	1+ (4/12 – 5/12)	2		Killed (opportunistic shooting)
Resident	C14	Male	Adult	7+ (6/12 – 2/13)	22	July 2012: 0 (1/60.2 km)	Survived
Resident	C18	Male	Subadult	4+ (5/13 – 9/13)	0		Killed (vehicle collision)
Resident	C06	Female	Adult	1+ (10/11 – 11/11)	2		Killed (opportunistic shooting)
Resident	C13	Female	Adult	6+ (6/12 – 1/13)	16	July 2012: 0.02 (1/60.2 km)	Survived
Resident[2]	C17	Female	Adult	10+ (5/13 – 3/14)	8		Survived
Resident	C01	Female	Subadult	4+ (7/11 – 11/11)	0		Killed (recreational trapper)
Resident	C03	Female	Subadult	5+ (9/11 – 2/12)	1	February 2012: 0 (0/4.4 km)	Killed (recreational trapper)
Resident	C15	Female	Subadult	1+ (5/13 – 6/13)	0		Killed (USDA Wildlife Services)
Resident with transient periods	C07	Male	Adult	11+ (4/12 – 3/13)[3] 4+ (3/13 – 7/13)	0	July 2012: 0 (0/10.5 km)	Killed (opportunistic shooting)
Resident with transient periods	C09	Male	Subadult	8+ (5/12 – 1/13)	3	July 2012: 0 (0/8.4 km)	Survived
Resident with transient periods	C10	Female	Adult	10+ (5/12 – 4/13)[3] 7+ (6/13 – 12/13)	6	July 2012: 0 (0/37.4 km) March 2013: 0.15 (2/13.4 km) July 2013: 0.09 (1/11.2 km)	Survived
Resident transitioned to transient	C02	Male	Subadult	3+ (8/11 – 11/11)	0		Killed (opportunistic shooting)
Resident transitioned to transient	C12	Female	Subadult	8+ (5/12 – 1/13)	14	July 2012: 0.11 (3/26.9 km)	Killed (recreational trapper)[4]
Resident transitioned to transient	C19	Female	Subadult	8+ (5/13 – 1/14)	0	July 2013: 0 (0/1.1 km)	Survived
Transient[5]	C05	Female	Subadult	10 + (10/11 – 8/12)	0	February 2012: 0 (0/10.4 km) July 2012: 0 (0/20.1 km)	Killed (USDA Wildlife Services)[6]
Transient[7]	C16	Female	Adult	8+ (5/13 – 1/14)	NA		Survived
Unknown	C11	Male	Adult	~1 (5/12)	12		Killed (opportunistic shooting)

[1] including months when individuals were not tracked.

[2] distance between successive centers was greater than 2 km for the last month tracked.

[3] Two individuals (C07 and C10) were captured in consecutive years and fitted with replacement collars after the first collar stopped transmitting resulting in 2 time periods when the animal was tracked.

[4] collar and carcass returned by recreational trapper February 2013 after collar had stopped transmitting relocations.

[5] transient 8 of 10 months tracked

[6] reported killed by Wildlife Services March 2013 after collar had stopped transmitting relocations.

[7] transient 7 of 8 months tracked

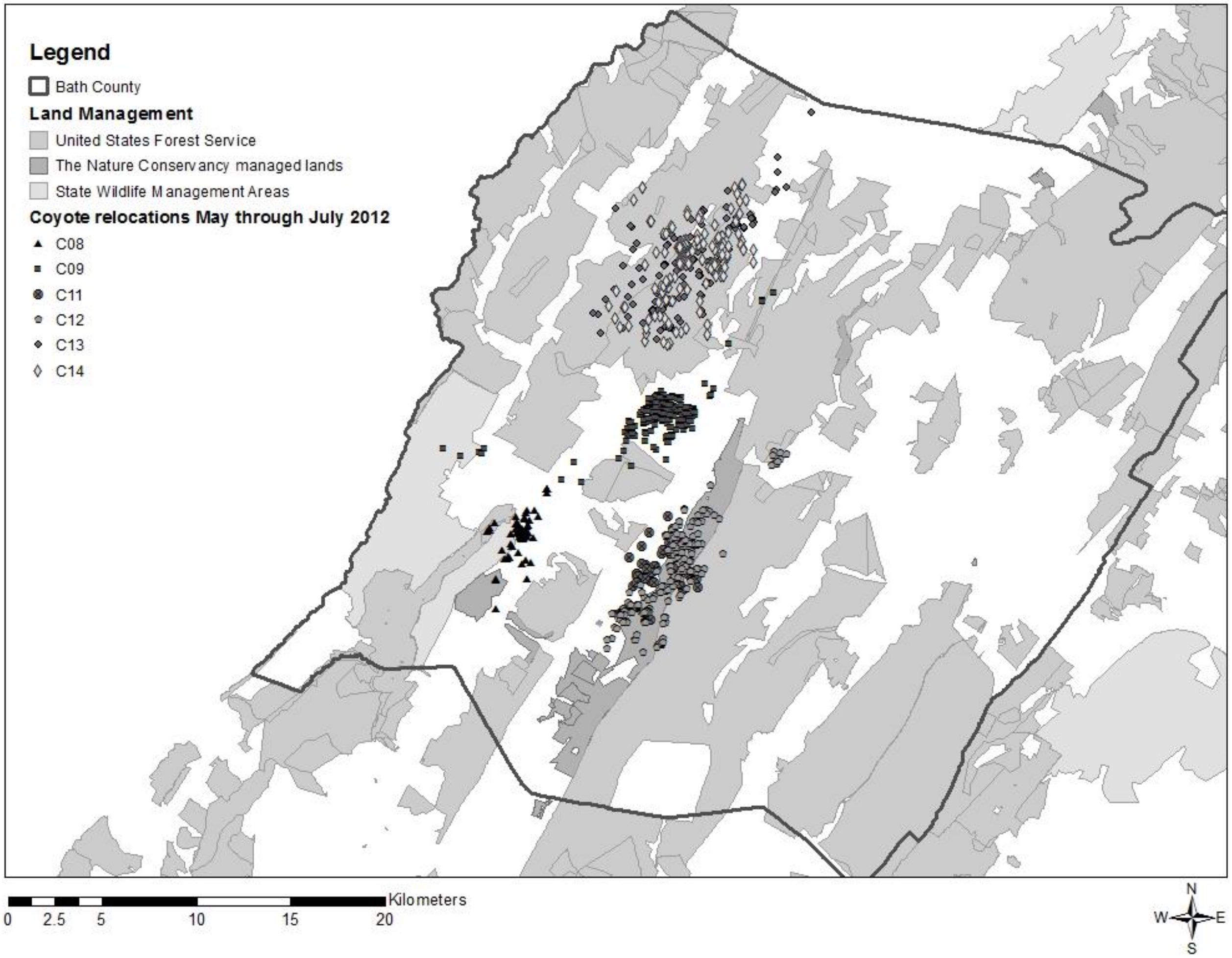


Figure 1. Bath County, Virginia, Study Area, displaying land ownership and collar relocations of resident Coyotes detected during scat surveys from May – July 2012.

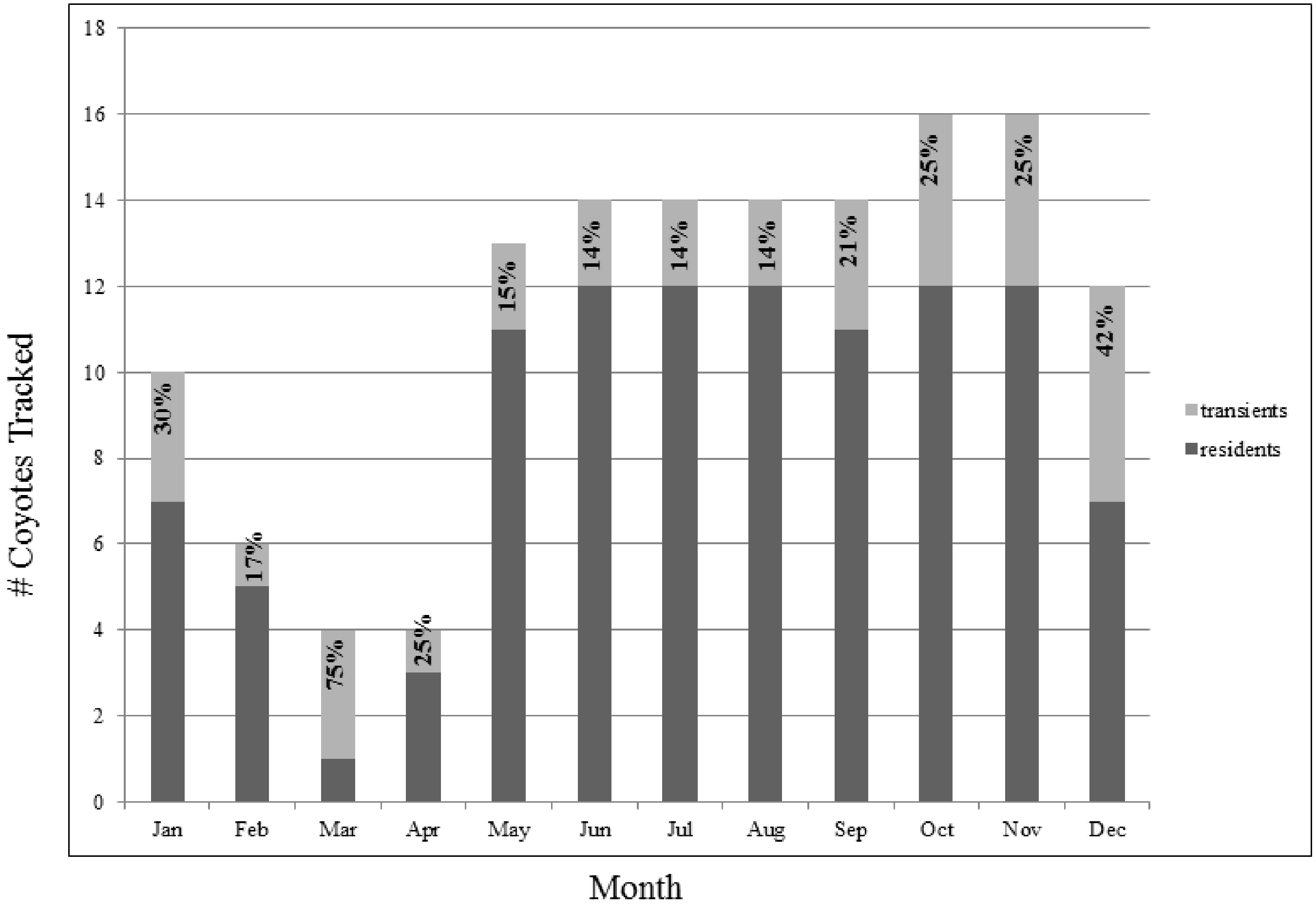


Figure 2. Proportion of tracked coyotes out of total number coyotes tracked each month (y-axis) behaving as transients each month as determined by distance between successive home range centers (Chapter 2).

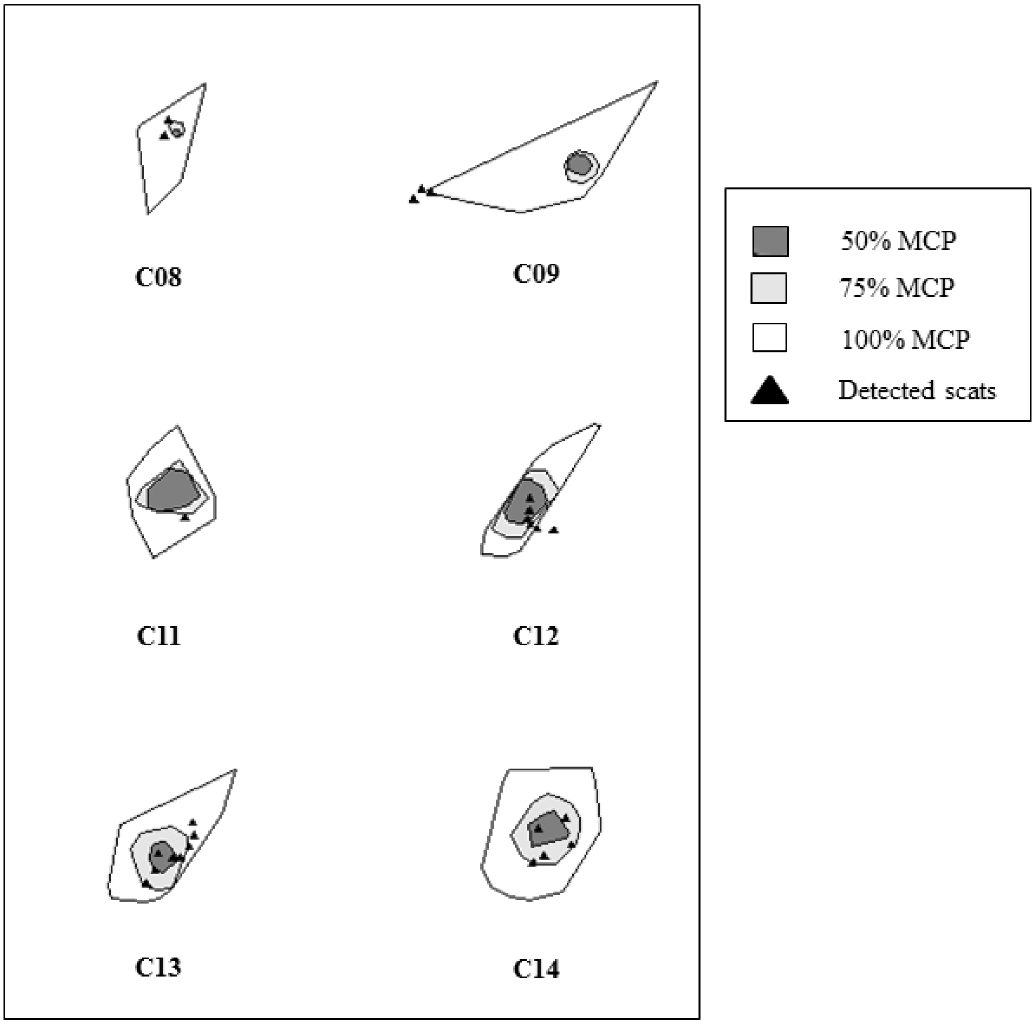


Figure 3. Locations of scats (black triangles) genotyped to the individual within that individual's home range May through July 2012. Number of scats occurring in the outer band between the 50% and 100% MCPs was compared to the number found within the core 50% MCP.

CHAPTER 5.

Can landscape-level habitat management reduce human-coyote conflict?

Target Journal: Journal of Wildlife Management

ABSTRACT Coyote populations have expanded in the southeastern US and current strategies for management of human-coyote conflicts have been largely ineffective. Previously, we identified patterns in second-order habitat selection that indicated class substructure for selection of territories where adult residents had a higher probability of mortality in high productivity/high risk habitats, compared to subadults and transients that were restricted to less productive habitats in a limited resource, risk-disparate environment. Here, we re-evaluated the role of class substructure in third-order habitat selection to understand how coyotes use habitats within their home ranges. Most coyotes used habitat within the overall home range in proportion to availability, but adult resident females more often selected for high-productivity/high-risk habitats when those habitats were available in core areas, intensively used areas. Risk of mortality was greatest from residents that established territories including high-productivity/high-risk habitats, and adult females showed more selection for those habitats within home ranges. Thus, the high local mortality rate could result in selection within the population for females that invest more in each reproductive opportunity (fast life history traits), as the landscape-scale habitat composition encourages risky behavior for greater rewards. Based on our results, we suggest landscape-scale habitat management as an alternative strategy to minimize human-coyote conflict and potential impacts to local prey populations.

KEY WORDS alternative human-wildlife conflict management, *Canis latrans*, coyote, eigenanalysis of selection ratios, habitat selection, landscape-scale management, optimal foraging theory, risk.

Journal of Wildlife Management 00: 000-000

INTRODUCTION

As coyotes (*Canis latrans*) have expanded into the eastern United States, natural resource agencies in the affected states have struggled to address human-coyote conflicts and find effective potential management strategies. In Virginia, the agency policy and legislative actions have focused on removing barriers to harvest, designating coyotes a nuisance species, establishing a continuous open season, and removing restrictions on hunting at night, with lights and/or electric calls. In addition, the state legislature passed a law allowing counties to designate bounties; currently there are 17 counties with bounties (11 funded) that range from \$25 to \$75. In addition, private and local stakeholder organizations have promoted "lotteries" intended to encourage the highest level of mortality possible, as a means to decrease the coyote population or human-coyote conflicts.

These actions all assume that coyote populations can be managed through predation, or increased mortality. However, despite numerous studies across North America (over 19,000 Google Scholar articles from a search of "*Canis latrans*" on April 27, 2015), few provide evidence that coyote removals have reduced coyote populations, and in the face of >100 years of concerted efforts to control coyote populations, the species has expanded its range substantially. Studies examining the impact of coyote removals to benefit prey populations have produced mixed or inconsistent results at high financial costs (Kilgo et al. 2014, Gulsby et al. 2015). Alternative remedies such as reducing the hunter harvest of female deer (*Odocoileus virginianus*) are now being proposed to counteract any additive mortality coyotes may generate (Robinson et al. 2014).

Coyotes are adaptable and exhibit a flexible life history strategy, with selection for increased reproductive rates (early age of first reproduction, larger litter sizes) when adult mortality is high (Knowlton et al. 1999). In a meta-analysis of demographic transient dynamics for 111 mammal species, coyotes were identified as singularly unique in their ability to respond to rapid population declines due to these life history traits (Gamelon et al. 2014). In another meta-analysis of coyote removal studies over multiple years, the single best predictor of the number of coyotes required to be removed to maintain a decrease in population was the number of coyotes removed the previous year, and the slope of the relationship indicated 1.34 more coyotes would need to be removed every year (Conner and Morris, submitted). In contrast, in high density or lightly exploited populations, coyote populations are typically limited by available territories (territory saturation), reproduction and recruitment decline (Windberg 1995, Knowlton and Gese 1995), adults maintain territories past reproductive senescence (Crabtree 1988), and reproductive rates "fall far short of the reproductive potential of the species" (Knowlton and Gese 1995, pg. 3).

In Chapter 3, we found evidence of density dependent coyote population dynamics, even at low densities in the ridge and valley region of central Appalachians in Virginia. The Bath County coyote population persisted at relatively consistent densities (5.53 – 9.04/100 km^2), despite very low 6-month apparent survival (0.442, 95% CI = 0.259 – 0.643), and in Chapter 4 we identified 3 potential "biding" strategies allowing for immediate recruitment into the local population through compensatory immigration (see also Baker and Harris 2006, Hernando and Perez 2012, Beasley et al. 2013, and Lieury et al. 2015). In contrast, the western Rockingham

County coyote population demonstrated “boundedness” (Murdoch 1994) at generally lower densities (median = 4.68 coyotes/100 km^2), higher apparent survival (0.863, 0.269 – 0.991), and recruitment inversely correlated with fluctuating densities. Thus, the population dynamics of coyotes in both study areas suggest there may be a negative feedback loop facilitating density-dependent regulation through competition for limited territories.

Encouraging an alternative human-coyote conflict management strategy.

Coyote conflict with livestock is a function of coyote abundance and coyote behavior (Knowlton et al. 1999). This is also likely true regarding impacts to prey (Hinton 2014, Chitwood et al. 2014a). In Chapter 2, we found differences in mortality risk based on how coyotes selected for habitats to include in home ranges (second-order habitat selection). We suggested this sets up a potential for territory-level source-sink dynamics in Bath County with high-risk territories along valley bottoms consistently refilled by new residents from the surrounding low-productivity mature deciduous forests. This dynamic begs the question “can we affect coyote behavior by altering the risk/reward landscape to reduce potential human-coyote conflict?”. In other words, is habitat management a viable alternative management strategy?

To consider the possibility of addressing human-coyote conflict in our study area through habitat changes we evaluated habitat selection at the third-order level in addition to the previous second-order analysis (Chapter 2) to better understand population class structure and individual behavior in relation to risk and reward. While second-order selection provides insight into interactions among individuals, third-order selection addresses individual selection within individual territories and may be more insightful in predicting potential sources of conflict. Therefore, we repeated the habitat selection analyses performed in Chapter 2, but at the third-order level, within home range.

We compared our results from analyses at both levels of selection to determine 1) if there was greater mortality risk as an effect of second- or third-order level selection behavior, and 2) if there were indications that coyote behavior could be influenced by habitat on the landscape. We predicted coyotes would show greater risk aversion at the third-order level compared to the second-order level. In other words, we expected the primary axis of each third-order eigenanalysis would distinguish between individual selection within home ranges for habitats associated with high risk as determined in Chapter 2 (agriculture, shrub, open/barren, and disturbed/developed habitats with higher potential for human interaction) at one end of the spectrum, and low risk (riparian, rocky outcrops and ridgelines, hardwood, softwood, and mixed forest stands and small grassy wildlife clearing) at the other end. We also predicted second-order habitat selection along the 95% UD risk axis (axis 2) would remain the best predictor of survival as we believe location of territory is a greater source of risk of mortality than individual behavior in selection within territories.

METHODS

For third-order analysis, we again used all 4 space-use classifications estimated from Biased Random Bridges (BRBs) calculated each month: 95% utilization distribution (UD) overall home range or territory, 50% UD core areas, 50% intensity distribution (ID) intensively used areas, and 50% recursion distribution (RD) frequently used areas (Benhamou 2011). We used the adehabitat package (Calenge 2006) in R (R Core Team 2013) using the coyote relocation data collected as described in Chapter 2 to allow inference regarding differences in how individual coyotes use the resources available to them within their home ranges for different purposes or activities. However, at this level of analysis, availability was considered at the individual level and was tabulated as the count of habitat raster cells within each home range designation for each individual for each month they were tracked (a coyote-month). For habitat use, we counted the number of relocations within each habitat type for the appropriate space-use classification. Using the eisera() function, these counts were transformed to proportions for eigenanalysis of selection ratios (Calenge and Dufour 2006). We extracted resource selection scores for each habitat type and the first and second component scores for each individual over each month (coyote-month) for further analyses including linear mixed models (LMMs) using the same candidate model set described in Chapter 2 (Table 1). In addition, we repeated the known-fate binomial generalized linear mixed model (GLMM) adding the third-order eigenanalysis selection ratios to the candidate set as explanatory variables and using AICc to select the best model representing the space-use level at which coyotes were most at risk of mortality.

RESULTS

Third-order eigenanalysis at the 95% UD home range level (Figure 1) indicated most individuals were using for habitat within the overall home range proportional to availability. Coyote C10, an adult resident female, showed strong selection for agricultural areas within its territory in November 2013, which creates the main trend on axis 1. However use was relatively proportional to availability for the 17 other months it was tracked. There was no evident trend towards risk or productivity on axis 2, distinguishing between selection for rocky habitats at negative values and mixed hardwood/softwood stands at positive values. Model selection for axis 1 and axis 2 LMMs (Table 2, Appendix 1) both suggest individual was the greatest source of variation in how coyotes select for habitat within their entire home range or territory (random intercept only model $\omega = 0.398$, and 0.409, respectively). In addition, visual inspection of boxplots and scatterplots for axis 1 and axis 2 suggest habitat selection within overall territories was generally proportional to availability, with occasional shifts by some coyotes for some months.

Third-order eigenanalysis of habitat selection at the 50% UD core home range level (Figure 2) evaluated how individuals selected habitats within their own core territories. Axis 1 again represented occasional strong selection for agriculture greater than availability at positive values. Axis 2 distinguished between selection within core home ranges for mixed forest stands (positive values) and rocky habitat (negative values). Model selection of LMMs suggested individual is again the most important source of variation on both axis 1 ($\omega = 0.235$) and axis 2 ($\omega = 0.380$) within available core home range areas (Table 2, Appendix 2), but there appears to be a trend for residents to select for agriculture and mixed forests, more productive habitats within territories, evident by the positive axis 1 values for successive distances less than 2 km ($\Sigma\omega = 0.419$). Males tended to select for habitat proportional to availability (mean axis 1 factor score = 0.005) and females exhibited a mean positive factor scores (0.056) with a greater range of variability suggesting weak selection for agriculture for within individual 50% UD core home range areas and evidence of differences in selection within core home ranges based on sex ($\Sigma\omega = 0.394$).

Third-order eigenanalysis of the 50% ID described how individuals select habitats within the areas they most intensively use (Figure 3). Axis 1 distinguished selection for agriculture and mixed forest stands at more extreme negative values compared to other habitat types. Axis 2 distinguished between selection within intensively used areas for mixed forest stands at moderate positive values, shrub-dominated habitats at moderate negative values, and agriculture and disturbed/developed habitats at extreme negative values. We found support for differential selection of habitats within intensively used areas for the axis 1 models including distance between successive home range centers (Σω = 0.554) and sex (Σω = 0.415, Table 2, Appendix 3). Transients showed stronger selection for hardwood forest stands, and males demonstrated greater variability in moderate selection for habitats within intensely used areas compared to females. Individual was the greatest source of variation in selection along axis 2 (random intercept only model ω = 0.421, Appendix 3). There also appeared to be greater variation in adult selection for habitats within areas intensively used (range = -1.664 –0.620) compared to subadults (range = -0.654 – 0.0356) that demonstrated weaker selection for habitats within intensively used areas.

Third-order eigenanalysis of the 50% RD describes how an individual selects for habitats within the areas they use frequently (Figure 4). Axis 1 distinguished selection for disturbed/developed and shrub dominated landscapes at moderate negative values, and strong selection for agriculture at extreme negative values compared to other habitat types. Axis 2 distinguished between strong selection for mixed forest stands at extreme positive values from selection for agriculture at negative values. The random effect intercept only model was ranked highest for the both axis 1 (ω = 0.408) and axis 2 (ω = 0.415) LMM candidate sets (Table 2, Appendix 4), indicating that individual was again the greatest source of variation for selection within areas frequently visited.

Second-order eigenanalysis axis 2, which differentiated selection between high-risk and low-risk habitats in selection of overall territories, remained the best explanatory variable (ω = 0.278) for survival probability in the known-fate binomial GLMM (Table 3). However, third-order selection along axis 1 of the 50% UD core home range was a competing model (ΔAICc = 1.962, ω = 0.104, β = -1.53, SE = 0.92). This axis distinguishes between habitat selection within core home ranges along a gradient of high and low risk for agriculture in one direction and comparative selection for all other habitats relatively proportional to availability and suggests adult females that showed greater selection for these habitats assumed more risk of mortality for high-productivity habitats.

DISCUSSION

Many of the observed trends in coyote space use were a result of the general habitat composition across the study area and disparity between good quality and poor quality habitat. Over 75% of available habitat consisted of low-productivity hardwood forest. Coyotes sought out and established home ranges containing the remaining habitat types, and frequently visited and intensively used these areas. This likely concentrated foraging in the limited habitat with higher prey abundance and diversity. If nutritional carrying capacity was already low for prey species due to the dominance of resource-depleted mature hardwood stands, or species are already at low population levels, additional predation or interspecific killing from coyotes could result in additive mortality for some prey or competitor species (Cypher and Spencer 1998, Palomares and Caro 1999, Kilgo et al. 2014, Chitwood et al. 2014b).

In addition, we have shown that resource disparity coupled with higher probability of mortality may increase risk-taking behavior for selection of habitats, particularly for female coyotes. However, risk is not just associated with habitat. Optimal foraging theory also predicts risk management in relation to “dangerous prey” (Mukherjee and Heithaus 2013). Taking of larger prey such as white-tailed deer is typically rare for smaller predators, such as coyotes, in part because there is a fitness trade-off between reward and risk of injury. However, there were four notable adult doe predation events by coyotes during a deer study at Fort Bragg, North Carolina (Chitwood et al. 2014a). In this case, three of four females were towards the end of pregnancy (the other unconfirmed but suspected), experiencing reduced mobility and considered “vulnerable” (Chitwood et al. 2014a). It could be assumed that perceived reward to coyotes as foragers increased in relation to perceived risk as the pregnant females were less threatening. It is not unreasonable to consider that the same circumstances in our study area may cause some individuals to consider larger, more dangerous and energetically costly, but very high reward prey.

Coyotes selected for agriculture at many space-use levels, increasing potential risk of mortality. However, it appears it is the open pasture land habitat and associated wildlife prey base, and not livestock or crops that attracts coyotes to agricultural areas in our study area. For example, at the 95% UD home range level, coyotes prioritized incorporation of grasslands within territories and agriculture within territories in a very similar manner. Figure 6 in Chapter 2 showed similar extreme negative values for both grasslands and agriculture along the axis 1 productivity gradient (Table 4), but divergent values on the axis 2 risk gradient. However, it should be noted that during a concurrent diet analysis study we did not find common agricultural crops in coyote scats and only one coyote sample contained livestock hair (Montague 2014). Thus, attraction to agricultural areas is likely due to habitat conditions and higher density prey populations in the open pastures and fields, and not individual propensity for damage.

In addition, seasonal trends at the second-order core home range level (50% UD) indicated selection for agricultural areas may be a result of changing risk and reward values in the usually low-risk forest stands. There was very little individual variability in habitat selection along axis 2 in June and July and selection was almost entirely for hardwood and softwood forest stands (Figure 8 in Chapter 2). These months likely corresponded with lowest risk and greatest food abundance in forested habitats, which in our study area is primarily the George Washington National Forest. These months had no open hunting seasons and followed a reproductive pulse for several prey species and fruiting of soft mast, all commonly found in coyote diet (Schrecengost et al. 2008; Montague 2014). However, from August through December there is a shift to incorporate more agricultural habitats, as shown by the negative selection values on axis 1, particularly by adult residents. This timing corresponded with likely depletion of seasonal food resources in the forest habitats and a pulse of increased human activity on National Forest lands. Bear (*Ursus americanus*) chase season starts in mid-August followed by archery deer season, and firearms deer season; hunter activity peaks in November during rifle season and we observed a corresponding peak in second-order core home range habitat selection variability. We suggest the increased risk and decreased reward values in the hardwood forest, commonly public lands, as human activity increases and forest food resources decline, stimulate a change in optimal foraging strategies, nullifying the safety benefit of less productive habitats and increasing selection for more risky but increasingly productive habitats, similar to how game species also respond to perceptions of danger from hunters (Kilgo et al. 1998, Frid and Dill 2002, Stankowich 2008). We propose coyotes in our study area are responding not only to changes in foraging opportunities, but also to changes in their own perceptions of increased predation risk from hunters in forested habitats during deer hunting seasons (Kie 1999, Frid and Dill 2002).

We have demonstrated that predator-prey species interactions and human conflict as a result of coyote space use and behavior in our study areas likely were functions of a disparity in productivity between high risk and low risk areas (Abrahams and Dill 1989). Therefore, potential actions to reduce human-coyote conflict could include increasing risk perception in habitats where we wish to deter use, and increasing the relative value of other habitats. Increased habitat quality across the study area to increase nutritional carrying capacity of prey would likely reduce potential additive mortality from coyote predation and disperse predator foraging focus across a wider landscape. In addition, large-scale habitat improvements would reduce the disparity in habitat quality, increasing the “energetic equivalent of risk” (Abrahams and Dill 1989), and likely decrease risk-taking behavior that otherwise seems to result in increased real or perceived human-coyote conflicts along the valley floors. Thus, improvements in habitat quality across the study area including prescribed fires and timber harvests could relieve potential sources of human-coyote conflict as well as produce positive impacts on prey populations, bringing to mind the idiom “a rising tide lifts all boats”.

ACKNOWLEDGMENTS

We would like to thank collaborators Robert Alonso, the Virginia Department of Game and Inland Fisheries, including Mike Fies, Dave Steffen, Al Bourgeois, and Nelson Lafon, US Forest Service, including Steve Tanguay, Carol Croy, Russ MacFarlane, and Lindsey Curtain, the Nature Conservancy and Marek Smith at the Warm Springs Mountain Preserve. In addition, we thank Mike Cherry, Joey Hinton, Colter Chitwood, Marcus Lashley, and Jim Nichols for conversations critical to converting pattern to process, Lisa Lyren, Ed and Jaime McArdle for logistic support, and Jason Woods for public relations and carcass/collar retrieval. Financial support provided by the Virginia Department of Game & Inland Fisheries came from the U.S. Fish & Wildlife Service through the Wildlife and Sport Fish Restoration Program, Project WE99R. Finally, we appreciated additional funding and support from the Appalachian members of the Virginia Deer Hunter Association, The Nature Conservancy, the Edna Bailey Sussman Foundation, and the Cunningham Fellowship (Virginia Tech Graduate School).

LITERATURE CITED

Abrahams, M. V., and L. M. Dill, 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70(4):999-1007.

Baker, P.J., and S. Harris. 2006. Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK?. European Journal of Wildlife Research 52:99-108.

Beasley, J.C., Z.H. Olson, W.S. Beatty, G. Dharmarajan, and O.E. Rhodes Jr. 2013. Effects of Culling on Mesopredator Population Dynamics. PLoS ONE 8:e58982.

Benhamou, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PloS one 6(1):e14592.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519

Calenge, C., A. B. Dufour. 2006. Eigenanalysis of selection ratios from animal radio-tracking data. Ecology 87(9):2349-2355.

Chitwood, M. C., M. A. Lashley, C. E. Moorman, C. S. DePerno. 2014a. Confirmation of coyote predation on adult female white-tailed deer in the southeastern United States. Southeastern Naturalist 3(13):N30-N32.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2014b. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer?. PloS one 10(3):e0119070-e0119070.

Conner, L.M. and G. Morris. In Preparation. Mesopredator removals studies: implications for conserving mesopredators and their prey.

Crabtree, R.L. 1988. Sociodemography of an unexploited coyote population. Dissertation, University of Idaho, Moscow, USA.

Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79(1): 204-214.

Frid, A., L. and M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1):11.

Gamelon, M., O. Gimenez, E. Baubet, T. Coulson, S. Tuljapurkar, and J.M. Gaillard. 2014. Influence of life-history tactics on transient dynamics: a comparative analysis across mammalian populations. American Naturalist 184:673-683.

Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39(2):248-255.

Herrando-Pérez, S., S. Delean, B. W. Brook, and C. J. Bradshaw. 2012. Decoupling of component and ensemble density feedbacks in birds and mammals. Ecology 93:1728-1740.

Hinton, J. W. 2014. Red wolf (*Canis rufus*) and coyote (*Canis latrans*) ecology and interactions in northeastern North Carolina. PhD Dissertation. University of Georgia, Athens, USA.

Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80(4):1114-1129.

Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of Hunting on the Behavior of White-Tailed Deer: Implications for Conservation of the Florida Panther. Conservation Biology 12(6):1359-1364.

Kilgo, J. C., M. Vukovich, H. S. Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. Journal of Wildlife Management 78(7):1261-1271.

Knowlton, F. F., and E. M. Gese. 1995. Coyote population processes revisited. In Symposium Proceedings--Coyotes in the Southwest: A Compendium of Our Knowledge, 1995: p. 26.

Knowlton, F. F., E. M. Gese, M. M. Jaeger 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52(5):398-412.

Lieury, N., S. Ruette, S. Devillard, M. Albaret, F. Drouyer, B. Baudoux, and A. Millon. 2015. Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. Journal of Wildlife Management 79:425-434.

Montague, D. M. 2014. Diet and Feeding Ecology of the Coyotes, Black Bears, and Bobcats in Western Virginia and Preliminary Assessment of Coyote Parasites. Thesis, Virginia Tech, Blacksburg, USA.

Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology 75:271-287.

Mukherjee, S., and M. R. Heithaus. 2013. Dangerous prey and daring predators: a review. Biological Reviews 88:550-563.

Palomares, F., and T. M. Caro, 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153(5):492-508.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Robinson, K. F., D. R. Diefenbach, A. K. Fuller, J. E. Hurst, and C. S. Rosenberry. 2014. Can managers compensate for coyote predation of white-tailed deer? Journal of Wildlife Management 78:571–579.

Schrecengost, J. D., J.C. Kilgo, D. Mallard, H.S. Ray, and K.V. Miller. 2008. Seasonal food habits of the coyote in the South Carolina coastal plain. Southeastern Naturalist 7:135-144.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159-2173.

Windberg, L.A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942-954.

TABLES

Table 1. Linear Mixed Model (LMM) candidate sets of multiple working hypotheses for sources of variability in coyote home range size and habitat selection. There are 18 response variables for which the same candidate set composed of 11 models was applied. Response and explanatory variables were transformed as necessary to approximate normality and c-hat was estimated using the global model, although this model was not included in the restricted candidate model sets due to the excessive number of parameters for a relatively small sample size (137 total observations of coyote home ranges over months).

<table>
<tr><th>Space Use Classification</th><th>Space Use Type</th><th>Response Variable</th><th>Candidate Set and model number used for each response variable</th></tr>
<tr><td rowspan="4">**Overall Home Range**</td><td rowspan="2">Partitioning of available habitat for territories among individuals</td><td>95% UD second order eigenanalysis axis 1</td><td rowspan="16">**model 1** ~ (1 | individual)
model 2 ~log(Successive Distance) + (1 | individual)
model 3 ~month + (1 | individual)
model 4 ~log(Successive Distance) + month + (1 | individual)
model 5 ~sex + (1 | individual)
model 6 ~log(Successive Distance) + sex + (1 | individual)
model 7 ~month + sex + (1 | individual)
model 8 ~stage + (1 | individual)
model 9 ~log(Successive Distance) + stage + (1 | individual)
model 10 ~month + stage + (1 | individual)
model 11 ~sex + stage + (1 | individual)</td></tr>
<tr><td>95% UD second order eigenanalysis axis 2</td></tr>
<tr><td rowspan="2">Selection for habitat within individual territories</td><td>95% UD third order eigenanalysis axis 1</td></tr>
<tr><td>95% UD third order eigenanalysis axis 2</td></tr>
<tr><td rowspan="4">**Core Home Range**</td><td rowspan="2">Partitioning of available habitat for core home range areas among individuals</td><td>50% UD second order eigenanalysis axis 1</td></tr>
<tr><td>50% UD second order eigenanalysis axis 2</td></tr>
<tr><td rowspan="2">Selection for habitat within individual core home range areas</td><td>50% UD third order eigenanalysis axis 1</td></tr>
<tr><td>50% UD third order eigenanalysis axis 2</td></tr>
<tr><td rowspan="4">**Core Home Range Areas Used Intensively**</td><td rowspan="2">Partitioning of available habitat for intensive use (long durations) among individuals</td><td>50% ID second order eigenanalysis axis 1</td></tr>
<tr><td>50% ID second order eigenanalysis axis 2</td></tr>
<tr><td rowspan="2">Selection for habitat within individual intensive use areas</td><td>50% ID third order eigenanalysis axis 1</td></tr>
<tr><td>50% ID third order eigenanalysis axis 2</td></tr>
<tr><td rowspan="4">**Core Home Range Areas Frequently Used**</td><td rowspan="2">Partitioning of available habitat for core home range areas among individuals</td><td>50% RD second order eigenanalysis axis 1</td></tr>
<tr><td>50% RD second order eigenanalysis axis 2</td></tr>
<tr><td rowspan="2">Selection for habitat within individual core home range areas</td><td>50% RD third order eigenanalysis axis 1</td></tr>
<tr><td>50% RD third order eigenanalysis axis 2</td></tr>
</table>

Table 2. Support for differential coyote space use by individual (random effect intercept), month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)) for 18 model sets (one model set for each response variable, with each model set consisting of 11candidate models). Bolded fields represent best supported variables based on cumulative (Q)AICc weights listed from linear mixed model (LMM) selection.

Candidate model response variable	**Axis[1]**	**status**	**month**	**sex**	**stage**	**Individual intercept only**	**Level of Inference**
95% UD Home Range Size[2]		**0.406**	0	0.238	**0.392**	0.254	overall home range/territory
95% UD second order habitat	1	NA[2]	NA	NA	NA	NA	selection between overall home ranges/territories
95% UD second order habitat	2	**0.995**	0.001	0.25	0.19	0.002	
95% UD third order habitat	1	0.250	0.013	0.251	0.25	**0.398**	selection within overall home ranges/territories
95% UD third order habitat	2	0.246	0.001	0.241	0.253	**0.409**	
50% UD Home Range Size		0.053	**0.987**	0.044	**0.763**	0.001	core home range area
50% UD second order habitat	1	0.263	0	0.238	0.276	**0.389**	selection between core home range areas
50% UD second order habitat	2	0.293	0	0.239	0.239	**0.393**	
50% UD third order habitat	1	**0.419**	0.005	**0.394**	0.275	0.235	selection within core home range areas
50% UD third order habitat	2	0.252	0.008	0.296	0.238	**0.380**	
50% ID second order habitat	1	**0.833**	0.001	0.223	**0.495**	0.069	selection between intensively used areas
50% ID second order habitat	2	NA[2]	NA	NA	NA	NA	
50% ID third order habitat	1	**0.544**	0	**0.415**	0.225	0.193	selection within intensively used areas
50% ID third order habitat	2	0.244	0	0.241	0.241	0.421	
50% RD second order habitat	1	0.241	0	0.246	0.249	**0.416**	selection between frequently visited areas
50% RD second order habitat	2	**0.341**	0	0.238	0.265	**0.348**	
50% RD third order habitat	1	0.249	0	0.254	0.244	**0.408**	selection within frequently visited areas
50% RD third order habitat	2	0.243	0.001	0.243	0.247	**0.415**	

[1] Axis refers to the primary (Axis 1 - x) and secondary (Axis 2 - y) component factor scores from each eigenanalysis of habitat selection ratios.

[2] Home range size and second order habitat selection from Chapter 2.

[3] Unable to fit LMM due to poor transformations and inadequate goodness of fit.

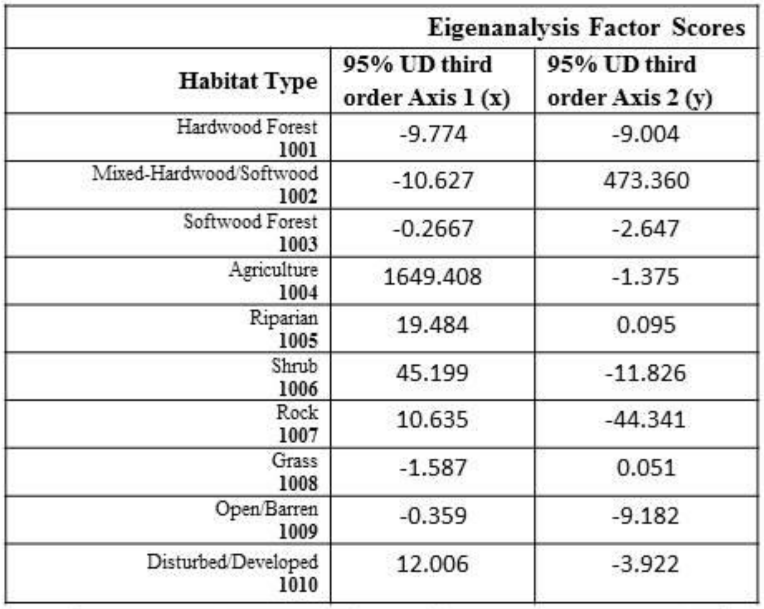
Table 3. Model Selection for known-fate binomial Generalized Linear Mixed Model. The response variable indicates survival from the beginning of one month to the next and the factor scores for each eigenanalysis axis were compared as explanatory variables (16 total, two for each order of habitat selection and two for each level of space use). Individual coyote was included as a random effect.

Model	Intercept	Eigenanalysis axis beta estimate	logLikelihood	Deviance	df	AICc	delta AICc	AICc model weight
2nd order 95% UD Axis 2	3.03 (0.48)	- 3.51 (1.60)	-35.6	71.2	134	77.399	0.000	0.278
3rd order 50% UD Axis 1	2.63 (0.47)	- 1.53 (0.92)	-36.6	73.2	134	79.361	1.962	0.104
2nd order 50% RD Axis 1	2.55 (0.39)	0.83 (0.50)	-36.7	73.3	134	79.496	2.097	0.098
2nd order 50% ID Axis 2	2.54 (0.45)	1.47 (1.00)	-36.9	73.9	134	80.056	2.657	0.074
2nd order 95% UD Axis 1	2.54 (0.34)	0.81 (0.48)	-37.0	74.0	134	80.219	2.820	0.068
2nd order 50% ID Axis 1	2.55 (0.42)	1.48 (1.09)	-37.1	74.2	134	80.399	3.000	0.062
2nd order 50% UD Axis 2	2.58 (0.43)	1.04 (0.89)	-37.3	74.7	134	80.867	3.468	0.049
3rd order 50% ID Axis 1	2.52 (0.44)	- 0.92 (1.30)	-37.7	75.4	134	81.574	4.175	0.035
3rd order 50% RD Axis 2	2.51 (0.43)	0.79 (1.20)	-37.7	75.4	134	81.589	4.190	0.034
3rd order 95% UD Axis 2	2.48 (0.43)	0.62 (1.11)	-37.8	75.6	134	81.753	4.354	0.032
2nd order 50% RD Axis 2	2.50 (0.41)	0.74 (1.28)	-37.8	75.6	134	81.800	4.401	0.031
3rd order 50% UD Axis 2	2.51 (0.43)	0.56 (1.13)	-37.9	75.7	134	81.885	4.486	0.030
3rd order 95% UD Axis 1	2.48 (0.43)	0.18 (0.73)	-37.9	75.9	134	82.068	4.669	0.027
3rd order 50% ID Axis 2	2.48 (0.42)	- 0.25 (1.31)	-38.0	75.9	134	82.098	4.699	0.027
2nd order 50% UD Axis 1	2.46 (0.49)	0.12 (1.12)	-38.0	75.9	134	82.124	4.725	0.026
3rd order 50% RD Axis 1	2.48 (0.42)	- 0.07 (0.76)	-38.0	75.9	134	82.130	4.731	0.026

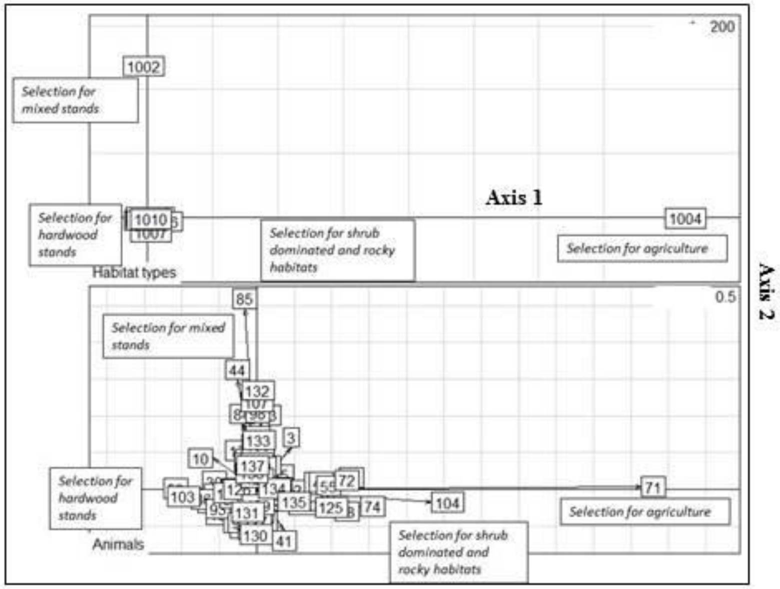
Table 4. Risk compared to productivity in prioritization of habitat selection at multiple scales and levels of space use as determined by eigenanalysis of selection ratios. Second order selection refers to how individuals select for habitat to incorporate in a home range unit. Third order selection refers to how individuals select for habitat within a home range unit. The primary axis is in bold and explains the greatest trend in variability.

Space Use Scale	Analysis Level	Component axis	Dichotomy for axes	% Variation explained
95% utilization distribution (UD), overall home range/territory	Second order	**Primary (axis 1: x)**	**productivity**	**38.67%**
		Secondary (axis 2: y)	risk	26.15%
	Third order	**Primary (axis 1: x)**	**none**	**52.33%**
		Secondary (axis 2: y)	none	25.14%
50% utilization distribution (UD), core home range	Second order	**Primary (axis 1: x)**	**productivity**	**27.51%**
		Secondary (axis 2: y)	undetermined	20.25%
	Third order	**Primary (axis 1: x)**	**risk**	**36.05%**
		Secondary (axis 2: y)	productivity	26.67%
50% intensity distribution (ID), intensive use areas	Second order	**Primary (axis 1: x)**	**risk (only productive habitats selected)**	27.82%
		Secondary (axis 2: y)	risk	26.24%
	Third order	**Primary (axis 1: x)**	**productivity**	**33.74%**
		Secondary (axis 2: y)	risk	27.38%
50% recursion distribution (RD), frequent use areas	Second order	**Primary (axis 1: x)**	**productivity**	**41.28%**
		Secondary (axis 2: y)	risk	19.11%
	Third order	**Primary (axis 1: x)**	**productivity**	**40.58%**
		Secondary (axis 2: y)	risk	36.74%

FIGURES



Eigenanalysis Factor Scores		
Habitat Type	**95% UD third order Axis 1 (x)**	**95% UD third order Axis 2 (y)**
Hardwood Forest **1001**	-9.774	-9.004
Mixed-Hardwood/Softwood **1002**	-10.627	473.360
Softwood Forest **1003**	-0.2667	-2.647
Agriculture **1004**	1649.408	-1.375
Riparian **1005**	19.484	0.095
Shrub **1006**	45.199	-11.826
Rock **1007**	10.635	-44.341
Grass **1008**	-1.587	0.051
Open/Barren **1009**	-0.359	-9.182
Disturbed/Developed **1010**	12.006	-3.922



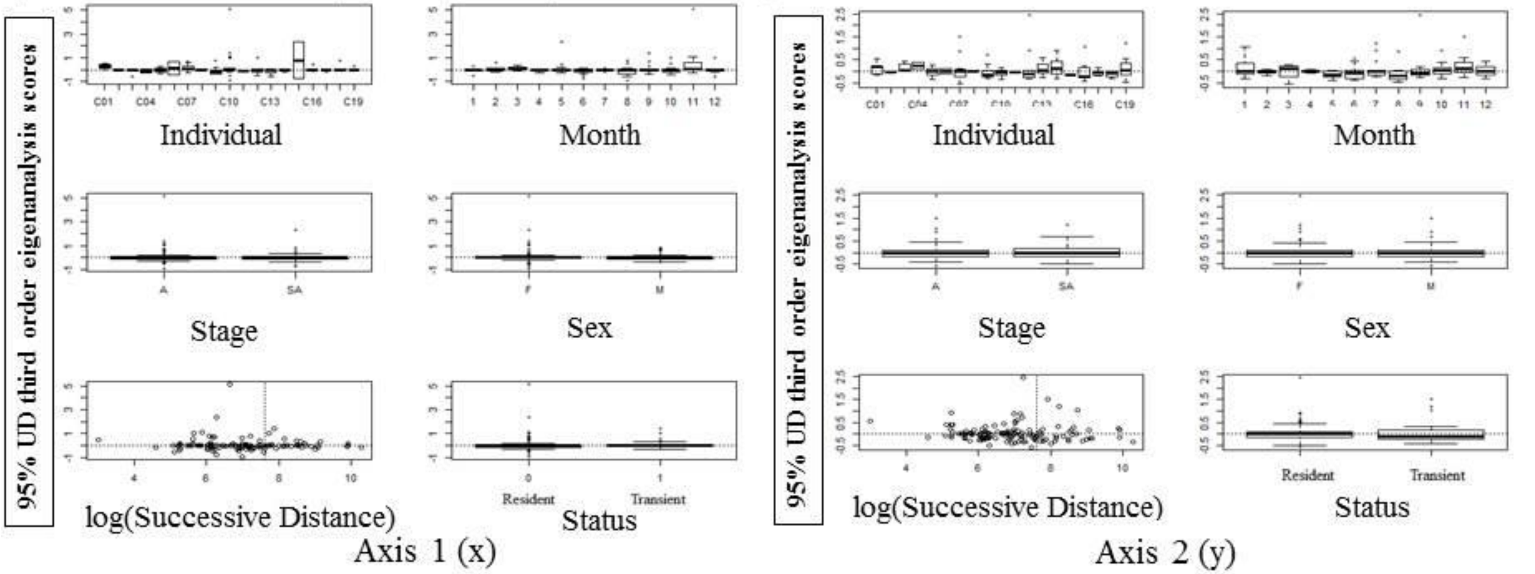
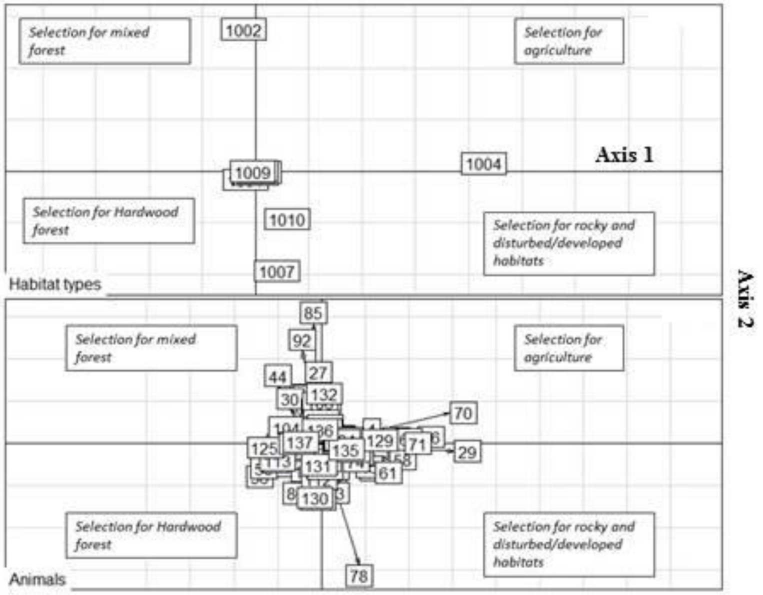
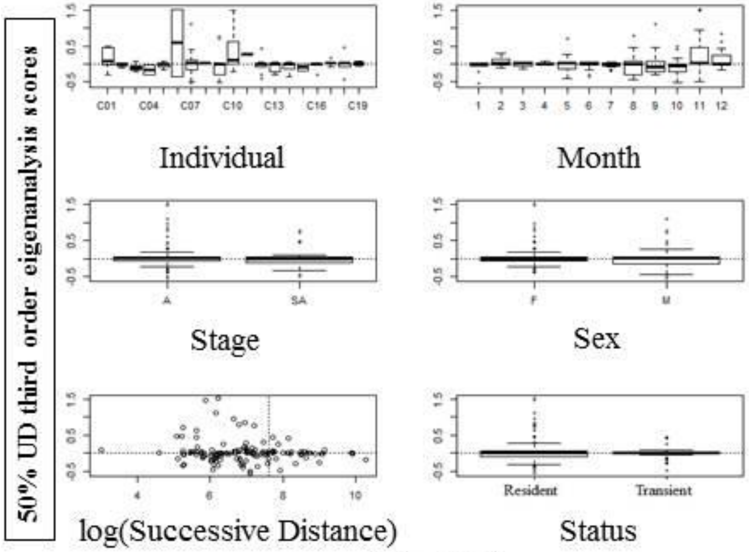


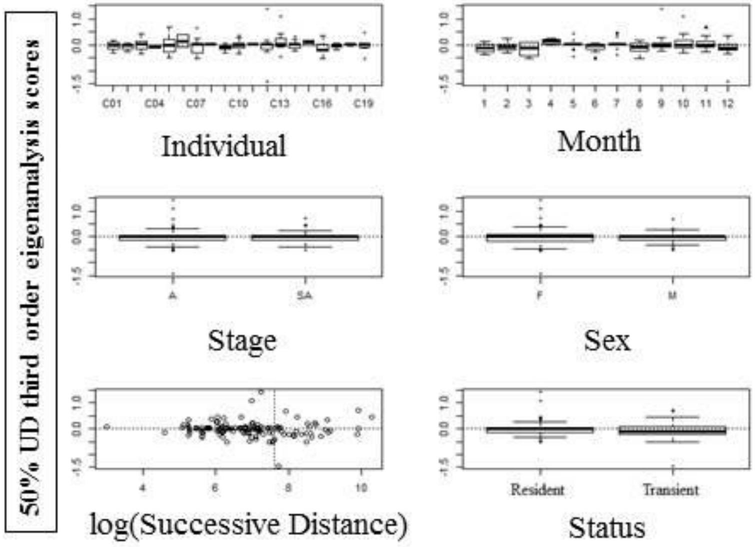
Figure 1. Third order habitat selection eigenanalysis biplots (top right) for 95% utilization distribution (UD) overall home range by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for each axis (top left pane) demonstrate differentiation and relative strength of selection for habitat types within individual home range territories. Values near zero (origin in biplots) represent similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Habitat selection within the overall home range was generally weak and most variability representing stronger selection for habitat types is at the individual level. The single point at the extreme of the positive range of axis 1 (box 71, right central pane) represents strong selection for agriculture by an adult resident female (C10) in November 2013. The single point at the extreme of the positive range of axis 2 (box 85, right central pane) represents strong selection for mixed forest stands by an adult resident female (C12) in September 2012 during a temporary exploratory stopover at the initiation of a dispersal event.

	Eigenanalysis Factor Scores	
Habitat Type	**50% UD third order Axis 1 (x)**	**50% UD third order Axis 2 (y)**
Hardwood Forest **1001**	-9.927	-8.469
Mixed-Hardwood/Softwood **1002**	-11.584	137.691
Softwood Forest **1003**	0.030	-0.510
Agriculture **1004**	214.468	7.527
Riparian **1005**	0.210	-3.772
Shrub **1006**	3.065	-1.464
Rock **1007**	20.422	-96.919
Grass **1008**	0	0
Open/Barren **1009**	-2.435	-0.454
Disturbed/Developed **1010**	29.887	-46.556





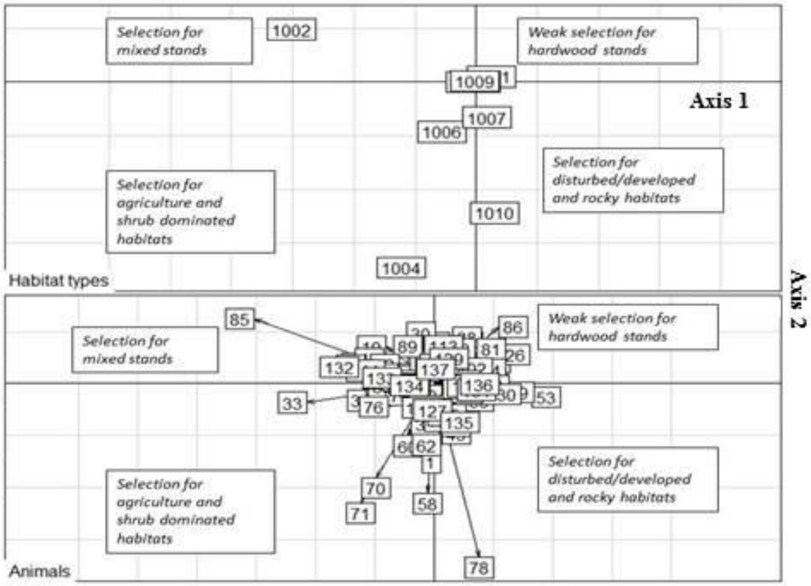
Axis 1 (x)

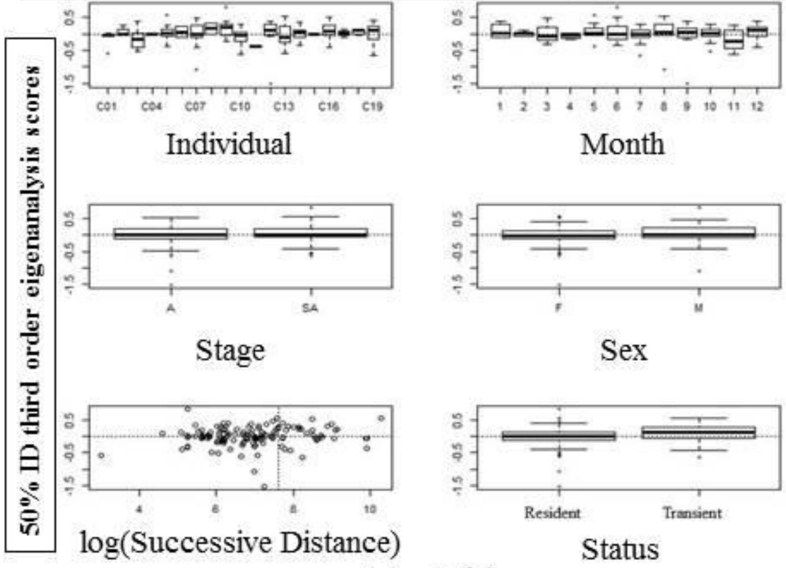


Axis 2 (y)

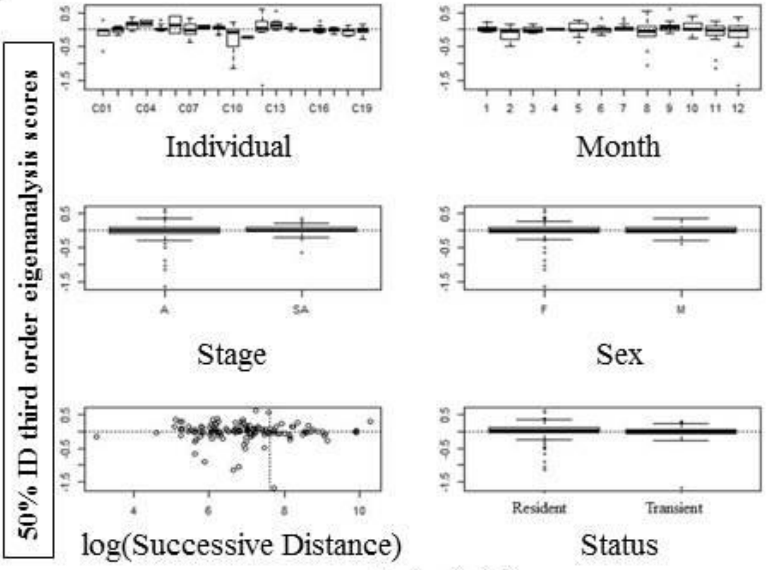
Figure 2. Third order habitat selection eigenanalysis biplots (top right) for 50% utilization distribution (UD) core home range by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat within core home range areas. Values near zero represent similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Residents show greater variability in selection for habitats within their core home range on axis 1 (lower left), including selection for agriculture. In addition, some females also demonstrated greater selection for agriculture. Individual variability was greatest along axis 2 (lower right).

Habitat Type	Eigenanalysis Factor Scores 50% ID third order Axis 1 (x)	 50% ID third order Axis 2 (y)
Hardwood Forest **1001**	12.486	4.780
Mixed-Hardwood/Softwood **1002**	-151.397	48.663
Softwood Forest **1003**	-0.109	-0.024
Agriculture **1004**	-61.591	-172.423
Riparian **1005**	-5.048	-0.086
Shrub **1006**	-27.633	-46.104
Rock **1007**	8.367	-33.165
Grass **1008**	-0.628	-0.198
Open/Barren **1009**	-0.683	0.741
Disturbed/Developed **1010**	15.503	-121.758





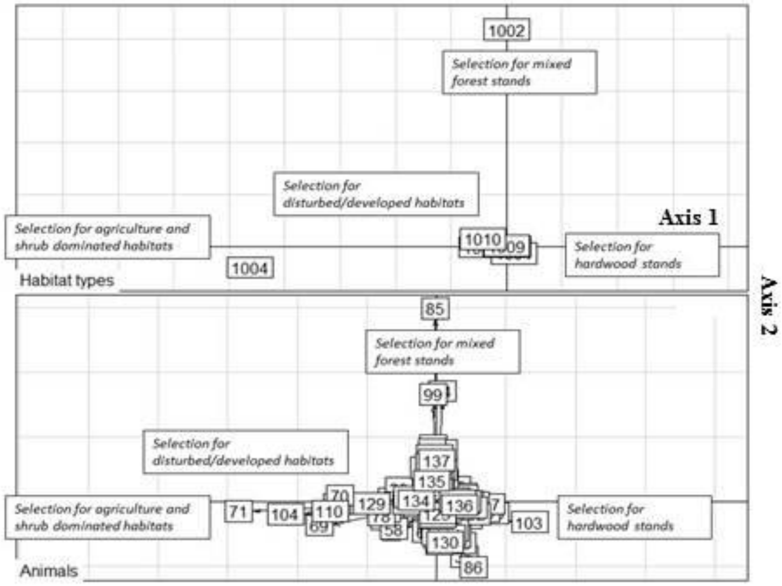
Axis 1 (x)

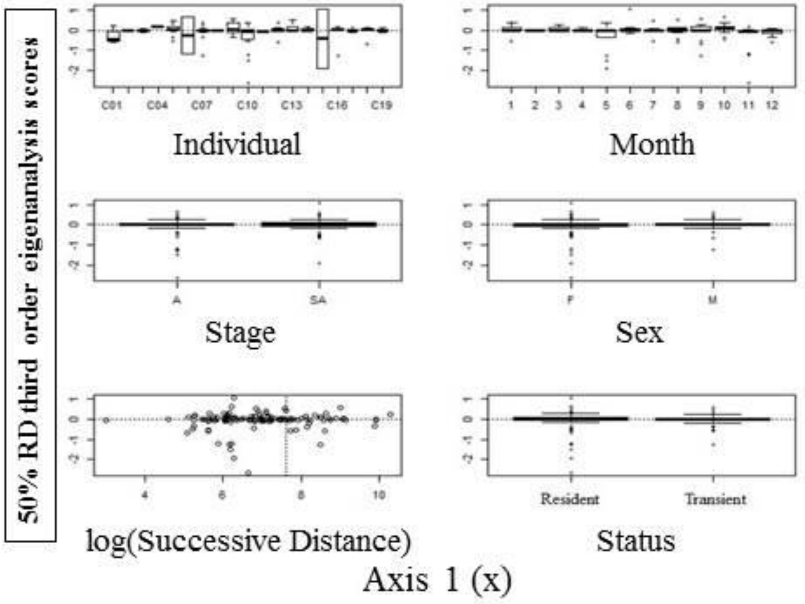


Axis 2 (y)

Figure 3. Third order habitat selection eigenanalysis biplots (top right) for 50% intensity distribution (ID) for intensively used areas by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat within areas individuals intensively use. Values near zero represent similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. Males and transients showed more variability in selection with greater selection for less risky hardwood and mixed forest stands along axis 1 (lower left) compared to residents and females. Adult females residents showed much greater variability in selection along axis 2, a gradient from agriculture and disturbed/developed to mixed forest stands compared to males, subadults, and transients, which showed very weak selection along this continuum with most values for axis 2 (lower right) near 0 (the origin).

	Eigenanalysis Factor Scores	
Habitat Type	**50% RD third order Axis 1 (x)**	**50% RD third order Axis 2 (y)**
Hardwood Forest **1001**	14.285	-13.6211
Mixed-Hardwood/Softwood **1002**	0.641	419.099
Softwood Forest **1003**	-0.498	-0.3227
Agriculture **1004**	-462.843	-40.584
Riparian **1005**	-1.186	1.016
Shrub **1006**	-43.694	-1.274
Rock **1007**	1.624	-0.710
Grass **1008**	-1.425	-0.369
Open/Barren **1009**	-0.326	0.744
Disturbed/Developed **1010**	-41.765	14.565





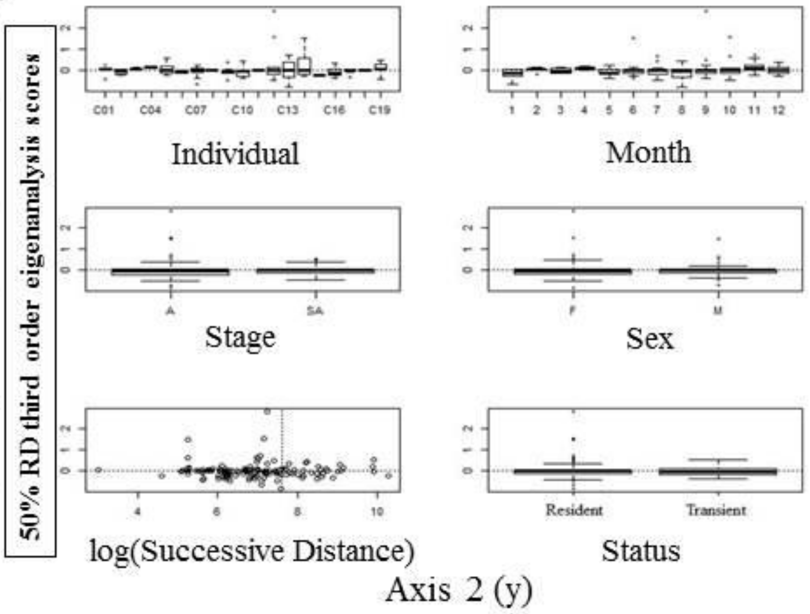


Figure 4. Third order habitat selection eigenanalysis biplots (top right) for 50% recursion distribution (RD) for frequently used areas by habitat type (boxed numbers in top right pane), and by individual during each month (coyote-month, boxed numbers in central right pane). Eigenanalysis factor scores for each axis (top left pane) demonstrate differentiation and relative strength of selection of habitat within areas individuals frequently use. Values near zero represent similar use proportional to availability. The lower panes display boxplots and scatterplots of coyote-month eigenanalysis factor scores (y-axis) for eigenanalysis axis 1 and eigenanalysis axis 2 by individual, month, stage, sex, successive distance between estimated activity centers, and status. The dashed vertical line for log(Successive Distance) represents log(2km), the threshold established for distinguishing residents from transients. In this particular eigenanalysis there is distinct differentiation between selection along axis 1 and selection along axis 2; when selection along one axis is strong, represented by high values, selection along the other axis is neutral, represented by values close to zero. On both axis 1 (lower left) and axis 2 (lower right), individual differences are the greatest source of variability. The single point at the extreme of the negative range of axis 1 (box 71, right central pane) represents strong selection for agriculture in frequent use areas by an adult resident female (C10) in November 2013. The single point at the extreme of the positive range of axis 2 (box 85, right central pane) represents strong selection for mixed forest stands in frequent use areas by an adult resident female (C12) in September 2012 during a temporary exploratory stopover at the initiation of a dispersal event.

APPENDICES

Appendix I. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from third order eigenanalysis (habitat selection within a home range) at the 95% utilization distribution (UD) overall home range level based on (Q)AICc. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A “+” sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	AICc	delta AICc	AICc model weight
Third Order 95% UD Overall Home Range Axis 1	1	1.016					3	17.760	-29.3	0	0.398
	8	1.020				+	4	17.814	-27.3	2.01	0.145
	5	1.020			+		4	17.808	-27.3	2.03	0.144
	2	1.047	(+) -0.005				4	17.804	-27.3	2.03	0.144
	6	1.062	(+) -0.006		+		5	17.878	-25.3	4.04	0.053
	11	1.024			+	+	5	17.861	-25.3	4.08	0.052
	9	1.049	(+) -0.004			+	5	17.852	-25.2	4.09	0.051
	3	0.974		+			14	26.288	-21.1	8.20	0.007
	4	1.029	(+) -0.008	+			15	26.443	-18.9	10.42	0.002
	10	0.977		+		+	15	26.356	-18.7	10.59	0.002
	7	0.981		+	+		15	26.323	-18.7	10.66	0.002
Third Order 95% UD Overall Home Range Axis 2	1	0.009					3	158.945	-311.7	0	0.409
	8	0.010				+	4	159.006	-309.7	2.00	0.150
	2	0.017	(+) -0.001				4	158.968	-309.6	2.08	0.145
	5	0.009			+		4	158.945	-309.6	2.12	0.141
	9	0.018	(+) -0.001			+	5	159.025	-307.6	4.12	0.052
	11	0.010			+	+	5	159.006	-307.6	4.16	0.051
	6	0.017	(+) -0.001		+		5	158.969	-307.5	4.23	0.049
	3	0.001		+			14	165.585	-299.7	11.98	0.001
	4	0.015	(+) -0.002	+			15	165.665	-297.4	14.35	0
	10	0.002		+		+	15	165.635	-297.3	14.41	0
	7	-0.002		+	+		15	165.616	-297.3	14.44	0

Appendix J. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from third order eigenanalysis (habitat selection within a home range) at the 50% utilization distribution (UD) core home range level based on (Q)AICc. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A “+” sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	QAICc	delta QAICc	QAICc model weight
Third Order 50% UD Core Home Range Axis 1	1	0.837					3	51.624	-97.1	0	0.235
	2	0.943	(+) -0.015				4	52.362	-96.4	0.65	0.170
	6	0.992	(+) -0.020		+		5	53.425	-96.4	0.68	0.167
	5	0.851			+		4	52.237	-96.2	0.90	0.150
	8	0.849				+	4	51.990	-95.7	1.39	0.117
	9	0.951	(+) -0.015			+	5	52.703	-94.9	2.12	0.081
	11	0.863			+	+	5	52.633	-94.8	2.26	0.076
	3	0.848		+			14	59.305	-87.2	9.90	0.002
	4	0.966	(+) -0.018	+			15	60.356	-86.7	10.32	0.001
	7	0.871		+	+		15	59.881	-85.8	11.27	0.001
	10	0.856		+		+	15	59.668	-85.4	11.7	0.001
Third Order 50% UD Corel Home Range Axis 2	1	-0.019					3	-25.800	57.8	0	0.380
	5	-0.006			+		4	-25.541	59.4	1.60	0.170
	2	0.028	(+) -0.007				4	-25.748	59.8	2.02	0.138
	8	-0.018				+	4	-25.797	59.9	2.12	0.132
	6	0.071	(+) -0.011		+		5	-25.416	61.3	3.51	0.066
	11	-0.005			+	+	5	-25.539	61.5	3.75	0.058
	9	0.029	(+) -0.007			+	5	-25.746	61.9	4.17	0.047
	3	0.130		+			14	-17.671	66.8	9.00	0.004
	7	0.170		+	+		15	-17.090	68.1	10.37	0.002
	10	0.132		+		+	15	-17.653	69.3	11.49	0.001
	4	0.133	(+) -0.001	+			15	-17.670	69.3	11.53	0.001

Appendix K. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from third order eigenanalysis (habitat selection within intensive use areas) at the 50% intensity distribution (ID) home range level based on (Q)AICc. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A “+” sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	QAICc	delta QAICc	QAICc model weight
Third Order 50% ID Intensive Use Axis 1	6	-0.302	(+) 0.040		+		5	-24.299	59.1	0	0.237
	2	-0.223	(+) 0.033				4	-25.453	59.2	0.15	0.219
	1	0.002					3	-26.641	59.5	0.41	0.193
	5	-0.019			+		4	-26.015	60.3	1.28	0.125
	9	-0.229	(+) 0.032			+	5	-25.284	61.0	1.97	0.088
	8	-0.011				+	4	-26.415	61.1	2.08	0.084
	11	-0.031			+	+	5	-25.798	62.1	3.00	0.053
	4	-0.292	(+) 0.036	+			15	-19.558	73.1	14.03	0
	3	-0.054		+			14	-21.003	73.4	14.39	0
	7	-0.100		+	+		15	-20.299	74.6	15.51	0
	10	-0.064		+		+	15	-20.732	75.4	16.37	0
Third Order 50% ID Intensive Use Axis 2	1	5.795					3	-250.710	73.1	0	0.421
	2	6.184	(+) -0.057				4	-250.598	75.3	2.13	0.146
	8	5.816				+	4	-250.698	75.3	2.15	0.144
	5	5.785			+		4	-250.707	75.3	2.15	0.144
	9	6.204	(+) -0.055			+	5	-250.588	77.5	4.31	0.049
	6	6.195	(+) -0.058		+		5	-250.598	77.5	4.31	0.049
	11	5.807			+	+	5	-250.696	77.5	4.34	0.048
	3	5.626		+			14	-243.278	96.9	23.74	0
	10	5.661		+		+	15	-243.227	99.4	26.29	0
	4	5.821	(+) -0.031	+			15	-243.247	99.4	26.30	0
	7	5.644		+	+		15	-243.274	99.5	26.31	0

Appendix L. Linear mixed model (LMM) selection for the first two factor component axes (Axis 1: x, Axis 2: y) from third order eigenanalysis (habitat selection within frequent use areas) at the 50% recursion distribution (RD) home range level based on (Q)AICc. Individual is a random effect. Fixed effects include month, and class structure variables including sex, stage (subadult or adult), and status (resident or transient, represented by on log(distance between successive activity centers)). A "+" sign indicates a fixed effect is included in a model.

Home Range Estimate	Model Number	Random Effect: Intercept (1 | individual)	Stability: log(Successive Distance)	Month	Sex	Stage	df	logLikelihood	QAICc	delta QAICc	QAICc model weight
Third Order 50% RD Frequent Use Axis 1	1	8.848					3	-294.108	79.1	0	0.408
	5	8.703			+		4	-293.556	81.2	2.02	0.149
	2	7.969	(+) 0.127				4	-293.758	81.2	2.07	0.145
	8	8.745				+	4	-293.868	81.2	2.10	0.143
	6	7.480	(+) 0.172		+		5	-292.917	83.2	4.06	0.054
	11	8.610			+	+	5	-293.307	83.3	4.15	0.051
	9	7.913	(+) 0.122			+	5	-293.537	83.3	4.21	0.050
	3	9.010		+			14	-285.803	102.8	23.66	0
	7	8.694		+	+		15	-285.100	105.2	26.06	0
	4	8.206	(+) 0.121	+			15	-285.476	105.3	26.15	0
	10	8.944		+		+	15	-285.580	105.3	26.18	0
Third Order 50% RD Frequent Use Axis 2	1	0.989					3	49.538	-92.9	0	0.415
	8	0.987				+	4	49.559	-90.8	2.08	0.147
	5	0.988			+		4	49.544	-90.8	2.11	0.144
	2	0.990	(+) -0.000				4	49.538	-90.8	2.12	0.144
	11	0.986			+	+	5	49.564	-88.7	4.23	0.050
	9	0.989	(+) -0.000			+	5	49.559	-88.7	4.24	0.050
	6	0.987	(+) 0.000		+		5	49.544	-88.6	4.27	0.049
	3	1.045		+			14	55.531	-79.6	13.28	0.001
	10	1.043		+		+	15	55.548	-77.1	15.77	0
	7	1.043		+	+		15	55.536	-77.1	15.79	0
	4	1.040	(+) 0.001	+			15	55.533	-77.1	15.80	0